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1859 • 1984

125th Anniversary
Missouri Botanical Garden

Henry Shaw (1800-1889)

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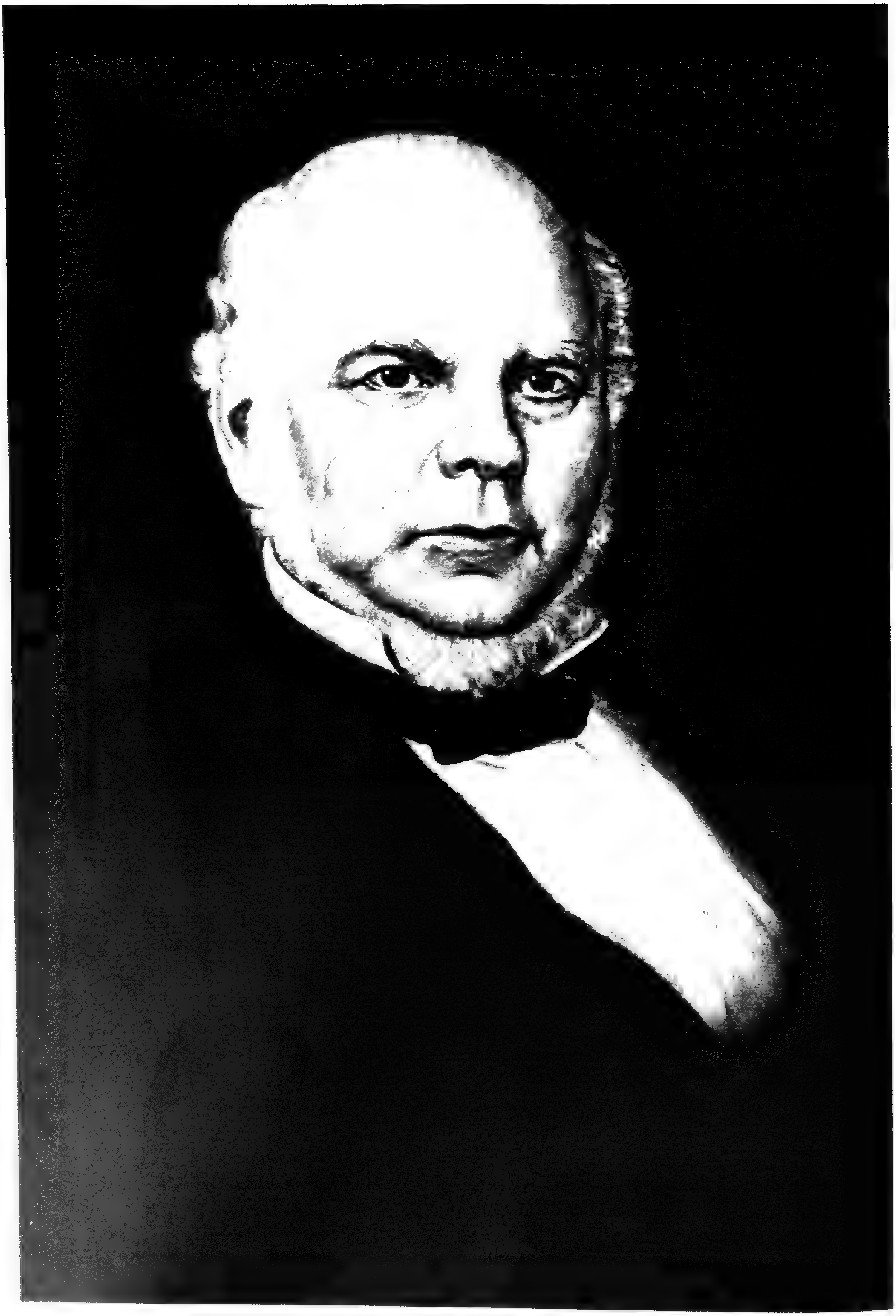

George Engelmann in 1860.

This volume of the ANNALS is dedicated to George Engelmann (1809–1884), who, though never formally associated with the Missouri Botanical Garden, was influential in establishing a program of scientific research here.

Engelmann was born in Frankfort-am-Main in the same year that Abraham Lincoln was born southwest of Frankfort, Kentucky, and Charles Darwin was born in England. His involvement with the Burchenschaft, a liberal German fraternal organization, caused his migration from the University of Heidelberg, to Berlin, to Würzburg, where he received his medical degree in 1831. He then spent a few months in Paris renewing old university acquaintances with Louis Agassiz, Karl Schimper, and Alexander Braun; botanizing in the Bois du Boulogne; and studying the latest cholera epidemic, before departing for the United States in the fall of 1832 as an emissary for his family, to investigate the advisability and feasibility of immigration to *Das Westland.*

The next two plus years were spent investigating and exploring western Illinois, Missouri, and Arkansas. By the fall of 1835 he was flat broke and established a medical practice in St. Louis with the goal of earning enough money in a few years to return permanently to Germany. But he never did. His medical practice boomed, because the population was growing rapidly, doubling every few years, due in no small part to German immigration, and, probably, because his European training was better than that of most local practitioners. In 1840 he returned to Germany to marry his long-time sweetheart, Dorothea Horstmann. On the return trip to St. Louis, Engelmann met Asa Gray in New York, establishing a close working relationship that would last the rest of his life.

The first of Engelmann's many publications on North American botany appeared in 1842, "A monography of North American Cuscutinae," in the American Journal of Science, "Silliman's Journal." Engelmann participated in the foundation of St. Louis's Western Academy of Science in 1835, and he, Adolphus Wislizenus, William Greenleaf Eliot, and Marie P. Leduc attempted to establish a botanical garden near the southwestern edge of the city in 1843. These ideas were, perhaps, just a bit ahead of their time: neither institution lasted long or contributed significantly to the advance of knowledge. However, by the late 1850's things had changed: in 1856 Engelmann was a founder of the St. Louis Academy of Science, which survives today as the St. Louis Museum of Science and Natural History, and he helped mold Henry Shaw's concept of a Botanical Garden to include a herbarium and library. Shaw opened his Missouri Botanical Garden to the public in 1859, and among its most handsome features was the Botanical Museum & Library, in which was installed the herbarium of J. J. Bernhardi of Leipzig, which Engelmann had purchased on Shaw's behalf for $400 while on an extended trip to Europe. The Bernhardi herbarium contained about 68,000 specimens.

Engelmann maintained a demanding medical practice. A reflection of his devotion to medicine is the fact that though he was one of the 50 original "incorporators" of the Congressionally established National Academy of Sciences in 1863, he resigned his membership four years later because his practice would not allow him to attend its sessions.

Monographic publications continued to pour from his steel pen until shortly before his death. *Cuscuta* was not the only difficult, tedious group on which he worked. Indeed, he concentrated his efforts on such groups: *Quercus, Vitis,* Cactaceae, conifers, *Isoëtes.* His detailed studies of these and other taxa laid the foundations for future workers.

Engelmann also contributed indirectly to our understanding of plants by acting as a middle-man between the West and the East. Strategically positioned in St. Louis, the gateway to much western trade, exploration, migration, and adventure, he hired and trained individuals—Joshiah Gregg, Ferdinand Lindheimer, Augustus Fendler— to collect and advised military leaders—John Charles Frémont, William Emory— as they lead their troops west, assuring a steady flow of specimens moving from the hitherto unexplored West to the botanical centers of the East, especially into the hands of John Torrey and Asa Gray.

The Thirtieth Annual Systematics Symposium, held at the Missouri Botanical Garden on 19 and 20 October 1984, also commemorated George Engelmann, concerning itself with our current knowledge of many of the taxa he studied, southwestern floristics, and his life and relations with contemporaries. The proceedings of the Symposium will appear in a future issue of the Annals.

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PARTITIONING AND SHARING OF POLLINATORS BY FOUR SYMPATRIC SPECIES OF *DALECHAMPIA* (EUPHORBIACEAE) IN PANAMA[1]

W. SCOTT ARMBRUSTER[2] AND ANN L. HERZIG[3]

ABSTRACT

Observations were made on distribution, floral morphology, and pollination of four species of *Dalechampia* (Euphorbiaceae) in central Panama. The four species occur sympatrically in various combinations throughout Panama and are pollinated by resin-collecting euglossine bees, and resin- and/or pollen-collecting stingless bees and megachilid bees. With one exception, these plant species overlap very little in pollinators or time of pollination. *Dalechampia heteromorpha* is pollinated early in the day by *Trigona* and *Hypanthidium* whereas a sympatric congener, *D. scandens,* is pollinated by the same species of bees late in the day. A third sympatric species, *D. dioscoreifolia,* is pollinated by euglossine bees. *Dalechampia heteromorpha* also occurs sympatrically with *D. tiliifolia*; the latter is pollinated by euglossine bees. Individuals of *Dalechampia dioscoreifolia* and *D. tiliifolia* were observed occurring together at only one site; here they shared pollinators (euglossine bees) and were receptive to pollination at the same time of day. Interspecific pollen flow was substantial and may have resulted in depressed seedset in *D. dioscoreifolia.*

A number of authors have suggested that plant communities are likely to be organized in ways that minimize reproductive interference (Levin, 1970; Levin & Anderson, 1970; Mosquin, 1971; Straw, 1972; Reader, 1975; Heinrich, 1975). [We here define the term "reproductive interference" to include all plant-plant interactions that have direct detrimental effects on reproductive processes, including competition for pollinator service, interspecific pollen transfer, and competition for agents of seed dispersal; this is more inclusive than the phrase "competition for pollination" used by Waser (1982).] There have been a number of studies that indicate such organization occurs in natural communities (Snow, 1966; Frankie, 1975; Reader, 1975; Heinrich, 1976a; Stiles, 1975, 1977; Feinsinger, 1978; Waser, 1978a; Brown & Kodric-Brown, 1979; Parrish & Bazzaz, 1979). However, as several authors have pointed out, before claiming that organizing processes have affected community structure it is necessary to show statistically that

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[1] We wish to thank the Smithsonian Tropical Research Institute for the use of their facilities, Don Windsor and Robert Dressler for assistance in Panama, Irene Baker for information on the paints, Kim Steiner and Robbin Foster for information on distribution and phenology, Robert Dressler for identifying euglossine bees, Dave Roubik for identifying the *Trigona,* Karen Harris for assistance in making greenhouse crosses, and Jim Ackerman, John Bryant, Terry Chapin, Steve MacLean, Kim Steiner, Ed Murphy, Grady Webster, Cheryl Crowder, and an anonymous reviewer for reading the manuscript and making valuable suggestions. Field work during 1980 was supported by grant #DEB78-24218 from the National Science Foundation.

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niche overlap in a community is less than that of a randomly generated assemblage of species (Connor & Simberloff, 1979; Poole & Rathcke, 1979; Strong et al., 1979). Further, as Grant (1972), Roughgarden (1976), Feinsinger (1978), Slatkin (1980), Waser (1983), and others have pointed out, the observed organization may be either the result of evolution of the component species in response to their biotic environments or the result of the sorting of preadapted species into "compatible" associations. It is difficult, at best, to distinguish between these two processes.

These limitations notwithstanding, we believe that it remains useful to investigate the ecological relationships between members of species assemblages. While detailed studies of a single community usually cannot demonstrate community organization, they may reveal the selective pressures that have been operating and the "cost" of not being adapted to sympatry.

We have been interested in how assemblages of sympatric species of *Dalechampia* (Euphorbiaceae) are organized, especially with respect to use of the pollinating fauna and to potential interspecific pollen flow. The pollination systems of three different pairs of sympatric species of *Dalechampia* in South America and Mexico have been discussed by Armbruster and Webster (1979, 1981, 1982). In each case the pollinators were effectively partitioned, and there was very little interspecific pollen flow. In this paper we describe the relationships between four species of *Dalechampia* (*D. dioscoreifolia, D. heteromorpha, D. scandens,* and *D. tiliifolia*) that occur in several combinations of sympatry in Panama and examine the relationships with pollinators, the extent of resource partitioning, and the amounts of interspecific pollen flow.

Dalechampia contains about 100 species, most of which are small to moderate-sized lianas of lowland neotropical habitats. All species are monoecious; the unisexual flowers are grouped together into functionally bisexual pseudanthial inflorescences (Webster & Webster, 1972). In most species studied, including those considered here, the inflorescence contains three pistillate flowers, 8–13 staminate flowers, and a gland-like structure that secretes resin (Armbruster & Webster, 1979). The whole inflorescence is subtended by two usually large and showy bracts.

In most species of *Dalechampia,* including the subjects of this study, the pistillate flowers are receptive several days prior to anthesis of the staminate flowers in the same inflorescence. Subsequently there is a bisexual phase during which the pistillate flowers are still receptive, but the staminate flowers are also open and pollen is being shed. During the bisexual phase self-pollination may occur; since all *Dalechampia* species that have been tested are self-compatible, self-fertilization may result (Armbruster, unpubl.). During the pistillate phase only cross-pollination is possible.

Most species of *Dalechampia* are pollinated by female bees that collect the resins secreted by the large secretory glands associated with the staminate flowers (Armbruster & Webster, 1979, 1981, 1982). The amount of resin secreted determines the size of the largest floral visitors. Apparently due to energetic constraints on foraging behavior, only small bees visit *Dalechampia* species that secrete small amounts of resin, whereas large bees (euglossines) visit only those species of *Dalechampia* bearing larger amounts of resin (Armbruster & Webster, 1981, 1982; Armbruster, in prep.).

Because of the viscous, sticky nature of floral resins, it is very difficult to measure the rate of resin secretion. Experimental removal of resin from glands of *D. scandens, D. heteromorpha,* and *D. tiliifolia* has shown that resin secretion occurs throughout the period that the bracts are open, and about 0.5–1.5 mm (depth) of resin accumulates across the surface of the gland daily (Armbruster, unpubl.). *Dalechampia dioscoreifolia* appears to follow this pattern as well. Because the rates of secretion are similar in all species studied and because of the difficulties in measuring secretion rates, the area of secretion is probably the best single field measurement of the average quantity of resin available to foraging bees.

The arrangement of the staminate and pistillate flowers also affects the size class of the effective pollinators. Species of *Dalechampia* in which the distances between the gland and the stigmas or the gland and the anthers is relatively large (>ca. 6 mm) are pollinated only by relatively large bees (>ca. 10 mm). Species of *Dalechampia* in which the gland-stigma and gland-anther distances are smaller (<ca. 4 mm) can be pollinated by smaller bees (Armbruster & Webster, 1981, 1982; Armbruster, in prep.).

MATERIALS AND METHODS

Observations on the reproductive biology of *Dalechampia* species were made in the Canal Zone of the Republic of Panama during three separate periods: 30 June–3 July 1978, 14–18 November 1978, and 9–27 January 1980. Intensive observations were made on three species, *D. dioscoreifolia* Poepp. & Endl., *D. heteromorpha* Pax & Hoffmann (Pax & Hoffmann, 1919; = *D. cissifolia* subsp. *panamensis,* Webster & Burch, 1968; Croat, 1978), and *D. scandens* L., where they occurred together at km 13 Pipeline Road. Intensive observations were also made on *D. dioscoreifolia, D. heteromorpha,* and *D. tiliifolia* Lam. where they occurred together at km 15 Pipeline Road. Additional observations were made on these species at 10 other sites in the Canal Zone, including elsewhere along Pipeline Road (as far as Rio Casanga), Madden Dam, Madden Reserve, Barro Colorado Island, and near the Summit Gardens.

For each species we tagged 19–52 inflorescences on 5–7 plants and daily monitored changes in number of staminate flowers open, amount of resin present, and the amount and, when possible, type of pollen on the stigmas. Resin amounts were estimated by observing the depth on the gland. Pollen grains, which are large (ca. 50–150 μm), were counted with the aid of a hand lens; we were able to distinguish between the pollen of *D. tiliifolia* and *D. dioscoreifolia* on the basis of size. *Dalechampia* pollen was distinguishable from pollen of other plants common in the area on the basis of size and color. At half-hour or hour intervals the position of the involucral bracts was assessed. Measurements were made of the gland size and minimum distances between the gland and stigmas, the gland and anthers, and the anthers and stigmas, using dial calipers accurate to 0.05 mm.

Observations on pollinators included counting floral visitors, noting the amount and color of their corbicular/scopal loads, recording their behavior and monitoring their movements. To facilitate these observations some bees were captured, marked on the scutum with correction fluid, and released. Effectiveness of pollinators was determined by monitoring changes in number of pollen grains on the stigmas of each species; effective pollinators (Table 3) are those that were observed to regularly transfer *Dalechampia* pollen to *Dalechampia* stigmas. Visitation rates were calculated for each pollinator species by summing the number of visits observed and dividing by the number of days of observation and by the mean number of inflorescences open in the observation area during the period of observation. Only days in which observations were made throughout the period of bract opening were included in calculating means. To assess the movement of pollen within and among species, staminate flowers of each species were dusted at short intervals with specific colors of powdered, non-toxic, fluorescent paint; transfer of paint granules was recorded periodically. Vouchers of plant species and floral visitors were collected. In the lab pollen loads were removed from visitors, slides made using Hoyer's medium, and pollen identified with a microscope. Plant vouchers have been deposited at DAV and SCZ.

Experimental intraspecific and interspecific crosses, measures of selfing ability and stigmatic receptivity, and tests of self-compatibility were performed on cultivated material of all four species in the greenhouses at the University of California, Davis from 1975 until 1980. Crosses were made by removing all staminate flowers while in bud and manually transferring pollen with a small camel's-hair brush. Stigma receptivity was tested by pollinating stigmas in emasculated inflorescences at various times during inflorescence development and by testing for peroxidase activity with Peroxtesmo KO paper.

RESULTS

DISTRIBUTION AND FLOWERING TIME

Dalechampia dioscoreifolia, D. heteromorpha, D. scandens, and *D. tiliifolia* are all locally common in forested and/or open areas of the Canal Zone and other parts of Panama. While at the majority of the 12 study sites only one or two species were present, at two sites we were able to observe three species occurring sympatrically (Table 1). *Dalechampia dioscoreifolia* occurred sympatrically with *D. heteromorpha* at four sites, and with *D. scandens* at three sites. *Dalechampia heteromorpha* occurred with *D. scandens* at one site and with *D. tiliifolia* at two sites. *Dalechampia dioscoreifolia* and *D. tiliifolia* occurred together at one site, but *D. tiliifolia* was restricted to the open scrub, whereas *D. dioscoreifolia* occurred in the forest (Table 1). The two species grew close together only at the ecotone of the forest and scrub communities.

The data on flowering phenology of Panamanian *Dalechampia* are limited; however, it is possible to make a first approximation based on our observations in 1978 and 1980, on available collections, and from the literature. The phenological data presented in Table 2 are based on our observations made in Panama during July, No-

TABLE 1. Observed co-occurrence and ecological distribution of four species of *Dalechampia* in central Panama.

	D. dioscoreifolia	*D. heteromorpha*	*D. scandens*	*D. tiliifolia*
Site:				
km 13, Pipeline Rd.	+	+	+	
km 15, Pipeline Rd.	+	+		+
km 17, Pipeline Rd.	+	+		
Madden Reserve	+		+	
Madden Dam	+		+	
Summit Gardens		+		+
Barro Colorado Island	+	+		
Habitat:				
Closed Forest	+	+	?	
Open Forest	+	+	+	
Forest Edge	+	+	+	+
Secondary Scrub		+	?	+
Open Fields		+		+

vember and January, nearly year-round observations of K. E. Steiner (pers. comm.), Croat's observations (1978), and examination of Panamanian specimens from SCZ, MO, and GH (*Dalechampia dioscoreifolia*: 5 sheets; *D. heteromorpha*: 4 sheets; *D. scandens*: 3 sheets; *D. tiliifolia*: 18 sheets). These data are further corroborated by our observations made on these four species in other parts of Mesoamerica and northern South America intermittently from 1975 to 1980. Considerable phenological information can be gleaned from examination of natural populations, even at a few times of the year: the previous 1–3 months' flowering activities are recorded in fruits of various stages of maturation or dehiscence; the future month of flowering activities can be predicted by examining plants for inflorescence buds. In all four species (as studied throughout the Neotropics), all "mature" members of the population produce new flowers throughout the blooming season.

Three of the species of *Dalechampia* bloom primarily during the late wet and dry seasons and reproductive interference between members of each sympatric species could be occurring at this time. Thus, there is potential reproductive interference with congeners affecting *D. tiliifolia*, *D. scandens*, and possibly *D. dioscoreifolia* throughout the flowering season of each. However, since *D. heteromorpha* blooms year-round, it may not be subject to reproductive interference from other species for about half of the year (cf. Table 2).

BREEDING SYSTEMS

Greenhouse and field bagging experiments have shown that *D. dioscoreifolia*, *D. heteromorpha*, *D. scandens*, and *D. tiliifolia* are self-compatible.

TABLE 2. Flowering phenology of *Dalechampia* species in central Panama. Table is based on personal observation, herbarium specimens, information presented in Croat, 1978, and verbal reports (K. Steiner, pers. comm.). Seasonal assignments follow Ackerman, 1984. (+ indicates abundant flowering occurs during that month.)

	Season and Month											
	Dry			Early Wet			Mid Wet			Late Wet		
Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
D. dioscoreifolia	+	+	+	+			+?				+	+
D. heteromorpha	+	+	+	+	+	+	+	+	+	+	+	+
D. scandens	+	+	+							+	+	+
D. tiliifolia	+	+	+								+	+

TABLE 3. Floral morphology of Panamanian *Dalechampia*. Numbers in table are means ± s.d. with N in parentheses.

Dalechampia Species	Number of Staminate Flowers	Gland Area (mm^2)	Gland-Stigma Distance (mm)	Gland-Anther Distance (mm)	Anther-Stigma Distance (mm)
D. dioscoreifolia	8–10	30.1 ± 12.3 (20)	5.5 ± 1.1 (20)	6.7 ± 1.5 (10)	10.2 ± 2.0 (9)
D. heteromorpha	8–10	6.5 ± 1.8 (16)	3.1 ± 0.6 (16)	2.2 ± 0.4 (9)	0.5 ± 0.6 (9)
D. scandens	9–10	8.7 ± 3.0 (30)	3.1 ± 0.8 (29)	2.8 ± 0.8 (20)	1.8 ± 0.8 (20)
D. tiliifolia	9–10	22.0 ± 4.8 (20)	8.9 ± 1.7 (20)	8.2 ± 1.0 (15)	3.0 ± 2.1 (15)

All four of these species set nearly full complements of seeds when inflorescences are manually self-pollinated and screened from pollinators. There are, however, differences among species with respect to the ability of each to self-pollinate and set seed in the absence of pollinators. Observations of pollen movement in a number of species have shown that the distance between the stigmas and the anthers is a primary determinant of the ability of a species to self-pollinate (Armbruster, in prep.). Accordingly, *D. heteromorpha* with a mean anther-stigma distance of only 0.5 mm (Table 3) sets abundant seed in the absence of pollinators. Plants screened from pollinators in greenhouse experiments produce 68% of the maximum possible seedset (N = 279). Manually selfed material had seedsets of 85% of maximum (N = 603), so depression of seedset by the lack of insect-mediated pollination, while significant ($P < 0.001$, d = 5.90, normal approximation of binomial distribution; Bailey, 1959), is relatively small.

Dalechampia scandens also has a relatively small mean anther-stigma distance (1.8 mm, Table 3); Panamanian material of this species grown in the greenhouse set abundant seed in the absence of pollinators. A population of *D. scandens* in Costa Rica with a mean anther-stigma distance of 3.6 mm produced 63% of maximum possible seedset (N = 27) when screened from pollinators.

Dalechampia tiliifolia also has a relatively small mean anther-stigma distance (3 mm, Table 3) and self-pollination when pollinators are absent may be relatively frequent. In a population in Costa Rica with a mean anther-stigma distance of 2 mm, inflorescences screened from pollinators produced 93% of maximum possible seedset (N = 84).

Dalechampia dioscoreifolia differs from the other three species in having a relatively large mean anther-stigma distance (10.2 mm, Table 3). This strongly suggests that self-pollination in the absence of pollinators is rare. In one plant screened from pollinators in the greenhouse only two out of eight inflorescences set seed. A closely related species, *D. aristolochiifolia* H.B.K. has a similar inflorescence morphology (distances between gland-stigma = 5.8 mm, gland-anther = 9.1 mm, anther-stigma = 7 mm; compare with Table 3) and set no seed when grown in the greenhouse and screened from pollinators (N = 108).

FLORAL DEVELOPMENT

The four species of *Dalechampia* considered in this study follow similar patterns of inflorescence development (Table 4). The involucral bracts remain closed when the inflorescences are in bud. On the first day that the bracts open, the stigmas of all four species are receptive. Seed was set in greenhouse material of *D. heteromorpha, D. scandens,* and *D. tiliifolia* that was pollinated on the first day of bract opening and subsequently emasculated and screened from pollinators. All four species show positive peroxidase reactions on the first day of bract opening. Similar tests show that the stigmas remain receptive throughout the period of anthesis of the staminate flowers.

Anthesis of the first staminate flower occurs on the second to fourth day after the bracts first open. Each day for the next four to seven days, one to two additional staminate flowers open. Staminate flowers persist two to three days after anthesis and then abscise. Anthesis of the "mature" staminate flower(s) occurs shortly after the bracts open each day (Table 4). In all four species, the anthers dehisce shortly after anthesis.

The involucral bracts open and close in a diurnal cycle characteristic for each of the four species. The bracts of *D. heteromorpha* open daily in the early morning, those of *D. scandens* in the early

TABLE 4. Inflorescence development and behavior. Numbers in columns 1 and 2 are means rounded to the nearest day with range and sample size in parentheses.

Species	Duration of ♀ Phase (days)	Duration of ⚥ Phase (days)	Time of Anthesis of Staminate Flowers (hrs)	Period Bracts Are Open (hrs)
D. dioscoreifolia	3 (2–5; 8)	4 (3–6; 4)	ca. 1500	(1400) 1500–1830
D. heteromorpha	3 (2–4; 9)	5 (4–6; 7)	ca. 0700	0600–1900(+)
D. scandens	2 (1–3; 10)	6 (5–6; 8)	ca. 1330	(1300) 1330–1830
D. tiliifolia	2 (1–3; 6)	5 (5–6; 11)	ca. 1430	1400–1800

afternoon, and those of *D. tiliifolia* and *D. dioscoreifolia* in the early to mid-afternoon. The bracts of all four species close shortly after sunset (Table 4).

In all four species, after ca. seven to nine days of receptivity, the inflorescence passes into the fruiting phase. The staminate cycle, including the resin gland, abscises. The bracts in *D. heteromorpha, D. scandens,* and *D. tiliifolia* close around the developing capsules. In the last two species the bracts suffuse with chlorophyll. In *D. dioscoreifolia* the bracts abscise when the fruits begin to develop (cf. Armbruster, 1982).

INFLORESCENCE MORPHOLOGY

The basic number and arrangement of staminate and pistillate flowers in the inflorescences is similar in all the four species considered in this study (Table 3, Figs. 1–4). However, there is considerable variation in the color and size of bracts, in the size of the resin glands, and in the distances between floral structures. *Dalechampia heteromorpha* has relatively small green bracts (10–25 mm), and relatively small resin glands (ca. 6.5 mm^2), gland-stigma distances (ca. 3.1 mm), and gland-anther distances (ca. 2.2 mm, Table 3). Similarly, *D. scandens* has relatively small, pale-green bracts (10–25 mm), and relatively small resin glands (ca. 8.7 mm^2), gland-stigma distances (ca. 3.1 mm) and gland-anther distances (ca. 2.8 mm, Table 3).

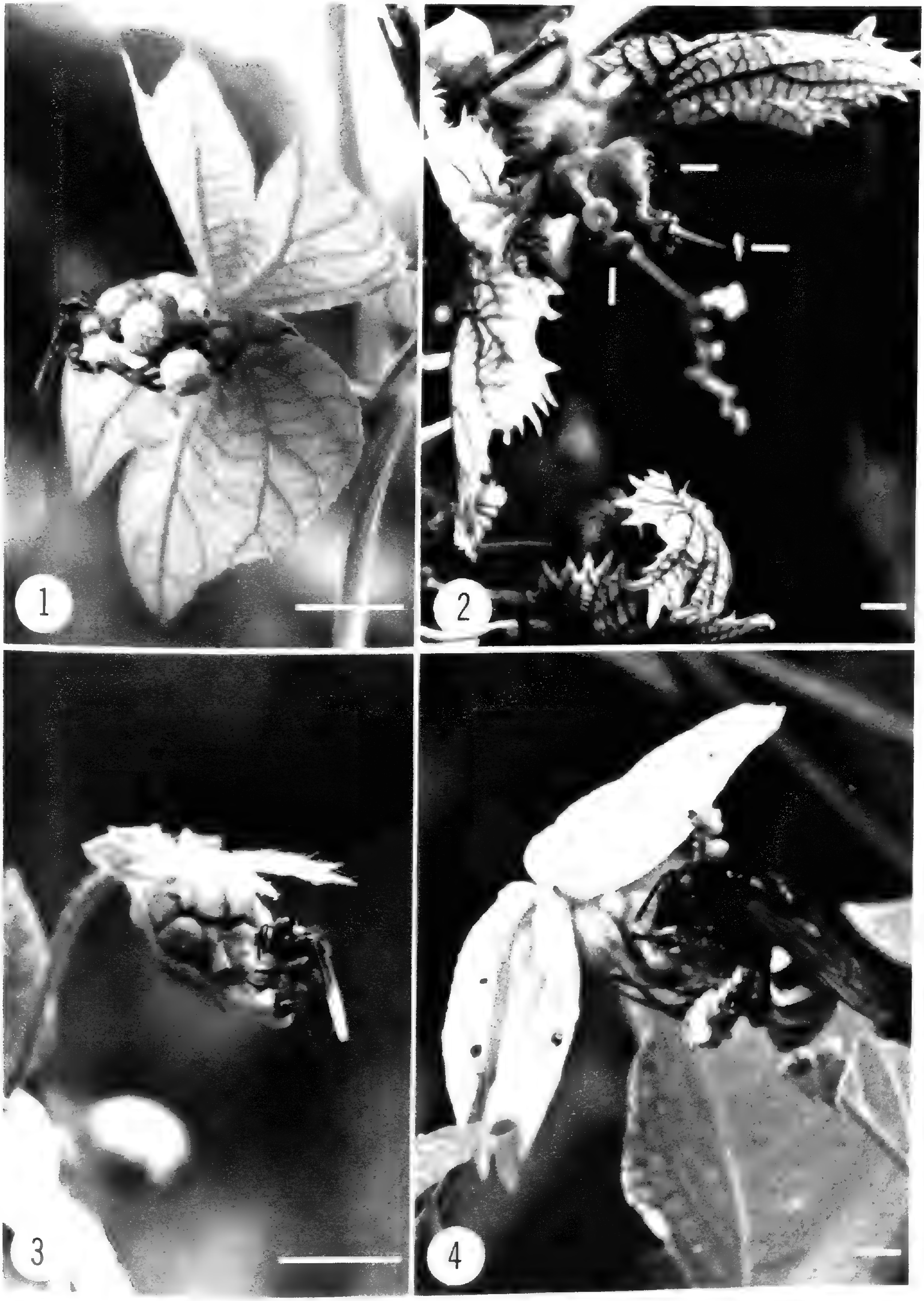
In contrast *D. tiliifolia* has relatively large white bracts (20–50 mm), and relatively large resin glands (ca. 22 mm^2), gland-stigma distances (ca. 8.7 mm), and gland-anther distances (ca. 8.2 mm, Table 3). Similarly, *D. dioscoreifolia* has relatively large pink bracts (40–50 mm), relatively large resin glands (ca. 30.1 mm^2), and moderately large gland-stigma distances (ca. 5.5 mm), and gland-anther distances (ca. 6.7 mm, Table 3).

The size of the stigmatic tip of the stylar column also varies considerably among the four species. In *Dalechampia heteromorpha* this structure is relatively small (ca. 0.7 mm^2); in *D. scandens* it is slightly larger (ca. 0.8 mm^2). In *Dalechampia tiliifolia* and *D. dioscoreifolia* the stigmatic tips are considerably larger (ca. 4 mm^2 and ca. 6 mm^2, respectively).

POLLINATION AND SEEDSET

As predicted from studies of other species of *Dalechampia* (cf. Armbruster & Webster, 1981, 1982), *D. heteromorpha* and *D. scandens* (both with small resin glands) were visited only by small bees, including *Hypanthidium panamense* and *Trigona* spp. (Table 5). These bees collected resin and/or pollen. We observed no visits by the larger euglossine bees during 42 hours of observation at the Pipeline Road study sites, although these bees were active in the area. Because the gland-stigma and gland-anther distances are small in both of these *Dalechampia* species, the small bees effectively transferred pollen to the stigmas. Pollen was deposited on the legs and ventral surface of the thorax and abdomen. The same species pollinated *D. scandens* and *D. heteromorpha* at other study sites where these plants were observed.

At the Pipeline Road study site, *D. tiliifolia* and *D. dioscoreifolia* were visited and pollinated by medium-sized to large euglossine bees (*Eulaema* spp., *Euglossa bursigera*), which collected resin from the large resin glands (Table 5). Pollen was deposited on the legs and on the ventral surface of the thorax and abdomen. These bee species were observed pollinating *D. tiliifolia* and *D. dioscoreifolia* at a number of different study sites in Panama and also in Costa Rica (Armbruster, unpubl.). Because of the large gland-stigma and gland-anther distances, smaller bees (such



FIGURES 1–4. Panamanian *Dalechampia* and pollinators. Scale bars are 5 mm.—1. *D. heteromorpha* in bisexual condition being visited by *Trigona jaty*.—2. *D. dioscoreifolia* in bisexual condition. Pointers indicate resin gland (top), staminate flower (middle), pistillate flower (bottom).—3. *D. scandens* in bisexual condition being visited by *T. perangulata*.—4. *D. tiliifolia* in bisexual condition being visited by *Eulaema cingulata*.

TABLE 5. Floral visitors to Panamanian *Dalechampia*. Visitation rates based on observations from 9–27 Jan. 1980. Numbers in column 5 are means ± s.d. with N in parentheses.

Dalechampia Species (Locality)	Floral Visitor (Size in mm)	Effective Pollinator?	Material Collected	Visitation Rate in Visits·Inflorescence^{-1}·day^{-1}	Number of Hours of Observation
D. dioscoreifolia					
(km 13, Pipeline Rd.)	*Eulaema cingulata* (Fabricius) (22)	+	resin	0.35 ± 0.47 (4)	8
	Eulaema cf. *meriana* (Olivier)[a] (24)	+	resin	1.22 ± 0.80 (4)	8
	Euglossa sp. (11)	+	resin	0.05 ± 0.08 (4)	8
(km 15, Pipeline Rd.)	*Eulaema cingulata* (22)	+	resin	0.81 ± 0.25 (5)	20
	Euglossa sp. (11)	+	resin	0.08 ± 0.08 (5)	20
D. heteromorpha					
(km 13, Pipeline Rd.)	*Hypanthidium panamense* Cockerell (7)	+	resin and pollen	0.97 ± 0.48 (3)	42
	Trigona perangulata Cockerell (6)	+	pollen	4.52 ± 1.54 (3)	42
	Trigona jaty Smith (5)	+	resin	0.05 ± 0.09 (3)	42
	Trigona fulviventris Guerin (6)	+	pollen	0.02 ± 0.03 (3)	42
	Trigona sp. (3)	–	resin	0.12 ± 0.06 (3)	42
D. scandens					
(km 13, Pipeline Rd.)	*Hypanthidium panamense* (7)	+	resin and pollen	0.32 ± 0.26 (3)	42
	Trigona perangulata (6)	+	pollen	5.25 ± 2.39 (3)	42
	Trigona jaty (5)	+	resin	0.08 ± 0.14 (3)	42
	Trigona sp. (3)	–	resin	0.10 ± 0.10 (3)	42
D. tiliifolia					
(km 15, Pipeline Rd.)	*Eulaema cingulata* (22)	+	resin	1.31 ± 0.86 (5)	20
	Euglossa bursigera Moure (11)	+	resin	0.005 ± 0.012 (6)	20
	Tetrapedia sp. (8)	–	pollen	0.05 ± 0.07 (5)	20

[a] This bee was only observed with binoculars. Due to extreme similarity of mimetic euglossines, we cannot be certain that this is *E. meriana* (cf. Dressler, 1979).

as *Paratetrapedia*, Table 5) are not effective pollinators of *D. tiliifolia* or *D. dioscoreifolia*.

In these four species of *Dalechampia*, a full complement of nine seeds usually develops if pollination is adequate (cf. Armbruster, 1982). There is no evidence suggesting that selective abortion occurs or that, in healthy plants, abscission of inflorescences is due to anything other than lack of pollination. In *D. dioscoreifolia*, of 19 pistillate flowers that had been tagged and monitored and later abscised, 16 (84%) lacked pollen on the stigmas, 3 (16%) had <5 grains per stigma and none had >5 grains per stigma. In *D. scandens*, of 15 monitored inflorescences that abscised, 8 (53%) had <5 grains per stigma, 6 (40%) had between 5 and 10 grains per stigma, and 1 (7%) had >10 grains per stigma.

The proportion of tagged pistillate flowers setting seed varied considerably among species. *Dalechampia heteromorpha* had 100% seedset (N = 30) at km 13 Pipeline Road; at this site *D. scandens* had 76% seedset (N = 87). At km 15 Pipeline Road, *Dalechampia tiliifolia* had 100% seedset (N = 48), whereas *D. dioscoreifolia* had only 42% seedset (N = 24).

POLLINATOR MOVEMENTS BETWEEN SPECIES

At the study site at km 13 Pipeline Road, *D. heteromorpha* and *D. scandens* grew together and were pollinated by the same bee species (Table

5). In the morning hours *Hypanthidium* and *Trigona* visited and pollinated *D. heteromorpha* (Fig. 5). On a number of occasions bees that had just visited *D. heteromorpha* attempted to visit inflorescences of *D. scandens*; however, the bracts of the latter were closed in the morning and successful foraging from, and pollination of, this species was usually not possible before 1300 hrs. Thus there was little potential for interspecific pollen flow in the morning hours.

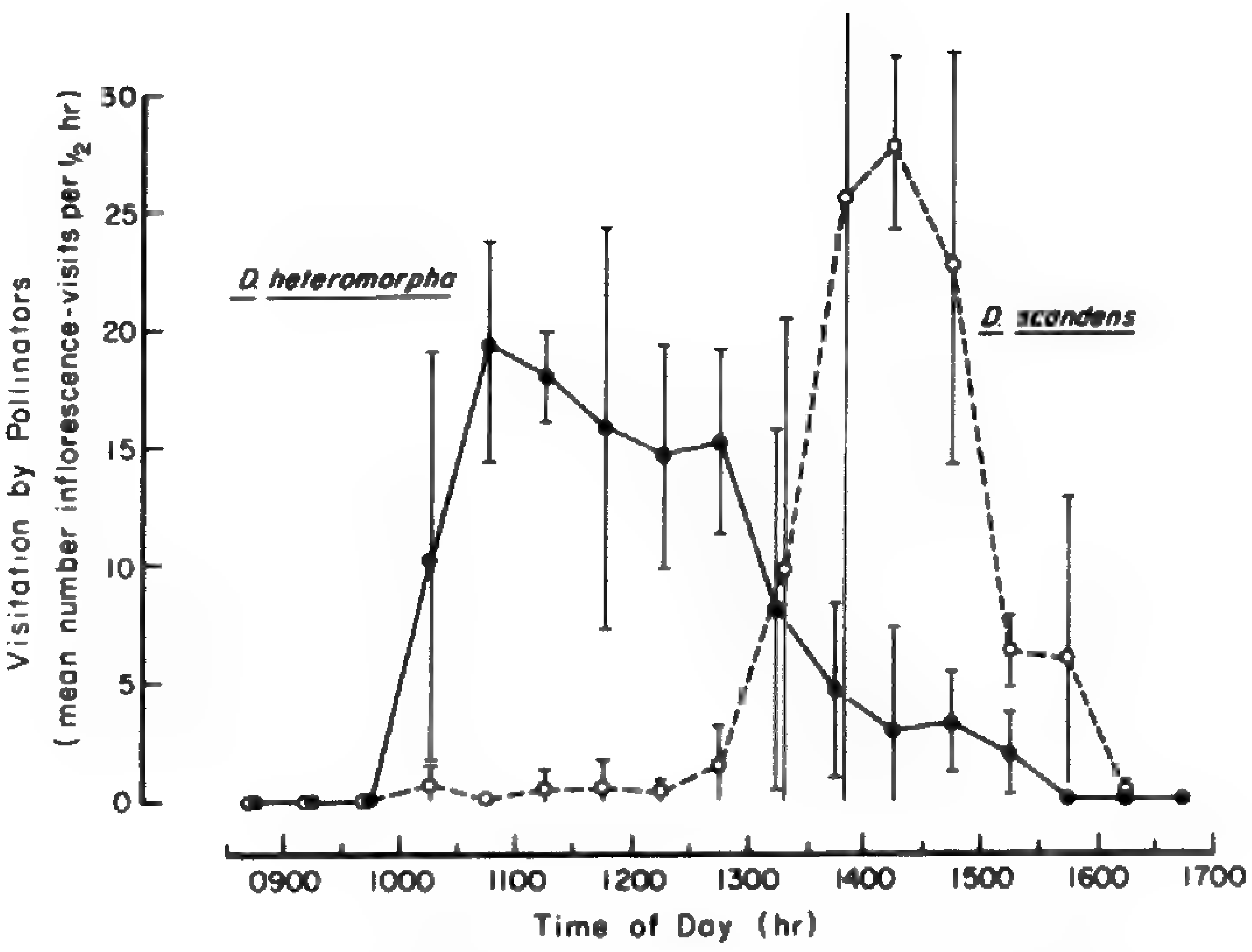


FIGURE 5. Rates of effective visitation by pollinators of *Dalechampia heteromorpha* and *D. scandens* at km 13 Pipeline Road, Canal Zone, Panama, 13–26 January, 1980. Bars are ± one standard deviation.

The majority of attempted visits by *Hypanthidium* and *Trigona* during the morning hours were to *D. heteromorpha.* Out of 599 recorded inflorescence visits during the period from 0800 to 1300 hrs, 535 (89.3%) were successful visits to *D. heteromorpha,* 39 (6.5%) were attempted visits to inflorescences of *D. scandens* that were closed, 13 (2.2%) were visits to old inflorescences of *D. scandens* that had ceased bract movement (and lacked pollen and resin resources), and 12 (2%) were to the rare inflorescences of *D. scandens* that were receptive and slightly open.

In the afternoon (after 1330 hrs) when the inflorescences of *D. scandens* were open, the pollinating bee species "switched" from foraging primarily from *D. heteromorpha* to foraging primarily from *D. scandens.* Of 483 recorded inflorescence visits during the period from 1330 to 1700 hrs, 429 (88.8%) were to *D. scandens* and only 54 (11.2%) were to *D. heteromorpha.* That the bees "preferred" *D. heteromorpha* in the morning and *D. scandens* in the afternoon is statistically highly significant ($P \ll 0.001$, $\chi^2 = 314.4$).

As a consequence of this daily shift in bee preference, the number of interspecific moves by pollinators was surprisingly low. *Dalechampia heteromorpha* and *D. scandens* grew together in the same hedgerow at the km 13 study site; they were frequently intertwined. The inflorescences were of approximately equal number (Table 6) and not spatially segregated to any great extent. Yet out of 576 recorded pollinator moves, only 32 (5.5%) were interspecific (Table 6).

Observations of the movement of paint granules that had been dusted on staminate flowers of both species of *Dalechampia* also suggest a low level of interspecific pollen flow. The frequency was somewhat higher than noted above; 5 (11.6%) of 43 paint transfers were interspecific. [However, the sample size is small and 11.6% is not significantly different from 5.5% (binomial probability, β (5; 43, 0.055) = 0.06).] The average distance of paint transfer was 1.45 m (N = 24) with a large standard deviation (1.87) and a range of 0.025 m to 7.62 m. Of 27 observed paint transfers in which both the source and destination were known, carry-over of paint (here defined as transfer of paint to inflorescences visited subsequent to the bee's first stop after visiting the source) was observed only twice (=7.4%). Presumably pollen carry-over is correspondingly low (cf. Waser & Price, 1982).

At the study site at km 15 Pipeline Road, *D. tiliifolia* and *D. dioscoreifolia* occurred near one another and were pollinated by the same bee species and individuals. Despite the fact that these two species of *Dalechampia* differ in bract color and morphology and in resin color (*D. tiliifolia*: white bracts, yellow resin; *D. dioscoreifolia*: pink bracts, maroon resin), on many occasions we observed individual *Eulaema cingulata* visit both species "indiscriminately" and to have mixed corbicular loads of yellow and maroon resin. The two plant species were highly segregated. An average of 82 open inflorescences of *D. tiliifolia* were present in an open grassy area, whereas an average of ten open inflorescences of *D. dioscoreifolia* were present at the edge of the forest. Thus even indiscriminate foraging on the part of the bees would result in fewer interspecific moves than would be expected were the plants evenly distributed. Out of 670 recorded moves between inflorescences, 23 (3.4%) were interspecific moves. This is considerably less than would be expected were the plants not spatially segregated (Table 7).

The small proportion of interspecific pollinator moves belies the significance of its effect on

TABLE 6. Observed movements of pollinators between ca. 20 inflorescences of *Dalechampia heteromorpha* and ca. 20 inflorescences of *D. scandens*, 13–26 Jan. 1980, Canal Zone, Panama. Expected values are calculated using 2 × 2 contingency assuming no pollinator constancy or spatial segregation of plants. Observed differs from expected at $P < 0.001$ ($\chi^2 = 445.9$).

	By *Trigona* spp.	By *Hypanthidium panamense*	Total Observed Pollinator Movements (%)	Total Expected Pollinator Movements
Intraspecific movements: *D. heteromorpha*	276	58	334 (58.0%)	213
Intraspecific movements: *D. scandens*	204	6	210 (36.5%)	89
Interspecific movements: From *D. heteromorpha* to *D. scandens*	13	2	15 (2.6%)	136
Interspecific movements: From *D. scandens* to *D. heteromorpha*	13	4	17 (2.9%)	138

D. dioscoreifolia. A comparison of the number of pollinator moves from inflorescences of *D. tiliifolia* to inflorescences of *D. dioscoreifolia* with the number of intraspecific moves among *D. dioscoreifolia* inflorescences (Table 7), indicates that nearly one-third of the visits to *D. dioscoreifolia* by *E. cingulata* are likely to have resulted in the deposition of pollen of *D. tiliifolia* on the stigmas of *D. dioscoreifolia*. The pollen grains of *D. tiliifolia* are much larger than those of *D. dioscoreifolia*. Stigmas of these two species were examined with a hand lens and pollen grains were identified and counted. All the stigmas examined in inflorescences of *D. dioscoreifolia* that had been visited by a bee coming from *D. tiliifolia* (N = 8) bore large amounts of pollen of *D. tiliifolia*. In two observations of the reverse interspecific move there was no transfer of *D. dioscoreifolia* pollen to the stigmas of *D. tiliifolia*.

The *D. dioscoreifolia* at this locality was thus subject to a substantial influx of pollen from *D. tiliifolia*. Of 15 stigmas of *D. dioscoreifolia* examined on 25 January 1980, 4 (27%) bore pollen of *D. tiliifolia*, 3 (20%) bore pollen of *D. dioscoreifolia*, and 8 (53%) had no pollen on the stigmas. *Dalechampia tiliifolia* at this site was much more abundant (Table 7) and was visited at a higher rate (Table 5). Of 51 stigmas of *D. tiliifolia* examined on 22 January 1980, 42 (82%) bore *D. tiliifolia* pollen and 9 (18%) bore none; no stigmas bore *D. dioscoreifolia* pollen. Thus, at least as compared to *D. tiliifolia*, *D. dioscoreifolia* showed substantial stigmatic contamination by heterospecific pollen and relatively low levels of conspecific pollination. However, part of the latter difference between the two species may be attributed to the fact that *D. tiliifolia* self-pollinates fairly readily and *D. dioscoreifolia* does not.

HYBRIDIZATION AND INTERSPECIFIC CROSSES

Despite extensive searches in numerous locations in Central and South America, we have never found any evidence of natural hybridization between species of *Dalechampia*. Experimental greenhouse crosses have been performed between *D. scandens* and *D. heteromorpha*. Out of 45 crosses made with *D. scandens* as the pistillate parent, only two produced seed. When these putative hybrids were grown and later selfed, we found that neither the F_1s nor F_2s were distinguishable from the pistillate parent; apparently these were the result of pollen contamination from the pistillate parent.

In the reverse cross (*D. heteromorpha* as the pistillate parent), of 51 crosses only three produced seed. These again appeared to be the result of contamination by pollen from the pistillate parent.

It has not been possible to make the combinations of crosses involving the other two species in this study. However, unsuccessful crosses made between four additional Central American species of *Dalechampia* suggest that interspecific incompatibility barriers are common among sympatric species of *Dalechampia*.

Experiments have also been performed to measure how contamination ("clogging") of stigmas with heterospecific pollen affects seedset. In one experiment using *D. scandens* as the pistillate parent, stigmas were pollinated with the pollen of *D. heteromorpha*; two days later they were manually self-pollinated. Other stigmas were

TABLE 7. Observed movements of pollinators between an average of 82 inflorescences of *Dalechampia tiliifolia* and an average of 9.6 inflorescences of *D. dioscoreifolia*, 20–27 Jan. 1980, Canal Zone, Panama. Expected values are calculated using 2 × 2 contingency assuming no pollinator constancy or spatial segregation of plants. Observed differs from expected at $P < 0.001$ ($\chi^2 = 314.6$).

	By *Eulaema cingulata*	By *Euglossa* sp.	Total Observed Pollinator Movements (%)	Total Expected Pollinator Movements
Intraspecific movements: *D. tiliifolia*	617	1	618 (92.2%)	591
Intraspecific movements: *D. dioscoreifolia*	27	2	29 (4.3%)	2
Interspecific movements: From *D. tiliifolia* to *D. dioscoreifolia*	13	0	13 (1.9%)	40
Interspecific movements: From *D. dioscoreifolia* to *D. tiliifolia*	10	0	10 (1.5%)	37

pollinated with a mixture of roughly equal parts of *D. scandens* and *D. heteromorpha* pollen. As a control, stigmas were manually self-pollinated. The results (Table 8) indicate significant depression of seedset (relative to the control) by heterospecific pollination prior to self-pollination ($P < 0.001$). Pollination with the two-species pollen mixture produced significantly more seeds than heterospecific pollination followed by self-pollination ($P < 0.05$). Pollination with the mixture produced fewer seeds than the control treatment, but the difference was not significant ($P = 0.076$).

In a similar experiment on *D. heteromorpha*, the stigmas were pollinated with heterospecific pollen followed by manual self-pollination two days later. The source of heterospecific pollen was *D. magnistipulata* Webster & Armbruster, a relative of *D. scandens* in sect. *Scandentes*. The control treatment was manual self-pollination. The experimental treatment again resulted in depression of seedset relative to the control ($P < 0.01$, Table 8).

DISCUSSION AND CONCLUSIONS

FLORAL CONSTANCY AND FORAGING STRATEGIES

There is considerable literature indicating that flower constancy is common or even the rule among wild bees (Chambers, 1946; Grant, 1950; Manning, 1956; Sprague, 1962; Free, 1966; Proctor & Yeo, 1972). These authors have suggested that individual bees that learn how to manipulate a flower species will forage most effi-

TABLE 8. Effect of heterospecific pollination on seed production. Numbers in rows 1 and 2 indicate the number of inflorescences in each class. Column 1 differs significantly from column 2 at $P < 0.05$, column 1 from 3 at $P < 0.001$, column 4 from 5 at $P < 0.01$; columns 2 and 3 are not significantly different, $P = 0.076$; χ^2 analysis.

	D. scandens (♀) × *D. heteromorpha* (♂)			*D. heteromorpha* (♀) × *D. magnistipulata* (♂)	
	Heterospecific pollination followed by self-pollination	Pollination with mixture of two pollens	Self-pollination (Control)	Heterospecific pollination followed by self-pollination	Self-pollination (Control)
0–4 seeds produced per inflorescence	26	11	8	8	10
5–9 seeds produced per inflorescence	9	15	34	2	30
Mean number seeds per inflorescence	1.97	3.95	6.93	4.6	8.0

ciently if they restrict their activities to that species, at least as long as it is abundant. Some authors, however, have argued that the foraging strategies of polylectic bees are not adequately described by the concept of simple temporary constancy, but that many bees are inconstant, facultatively constant, or have "majors" and "minors" (e.g., Hobbs, 1962; Macior, 1966; Mosquin, 1971; Heinrich, 1975, 1976b).

The observations on foraging bees made in this study are also inconsistent with the assertion that simple floral constancy is the primary pattern of foraging by bees. We observed numerous individual *Eulaema* foraging from *D. tiliifolia* and *D. dioscoreifolia* without apparent "regard" for species; yet these bees could surely distinguish between these markedly dissimilar *Dalechampia* species. Similarly, we observed individual *Hypanthidium* and *Trigona* on several occasions visit *D. scandens* and *D. heteromorpha* indiscriminately, moving to nearest neighbors as encountered on their foraging routes.

Yet bees did distinguish between species of *Dalechampia* under certain conditions. *Trigona* and perhaps *Hypanthidium* appeared to distinguish between *D. scandens* and *D. heteromorpha* when there were differences in the available resources. When inflorescences of *D. scandens* were closed in the morning and pollen and resin resources were unavailable to foraging bees, *Trigona* and *Hypanthidium* foraged from *D. heteromorpha* on 89.3% of the inflorescence visits (N = 599). In the afternoon when the pollen and resin resources were depleted in *D. heteromorpha,* these same bee species foraged "preferentially" from *D. scandens,* visiting this species on 88.8% of all inflorescence visits (N = 483).

Similar observations were made by Armbruster and Webster (1982) on the behavior of *Hypanthidium* nr. *melanopterum* foraging on *Dalechampia scandens* and *D. affinis* Muell.-Arg. in Brazil. In this community *D. scandens* opened in the morning and *D. affinis* opened in the afternoon. In the morning *Hypanthidium* visited only *D. scandens*; of 19 visits observed prior to 1400 hrs, all were to *D. scandens.* In the afternoon, after the inflorescences of *D. affinis* opened and the pollen and resin resources of *D. scandens* were depleted, the same individual bees "preferentially" visited *D. affinis*; after 1430 hrs 21 (84%) of 25 observed visits were to *D. affinis* even though inflorescences of *D. scandens* were still open (cf. Fig. 2 in Armbruster & Webster, 1982).

When there are differences in the resource available, euglossine bees, as well, forage preferentially from one species of *Dalechampia* over another. It has been pointed out several times that euglossine bees (of medium to large size) collect resin preferentially from *Dalechampia* species with large resin glands, "ignoring" those species with smaller glands (Armbruster & Webster, 1981, 1982). This behavior was exhibited during this study as well.

Thus it appears that at least some species of the diverse genera *Eulaema, Euglossa,* and *Hypanthidium* employ a "strategy" of facultative constancy which "maximizes" resource harvest. They do not discriminate between similar flower species when there is no advantage in doing so. However, these bees do discriminate between similar flower species when they perceive that there are differences between them in the resources available. Zimmerman (1981) has suggested that bumblebees employ this same strategy, and Simpson and Neff (1981) have drawn similar conclusions from their studies of *Centris* foraging oils in Texas. This pattern may also hold for individual *Trigona* (a social species); however, because of the possibility of sequential foraging on different *Dalechampia* species by different workers from the same hive, many more marked individuals need to be observed.

REPRODUCTIVE INTERACTIONS BETWEEN PLANT SPECIES

Recently there has been considerable interest in the nature of reproductive interactions between sympatric plant species (Waser, 1983). Under certain conditions, co-occurring plant species may mutualistically facilitate each other's reproduction (Macior, 1971; Brown & Kodric-Brown, 1979; Waser & Real, 1979; Schemske, 1981). Perhaps more common, however, is reproductive interference between co-occurring species. Reproductive interference is manifested in several ways. Simultaneously flowering sympatric species may compete for pollinator service if pollinators are not abundant enough to effect full pollination of all flowers of both species (Levin, 1970; Levin & Anderson, 1970; Mosquin, 1971). If a pollinator is constant and prefers one species over another, the second species will suffer from lower rates of pollination as a consequence of its sympatry with the first species. Even if a pollinator does not "prefer" one flower species over another, both species may have lower rates of effective pollination as a result of the large number of wasted interspecific pollinator moves. This has especially dire consequences on the numerically minor species (Levin & Anderson, 1970; cf. Lewis, 1961).

Another detrimental effect may accrue from sharing pollinators even when pollinators are sufficiently abundant to adequately pollinate all flowers of both species. If shared pollinators results in interspecific pollen flow, the reproductive fitness of sympatric plants may be depressed in several ways. If the species are cross-compatible but produce sterile hybrids, reproductive fitness is lowered and severe selection operates against individuals sharing pollinators (Lewis, 1961; Grant, 1966). Interspecific pollination also represents a major loss of genomic copies (pollen); any plant that is effective in getting its pollen to conspecific stigmas will be at a substantial selective advantage (Charnov, 1979). We have presented evidence of a third consequence of interspecific pollen flow: seedset is depressed by the presence of heterospecific pollen on stigmas, even if there is adequate conspecific pollination (also cf. Waser, 1978a, 1978b; Sukada & Jayachandra, 1980; Thomson et al., 1981). One or several of these processes presumably generates selective pressures that may lead to partitioning of pollinator resources by coexisting plant species, and thereby reduction of competition for pollinator service and/or reduction of interspecific pollen flow.

Several of these selective pressures may be operating in assemblages of *Dalechampia* species. We have shown that one consequence of pollinator sharing by *D. tiliifolia* and *D. dioscoreifolia* is substantial interspecific pollen flow, and that interspecific pollen flow between *D. scandens* and *D. heteromorpha* can reduce the number of seeds produced by members of both species. It thus seems likely that populations of sympatric species will have adapted to coexistence with their congeners, at least if their ranges overlap substantially and they have co-occurred for a sufficiently long period of time. Previous studies of two-species assemblages of *Dalechampia* supported this expectation (Armbruster & Webster, 1979, 1981, 1982). In the present study we found that most of the coexisting species partition pollinators in ways that result in low levels of interspecific pollen flow. At km 13 Pipeline Road, *D. dioscoreifolia* was the only species that produced large quantities of resin and had relatively large interfloral distances; it alone was pollinated by euglossine bees. *Dalechampia heteromorpha* and *D. scandens,* with smaller resin glands and smaller interfloral distances were not visited by euglossines, but instead were pollinated by small megachilid and meliponine bees. Although these two species were visited by the same bee species and individuals, the levels of interspecific bee movement, and presumably pollen flow, were relatively low; *D. heteromorpha* was pollinated primarily in the morning, *D. scandens* in the afternoon.

Dalechampia tiliifolia and *D. heteromorpha* occurred together at several sites. These species utilized different pollinators as well; *D. tiliifolia* was pollinated by euglossine bees, *D. heteromorpha,* again, by megachilid and meliponine bees. We did not observe *D. tiliifolia* and *D. scandens* growing together in Panama. It is possible that they do occasionally occur together; if so, they probably do not share pollinators.

At km 15 Pipeline Road, we observed *D. tiliifolia* and *D. dioscoreifolia* growing together. Both species have large resin glands and relatively large interfloral distances; they are both pollinated by species of euglossine bees. The most frequent pollinator of these two species at this site, *Eulaema cingulata,* moved between the two species with sufficient frequency to effect considerable interspecific pollination.

Dalechampia dioscoreifolia was less abundant than *D. tiliifolia* at this site (with averages of ten and 82 inflorescences, respectively). As a consequence it was subject to substantial pollen flow from *D. tiliifolia* and must have lost much pollen to foreign stigmas. The effects of interspecific pollination on *D. tiliifolia* were diluted among a larger number of inflorescences and were probably of minor significance.

This relationship may have detrimentally affected the reproductive output of individuals of *D. dioscoreifolia* at this site. With respect to the male component of fitness, probably over 25% of the pollen was lost to heterospecific stigmas during our study (Table 7). The female component of fitness may also have been affected; a substantial proportion of the monitored stigmas of *D. dioscoreifolia* bore alien pollen (e.g., 27% on 25 Jan. 1980). We lack data on the effect of alien pollen on the seedset of *D. dioscoreifolia,* but the effect may be similar to that on other *Dalechampia* species. In *D. scandens* and *D. heteromorpha* there was marked depression of seedset if alien pollen reached the stigmas first; however, these two species have smaller stigmas and may be more sensitive to stigma contamination and/or stylar "clogging" than *D. dioscoreifolia.*

Only a small proportion of the stigmas of *D. dioscoreifolia* at km 15 bore significant amounts of conspecific pollen (e.g., 20% on 25 Jan. 1980). Those stigmas lacking conspecific pollen were either devoid of pollen (53%, 25 Jan. 1980) or bore pollen of *D. tiliifolia* (27%, 25 Jan. 1980). This suggests that effective pollinator service was in short supply; in view of the rarity of self-pollination in *D. dioscoreifolia,* reduced pollinator service probably resulted in reduced seed production.

There is some evidence that *D. dioscoreifolia* suffered from lower rates of effective pollination as a result of its proximity to *D. tiliifolia.* Nearly one-third of the pollinator visits to *D. dioscoreifolia* were "wasted," bringing loads of *D. tiliifolia* pollen. When we factor the "wasted" visits out of the visitation rates, we find that *D. dioscoreifolia* at km 15 Pipeline Road had significantly lower rates of effective visitation than did *D. dioscoreifolia* at km 13 Pipeline Road. During three hours of observation on each of two days when the number of open inflorescences were the same in the two populations, we observed 19 visits by *Eulaema cingulata* and 24 visits by *E.* cf. *meriana* at km 13; at km 15 we observed only ten visits by *E. cingulata,* of which one-third could be expected to be ineffective. Thus the rate of effective visitation to *D. dioscoreifolia,* even by *E. cingulata* alone, was significantly lower at km 15 than at km 13 ($7 < 19$, $P < 0.015$, assuming Poisson distribution, Pearson & Hartley, 1958).

Additional evidence suggests that *D. dioscoreifolia* was at a competitive disadvantage relative to *D. tiliifolia* at the Pipeline Road study site, and that this contributed to lower rates of pollinator visitation. If bees visit these two species without preference and without regard to the spatial distribution of the two species, we would expect that the number of visits to each species would be proportional to the number of open inflorescences of each species. The frequency of visits to *D. tiliifolia,* then, should have been 0.895 (its average floral frequency) and the frequency of visits to *D. dioscoreifolia* should have been 0.105. The observed frequencies of visits were 0.937 and 0.063 respectively, which are significantly different from the expected at $P < 0.001$ ($N = 670$; normal approximation of binomial distribution; Bailey, 1959). Thus the rate of visitation to *D. dioscoreifolia* is significantly lower than expected; apparently the bees either have a weak "preference" for *D. tiliifolia* or they are foraging in a manner that causes them to encounter *D. tiliifolia* more frequently.

The expected consequence of sharing pollinators with *D. tiliifolia* is reduced seedset in *D. dioscoreifolia.* Seedset is much lower in the population of *D. dioscoreifolia* at km 15 Pipeline Road than is the seedset for other species. However, the truly critical data are lacking. We have only subjective comparisons between populations of *D. dioscoreifolia*; the population of *D. dioscoreifolia* at km 15 Pipeline Road appeared to produce less fruit than did the populations of similar size we observed at km 13 Pipeline Road, and on Barro Colorado Island, where *D. tiliifolia* was absent.

A puzzling question emerges from this study. There appears to be ample evidence of selective disadvantage to individual plants sharing pollinators and exchanging pollen with members of other species. Most species of *Dalechampia* considered in this study appear to be adapted (or preadapted) to coexisting with each other. *Dalechampia tiliifolia* and *D. dioscoreifolia,* however, share pollinators, exchange pollen, and do not appear to be adapted to coexistence.

The adaptive explanation of pollinator sharing leading to higher rates of pollination for relatively rare or few-flowered species (Schemske, 1981) does not seem applicable here because both species of *Dalechampia* are fairly common and produce relatively large numbers of flowers; also *D. dioscoreifolia* appears to have suffered reduced rates of effective pollination and possibly lower reproductive output as a consequence of its proximity to *D. tiliifolia.* Instead, the explanation may be that these two species are not adapted to coexistence because they rarely occur together. We have observed *D. tiliifolia* at 14 sites and *D. dioscoreifolia* at nine sites in Central and South America (Armbruster, unpubl.), but only at the Pipeline Road site were the two species growing together. The two species usually occur in different habitats; in Panama *D. dioscoreifolia* occurs predominately in forest, and *D. tiliifolia* occurs predominately in open scrub (Table 1). Thus the distribution of these two species is better described as parapatric than as sympatric. Since reproductive interference impacts only a very small peripheral segment of the population of *D. dioscoreifolia,* there would not occur population-wide evolutionary adjustments to sympatry with *D. tiliifolia.* Local adaptation would be possible only if gene flow were very localized, which seems unlikely in this species (cf. Janzen, 1971).

RESOURCE PARTITIONING AND COMMUNITY STRUCTURE

The four species of *Dalechampia* we observed in Panama may be an important part of this tropical forest ecosystem. While the flowers provide resin resources for only four genera of bees, these genera are themselves sufficiently abundant to be important pollinators of many other tropical plants (cf. Gilbert, 1980). Female euglossine bees visit a large variety of plants for nectar and pollen resources, while the males visit and pollinate dozens of species of orchids (Ackerman, 1984; Dressler, 1982). Similarly, *Trigona* and *Hypanthidium* visit numerous other plant species for pollen and nectar. We observed both *Trigona* and *Hypanthidium* visiting a number of weedy roadside species in our study areas.

Most of the literature addressing pollination at the community level concludes that plant species that coexist in stable communities occupy different "pollination niches" (Levin, 1970; Levin & Anderson, 1970; Mosquin, 1971; Frankie, 1975; Heinrich, 1975, 1976; Reader, 1975; Stiles, 1975, 1977; Feinsinger, 1978; Waser, 1978). However, some authors suggest that niche separation is not the only expected outcome of ecological processes (Brown & Kodric-Brown, 1979; Grant & Grant, 1968; Proctor & Yeo, 1972; Macior, 1971; Schemske, 1981), and others argue that observing niche separation in a single community does not demonstrate that any ecological or evolutionary processes have occurred (Connor & Simberloff, 1979; Strong et al., 1979; Poole & Rathcke, 1979; Waser, 1983).

Most of the species of *Dalechampia* that occur together at our study sites in Panama are either pollinated by different bees or are pollinated at different times of the day. This is consistent with theoretical expectations. The only exception, pollinator sharing between *D. dioscoreifolia* and *D. tiliifolia*, may be a case of two species lacking adaptation for sympatry because they rarely occur together; when they do occur sympatrically it may impact only a small portion of each population. If so, this is compatible with the resource-partitioning theory as well. Before we can make strong claims of community organization, however, it will be necessary to collect more data on the relative frequency of co-occurrence of species, pollen-flow dynamics, reproductive consequences of interspecific pollination, and comparative reproductive performance of populations of each species as they occur with and without sympatric congeners. Especially useful would be establishment of experimental populations of *D. tiliifolia* and *D. dioscoreifolia* in varying ratios, to determine the effects of sympatry on pollination rates and reproductive performance.

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POLLINATION BIOLOGY AND THE BREEDING SYSTEM OF *ACACIA RETINODES* (LEGUMINOSAE: MIMOSOIDEAE)[1]

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ABSTRACT

Coastal populations of *Acacia retinodes* Schldl. var. *uncifolia* J. M. Black are protogynous and highly self-incompatible. Flowers are nectarless but insects appear to be attracted to the inflorescences both by the yellow floral color and distinctive fragrance. Neutral red tests suggest that the scent originates from the stigma and epidermal cells of the anthers. Floral foragers represented three insect orders but interpretations of field observations and pollen load analysis of insects indicate that solitary bees in the Colletidae and Halictidae are the major pollen vectors. The method for removal of pollen from the anthers is via thoracic vibration. Because female phase flowers offer no pollen, foraging by bees on such flowers is interpreted as a trend towards partial pollination by deceit.

In Australia, the large number of *Acacia* species (ca. 900, Pedley, 1978, 1979), suggest that this country is a center of speciation and evolution; taken together with the fact that *Acacia* represents the largest genus of angiosperms, we might expect its reproductive biology to be well known. Regrettably, this is not the case. Research into the mechanisms of pollination and seed-setting of Australian species of *Acacia* has been spasmodic and fragmentary. Variation in the number of grains per polyad was documented by Mueller (1887–1888), but it was not until the 1930s that the first cytological studies of pollen germination and pistil interactions were carried out, based primarily on *A. baileyana* F. Muell. (Newman, 1933, 1934a, 1934b). Later, with the advent of electron microscopy, the structural relationships and taxonomic significance of the polyad was established for many species (Guinet & Lugardon, 1976; Guinet, 1981).

Pioneering studies of the breeding system of two Australian species of *Acacia* were carried out at the South African Wattle Research Institute. Philp and Sherry (1946, 1949) established that *A. decurrens* and *A. mearnsii* are only partially self-compatible, and are largely outbreeding. The vectors that assure effective pollination have not been established, although several brief reports have been published suggesting that bees are involved (Armstrong, 1979), or birds in some species (Ford & Forde, 1976). Vogel (1978) considers that *Acacia* is melittophilous.

The question arises whether research into the pollination biology of other mimosoids is further advanced. Arroyo (1981) noted that the basic unit of reproduction in the Mimosoideae is the inflorescence not the individual flower, because the flowers tend to be tiny, numerous, and densely massed. Furthermore, floral sexuality, within a single inflorescence, may intergrade subtly from functionally hermaphroditic through the various forms of decliny (Lewis & Elias, 1981). Therefore, the basic floral morphology of the Mimosoideae offers several obstacles in attempts to interpret pollinator-flower interactions and breeding systems. Modification of the size, floral attractants, and sexuality of the flowers, composing the mimosoid inflorescence, has permitted the exploitation of all animal groups commonly associated with the major trends in pollen dispersal. This includes bees e.g., in *Prosopis* (Simpson et al., 1977) and Mesoamerican *Acacia* (Janzen, 1974); bats e.g., in *Parkia* (Baker & Harris, 1957; Hopkins, 1981); birds e.g., in *Calliandra* (Arroyo, 1981) and *Inga* (Koptur, 1983); and marsupials e.g., in *Inga* and *Acacia* (Turner, 1983). Zoophilous syndromes intergrade in the Mimosoideae. Generalist entomophily occurs in *Acacia macracantha* Humb. & Bonpl. ex Willd. (Zapata & Arroyo, 1978) while some *Inga* spp. are pollinated by hummingbirds and Lepidop-

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tera (Koptur, 1983). Reliable information pertaining to the breeding systems remains fragmentary and inconclusive. *Neptunia* and *Parkia* are probably self-compatible (Windler, 1966; Baker & Harris, 1957), while self-incompatibility has been tentatively shown to occur in a few neotropical *Acacia* species (Janzen, 1974; Zapata & Arroyo, 1978).

There is therefore an urgent need to explore the reproductive biology of Australian species of *Acacia*. At Melbourne, we have initiated a long-term research program into the role of the polyad in reproduction, using a multi-disciplinary approach. We have established that variation in polyad grain number (4–16 in different species) is matched with ovule number in the ovary (Kenrick & Knox, 1982). However, the polyad grain number/ovule number ratio is very low, 1.2 (Knox & Kenrick, 1983) compared with about 4 in mimosoids with free pollen grains (Cruden, 1977). This suggests that the polyad of *Acacia* has a considerable selective advantage, and is a highly efficient reproductive unit. The compound grains also make for efficient use of available pollinators.

In the present paper, we have investigated the nature of the breeding system in a summer-flowering species of *Acacia, A. retinodes,* and explored its pollinator relationships. We have previously published a preliminary account showing that this species is self-incompatible (Knox & Kenrick, 1983). We now confirm this finding, and relate our results to work on other Mimosoideae.

MATERIALS AND METHODS

Acacia retinodes Schldl. var. *uncifolia* J. M. Black is restricted to coastal sites in South-eastern Australia where it is locally abundant on calcareous sands and is commonly called the Wirilda. Henceforth, in this paper, it is referred to as *A. retinodes*. This study was conducted in an area towards the eastern end of its distribution where *A. retinodes* is a dominant component of the remnants of the coastal flora. Two study sites were chosen at Cape Schanck, Victoria; the first site in the Cape Schanck National Park and the second about 2.5 km away at the Cape Country Club. Both sites are naturally occurring populations.

Breeding system analysis. The peak of flowering of *Acacia retinodes* in the populations at Cape Schanck is from early December until late February; however, occasional trees may be found sparsely flowering at any time of the year. Thirty trees were tested in this study, and each was labelled with a metal tag. Immature flowering shoots containing about three to 15 racemes of inflorescences were enclosed to prevent cross-pollination when the majority of buds were approaching the yellow bud stage (Newman, 1933). Open flowers and phyllodes were removed. The shoots were enclosed in cellulose acetate bags. These were 180 mm by 115 mm in size with 30 mm gussets on either side, and were tied on with plastic covered wire ties. These bags are permeable to air and water molecules, and provide suitable protection from pollinators.

Two or three days later, the shoots were uncovered either for pollen collection, or for pollination. For manipulated pollinations, shoots were trimmed of senescent flowers and unopened buds following the method of Philp and Sherry (1946, 1949). The aim was to pollinate when the maximum number of inflorescences were at the female phase (see Results, Floral Behavior and Dichogamy) with anthers still folded but styles extended.

For each series of crosses, all bagging was done at the same time and five replicate bagged flowering shoots were employed for each type of cross. Several types of pollination were undertaken:

1. Control, pollinators excluded. Because of the small size of the inflorescences, it is quite impractical to emasculate the flowers to prevent accidental self-pollination. Accordingly, to determine whether mechanical autogamy occurred in the absence of pollinators, five samples of flowering shoots on each tree remained bagged during the life of the flowers, i.e., a total of ten to 12 days.
2. Manipulated self-pollination. When the majority of inflorescences in a bag reached early anthesis (see Results for description), the bag was taken off and fully open male phase flowers and unopened buds removed before the inflorescences were self-pollinated. Pollen was applied to the stigmas from the inner surface of 2 ml specimen vials, made of polyvinyl chloride, which had been coated with pollen by pressing fully open flowers against the inside of the vial, to retain only the polyads. The shoots were bagged until the flowers were senescent.
3. Manipulated cross-pollination. These were carried out as described for self-pollinations,

TABLE 1. Variation in number of floral organs in two populations of *Acacia retinodes* at Cape Schanck, Victoria. Explanation of abbreviations: $\bar{x}$, mean; s.d., standard deviation; N, number in sample.

Tree Number:	Population 1				Population 2				Overall Data
	1	3	5	6	20	23	31	34	
A. Number of Flowers/Inflorescence									
$\bar{x}$	22.2	20.2	23.6	21.6	23.0	23.0	30.8	24.2	23.9
s.d.	2.05	0.84	3.44	0.89	1.73	2.86	2.28	2.68	3.73
N	5	5	5	5	5	5	5	5	40 (total)
B. Number of Anthers/Flower									
$\bar{x}$	52.9	56.8	59.2	58.7	62.2	78.0	71.6	72.0	63.5
s.d.	4.03	11.06	7.10	6.03	5.97	8.88	6.08	6.76	10.84
N	25	25	25	19	25	20	25	21	160 (total)
C. Number of Ovules/Ovary									
$\bar{x}$	12.7	13.7	11.9	11.8	12.7	13.2	12.5	12.3	12.6
s.d.	0.82	0.67	0.74	1.03	0.95	1.14	0.53	1.16	1.05
N	10	10	10	10	10	10	10	10	80 (total)

except that the pollen was from another nominated tree.

Pod counting. Pods were counted ten to 28 days after pollination. The number of pods set per infructescence was scored. A comparison was made between pod set following open-pollination and that following controlled pollination in one tree (number 23).

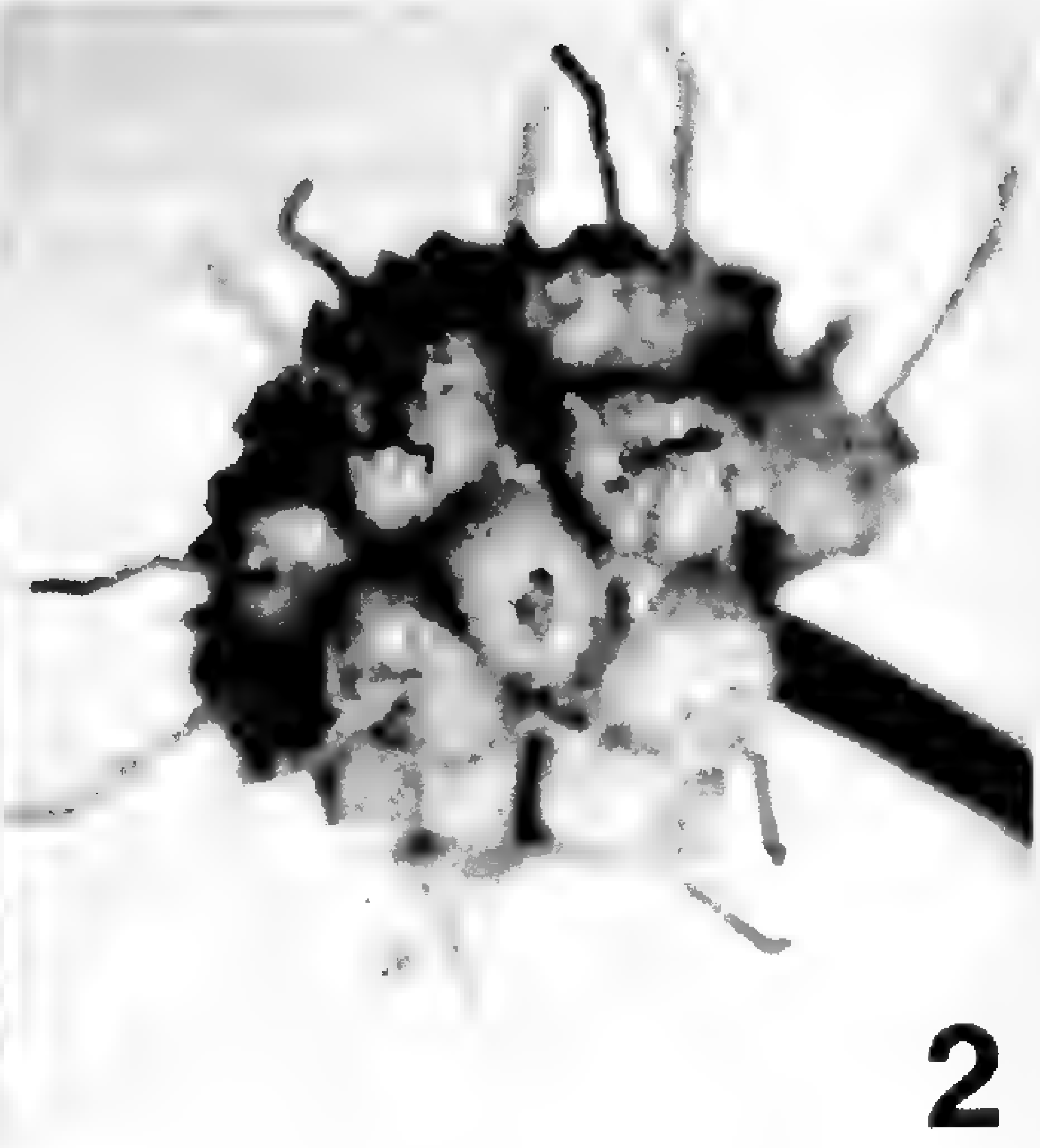
Floral statistics. Data for number of flowers/inflorescence and number of anthers/flower were counted in the laboratory using a high power binocular dissector on fresh or FAA-fixed material. Number of ovules/ovary was observed by fluorescence microscopy after ovaries, dissected from FAA fixed material were stained with decolorized aniline blue (Linskens & Esser, 1957; as modified by Kenrick & Knox, 1981a). The number of polyads/style was scored from open-pollinated, FAA-fixed flowers, which were rinsed in distilled water and stained with Calberla's solution (Ogden et al., 1974) and observed by bright field microscopy. Neutral red staining for detection of osmophores was employed as described by Boyer (1963).

Pollen vector analysis. To determine the pollen vectors of *Acacia retinodes,* insects were selectively collected, from 15 Dec. 1981 to 12 Feb. 1982 from 7:00 A.M. to 4:00 P.M. Collecting periods from 1:00 P.M. to 4:00 P.M. were finally dropped because no insect activity was recorded. Insects were collected *only* when they foraged on the flowers of *A. retinodes.* Foraging is defined here as the active removal of pollen or the probing of floral structures with insect mouthparts. Insects were killed together in jars containing ethyl acetate vapor. To determine the presence of pollen, insects were first observed under dissecting microscopes. To analyze pollen species the same insects were gently pressed against glass slides, to dislodge grains. Samples were stained with Calberla's solution and observed under light microscopy. Because insects had been killed in the same jar there was a continual danger of contamination. Therefore, pollen species were not recorded on a particular insect as present unless 25 individual polyads (for *A. retinodes*) or 25 separate grains (for all other species) could be counted in a single, stained sample. Foraging behavior of insects was noted on *A. retinodes* and on co-blooming species within the study sites.

RESULTS

Floral morphology. The globose inflorescences of *A. retinodes* contain 18 to 34 flowers (Table 1A). Inflorescences are arranged in "racemes" of five to seven inflorescences in the axil of a phyllode; however, at peak flowering, development of the phyllodes is evidently suppressed, and the apices of branches appear to be panicles of globose inflorescences (Fig. 1). After flowering, suppressed phyllodes may develop, and new vegetative growth may occur even from the tips of the racemes.

Each inflorescence bud develops in the axil of a reddish bracteole that ceases expansion at an



FIGURES 1, 2. A flowering shoot of *A. retinodes* var. *uncifolia.*—1. Note that there is usually more than one globose inflorescence per raceme and that inflorescences on the same branch tend to flower acropetally (×0.3).—2. Inflorescence in the female phase (×10).

early stage (Jobson et al., 1985). The calyx has five fused, reduced red sepals and the corolla has five yellow petals, that are reflexed at anthesis. The 34 to 91 stamens in each flower (Table 1B) have anthers that contain eight, 16-grain polyads that dehisce through longitudinal slits (Kenrick & Knox, 1979). The single ovary contains ten to 14 ovules (Table 1C).

The long, narrow style is generally equal to or exceeds the length of the stamens. The terminal cup-shaped stigma is of the wet type (WN) in the classification of Heslop-Harrison (1981). The flowers on most trees examined were hermaphrodite although in 25% of trees, some occasional flowers had undeveloped pistils. No nectaries have been found on the floral axis around the ovary, as occurs in some African species (Robbertse, 1974).

Floral behavior and dichogamy. Inflorescences flower acropetally and the flowers open synchronously within an inflorescence. The majority of styles emerged before 8:00 A.M., and are at first folded in a zigzag pattern, but soon straighten (Kenrick & Knox, 1981a). At this stage, the flower petals are only partially exserted and stamens are compressed beneath the petals. An inflorescence can be said to be truly protogynous since flowering is synchronous. At this point the inflorescence resembles a spiked club, and is referred to as a female phase inflorescence (Fig. 2).

Stamens normally do not fully extend until after mid-day, depending on the weather conditions. When the anther filaments are fully extended the styles are generally hidden. This state marks the beginning of the male phase, although dehiscence usually does not take place until the following day. Rate of floral development may vary according to the prevailing climatic conditions: dry sunny conditions accelerating and cool cloudy weather retarding development.

A fruity odor, reminiscent of ripe cantaloupe melon, is first detectable during the female phase. Neutral red tests for detection of osmophores, during this phase, stain the stigma only. However, scent is most pronounced during the male phase, when the anther epidermal cells stain intensely.

Breeding systems. The data obtained from controlled pollinations demonstrate that *A. retinodes* is highly self-incompatible (Table 2). Cross-pollinations with other trees resulted in high levels of pod set, while self-pollinations gave few or no pods. Higher levels of pod set resulted from interpopulation crosses than intrapopulation crosses.

The self-sterility is almost complete. Control flowering shoots, kept in bags during the flowering period to exclude pollinators showed similar low levels of pod set. In fact, the level is approximately 10% of that of the controlled self-pollinations (Table 2). These controls involved a much larger sample of trees in both populations than the manipulated pollinations. These data indicate that for effective seed set, pollen requires to be transferred from one tree to another. Trees existing very close together, suggesting a common origin from a single parent by root coppicing, were tested for the presence of self-incom-

TABLE 2. Comparison of the breeding systems of two populations of *Acacia retinodes* from Cape Schanck, Victoria following controlled pollinations.

Pollen Source	Number of Trees Tested	Number of Inflorescences Pollinated	Number of Infructescences	Total Number of Pods Set	Pod Set Ratio (4/2)
Female Trees of Population 1:					
Population 1	6	912	209	665	0.73
Population 2	4	581	199	863	1.49
Same tree (selfed)	6	393	4	5	0.013
Control, pollinators excluded	7	3,360[a]	5	12	0.001
Female Trees of Population 2:					
Population 2	8	1,879	320	1,012	0.54
Population 1	3	1,612	355	1,256	0.78
Same tree (selfed)	4	573	12	15	0.03
Control, pollinators excluded	20	4,104[a]	9	37	0.009
Total:	27[b]	13,414	1,113	3,865	0.29

[a] Estimated by using the number of shoots enclosed times 24 (the mean number of inflorescences pollinated per shoot).

[b] Actual number of trees employed.

patibility. In one such system (20A, B, C), the individuals were reciprocally cross-incompatible.

Natural pollination results in significantly lower levels of pod set ($P = 0.001$), than controlled pollination (Fig. 3). Six pods/infructescence were the greatest number set after open-pollination, compared with 13 after controlled pollination on the same tree. It is important to establish the probable frequency of natural pollination to determine the effectiveness of the pollination mechanism(s). Observations of the presence of polyads on random samples of pistils from six different trees showed that there is considerable variation (Table 3), with pollination ratios varying from 0.1 through 0.9, and a mean ratio of 0.37.

Diversity of floral foragers. Floral foragers were active between 7:00 A.M. and noon with the greatest density observed between 8:00 A.M. and 11:00 A.M. Foragers represented three insect orders (Table 4). While dipterans (flies) and hymenopterans (bees) were collected throughout the duration of the field study, coleopterans (beetles) were found visiting flowers only from 15 Dec. 1981 to 4 Jan. 1982.

Native species of solitary bees, and the introduced *Apis mellifera* (feral Caucasian strains) made up more than 70% of the insect collection and were the dominant polyad vectors. Over 55% of the bees collected were *Lasioglossum* (subg. *Parasphecodes*) spp. of the family Halictidae (Table 4).

Insect foraging behavior. Beetles usually ploughed through individual inflorescences in male phase eating pollen and stamens. *Acacia* polyads were deposited sterno- and nototribically with the greatest density confined to the thoracic region. Whole stamens were found in the mandibles of *Stenoderus suturalis* (Coleoptera). Flies landed on inflorescences in male (staminate) and female (pistillate) phase and probed stamens and styles with their probosces. *Acacia* polyads were found infrequently on these insects (Table 5) and were deposited sternotribically on the legs, thorax, and abdomen. Larger bees such as *Lasioglossum* spp., *Apis mellifera,* and *Megachile* sp. landed on inflorescences and crawled over the entire hemisphere continuously scraping the anthers with the two pairs of forelegs and raking with the hind legs. Thoracic vibration was audible at this time suggesting that polyads were harvested by the wing vibration technique as described in *Bombus* (Heinrich, 1976; Bernhardt & Montalvo, 1979) and on other members of the Mimosoideae (Arroyo, 1981). The smallest bees in the genera *Leioproctus* (Colletidae) and *Homalictus* (Halictidae) appeared to visit *each* male phase flower on an inflorescence sequentially. Polyad collection then proceeded as observed for larger bees. *Acacia* polyads were deposited sternotribically on all bee taxa, on the legs, thorax,

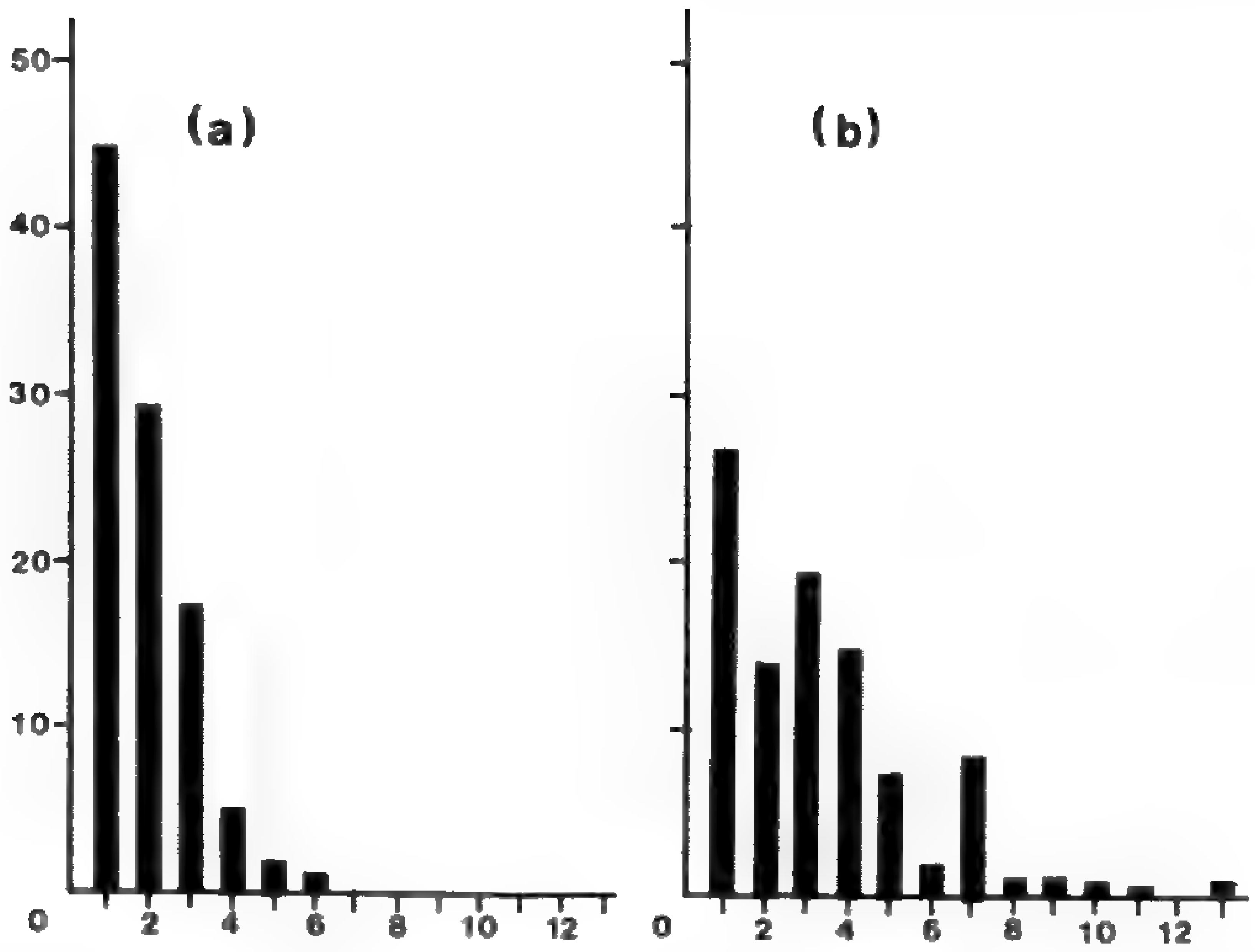


FIGURE 3. Histograms of the percentage frequency of pods set under (a) natural open pollination and (b) manipulated cross pollination on the same tree (number 23). Differences between (a) and (b) are significantly different (D = 7.97, $P = 0.001$).

TABLE 3. Frequency of natural pollination of *Acacia retinodes* at Cape Schanck, Victoria.

Tree Number	% of Pistils Pollinated	Number of Pistils Scored
Population 1:		
1	60	90
3	7	114
6	31	96
Population 2:		
20	54	37
23	24	89
34	88	52
Total:	$\bar{x} = 37$	478

and abdomen (Fig. 4). Pollen was eventually transferred to the abdomen or scopae of the hind legs of bees (Fig. 5) belonging to asocial families (Colletidae, Halictidae, Megachilidae) or to the corbiculae in *Apis mellifera*.

The amount of time a bee spent on an inflorescence appeared to be directly proportional to the number of flowers in the male phase. *Apis mellifera* and *Lasioglossum* spp. attempted to forage on inflorescences in the female phase but normally abandoned them before covering the full circumference. Small halictids and colletids usually visited all flowers on an inflorescence providing at least one-third of them had just emergent anthers. Undehisced anthers were found in the scopae and corbiculae of all bee taxa collected suggesting that insects did not regularly distinguish between polyads and indehiscent anthers.

Pollinator fidelity and co-blooming plants. Over 62% of bees, the largest group of pollen vectors, carried *Acacia* polyads in association with one or two other species (Table 4). Four pollen species were counted on one *Homalictus brisbanensis* and one *Lasioglossum* (*Parasphecodes*) sp. All bees carrying *Acacia* polyads mixed with the pollen of other species bore, at least, one species of pollen from a flower that also produced nectar (Table 4). A total of eight different pollen taxa were found on insects collected (Table 5). At least four pollen species came from angiosperms that were introduced to Australia and had become naturalized on the Cape Schanck peninsula and throughout Victoria (Willis, 1972).

Bees and flies observed foraging on *Hypochaeris radicata, Lycium ferocissimum, Salpichroa origanifolia,* and *Melaleuca lanceolata* were found to collect nectar from these plants before attempting to remove their pollen. *Hypochaeris radicata* was in flower when the field study began and was collected on insect bodies until 19 Jan. 1982 when its flowering season appeared to conclude on Cape Schanck. The two species of Solanaceae (*L. ferocissimum* and *S. origanifolia*), were also in flower when the field study began and their pollen was found on insects' bodies until the end of the field study. *Melaleuca lanceolata* was not found in flower until mid-January and the first insect bearing its pollen (*Leioproctus metallescens*) was not collected until 18 Jan. 1982.

DISCUSSION

Self incompatibility and the breeding system. The controlled pollination data now reported demonstrate that *Acacia retinodes* var. *uncifolia* is highly self-incompatible. The analysis is based on experiments involving nearly 6,000 inflorescences from trees in two populations. Following self-pollination, less than 2% of inflorescences set any pods; while following intrapopulation crosses, up to 23% of inflorescences set pods, which increased to 34% in interpopulation crosses. All manipulated pollinations were carried out in the field under the same conditions as unmanipulated controls.

A summary of published information on the

TABLE 4. Pollen load analysis of insects collected while foraging on *Acacia retinodes* var. *uncifolia.*[a]

	Pollen Load			
Insect (Order and Species)	*Acacia* Only	*Acacia* and Other spp.	Other spp. Only	No Pollen
Coleoptera:				
Automolus depressus	—	1	—	1
Belidae	—	—	—	1
Cleobora mellyimules	—	1	—	—
Rhyparida polymorpha	—	—	—	1
Stenoderus suturalis	1	1	—	1
Total:	1	3	—	4
Diptera:				
Eristalis copiosus	1	1	—	—
E. punctulatus	—	2	—	—
Incurviseta sp.	—	—	—	1
Melanguna viridicens	—	1	—	—
Pyrellia sp.	—	1	—	—
Musca vetustissimus	—	—	1	2
Senostoma sp.	—	—	1	—
Stomorhina subapicalis	—	—	—	1
Syrphus damaster	1	—	—	5
Trichareae brevicornis	1	—	—	5
Xanthogramma grandicornis	—	—	1	3
Total:	3	5	3	17
Hymenoptera:				
Anthobosca spp.	—	2	—	1
Apis mellifera	14	4	—	—
Homalictus brisbanensis	8	2	—	—
H. oxoniellus	2	2	—	—
Lasioglossum (*Chilalictus*) sp.	1	—	—	—
Lasioglossum (*Parasphecodes*) sp.	16	52	2	1
Leioproctus metallescens	1	14	—	—
L. plumosus	—	1	—	—
Megachile spp.	—	2	—	—
Total:	42	79	2	2
Grand Total:	46	87	5	23

[a] Combines collections made at both study sites.

breeding system and occurrence of self-incompatibility in *Acacia* and other Mimosoideae is given in Table 6. Very little data are available; only 12 species of *Acacia* and five other genera of Mimosoideae are listed. Data are often brief, and entirely qualitative, and the methods and results are frequently not given. Evidence suggesting the existence of self-incompatibility is given for *A. decurrens, A. harpophylla, A. macracantha, A. mearnsii* and now, *A. retinodes*; and for three other mimosoid taxa, *Calliandra laxa, Enterolobium cyclocarpium,* and *Pithecellobium saman* (Table 6).

Bawa (1974) developed criteria of self-incompatibility: (a) either no more than a third of the individuals are self-compatible and/or (b) cross-pollinations should yield five times more fruit than self-pollinations. Zapata and Arroyo (1978) developed an Index of Self-Incompatibility (ISI), calculated by dividing the average seed set per flower following manipulated selfing, by the results of manipulated cross-pollination. Self-compatible species score >1, while partially self-incompatible species score <1, and complete self-incompatible species score <0.2. In our results with *A. retinodes,* all ten plants that were both

TABLE 5. Pollen analysis of those insects collected bearing *Acacia* mixed with other species.

Insect (Order and Species)	Pollen Species[a]							
	Ac	Hyp	Lyc	Sal	Mel	Pol	Euc	Mal
Coleoptera:								
Automolus depressus	1	1	—	—	—	—	—	—
Cleobora mellyimules	1	1	—	—	—	—	—	—
Stenoderus suturalis	1	—	1	—	—	—	—	—
Diptera:								
Eristalis copiosus	1	—	—	1	—	—	—	—
E. punctulatus	2	—	1	1	—	—	—	—
Melanguna viridicens	1	—	—	—	—	—	—	1
Hymenoptera:								
Anthobosca spp.	2	2	1	—	—	—	—	—
Apis mellifera	4	1	2	—	2	—	—	—
Homalictus brisbanensis	2	1	1	2	—	—	—	—
H. oxoniellus	2	1	—	1	—	—	—	—
Lasioglossum (*Paraspechodes*) spp.	52	17	9	8	28	1	—	—
Leioproctus metallescens	14	—	2	—	12	—	1	—
L. plumosus	1	—	—	1	—	—	—	—
Megachile spp.	2	2	—	—	—	—	—	—

[a] Pollen species: Ac = *Acacia retinodes* var. *uncifolia* J. M. Black; Hyp = *Hypochaeris radicata* L.; Lyc = *Lycium ferocissimum* Miers; Sal = *Salpichroa origanifolia* (Lam.) Baill.; Mel = *Melaleuca lanceolata* Otto; Pol = *Polygala myrtifolia* L.; Euc = *Eucalyptus* spp.; Mal = Unidentified Malvaceae.

self- and cross-pollinated gave overall ratios of self- to cross-pollinated fruit set in populations 1 and 2 of 0.01:0.73, and 0.03:0.57, respectively. This level is also consistent with experimental results from gametophytic self-incompatible cultivars of *Lolium perenne* L. with ratios of 0.26:10.88 pistils pollinated which produced seed (Cornish et al., 1980) and *Trifolium pratense* L. in which only 0.2% of selfed pistils produced seed (Denward, 1963). The overall results with *A. retinodes* give an ISI score of 0.03 on a pod set basis indicating a high level of self-incompatibility; in fact, a score that is seven times lower than required.

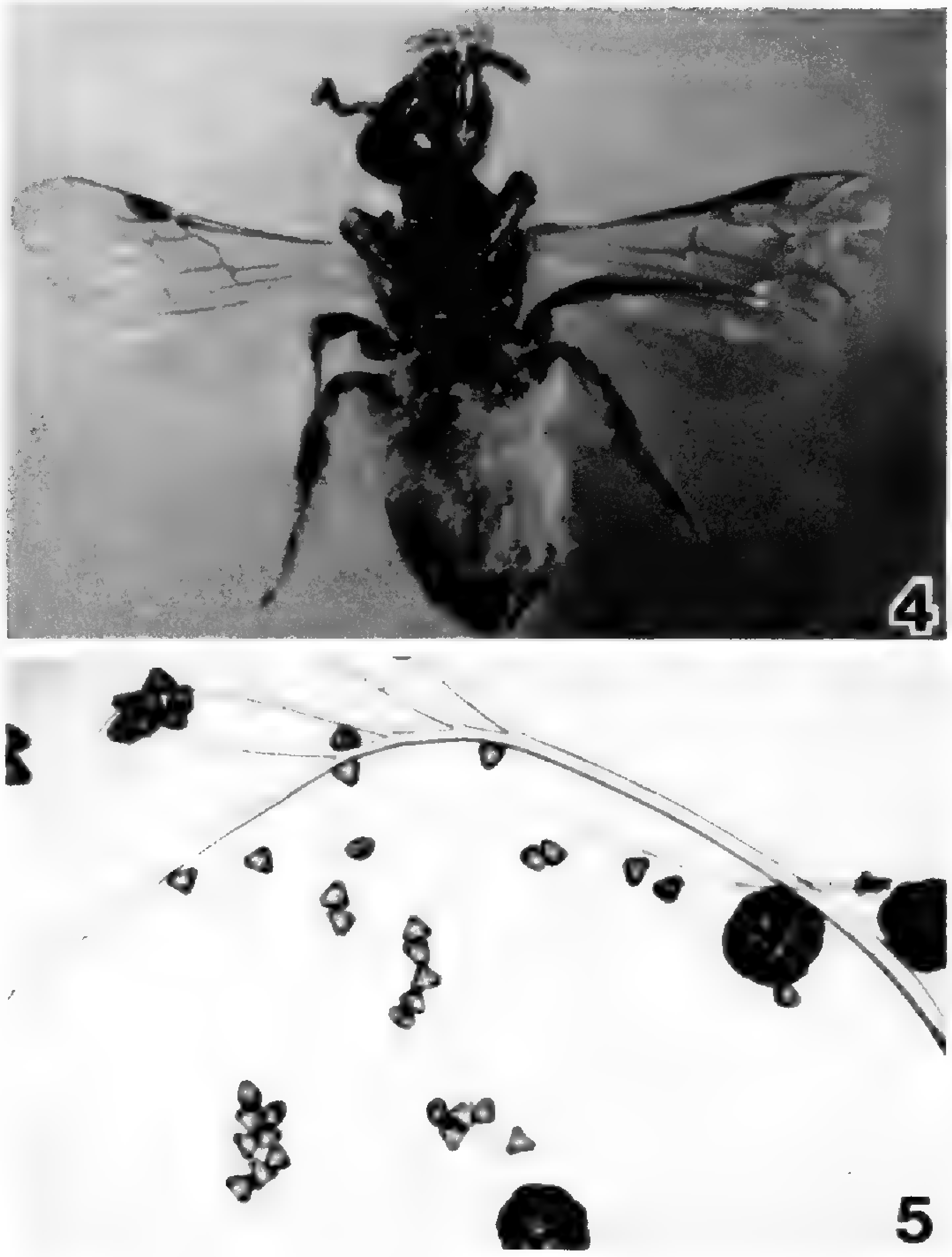
The existence of protogyny has now been reported in several *Acacia* spp. e.g., *A. baileyana* (Newman, 1934a), *A. decurrens, A. mearnsii* (Philp & Sherry, 1946), *A. subulata* (Kenrick & Knox, 1981a). Our data extend these observations to *A. retinodes,* and further demonstrate the existence of a female phase at stigma exsertion which is especially favorable for cross-pollination. In this summer-flowering species, the female phase is coincident with the period of greatest activity of insect pollinators, and may be as short as 2–3 hr. Pollinations made following days of temperatures >30°C show drastically reduced pod set (Kenrick & Knox, unpubl. data). It appears that high temperatures may intensify the expression of self-incompatibility in the stigma and style, or make pollen inviable or stigma unreceptive. The data indicate that for successful pod set, pollen must be transferred from one tree to another.

Pollination biology of Acacia. Bees appear to be the only consistent pollen vectors of *A. retinodes* despite the presence of other floral foragers representing two more insect orders. *Acacia retinodes* should be regarded as a "generalist" mellitophile, as pollinating bees span three native families of solitary Apoidea as well as the naturalized, eusocial *Apis mellifera* (primitively eusocial Halictidae do not occur in Australia; C. D. Michener, pers. comm.). These results parallel observations by Janzen (1974) concerning the swollen thorn acacias of Mesoamerica. Although the polyads of *Acacia* are not shed, as in annonalian or aroid taxa (Vogel, 1978), they do protrude during dehiscence and remain exposed on the surface of the anther (Kenrick & Knox, 1979). This should encourage generalist entomophily as in the American *Prosopis* species (Simpson et al., 1977; Arroyo, 1981), as specialized foraging habits are not required to remove polyads from dense, brushlike inflorescences. *Acacia retinodes,* though, receives a less varied spectrum of pollinators than *Prosopis* as it lacks floral nectaries. *Acacia retinodes* is of little interest to moths, most butterflies, wasps, carrion, and dung flies etc. that do not require the protein and lipids in pollen for ovulation or as a food source for larvae. Post-pollination exudate is not a nectar substitute! Secretions occur very briefly *after* pollination has occurred and if insects were attracted to the fluid they would undoubtedly interfere with the polyad-stigma interface (Kenrick & Knox, 1981b).

Furthermore, female phase inflorescences of *A. retinodes* offer no edible reward but they do offer color and scent as floral attractants. Cross-pollination must occur most frequently via "partial pollination by deceit" (sensu Vogel, 1978; Bernhardt & Montalvo, 1979). The discrepancy between natural and artificial (hand-pollinated) pod set may be based in part, on the foraging of bees that learn to discriminate between male and female phase inflorescences. Bees typically do not visit all of the flowers on a female phase inflorescence but an objective, artificial cross-pollination will probably result in a higher number of successful fertilizations.

Self-incompatibility undoubtedly limits the success of pod set between siblings or parents and their progeny. Interpopulational crosses are, therefore, superior to intrapopulational crosses. Long distance pollinations seem most unlikely with primary pollinators belonging to the Halictidae and Colletidae. Ironically, if such pollinations occur naturally in this region, they would be effected only via the "trap-line" foraging of the introduced honeybee!

Is natural seedset lowered in *A. retinodes* by competition for pollinators with so many naturalized plant species? Simpson et al. (1977) and Arroyo (1981) suggested that the most efficient bee pollinators of many Leguminoseae were those with polylectic-oligolectic (not monolectic) foraging patterns. This increases the frequency of cross-pollinations as small bodied bees, dependent on only one plant species for pollen, rarely visit more than one large shrub during a foraging bout. Narrow polylectic foraging seems to be the norm in bees associated with Australian *Acacia* species as these insects must obtain their chemical energy (floral nectar) from co-blooming taxa (Bernhardt, 1983; Bernhardt & Walker, 1983a, 1983b). The only established competitor for the pollinators of an *Acacia* species is another *Acacia* species (Bernhardt, 1983; Bernardt & Walker 1983a). True "pollen flowers" (sensu Vogel, 1978) have overlapping flowering periods with sympatric, nectariferous plants pollinated by the same bees (Heinrich, 1976; Bernhardt & Montalvo, 1979; Bernhardt, 1984). This has been interpreted as selectively advantageous as the limited pollinator resource is shared. It seems most likely that the invasion of European and South African plants has not put pressure on *A. retinodes* but has supplanted the original nectar flora, excluding *Melaleuca lanceolata* (Willis, 1972).



FIGURES 4, 5. 4. Ventral view of *Leioproctus metallescens* caught on *A. retinodes* showing the build-up of pollen on the hind legs and abdomen in contrast to the forelegs and thorax (×9.4).—5. Scopal hair of *Lasioglossum* (*Paraspechodes*) sp. bearing a mixed load of polyads of *A. retinodes* and grains of *Melaleuca lanceolata* (×640).

Unlike the majority of mimosoids studied so far, *Acacia retinodes* should be regarded as a "Papaver Type" pollen flower (sensu Vogel, 1978) due to the absence of floral nectaries and the accessibility of polyads retained on the anthers. Self-incompatibility and synchronous protogyny encourage cross-pollination in *A. retinodes* but also reduce the success of bee-mediated geitonogamy. The absence of floral and extra-floral nectar reduces the spectrum of potential pollen

TABLE 6. Breeding system of selected species of *Acacia* and other genera of Mimosoideae.

Species	Interpretation[a]	Number of Trees Sampled[c]	Number of Flowers Tested per Pollination per Tree[c]	Pollination Tests[b,c]	Reference
1. *Acacia*					
A. aroma Hook. & Arn.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
A. constricta Benth.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
A. cornigera L.	outbreeding	NG	NG	seed set in glasshouse	Janzen, 1974
A. decurrens Willd.	outbreeding	14	flowering branches, 8.3/tree	open 71.9%, self 26.8%, 400 ovules/tree	Philp & Sherry, 1946; Moffett & Nixon, 1974
A. drepanolobium Harms. ex Sjöstedt	SI	42	NG	seed set in glasshouse	Hocking, 1970
A. furcatispina Burk.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
A. greggii Gray	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
A. harpophylla F. Muell. ex Benth.	outbreeding	17	NG	number of pods/cluster, cross 0.47%, self 0.19%–0.26%	Coaldrake, 1971
A. macracantha H. & B.	SI	6–7	3,786–15,780	cross 0.19%, self 0%, control 0%	Zapata & Arroyo, 1978
A. mearnsii De Wild. (syn. *A. mollissima*)	outbreeding	24	flowering branches	number of viable seeds/pod, open 6.8%, self 2.7%	Moffett, 1956
2. Other Mimosoidea					
Calliandra laxa Benth.	SI	5–6	136–139	cross 11.76%, self 0%, control 0%	Zapata & Arroyo, 1978
C. eriophylla Benth.	SI	>1	1 flowering branch	NG	Simpson, 1977

TABLE 6. Continued.

Species	Interpretation[a]	Number of Trees Sampled	Number of Flowers Tested per Pollination per Tree	Pollination Tests[b]	Reference
Enterolobium cyclocarpum (Jacq.) Griseb.	SI	3–5	15–100	number of flowers setting seed, self 0%, cross 0.28%	Bawa, 1974
Leucaena trichodes (Jacq.) Benth.	SI	NG	NG	NG	Hutton & Eddie, 1982
L. esculenta (MCC & Sesse) Benth.	SI	NG	NG	NG	Hutton & Eddie, 1982
L. collinsii Britton & Rose	SI	NG	NG	NG	Brewbaker, 1982
L. lanceolata S. Watson	SI	NG	15	NG	Brewbaker, 1982
L. macrophylla Benth.	SI	NG	4	NG	Brewbaker, 1982
L. pulverulenta (Schlecht.) Benth.	SI	NG	18	NG	Brewbaker, 1982
L. shannoni Donn. Smith	SI	NG	15	NG	Brewbaker, 1982
Pithecellobium saman Jacq.	SI	3–5	15–100	self 0%, cross 0.28%	Bawa, 1974
Prosopis chilensis Mol. Stuntz emend. Burk.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
P. flexuosa DC.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
P. velutina Woot.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977
P. torquata (Lag.) DC.	SI	>1	1 flowering branch	cross, self, control	Simpson, 1977

[a] SI = self-incompatible.

[b] Control pollinations: inflorescences bagged but unmanipulated.

[c] NG = not given.

vectors, excluding vertebrates like arboreal marsupials (Turner, 1983) and birds (Ford & Forde, 1976; Kenrick et al., 1983), but it may also encourage cross-pollination as bees are forced to leave individual plants periodically when their supply of chemical energy is depleted.

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FLAVONOIDS OF ONAGRACEAE[1]

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ABSTRACT

Analyses of foliar flavonoids have been completed for approximately half of the species of Onagraceae and preliminary surveys have been carried out for at least one species of each of the 17 genera. Some 40 flavonoids, including glycoflavones, flavonols, and flavones, have been isolated and identified. Flavonols occur in all genera and in most species. Glycoflavones, either as the sole flavonoid constituent or co-occurring with flavonols, characterize the more generalized tribes, whereas only flavonols are found in the relatively specialized tribe Epilobieae. Glycoflavones, presumed primitive, occur in some members of all tribes except Fuchsieae and Epilobieae, whereas flavones occur only in Circaeeae, Fuchsieae, and Onagreae. In general, flavonoid data are strongly supportive of conclusions drawn from other lines of phylogenetic investigation about the relative degree of advancement of taxa, but they do not provide strong indications of phylogenetic relationship between genera or tribes.

Most studies of flavonoids in Onagraceae have concentrated on the compounds found in the leaves of these plants, and this paper will emphasize such studies. First, however, it seems worthwhile to review those studies that have been concerned with the floral pigments of this family. In the later sections of the paper, when dealing with foliar flavonoids, we shall not concern ourselves with anthocyanins. The anthocyanins of the flowers of *Fuchsia* and their influence on flower color have been investigated by several workers (Nozzolillo, 1969; Yazaki & Hayashi, 1967; Harborne, 1967; Crowden et al., 1977). The 3-glucosides and the 3,5-diglucosides of all six common anthocyanins are responsible for flower color in this genus. Variants in color appears to be almost wholly determined by these anthocyanins (Crowden et al., 1977). One of them, malvidin 3,5-diglucoside, also has been reported from the flowers of *Epilobium* and *Clarkia*, and another, cyanidin 3-glucoside, also from the flowers of *Clarkia* (Harborne, 1967). Dement and Raven (unpubl. data) examined the floral anthocyanins of 12 genera of the family. They found four widespread anthocyanins, and noted that several other anthocyanins seemed to have evolved independently in several lines. Cyanidin 3-glycoside was the most commonly encountered anthocyanin in Onagraceae, being present in *Calylophus, Gaura, Gongylocarpus, Hauya,* and *Xylonogra.*

A member of another class of floral pigments, the chalcone isosalipurposide, was reported as a floral pigment in 13 species from five genera of Onagraceae by Dement and Raven (1973, 1974). This chalcone is of particular interest because it represents a class of flavonoids that is apparently not found in the leaves of any Onagraceae. This chalcone plays an important ecological role in yellow-flowered Onagraceae, not reflecting light in the ultraviolet wavelengths so conspicuous in the portions of the same flowers where carotenoids predominate. Here it contributes to the formation of floral markings strikingly visible under ultraviolet light, and thus to the insects that visit the flowers of these plants.

At least one species from each genus and most subgenera within the family have been analyzed for its foliar flavonoids. Some 40 compounds have been isolated and identified from Onagraceae, not including anthocyanins. These include seven glycoflavones and six flavones. The remainder are flavonols based on kaempferol (5), quercetin (14), or myricetin (7). Most of the flavonols are 3-O-mono- and diglycosides with relatively few exhibiting seven or B-ring (3′ or 4′) substituents. At least four sulphated compounds, occurring in two different tribes, have been detected in the family. These data are summarized in Table 1. Base compounds and numbering systems are shown in Figure 1. Results for the individual tribes (summarized in Table 2) follow.

Jussiaeeae. Jussiaeeae include the single genus *Ludwigia,* with about 80 species. The species

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TABLE 1. Flavonoids in the Onagraceae.[a]

Flavonols			Glycoflavones	Flavones
kaempferol	quercetin	myricetin	vitexin	apigenin
3-O-gal	3-O-gal	3-O-gal	isovitexin	7-O-glu
3-O-glu	3-O-glu	3-O-glu	orientin	7-O-glucuronide
3-O-rha	3-O-rha	3-O-rha	isoorientin	7-O-glucoronide-sulphate
3-O-ara	3-O-ara	3-O-ara	orientin-o-acylate	
3-O-rha-glu	3-O-rha-glu	3-O-rha-glu		luteolin
	3-O-rha-gal	3-O-diglu	vitexin-o-acylate	7-O-glu
	3-O-diglu	3-O-me-7-O-glu		7-O-glucuronide
	3-7-O-diglu		lucinin	tricinin
	7-O-rha			7-O-glucuronide-sulphate
	3-O-me, 7-O-glu			
	3-O-xyl-gal			
	3-O-sulphates			
	3′-O-me			
	3-O-glucuronide			

[a] Gal = galactose, glu = glucose, rha = rhamnose, ara = arabinose, xyl = xylose.

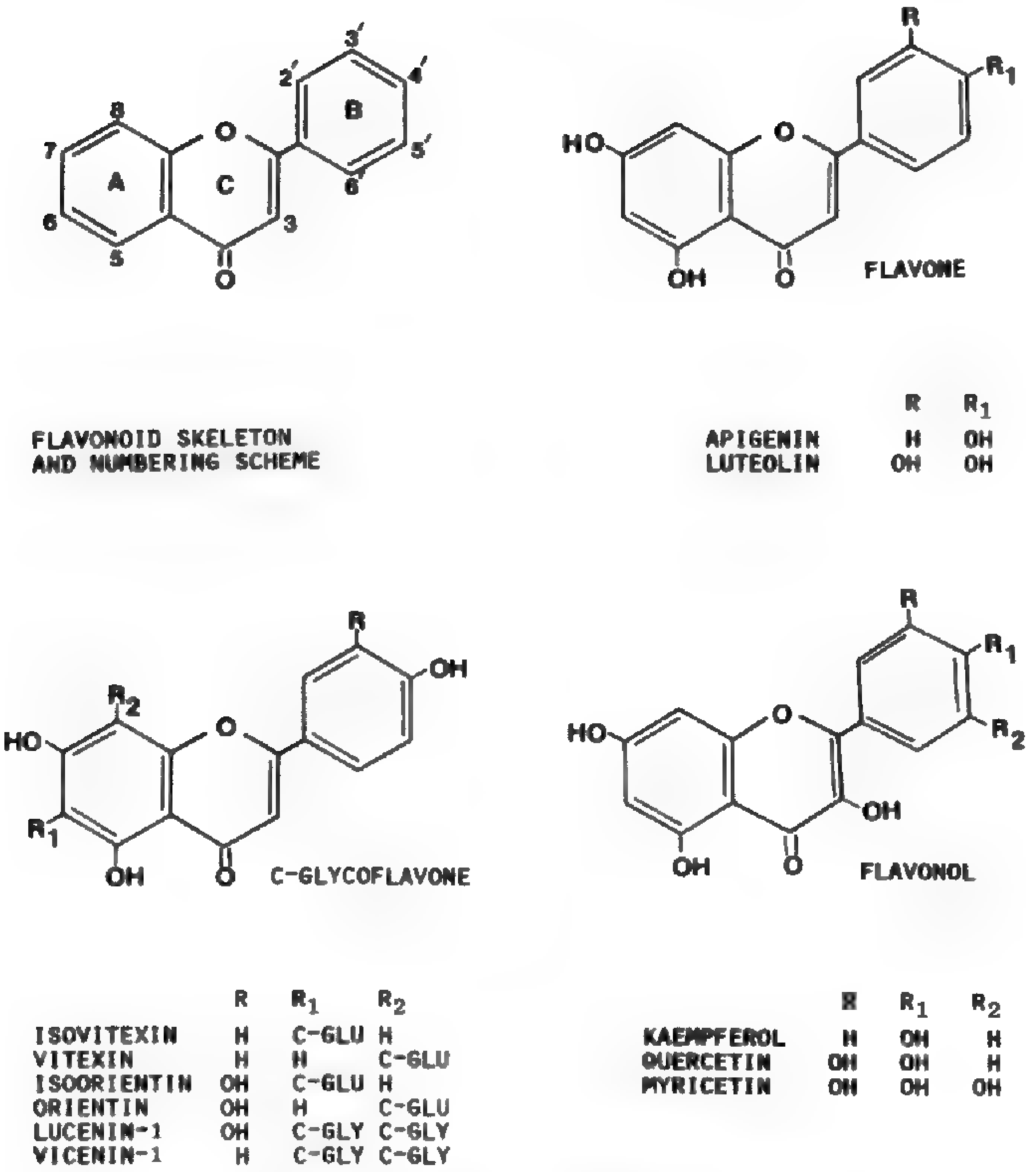
are unevenly divided among 17 sections. As demonstrated by Eyde (1978, 1979), *Ludwigia* represents a phylogenetic line distinct from all other genera, which are, therefore, more closely related to one another than any one is to *Ludwigia*. All but a few of the species of this genus have been examined for their foliar flavonoids (Averett et al., unpubl. data).

Eight flavonoids, including three glycoflavones based on orientin and isoorientin and five flavonol 3-O-glycosides, all based on quercetin, have been identified in *Ludwigia*. Both classes of flavonoids are found among the more primitive sections *Myrtocarpus, Michelia,* and *Pterocaulon*. Only flavonols are found in sections *Tectiflora, Humboldtia, Oligospermum,* and *Caryophylloidea*; only glycoflavones are found in the remaining ten sections. Even within sect. *Pterocaulon*, only two of the five species have flavonols. Thus, with increasing specialization of the taxa, there is evidently a corresponding loss of either glycoflavones or flavonols. Overall, glycoflavones predominate. Another point to be noted is that all of the flavonols are based on quercetin and that all of the substituents are relatively simple 3-O-glycosides.

Circaeeae. The only genus, *Circaea*, has no clear affinities to any of the other tribes in the family. It is, however, clearly a generalized early phyletic offshoot. Previous studies (Boufford et al., 1978) reported the presence of glycoflavones and the possible presence of flavones. The earlier study was considered preliminary, was concerned with hydrolysates, and included a limited number of species. Subsequent work with additional species, especially Asian ones, has confirmed the presence of some 14 compounds among the species of *Circaea*. These include eight glycoflavones, four flavones, and two flavonols.

Fuchsieae. *Fuchsia* is the only genus of the tribe. Eighteen flavonoid glycosides have been identified from six ornamental species of *Fuchsia* and seven of their hybrids by Williams et al. (1983). The compounds include 11 flavonol glycosides and six flavone glycosides. Three of the six flavones are sulphates. Among the approximately 100 remaining species of *Fuchsia*, we have identified 12 flavonoid glycosides, including four flavones and eight flavonols. The flavones include two sulphates. The flavonols include six 3-O-glycosides based on kaempferol, quercetin, or myricetin; and two methyl ethers. Flavonol glycosides are found in each of the species examined. Flavones are consistently present in each of the four species of sect. *Skinnera*, occasional in the single species of sect. *Kierschlegeria*, and sporadic among one or a few species of sections *Fuchsia, Ellobium,* and *Quelusia*. The flavone sulphates are restricted to sect. *Skinnera*. With this feature, coupled with the consistent presence of other flavones, sect. *Skinnera* is the most distinct of the genus with respect to its flavonoid chemistry. This New Zealand-Tahitian group of what is otherwise an American genus is equally distinctive morphologically, although clearly a member of the genus, which is quite diverse even excluding sect. *Skinnera*.

Although both flavones and flavonols are pres-



	R	R1
APIGENIN	H	OH
LUTEOLIN	OH	OH

	R	R1	R2
ISOVITEXIN	H	C-GLU	H
VITEXIN	H	H	C-GLU
ISOORIENTIN	OH	C-GLU	H
ORIENTIN	OH	H	C-GLU
LUCENIN-1	OH	C-GLY	C-GLY
VICENIN-1	H	C-GLY	C-GLY

	R	R1	R2
KAEMPFEROL	H	OH	H
QUERCETIN	OH	OH	H
MYRICETIN	OH	OH	OH

FIGURE 1. Base structures and numbering scheme for flavonoids discussed in the text.

TABLE 2. Distribution of flavonoids among the tribes of Onagraceae.

	Flavonols	Glyco-flavones	Flavones
Tribe:			
Jussiaeeae	●	●	
Circaeeae	●	●	●
Fuchsieae	●		●
Lopezieae	●	●	
Hauyeae	●	●	
Onagreae	●	●	●
Epilobieae	●		

ent in *Fuchsia*, the flavones occur only in a few scattered species. In contrast to this pattern, flavonols are characteristic of the genus, occurring in every species.

Lopezieae. Preliminary data indicate the presence of six flavonol 3-O-glycosides and at least four glycoflavones in *Lopezia*, the only genus of the tribe. To date, glycoflavones have been detected in one of the more primitive sections of *Lopezia*, sect. *Jehlia*, and in both species of the very distinctive sect. *Riesenbachia*, which is evidently an early offshoot. Flavonols occur in both sections but are absent in one of the two species of sect. *Riesenbachia*, *L. riesenbachia*. Only flavonols are present in the remaining sections. Neither methylated nor sulphated flavonoids have been detected in *Lopezia*.

Hauyeae. *Hauya*, the single genus of the tribe, has two species. One of them, the tetraploid and hexaploid *H. elegans* DC., consists of four subspecies that range from central Mexico to Costa Rica. In all taxa of *Hauya*, four flavonol 3-O-glycosides are typically present, with an additional two occurring sporadically. In at least some populations of each of the four subspecies of *H. elegans*, however, glycoflavones are also present. The second species, the diploid *H. heydeana* Donn. Sm. & Rose, lacks glycoflavones.

Onagreae. Flavonoid analyses of Onagreae have been confined largely to *Oenothera*, but at least some data are available for each of the other genera (Kagan, 1967; Zinsmeister & Bartl, 1971; Zinsmeister et al., 1977; Howard et al., 1972; Averett et al., 1982; Averett & Raven, 1983a, 1983b). Only flavonols have been reported for this group but studies in progress have identified glycoflavones and flavones, as well, in a few species of *Oenothera* and *Gaura*. Some 20 compounds, including compounds with 3; 3,7; 7; and B-ring substituents, have been isolated and identified from the tribe. The substituents include monoglycosides, diglycosides, sulphates, and methyl ethers. Typically, four to six compounds are found in any one genus but these range from three in *Stenosiphon* to more than 15 in *Oenothera*, taking the genus as a whole. Additional chemosystematic analyses in the tribe are needed, especially in *Calylophus, Camissonia, Clarkia*, and *Gaura*, in view of the diversity of compounds in this tribe. Preliminary surveys both of *Gaura* and of hitherto unexamined species of *Oenothera* indicate the presence of a great diversity of systematically interesting flavonoids, both unusual flavonols and glycoflavones.

Epilobieae. Seven compounds, all 3-O-monoglycosides of kaempferol, quercetin, or myricetin, are found among the species of *Epilobium* and *Boisduvalia*, the two genera of this tribe. Four compounds, the 3-O-rhamnosides and 3-O-glucosides of quercetin and myricetin, are typically present in each of the sections of both genera except for the monotypic *Epilobium* sect. *Xerolobium*. In this species, myricetin 3-O-rhamnoside is absent. The additional compounds are found in *Boisduvalia* sect. *Boisduvalia* and in *Epilobium* sects. *Zauschneria* and *Chamaenerion* (Averett et al., 1978, 1979).

The lack of flavonoid diversity among so many species is striking, with only seven compounds, each a simple monoglycoside, present. Variation is largely in the presence or absence of glycosylation by an arabinosyl moiety and in the presence or absence of the single kaempferol compound. In general, the more advanced taxa have fewer compounds, representing the absence of molecules with one glycosidic substitution and/or the absence of kaempferol-based compounds. Epilobieae are highly specialized in other characteristics; the flavonoids they exhibit seem to represent an example of secondary loss of substituents; i.e., highly advanced in the terminology of Gornall and Bohm (1978). The trend is apparent both within the tribe and in comparisons between it and other tribes.

DISCUSSION

Harborne (1966, 1976, 1977) has considered complex glycosylation and methylation as advanced characters and the presence of glycoflavones as primitive. Gornall and Bohm (1978), although in general agreement with the primitive nature of glycoflavones, have suggested a third state, highly advanced, where substituents, once gained, are then lost. We also have suggested that a loss of substituents may be correlated with evolutionary advancement within a given taxon (Averett, 1973; Averett et al., 1978, 1979). The distribution of flavonoid types in Onagraceae (Table 2) is interesting in relation to these suggestions.

Jussiaeeae, as mentioned above, represent a distinct line within the family, a line that is characterized by the presence of glycoflavones. Flavonols are widespread in Jussiaeeae, but are relatively simple glycosides of only one base aglycone. Glycoflavones and flavonols in *Ludwigia* are found together only in the more primitive sections. The sections considered to be more specialized have lost one or the other of these two classes of flavonoids.

The rest of the family constitutes a second main line of evolution in the family. Within this line, *Circaea, Fuchsia, Hauya,* and *Lopezia*—each constituting a monogeneric tribe—seem to be relatively generalized in their characteristics, Onagreae and Epilobieae more specialized. *Lopezia* and *Hauya* have both glycoflavones and flavonols. In *Lopezia,* however, glycoflavones are restricted to a few of the most generalized taxa, apparently having been lost during the course of evolution of the genus. Flavonols, on the other hand, occur in every species examined of both *Lopezia* and *Hauya* except for one species of *Lopezia, L. riesenbachia,* which is obviously specialized. Thus, flavonols clearly predominate in these two genera, but the ones that are present are generally simple in structure, and glycoflavones are frequent in the generalized species.

Fuchsia has both flavonols and flavones but no glycoflavones, whereas *Circaea* has all three classes of compounds. In contrast, the two more specialized tribes, Onagreae and Epilobieae, differ markedly in their flavonoid constituents. Onagreae, like *Circaea,* have glycoflavones, flavones, and flavonols, whereas Epilobieae have the least diverse pattern of any tribe, having only flavonol 3-O-monoglycosides.

If the presence of glycoflavones is a primitive characteristic, as Harborne (1976) has postulated, the fact that this class of compounds occurs in all groups except *Fuchsia* and Epilobieae is notable. Epilobieae is a group that is clearly advanced in many of its characteristics, and one might assume that glycoflavones have been lost in the evolution of *Fuchsia* also.

Especially noteworthy in considerations of flavonoid evolution in Onagraceae is the presence of flavones in *Circaea, Fuchsia,* and the tribe Onagreae. Extensive surveys of flavonoids have not been completed in other families of the order Myrtales, but thus far, flavones have not been detected in any family other than Onagraceae (Gornall et al., 1979; Dahlgren & Thorne, 1984). This pattern suggests that ability to synthesize flavones may have evolved within Onagraceae, possibly in the ancestor of the "non-*Ludwigia*" branch of the family. If this hypothesis is correct, flavones were subsequently lost in most species of the family, including all of *Hauya, Lopezia,* and the tribe Epilobieae. It seems very unlikely that the biochemical pathway leading to the synthesis of flavones originated independently in the three groups in which they occur. Despite this, it also seems unlikely that these groups could share an immediately common ancestor in view of the major differences between them. Thus, if it can be interpreted properly, the occurrence of flavones in these three tribes might offer valuable clues to relationships within the family.

Overall, the pattern of distribution of glycoflavones and flavones in Onagraceae tends weakly to support the hypothesis that *Fuchsia* and *Circaea* might be early offshoots of the phylogenetic line leading to the tribe Onagreae, and that *Hauya, Lopezia,* and the tribe Epilobieae might not belong to this same line. Furthermore, there is some suggestion in its diversity of compounds that the tribe Onagreae might be heterogenous in origin, and new detailed information about the distribution of flavonoids in the species and genera that make up this large tribe might be helpful in evaluating this possibility.

Summarizing for the family as a whole (Table 2), glycoflavones characterize the more primitive elements but are occasionally present in all tribes except Fuchsieae and Epilobieae. Onagreae exhibit the greatest diversity of compounds, including flavonol 7-O-glycosides and B-ring substitutions. The Epilobieae exhibit the least diverse pattern, having only flavonol 3-O-monoglycosides. If these data represent, as indeed we believe they do, a proliferation of compounds during the course of evolution of the family with a reduction of compounds with further advancement, they are in general agreement with assessments of relative evolutionary states of these taxa derived from other lines of investigation. In context, however, the lack of glycoflavones in *Fuchsia* is unexpected in view of the ubiquitous distribution of this class of compounds among all other genera of the family with relatively primitive characteristics.

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A PALYNOLOGICAL STUDY OF THE GENUS *FUCHSIA* (ONAGRACEAE)[1]

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ABSTRACT

The pollen of 76 collections representing 48 of the ca. 100 species and all nine sections of *Fuchsia* was examined in light (LM) and scanning electron microscopy (SEM), and a selected group in transmission electron microscopy (TEM). The pollen of *Fuchsia* is shed as monads and is mostly 2-aperturate or very rarely 3-aperturate; the exine sculpture is composed of globular elements, or more rarely elongated elements; the viscin threads are segmented, more rarely smooth; the exine is composed of two layers, an outer spongy undifferentiated ektexine, and an inner solid, massive endexine. The polyploid sects. *Quelusia* (eight species) and *Kierschlegeria* (one) are characterized by 3-aperturate pollen as are several tetraploid species in sects. *Fuchsia* and *Hemsleyella*. As far as is known, 3-aperturate grains usually occur only in polyploid species; but not all polyploids have 3-aperturate pollen. Two-aperturate grains do occasionally occur in both sects. *Kierschlegeria* and *Quelusia*, where they doubtless represent the condition of the diploid ancestors. It may be concluded that the common ancestor of all extant sections of *Fuchsia* had 2-aperturate pollen, although ultimately, within the Onagraceae, the 2-aperturate condition must have been derived from 3-aperturate pollen. Most species of *Fuchsia* have a globular-type sculpture element, but sects. *Encliandra* (six species) and *Kierschlegeria* have elongated elements, a derived condition. Most species of *Fuchsia* have segmented-beaded viscin threads, but sects. *Schufia* (two species), *Jimenezia* (one) and *Kierschlegeria* (one) and some species of sect. *Encliandra* have smooth viscin threads, another derived condition. A combination of aperture number, sculpture element, and viscin thread morphology could separate the nine sections of *Fuchsia*, although palynology provides, at best, only weak evidence for distinguishing sections.

In the already highly distinctive Onagraceae, the large genus *Fuchsia* L. (100 species; Munz, 1943; Breedlove, 1969; Breedlove et al., 1982; Berry, 1982) is further distinguished by 2-aperturate pollen in most species and a berry-type fruit, two characteristics not found in any remaining taxa. Most species of this genus are shrubs and trees with red, tubular, bird-pollinated flowers, although a few have shorter flowers, not so brightly colored, yet still red or reddish in hue. Because of the distinctive flowers and berries, *Fuchsia* has traditionally been treated as a monogeneric tribe of Onagraceae. In fact, it has no obvious relationships to any other genus.

Although all the distinctive features of *Fuchsia* are clearly advanced, in overall characteristics, *Fuchsia* is one of the less specialized of the 17 genera of Onagraceae. Evidence from floral anatomy (Eyde & Morgan, 1973), wood anatomy (Carlquist, 1975), cytology (Kurabayashi et al., 1962), and leaf architecture (Hickey, 1980) support this conclusion. The ovary of *Fuchsia* is 4-locular with a biseriate row of ovules in each. The placentation is axile but more importantly the placentas are deeply cleft, a primitive condition. *Fuchsia* is one of only three genera, *Hauya* Moc. & Sesse and *Ludwigia* L. being the other two, that lack interxylary phloem, a clearly primitive condition. Most species of *Fuchsia* are diploid, with a gametic chromosome number of $n = 11$, basic in Onagraceae. In addition, the chromosomes are relatively large for Onagraceae, lack reciprocal translocations as a regular part of the adaptive system, and are poorly differentiated into heteropycnotic and eupycnotic segments (Kurabayashi et al., 1962). In addition, Baker and Baker (1983) characterized the starchless condition found in the pollen grains of *Fuchsia* and *Lopezia* Cav. as the ancestral one, and sug-

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TABLE 1. *Fuchsia* specimens illustrated, with collector, locality to country, and Figure number(s).

Sect. *Ellobium*			
Fuchsia decidua Standley	*Boutin 3036* (MO)	Mexico	7–9
F. fulgens DC.	*Oliver & Voerhoek-Williams 562* (MO)	Mexico	10–12
F. splendens Zucc.	*Burger & Stolze 5969* (MO)	Costa Rica	13–14
	Croat 515 (MO)	Costa Rica	15, 115–117
Sect. *Encliandra*			
F. cylindracea Lindley (*F. parviflora* sensu Breedlove, non Lindley)	*Breedlove 36037* (MO)	Mexico	67, 72
	Breedlove 15831 (DS)	Mexico	144–146
F. encliandra Steudel subsp. *encliandra*	*Davidse & Davidse 9672* (MO)	Mexico	69
	Kalin 7089 (MO)	Mexico	59, 60
	Breedlove 15849 (DS)	Mexico	138–141
F. encliandra Steudel subsp. *tetradactyla* (Lindley) Breedlove	*Breedlove 25920* (MO)	Mexico	135–137
F. microphylla H.B.K. subsp. *aprica* (Lundell) Breedlove	*Breedlove 31744* (CAS)	Mexico	120–123
F. microphylla H.B.K. subsp. *hemsleyana* (Woodson & Siebert) Breedlove	*Utley 4297* (MO)	Costa Rica	64, 65
	Raven 20975 (DS)	Mexico	129, 130
F. microphylla H.B.K. subsp. *hidalgensis* (Munz) Breedlove	*Breedlove 15881* (US)	Mexico	124–128
F. microphylla H.B.K. subsp. *microphylla*	*Arizmendi 259* (MO)	Mexico	66
F. microphylla H.B.K. subsp. *quercetorum* Breedlove	*Breedlove 22959* (CAS)	Mexico	131–134
F. obconica Breedlove	*Breedlove 18711* (CAS)	Mexico	70, 142, 143
	Ventura 1457 (MO)	Mexico	58
F. ravenii Breedlove	*Kalin 7090* (MO)	Mexico	61–63, 71, 118–119
F. thymifolia H.B.K. subsp. *minimiflora* (Hemsley) Breedlove	*Breedlove 22788* (CAS)	Mexico	147–150
F. thymifolia H.B.K. subsp. *thymifolia*	*Anderson & Laskowski 3993* (MO)	Mexico	57
	Pringle 9794 (MO)	Mexico	55, 56, 68
Sect. *Fuchsia*			
F. ayavacensis H.B.K.	*Berry & Escobar 3601* (MO)	Peru	91
F. boliviana Carrière	*Berry 3552* (MO)	Colombia	101
	Berry & Aronson 3044 (MO)	Peru	151–154
F. corollata Benth.	*Berry 3173* (MO)	Ecuador	108
F. cuatrecasasii Munz	*Berry 3594* (MO)	Colombia	97
F. dependens Hook.	*Berry 3166* (MO)	Ecuador	94
F. gehrigeri Munz	*Berry 3098* (MO)	Venezuela	90
	Berry 3296 (MO)	Venezuela	96
F. hartwegii Benth.	*Berry 3568* (MO)	Colombia	112
	Bristol 876 (DS)	Colombia	158, 159
F. hirtella H.B.K.	*Berry 3543* (MO)	Colombia	95
F. macrophylla Johnston	*Berry & Aronson 3080* (MO)	Peru	103, 104

TABLE 1. Continued.

F. macrostigma Benth.	*Escobar 1094* (MO)	Ecuador	92, 93
F. mathewsii Macbride	*Berry 3603* (MO)	Peru	113
F. pallescens Diels	*Berry 3570* (MO)	Colombia	98
F. petiolaris H.B.K.	*Berry 3539* (MO)	Colombia	114
	Berry 3560 (MO)	Colombia	99
F. pringsheimii Urban	*Tuerckheim 3151* (MO)	Dominican Republic	89
F. putumayensis Munz	*Berry 3562* (MO)	Colombia	102
F. scabriuscula Benth.	*Berry 3593* (MO)	Colombia	107
F. tincta Johnston	*Berry et al. 2597* (MO)	Peru	100, 105, 106
F. triphylla L.	*Davidse 2689* (MO)	Dominican Republic	88, 94
F. verrucosa Hartweg	*Berry 3286* (MO)	Venezuela	111, 155–157
	Grant 10260 (US)	Colombia	109, 110
Sect. *Hemsleyella*			
F. apetala Ruiz & Pavón	*Berry & Aronson 3033* (MO)	Peru	74, 75, 78, 84
	Berry & Aronson 3070 (MO)	Peru	73
F. chloroloba Johnston	*Berry et al. 2599* (MO)	Peru	82, 86, 87
F. garleppiana Kuntze & Wittm.	*Linderman 2030* (MO)	Bolivia	160–163
F. inflata Schulze-Menz	*Berry & Aronson 3012* (MO)	Peru	76
F. juntasensis Kuntze	*Berry 3638* (MO)	Bolivia	83
F. membranacea Hemsley	*Berry 3278* (MO)	Venezuela	85
F. tillettiana Munz	*Berry 3267-B* (MO)	Venezuela	79–81, 164–167
	Berry 3463 (MO)	Venezuela	77
Sect. *Jimenezia*			
F. jimenezii Breedlove, Berry & Raven	*Allen 4965* (MO)	Panama	1, 2, 168, 169
	Croat 36223 (MO)	Costa Rica	3
Sect. *Kierschlegeria*			
F. lycioides Andrews	*UC Bot. Gard. Berk. 53.1303-S2* (RSA) (from Hartweg in 1953)	Chile	6
	Zöllner 8089 (MO)	Chile	4, 5, 170–173
Sect. *Quelusia*			
F. bracelinae Munz	*Mexia 4013* (US)	Brazil	17, 18
F. campos-portoi Pilger & Schulze	*Brade 18008* (S)	Brazil	19, 25
F. coccinea Sol.	*Irwin et al. 30326* (NY)	Brazil	31–33
F. magellanica Lam.	*Solomon & Solomon 4599* (MO)	Chile	20–24, 175
	Raven 20560 (MO)	New Zealand	174
F. regia (Vand. ex Vell.) Munz	*Davidse et al. 11076* (MO)	Brazil	34–36
	Hoehne 19661 (RSA)	Brazil	26–30
	Ramamoorthy 680 (MO)	Brazil	16
Sect. *Schufia*			
F. arborescens Sims	*Feddema 2872* (MO)	Mexico	37–40, 191, 192
F. paniculata Lindley	*Croat 35428* (MO)	Costa Rica	41, 42
	Allen 713 (MO)	Costa Rica	193, 194

TABLE 1. Continued.

Sect. *Skinnera*			
F. cyrtandroides Moore	*van Balgooy 1785* (MO)	Tahiti	46, 49, 50, 181–185
F. excorticata (J. R. Forster & G. Forster) L. f.	*McMillan 65/91* (MO)	New Zealand	43, 44, 51, 54, 178, 180
	Carse 2312 (MO)	New Zealand	176, 177, 179
F. perscandens Cockayne & Allen	*Raven et al. 25212* (MO)	New Zealand	45, 53, 186, 187
F. procumbens Cunn.	*Walker 4730* (MO)	New Zealand	47, 48, 52
	Cultivated Univ. of California Botanical Garden, Berkeley UCB 49.812 (UC)	New Zealand	188–190

gest that the starchy condition found in all remaining genera may be derived. The geographical distribution of *Fuchsia* could also be cited as evidence of its relative primitive position within the subfamily, since it clearly centers in South America (where the family almost certainly originated; Raven & Axelrod, 1974; Raven, 1979), with others in New Zealand-Tahiti and in Central America-Mexico.

Fuchsia is modally outcrossing, largely because of a combination of protogyny and spatial separation of anthers and stigma (Raven, 1979; Berry, 1982). In addition, male-sterility occurs in the sects. *Encliandra, Kierschlegeria, Schufia,* and *Skinnera,* and, together with female-sterility in most of the same species enforces outcrossing by dioecism, subdioecism, or, in two species of sect. *Skinnera,* by gynodioecism.

Advanced features in *Fuchsia* include those associated with bird pollination—red, tubular flowers—and bird dispersal of seeds—berries. These features make it very unlikely that plants with the characteristics of *Fuchsia* could have evolved before the Eocene (Raven, 1979; Sussman & Raven, 1978), whereas the known fossil record of the family extends back to the uppermost Cretaceous (Eyde & Morgan, 1973). The 2-aperturate pollen of most species of *Fuchsia* is unique in Onagraceae and nearly so in all of the Myrtales, and is a clearly derived feature. The nine sections of *Fuchsia* may be summarized as follows:

Sect. *Ellobium* consists of three species in Mexico and Central America formerly assigned to sects. *Fuchsia* and *Hemsleyella* (Breedlove et al., 1982). Sect. *Ellobium* combines characteristics of each of these basically South American sections, having petals as in sect. *Fuchsia* and band-nectaries as in sect. *Hemsleyella.* Sect. *Ellobium* may represent a Neogene invasion of Central America-Mexico by the same stock that gave rise to these sections.

Sects. *Encliandra* (Breedlove, 1969), *Jimenezia,* and *Schufia* have seven, one, and two species respectively, and occur in Mexico and Central America. The presence of small flowers, lobed-adnate nectaries, and smooth viscin threads suggest a common ancestry (Berry, 1982), as does the geographical proximity of these sections. All nine species are diploid, with $n = 11$ (Breedlove, 1969; Breedlove et al., 1982). Sect. *Schufia* can be easily distinguished from all other species of *Fuchsia* by the large, many-flowered, terminal panicles in which the small flowers have stamens exserted beyond the floral tube. These three sections apparently represent an earlier invasion of Central and North America than that which gave rise to sect. *Ellobium.*

Sect. *Fuchsia* includes 61 species, 59 from the tropical Andes of South America, and the other two in Hispaniola (Berry, 1982). This is the only section with annular nectaries in all but three species. The flowers have petals, in contrast to those of the sympatric sect. *Hemsleyella,* and the floral tubes are longer than the sepals, *F. verrucosa* excepted. Of the 43 species in sect. *Fuchsia* for which chromosome numbers have been reported, 37 were diploid with $n = 11$, five were tetraploid with $n = 22$, and one included both diploid and tetraploid individuals.

Sect. *Hemsleyella,* the second largest with 14 species, is found in the tropical Andes, as is sect.

Fuchsia. It differs from the latter by the absence of petals and its adaptations to a largely epiphytic habitat: tuberous stems and dry-season flowering and leaf drop (Berry, 1982). In fact, most herbarium specimens of sect. *Hemsleyella* lack leaves. Some species are polyploid (Berry, unpubl. data).

Sect. *Kierschlegeria* has a single species, the only one in the genus to occur in a seasonally dry habitat (Berry, 1982). *Fuchsia lycioides* has small deciduous leaves, spinose leaf bases, and thick seed coats, characteristics associated with xerophytic conditions. The flowers are small and solitary in the axils of leaves on (mostly) unbranched, peculiarly straight stems. It is subdioecious (Atstatt & Rundle, 1982). Like sect. *Quelusia*, it is tetraploid and has 3-aperturate pollen.

Sect. *Quelusia* exhibits a common pattern of disjunct distribution, seven species in southeast coastal Brazil, and an eighth, the widely cultivated *F. magellanica*, in the southern half of Chile and eastward into the western slopes of the Andes in Argentina. All species are polyploid and all have 3-aperturate pollen.

The four species of sect. *Skinnera* are the only representatives of the genus that occur in the Old World, three in New Zealand and one in Tahiti. These species are characterized by reduced petals, band-type nectaries, and the smallest and most numerous seeds in the genus. It seems likely that sect. *Skinnera* separated in Paleogene time from the ancestral stock, as judged from fossil evidence and the time needed to produce the present diversity in habit among the three New Zealand species, one a creeper, the second a liana, and the third a tall forest tree (see discussion in Berry, 1982).

This paper is intended to be a companion report to Praglowski et al. (1983), which comprises a survey of *Fuchsia* and *Ludwigia* pollen using predominantly light microscopy.

MATERIALS AND METHODS

Anthers were removed from herbarium specimens, all material for LM and SEM was acetolyzed according to procedures outlined in Erdtman (1966). Samples for SEM were either sputter or vacuum coated with gold and examined with an ISI Super II, a Cambridge Stereoscan MK IIa and S410, or a Coates and Welter 106B Field Emission Microscope.

The species examined, collection data, and figure number(s) are given in Table 1. Most of the collections used in this study were also reported in Praglowski et al. (1983), and there are presented both illustrations and extensive pollen morphological data on all collections. Although virtually all of the collections cited in the earlier study were examined for this report, not all specimens are illustrated here, either because of closely similar morphology (especially in sect. *Fuchsia*) or because they were illustrated already in Praglowski et al. (1983).

For TEM, pollen samples were acetolyzed or rehydrated (unacetolyzed). In the former, the residue was incorporated into agar, dehydrated through a graded acetone series and embedded in Araldite-Epon resins. Prior to incorporation in agar, the pollen was stained in 1–2% OsO_4 buffered with sodium cacodylate at pH 7.2–7.4 for 1–2 hours at room temperature. Unacetolyzed pollen was rehydrated by Alcian blue (Rowley & Nilsson, 1972) or by softening in Vatsol (Pohl, 1965), soaking for 2–3 days in 2.5% sodium cacodylate buffered (pH 7.2) glutaraldehyde. Dehydration and embedding follows that described above, except that agar was not used.

Sections approximately 10 nm thick were cut with diamond knives, collected on uncoated copper grids, and stained for 5 minutes each in 0.5% aqueous uranyl acetate and lead citrate, or in rehydrated pollen only in lead citrate. Observations and electron micrographs were made with either a Philips model 200 or Zeiss 10 electron microscope at 40 kV.

The terms for sculpture elements that are used in the palynological description of *Fuchsia* in this paper are documented elsewhere (Praglowski et al., 1983).

Light slides of all samples are deposited at the Palynological Laboratory, Department of Botany, Smithsonian Institution.

RESULTS

Mature pollen of *Fuchsia* is shed as monads, is paraisopolar to heteropolar, 2-aperturate and bilaterally symmetrical (Figs. 1, 7, 10, 13, 37, 40, 41, 43–48, 55, 58–61, 64, 73, 74, 79, 82–86, 88–92, 103–107, 109, 112–114), or, more rarely, 3-aperturate and radially symmetrical (Figs. 4, 16–21, 33–36, 76, 108, 180, 181).

SHAPE

The shape in polar view is ± elliptic in 2-aperturate grains (e.g., Figs. 1, 10, 40, 59, 89, 92, 109, 114), or triangular in 3-aperturate grains (e.g., Figs. 4, 17, 19, 20, 36, 76, 108). The shape in aperture-centered equatorial view is ± ovoid in 2-aperturate grains (Figs. 85, 86, 103, 105), or apiculate in 3-aperturate grains (Figs. 18, 21). The shape in mesocolpus-centered equatorial view is ± apiculate in both 2- and 3-aperturate grains (Figs. 34 uppermost grain, 43, 55, 58, 84, 104, 106).

APERTURES

The apertures protrude and are formed by a cone-like extension of the exine (Figs. 35, 93, 122, 128, 132, 136, 143, 155, 171, 176, 177, 191, 193). The endoaperture is complex and consists of a massive deposition of endexine in the form of ring(s). The chamber-like area delimited by the endoapertural ring proximally and by the ectoaperture (see below) distally, has been designated as the vestibulum (Praglowski et al., 1983). At the base of the cone and partially extending into the body of the grain the endexine is coarsely granular; within the vestibulum it is also finely channeled (Figs. 119, 122, 128, 132, 136, 143, 155, 163, 171, 174, 176, 177, 188, 191, 193). The ectoaperture is irregular in shape (Figs. 38, 51, 85, 86, 103, 105), only rarely a well-defined pore (Figs. 28, 93) or a horizontally-oriented colpus. Rare 4-aperturate grains were observed (Fig. 32) in the 3-aperturate sect. *Quelusia,* and 3-aperturate grains were noteworthy in *F. inflata* (sect. *Hemsleyella*), and *F. procumbens, F. excorticata* (Fig. 180), and *F. cyrtandroïdes* (Fig. 181) of sect. *Skinnera,* which is characterized by 2-aperturate pollen.

EXINE

The exine is distinctly bizonal (cf. many examples illustrated in Figs. 115–194), composed of ektexine and endexine. The ektexine consists of an outer spongy or paracrystalline-beaded layer without organization into distinct tectum, columellae, and foot layer components. The endexine is the mostly solid and continuous layer. The inner surface is finely granular in the body of the grain and very coarsely granular and/or lamellate within the apertures (see numerous examples in Figs. 115–194). The two exine layers are closely associated with one frequently appearing to extend into the other (e.g., Figs. 121, 124, 125, 130, 133–135, 138, 142, 149, 150, 160, 161, 168–170, 172, 178, 179, 183, 186, 189, 192, 194).

Sculpturing of the ektexine consists of elements which are primarily globular or irregular spheres (Figs. 2, 3, 14, 15, 27, 30, 53, 54, 57, 95, 98–102, 126, 147, 182), or elongated units (Figs. 5, 6, 56, 63, 66, 70–72, 129). Sometimes the elements were transitional and therefore difficult to categorize (i.e., Fig. 144).

VISCIN THREADS

Viscin threads are extensions of the ektexine (Figs. 126, 130, 138, 141, 142, 144, 145, 147, 152, 153, 158–161, 164, 172, 178, 179, 182, 183, 186, 190, 192). While they are usually located near or about the central region of the proximal face (Figs. 1, 10, 17, 59, 73, 88, 89, 92, 109, 112, 114, 181), they have also been noted to or on, the apertural protrusion (Figs. 141, 145, 188, 190). In freshly collected or rehydrated pollen, the viscin threads are enclosed by a membrane (Figs. 117, 152–154, 164–167, 172, 173, 178, 192). Threads are mostly segmented-beaded (Figs. 9, 12, 14, 15, 22–27, 52–54, 75, 87, 94–97, 101, 102, 117, 153, 154, 158–161, 165–167, 178, 182–187, 190) to segmented-ropy (Figs. 57, 98–100, 126, 147), or less commonly smooth (Figs. 2, 3, 5, 6, 31, 39, 42, 49, 50, 62, 63, 65, 66, 69–72, 110, 111, 123, 130, 131, 138–141, 144, 145, 157, 173).

In some species it is difficult to recognize the morphological pattern and the threads consist of both smooth and segmented portions (see, for example, *F. ravenii,* Fig. 71). Light segmentation (e.g., *F. cyrtandroides,* Figs. 49, 50, 182, 185; *F. perscandens,* Fig. 187) characterizes some species and usually requires supporting evidence from transmission electron microscopy (Figs. 183, 184, 186).

Localized distentions also contribute to thread morphology. One type, illustrated by *F. cyrtandroides* (Fig. 50) and *F. verrucosa* (Fig. 111) shows inflated bases and results from several threads originating from the exine surface within a confined area. This is common throughout Onagraceae, most notably in *Epilobium* (Skvarla et al., 1978). Another type is that of nodular distensions along the threads (e.g., *F. coccinea,* Fig. 31; *F. cyrtandroides,* Fig. 49), which probably represents a "rolling up" of certain thread regions. Threads characterized by nodular or "ball-like" distensions are usually associated with the more complex compound threads of *Epilobium* and *Boisduvalia.* The last type of distension occurs on smooth threads and appears cylindrical. This is observed on most smooth threads throughout the family (Skvarla et al., 1978).

TABLE 2. Pollen morphology in *Fuchsia*.

Sections	Number of Species in Section	Pollen Apertures	Predominant Ektexine Sculpture	Viscin Threads[a]
Ellobium	3	2	globular-type	segmented-beaded
Encliandra	7	2	elongated	smooth, sparsely segmented (segmented-ropy)
Fuchsia	61	2 (3)	globular-type[b]	segmented-beaded[c]
Hemsleyella	14	2 (3)	globular-type	segmented-beaded
Jimenezia	1	2	globular-type	smooth
Kierschlegeria	1	3	elongated	smooth
Quelusia	8	3	globular-type	segmented-beaded
Schufia	2	2	globular-type	smooth
Skinnera	4	2 (3)	globular type	segmented-beaded

[a] Term for viscin thread morphology follows Skvarla et al. (1978).
[b] Elongated in *F. verrucosa*.
[c] Smooth in *F. verrucosa*.

The pollen morphology of the sections of *Fuchsia* is characterized briefly as follows, and summarized in Table 2:

Sect. *Ellobium* (Lilja) Breedlove, Berry & Raven. Figures 7–15, 115–117.

Three species, Mexico and Central America.

Pollen was similar, 2-aperturate with a globular type ektexine sculpture and segmented-beaded viscin threads.

Sect. *Encliandra* (Zucc.) Endl. Figures 55–72, 118–150.

Seven species, Mexico and Central America.

Pollen of sect. *Encliandra* was predominantly 2-aperturate with an elongated type of ektexine sculpture. Viscin threads in this section were primarily smooth (Figs. 65, 66, 69, 71, 144), although sparsely segmented (Figs. 62, 63, 67, 68, 70–72), and segmented-ropy (Figs. 57, 147) threads were also common.

Sect. *Fuchsia*. Figures 88–114, 151–161.

Sixty-one species, tropical Andes and Hispaniola.

Almost all species examined in sect. *Fuchsia* had similar pollen: 2-aperturate (Figs. 88–92, 103–107, 109, 112–114) with globular type ektexine sculpture and segmented-beaded viscin threads, two characteristics illustrated best at high magnification (×15,000), Figures 100–102. One collection of *Fuchsia corollata, Berry 3173*, had predominantly 3-aperturate grains.

The type species for this section and thus for the genus is *F. triphylla* (Figs. 88, 94) endemic to Hispaniola, as is one other species *F. pringsheimii* (Fig. 89). Both are tetraploid, but have 2-aperturate grains (for discussion, see Berry, 1982: 37).

Fuchsia verrucosa (Figs. 109–111) differed in thread type and ektexine sculpture. The threads were smooth and usually originated from a "whorled base," and the sculpture element in the Colombian collection is elongated (Fig. 110), and more irregularly-shaped in the Venezuelan collection (Fig. 111). Berry (1982) considered this species one of the most distinctive in the section on the basis of its short floral tubes, antesepalous nectary lobes, and tetraploidy with 2-aperturate pollen grains.

Sect. *Hemsleyella* Munz. Figures 73–87, 162–167.

Fourteen species, tropical Andes of South America.

Pollen of all species of sect. *Hemsleyella* was similar: predominantly 2-aperturate, segmented-beaded viscin threads and with a globular type sculpture element. In one collection of *F. inflata, Berry & Aronson 3012* (Fig. 76), approximately three-fourths of the grains were 3-aperturate. An equatorial ridge appeared particularly pronounced in some species of sect. *Hemsleyella*, e.g., *F. tillettiana*, Figure 79 (see Praglowski et al., 1983: 5).

Sect. *Jimenezia* Breedlove, Berry & Raven. Figures 1–3, 168, 169.

One species, Costa Rica and Panama.

Pollen of *F. jimenezii* was 2-aperturate with a globular type sculpture and smooth viscin threads that can be single or compound. In this species the viscin threads originated over a wide area of the proximal surface.

Sect. *Kierschlegeria* (Spach) Munz. Figures 4–6, 170–173.

One species, coastal Chile.

Pollen of *F. lycioides*, a tetraploid species, was 3-aperturate with an ektexine that had an elongated element sculpture and smooth viscin threads.

Sect. *Quelusia* (Vand.) DC. Figures 16–36, 174, 175.

Eight species, SE coastal Brazil, Chile, and Argentina.

Pollen of sect. *Quelusia* was 3-aperturate (Figs. 16, 17, 33–36) with a globular type of ektexine sculpture. Rare 4-aperturate grains were noted (Fig. 32). The viscin threads were segmented-beaded (Figs. 22–27, 29, 30). In *F. coccinea* (Fig. 31) the threads were only slightly segmented and had nodular distensions (see also *F. cyrtandroides*, Fig. 49). All species of this section are polyploid.

Sect. *Schufia* (Spach) Munz. Figures 37–42, 191–194.

Two species, Mexico to Panama.

Pollen of the closely related *F. arborescens* and *F. paniculata* was similar: 2-aperturate with a globular type ektexine sculpture and smooth viscin threads.

Sect. *Skinnera* (Forster) DC. Figures 43–54, 176–190.

Four species, three in New Zealand and one in Tahiti.

The pollen of sect. *Skinnera* was 2-aperturate (a few 3-aperturate grains in *F. cyrtandroides*, Fig. 181; *F. excorticata*, Fig. 180; and *F. procumbens*) with a mostly globular type ektexine sculpture (slightly elongate in *F. cyrtandroides*, Fig. 50). A trend in viscin thread segmentation was evident: prominent segmented-beaded threads in *F. excorticata* (Figs. 54, 163, 164) and *F. procumbens* (Figs. 52, 190), less prominent segments in *F. perscandens* (Figs. 53, 186, 187), and light segmentation in *F. cyrtandroides* (Figs. 49, 50, 182–185). At low-intermediate SEM magnifications (Figs. 49, 50) segmentation in *F. cyrtandroides* was not clearly evident and thread morphology appeared smooth (see Praglowski et al., 1983: 21). At higher SEM magnification light segmentation was evident in the threads (Figs. 182, 185). These segments were better defined with TEM (Figs. 183, 184).

DISCUSSION

The most conspicuous variation in the pollen of *Fuchsia* is that of aperture number, which also determines shape of the grain and the type of symmetry. Most of the species in the largest section, sect. *Fuchsia* (Figs. 88–92, 103–107, 109, 112–114) have predominantly 2-aperturate grains, as do the species of sects. *Jimenezia* (Fig. 1), *Ellobium* (Figs. 7, 10, 13), *Schufia* (Figs. 37, 40, 41), *Skinnera* (Figs. 43–48), *Encliandra* (Figs. 55, 58–61, 64), and *Hemsleyella* (Figs. 73, 74, 79, 82–86). The entirely polyploid sects. *Quelusia* (Figs. 16–21, 32–36) and *Kierschlegeria* (Fig. 4) are characterized by 3-aperturate grains as are several polyploid species in sects. *Fuchsia* and *Hemsleyella*. In one collection of *F. inflata* (sect. *Hemsleyella*), *Berry & Aronson 3012*, the majority of the grains were 3-aperturate (Fig. 76). In many other plants the number of apertures in the pollen is affected by level of polyploidy. Our data (for the entire family) support this contention: deviations from the standard 3-aperturate conditions—i.e., four or five—are found in polyploids. Warth (1925) reported that a single tetraploid individual of sect. *Encliandra* had about 50% 3-aperturate pollen in contrast to the consistently diploid and 2-aperturate condition of other plants in this section. Similarly, Berry (1982: 37) has reported high proportions of 3-aperturate pollen in two of the six wholly or partly tetraploid taxa of sect. *Fuchsia*.

The wide distribution of 2-aperturate pollen in diverse sections of *Fuchsia*, including the very distinctive and only Old World section, sect. *Skinnera*, would favor the hypothesis that the 3-aperturate condition of a few species in the genus is directly associated with polyploidy and derived wherever it occurs.

In *F. lycioides* (sect. *Kierschlegeria*), about 25% of the grains examined by Praglowski et al. (1983) were 2-aperturate, as were occasional grains of one sample of *F. magellanica* (sect. *Quelusia*). Most likely these examples represent reversions to the ancestral condition of the diploids from which the tetraploids were derived, rather than separate origins of a character that is otherwise unknown in the family. We may conclude that the common ancestor of all extant species of *Fuchsia* had 2-aperturate pollen.

The predominant exine sculpture in *Fuchsia* and in most Onagraceae consists of globular type elements, which have varying degrees of distinction, e.g., in Figures 2 and 3 (*F. jimenezii*) the elements protrude, some even appear to be discrete spheres, whereas in Figures 27 (*F. regia*) and 77 (*F. tillettiana*) the elements appear more "submerged." This condition, globular-type elements, is probably primitive for the genus. The second sculpture type consists of elongated elements and is illustrated best in Figures 5 (*F. lycioides*), 65 (*F. microphylla* subsp. *hemsleyella*), and 70 (*F. obconica*). In general, the six species of the advanced sect. *Encliandra* and the only species in sect. *Kierschlegeria* mainly have elongated exine elements.

Judging from the data presented in this paper, as well as that of Skvarla et al. (1978), the viscin threads of *Fuchsia* are among the most copious in Onagraceae (Figs. 29, 75, 77, 78, 86, 96, 106, 112) and their interpretation as extensions of the ektexine (Skvarla et al., 1978) is strikingly illustrated (e.g., Figs. 130, 138, 141, 142, 145, 152, 153, 158–161, 178, 179, 186, 190, 192). These threads hold large masses of pollen together, presumably for more efficient pollination. The copious aspect of *Fuchsia* threads may be associated with bird pollination. The fact that these threads maintain the pollen in masses even after acetolysis would substantiate their effectiveness in nature. As pointed out by Raven (1979), sparse development of viscin threads is associated with pollination by bees, which are actually concerned with gathering pollen as food.

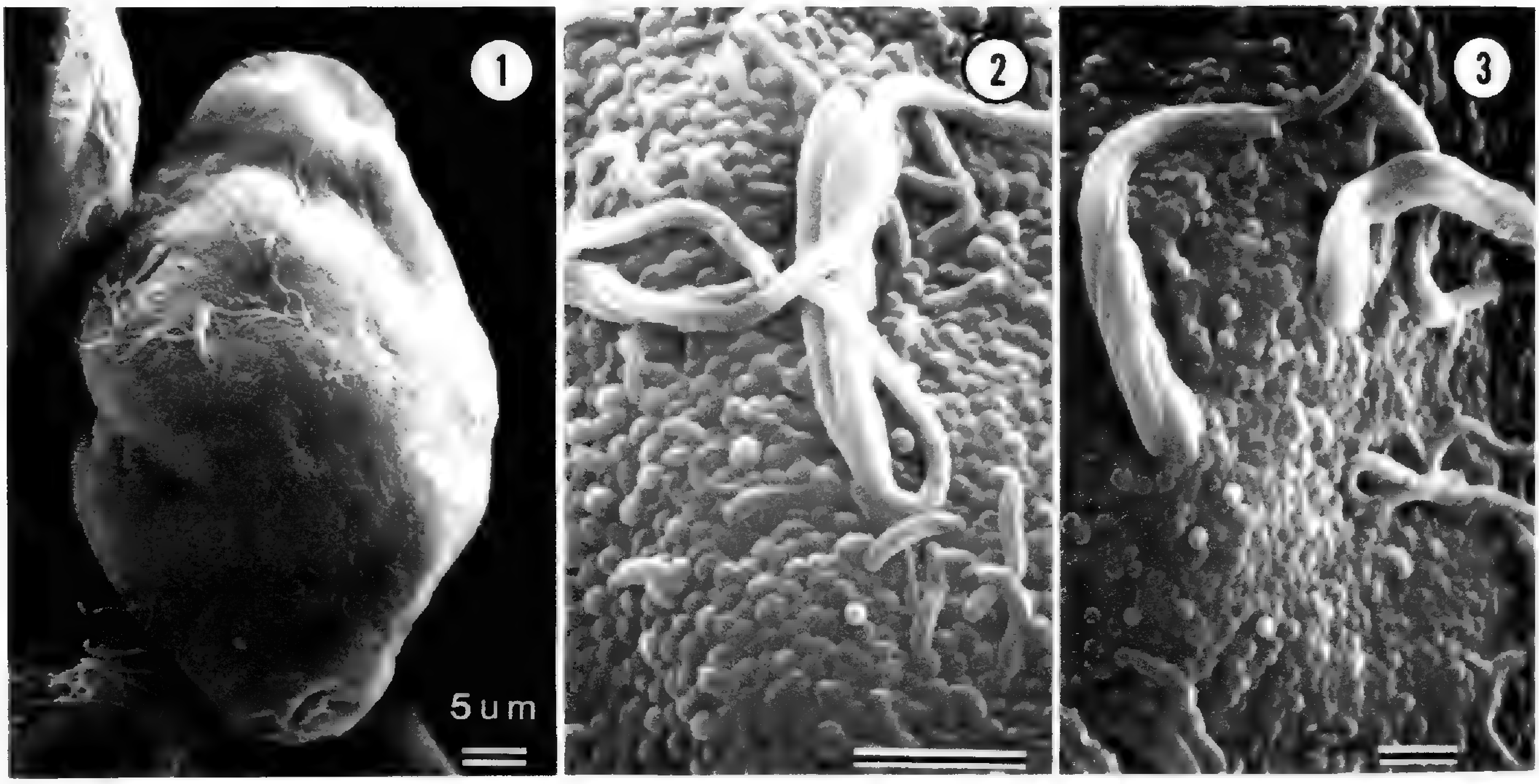
As shown in Table 2, segmented viscin threads are characteristic of most species of *Fuchsia*, and this is clearly the primitive condition in the genus. Smooth viscin threads of the derived and presumably directly related sects. *Encliandra, Jimenezia*, and *Schufia*, as well as those of the unrelated but still clearly derived sect. *Kierschlegeria*, clearly represent an advanced condition in these groups. There is a considerable amount of variability in viscin thread morphology in *Fuchsia microphylla* (sect. *Encliandra*): one subspecies, *F. microphylla* subsp. *hidalgensis* (Fig. 126), had segmented-ropy viscin threads; while others, subspp. *aprica* (Fig. 123), *hemsleyana* (Figs. 64, 130), *microphylla* (Fig. 66), and *quercetorum* (Fig. 131), had smooth threads.

In a recently published paper, Hesse (1982) described the development of viscin threads in *Epilobium angustifolium* and an unnamed species of *Fuchsia*. According to him, viscin threads develop in a granular matrix, and then the threads "approach towards" the microspores and "tend to fuse with the ektexine." In all Onagraceae the viscin threads are attached on the proximal face near the pole. In the case of pollen that is shed as tetrads, it is difficult for us to visualize a migration of threads between closely associated tetrad members, and their subsequent attachment to the pole.

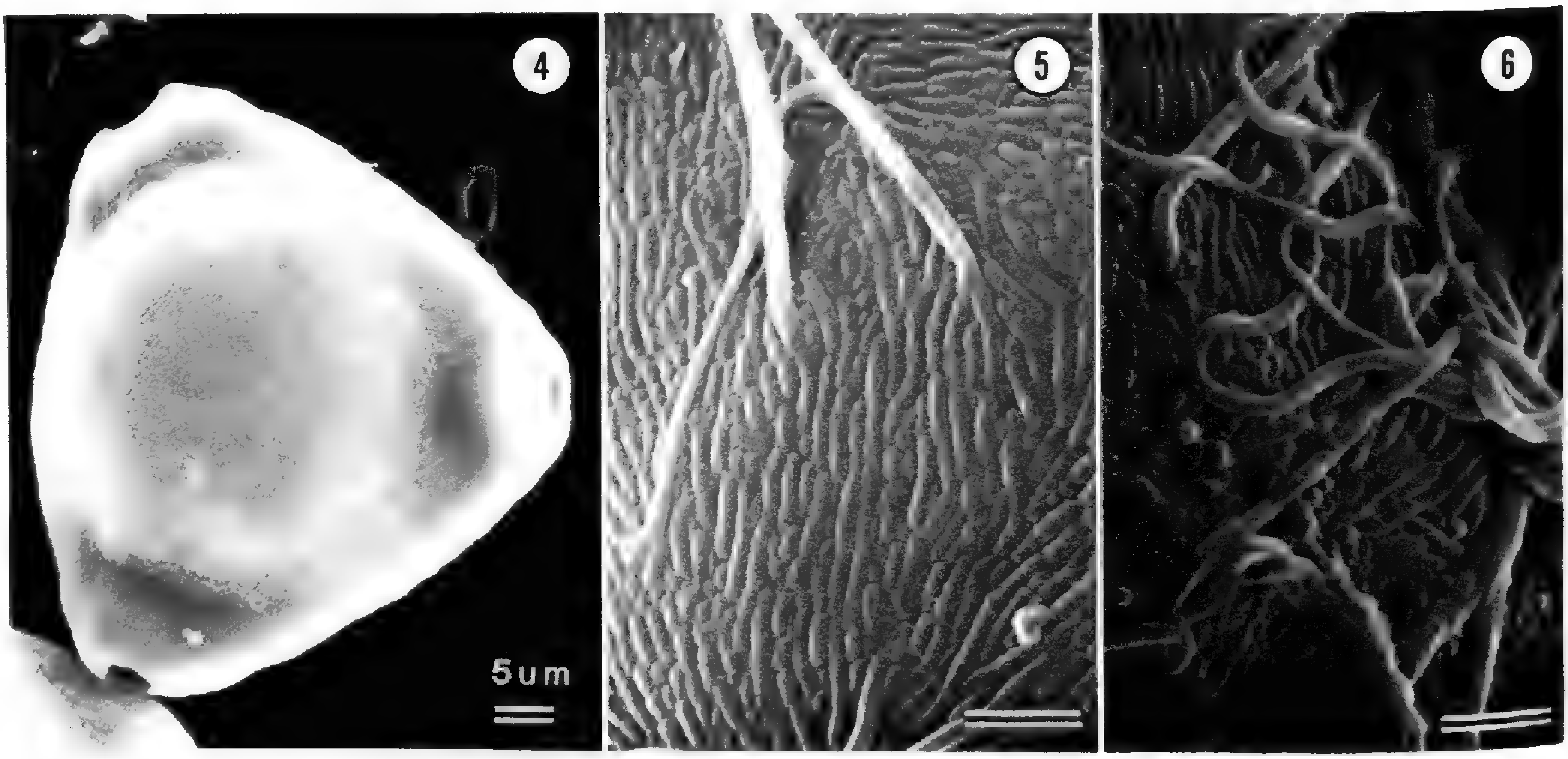
The structure of the exine in *Fuchsia* and in most other Onagraceae (Skvarla et al., 1976) is unique within the angiosperms (Patel et al., 1984). The ektexine is not differentiated into tectum, columellae, and foot layer units; instead, it consists of a spongy or paracrystalline layer, which is united with the endexine at numerous points along the ektexine-endexine interface. This selected union (rather than a total union or blanketing which would be expected in columellaless pollen) can result in a misleading impression that vestigial or incipient columellae are present. These structural relationships are clearly evident by perusal of many of the TEMs in Figures 115–194 as well as in SEM of fractured pollen (see particularly Figs. 120, 129). The ektexine is relatively uniform within a grain, differing sometimes in thickness between the distal and proximal faces (Praglowski et al., 1983; e.g., Figures 115, 116, 124, 125, 145, 146, 189, 190), and in the degree of fusion of the spongy elements. Organization of the spongy-paracrystalline ektexine suggests that some ektexines are more "complete" than others. For example, the ektexine in *F. microphylla* subsp. *hidalgensis* (Figs. 124, 125) seems to have more fused elements, hence more ektexine area than *F. garleppiana* (Fig. 162). Although this has certain validity, examination of the included TEMs (Figs. 115–194) will show that "completeness" or "incompleteness" of the ektexine will vary within the nine sections of *Fuchsia* and possibly even within species (compare TEM of subspecies of *F. microphylla*, Figs. 121, 122, 124, 125, 128, 130, 132–134). The second exine layer, the endexine, is primarily massive and uniform. As mentioned elsewhere, the lower or inner margin is usually finely granular throughout the pollen grain body, while in the aperture protrusions the endexine is extraordinarily channeled as well as being coarsely granular.

These results agree with previous work which considered the ektexine pattern of *Fuchsia* as having "tectum and columellae virtually indistinguishable" (Skvarla et al., 1976: 452). In this earlier study the ektexine pattern of *F. microphylla* subsp. *quercetorum* was described and illustrated (p. 51 and pl. 1F) as having "tectum and columellae distinct." Reexamination of this taxon clearly shows that the "columellae" were enhanced because the sectional view was exactly at the junction of the exine and cone-like aperture protrusion. Therefore, it is now more appropriate to recognize this exine layer simply as ektexine.

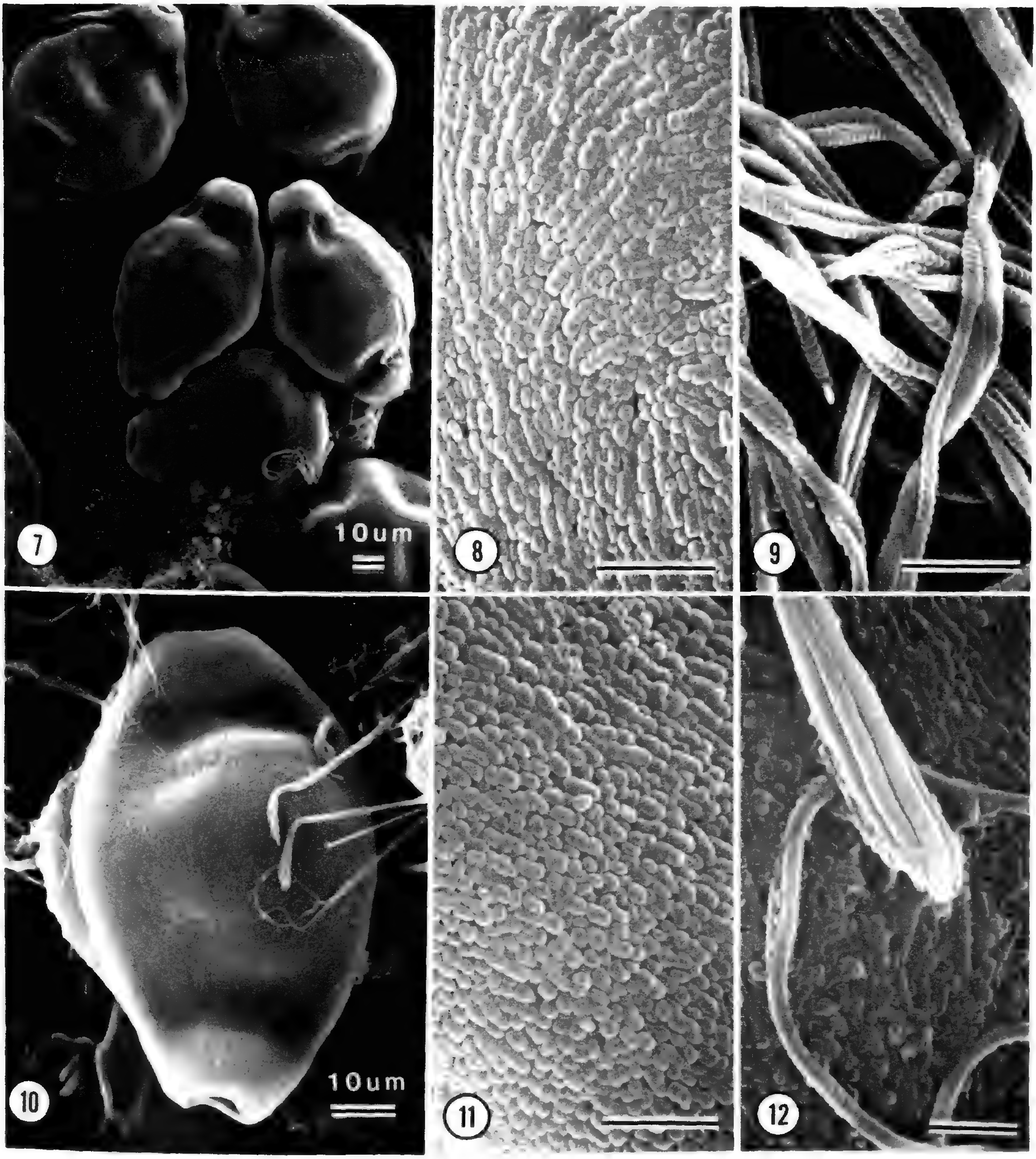
In the pollen of *Fuchsia*, two characteristics



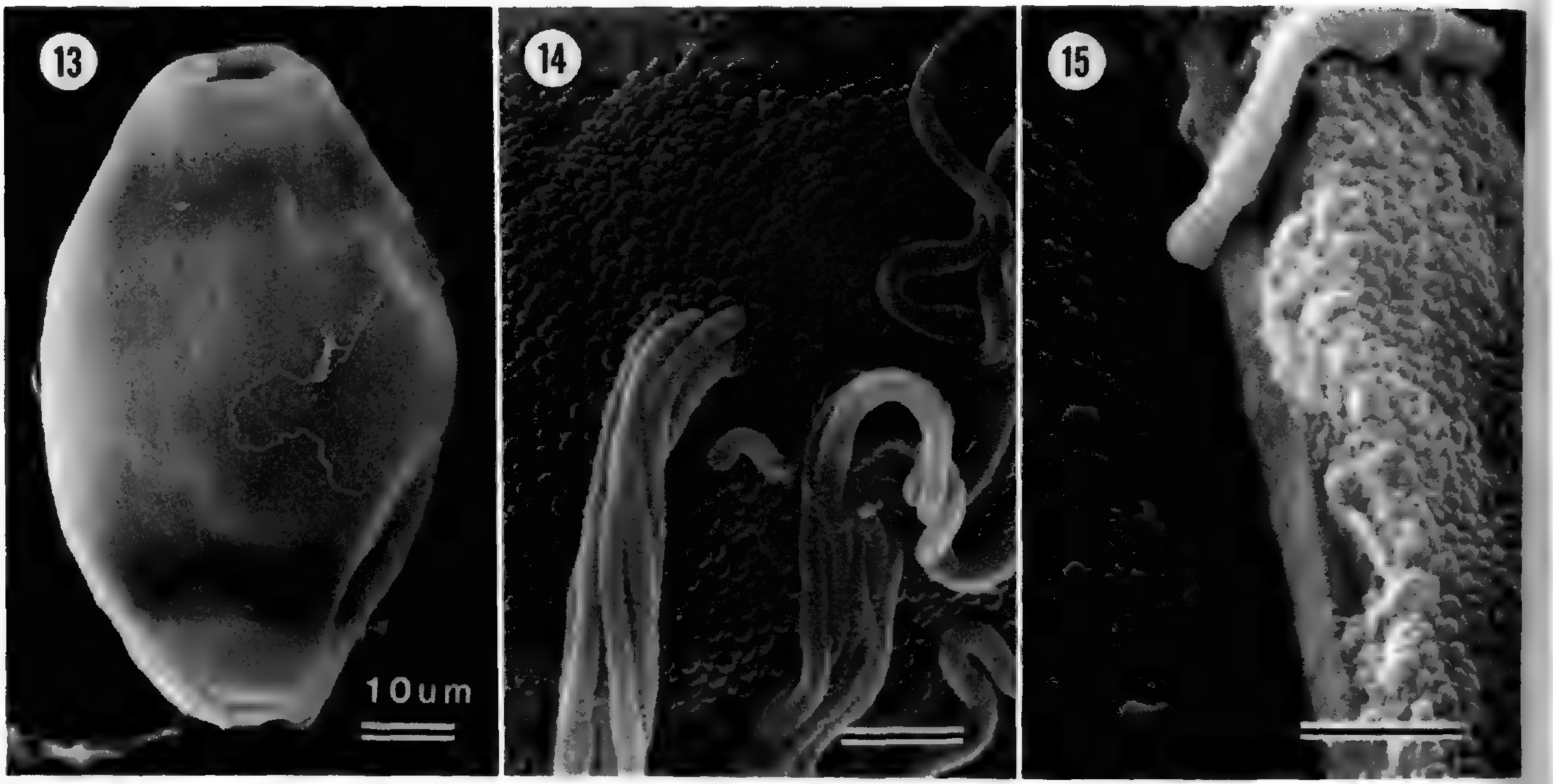
FIGURES 1–3. Scanning electron micrographs of *Fuchsia* sect. *Jimenezia, F. jimenezii.*—1. Slightly oblique polar view.—2. Ektexine with globular element sculpture and smooth viscin threads.—3. See legend of Figure 2. The scale equals 2 μm, unless otherwise indicated.



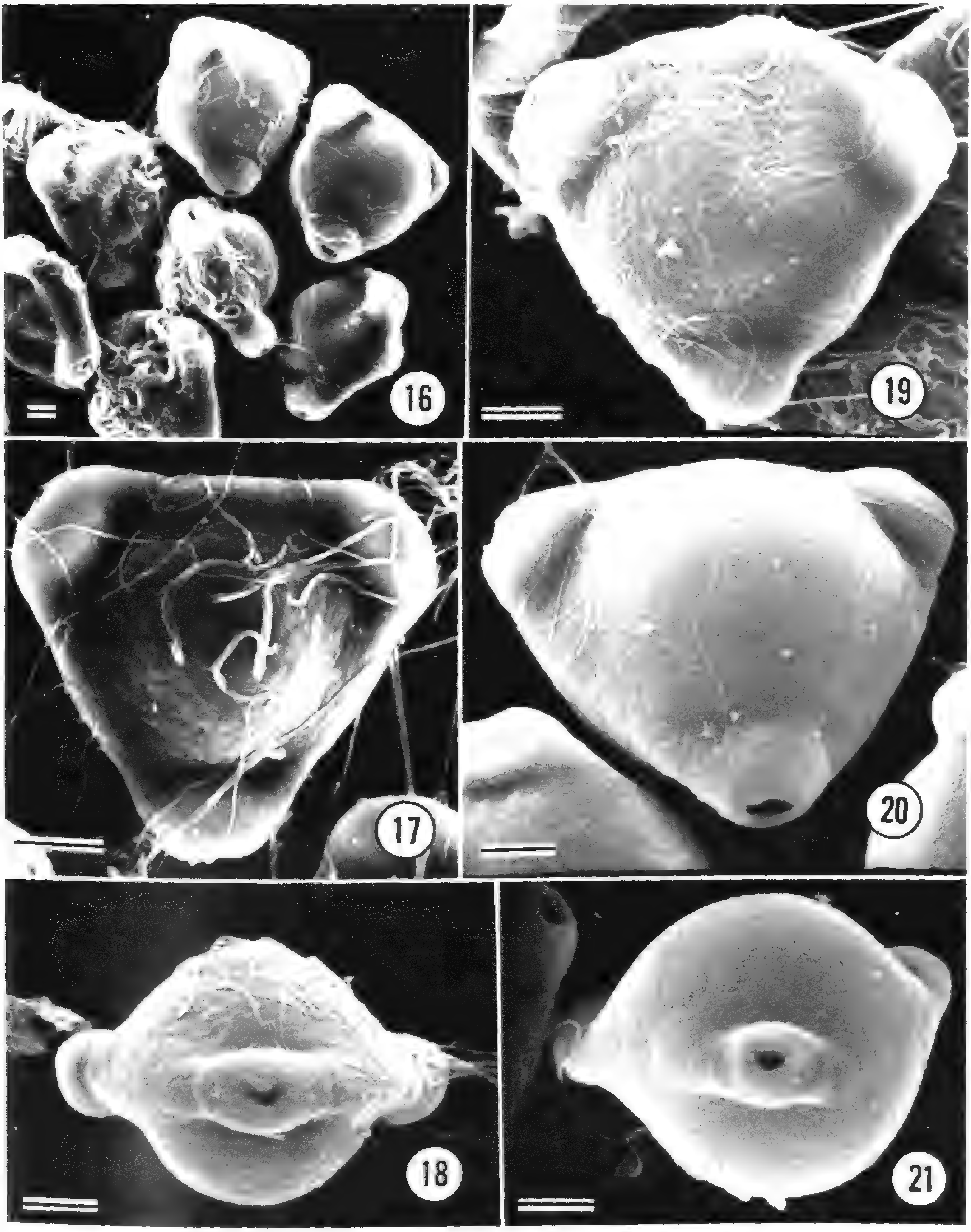
FIGURES 4–6. Scanning electron micrographs of *Fuchsia* sect. *Kierschlegeria, F. lycioides.*—4. Distal polar view.—5. Ektexine with elongated element sculpture and smooth viscin threads.—6. See legend of Figure 5. The scale equals 2 μm, unless indicated.



FIGURES 7–12. Scanning electron micrographs of *Fuchsia* sect. *Ellobium*. 7–9. *F. decidua*.—7. Low magnification of group.—8. Ektexine with globular-elongated element sculpture.—9. Segmented viscin threads. 10–12. *F. fulgens*.—10. Proximal polar view illustrating thread attachment.—11. See legend of Figure 8.—12. Segmented viscin threads. The scale equals 2 μm, unless indicated.



FIGURES 13–15. Scanning electron micrographs of *Fuchsia* sect. *Ellobium, F. splendens.*—13. Slightly oblique polar view.—14. Proximal pole with attached threads.—15. Exine fracture illustrating spongy ektexine and massive, solid endexine. The scale equals 2 μm, unless indicated.



FIGURES 16–21. Scanning electron micrographs of *Fuchsia* sect. *Quelusia.*—16. *F. regia,* low magnification of group. 17, 18. *F. bracelinae.*—17. Proximal polar view.—18. Aperture-centered equatorial view.—19. *F. campos-portoi,* polar view. 20, 21. *F. magellanica.*—20. Slightly oblique distal polar view.—21. Aperture-centered equatorial view. The scale equals 10 μm.

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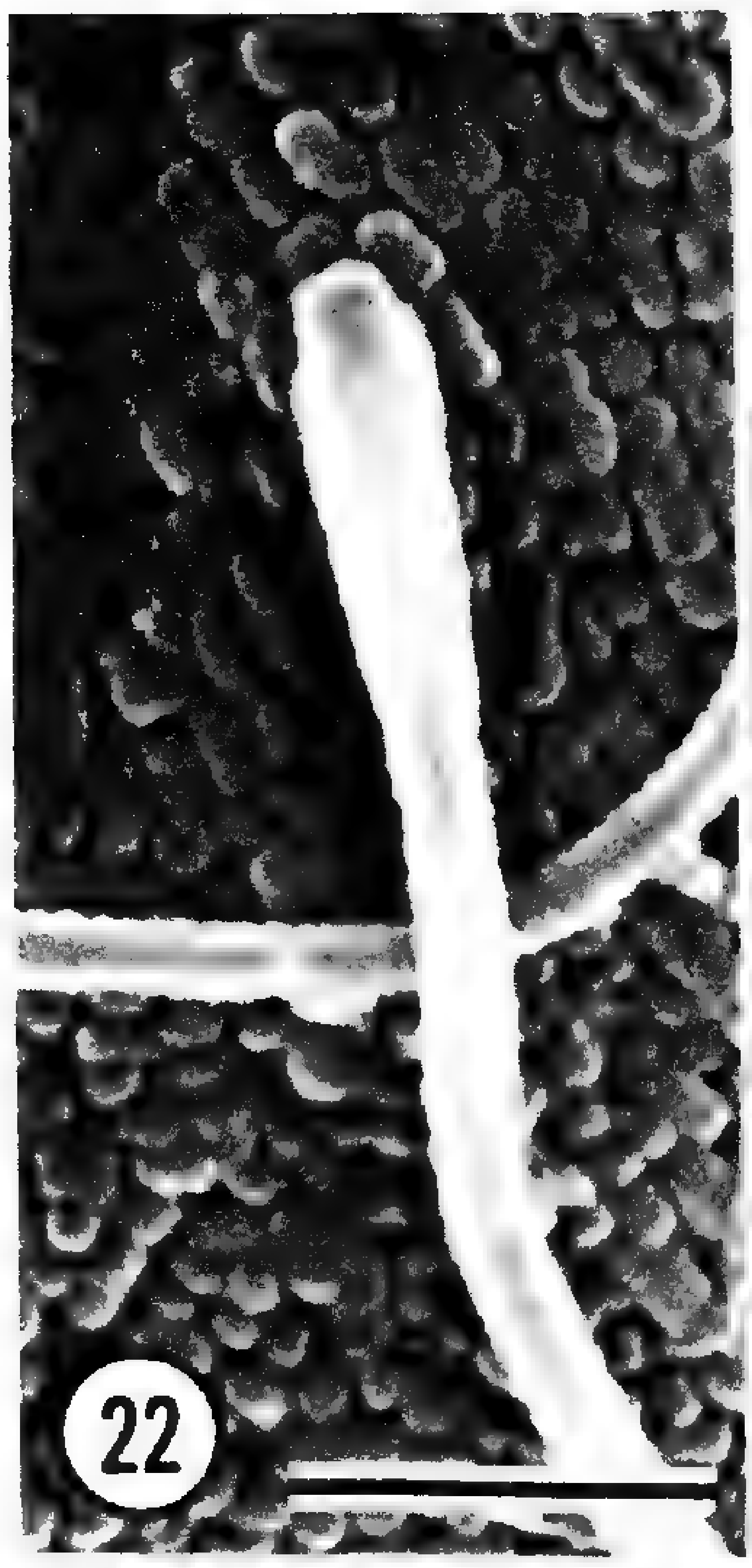
FIGURES 22–30. Scanning electron micrographs of *Fuchsia* sect. *Quelusia.*—22–24. *F. magellanica,* variation in thread attachment and ektexine sculpture within a sample, all threads segmented.—25. *F. campos-portoi,* segmented viscin threads. 26–30. *F. regia.*—26–27. Segmented viscin thread.—28. Pore.—29. Note the high density of threads in some grains.—30. Segmented viscin threads. The scale equals 2 μm.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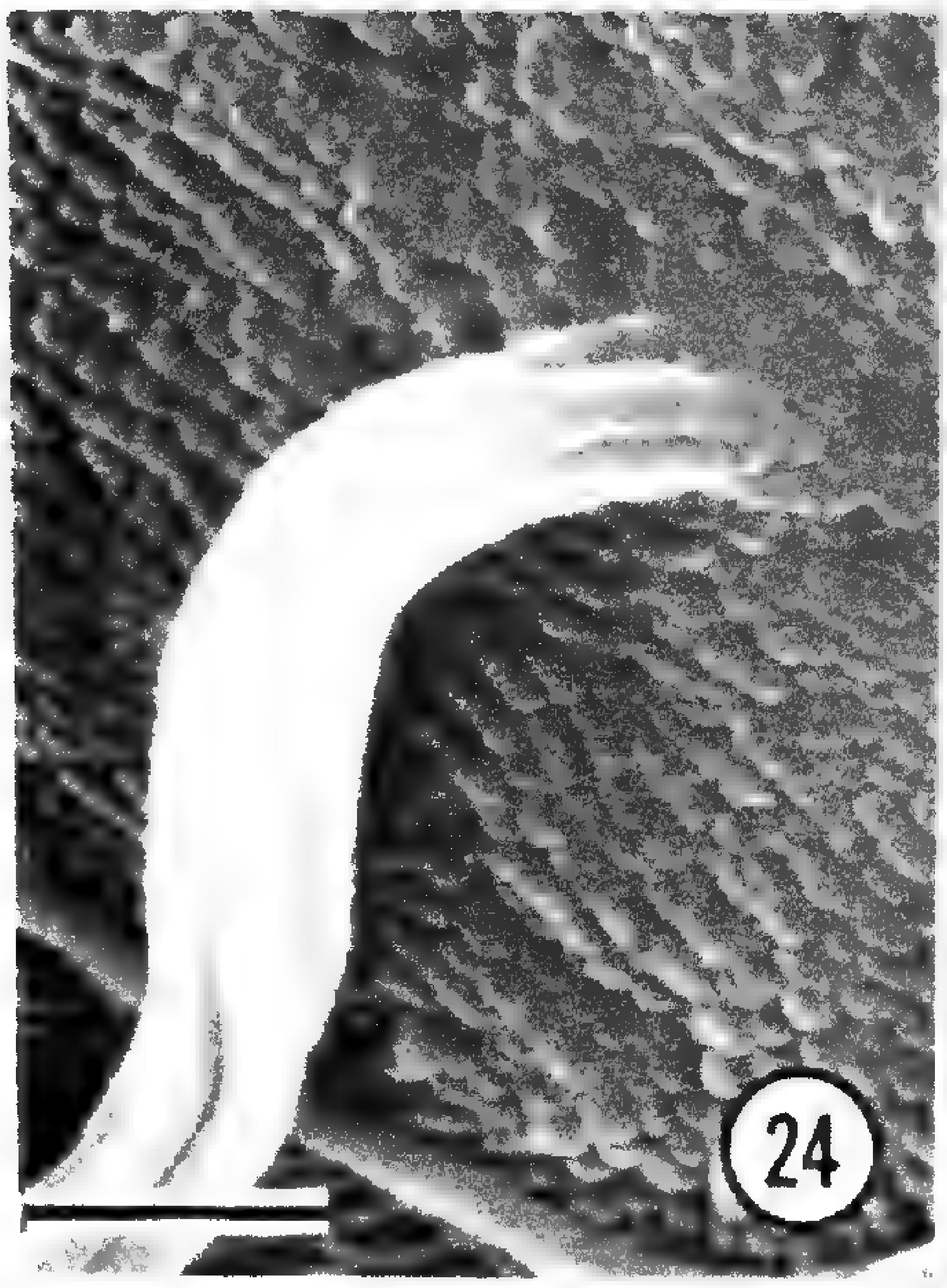
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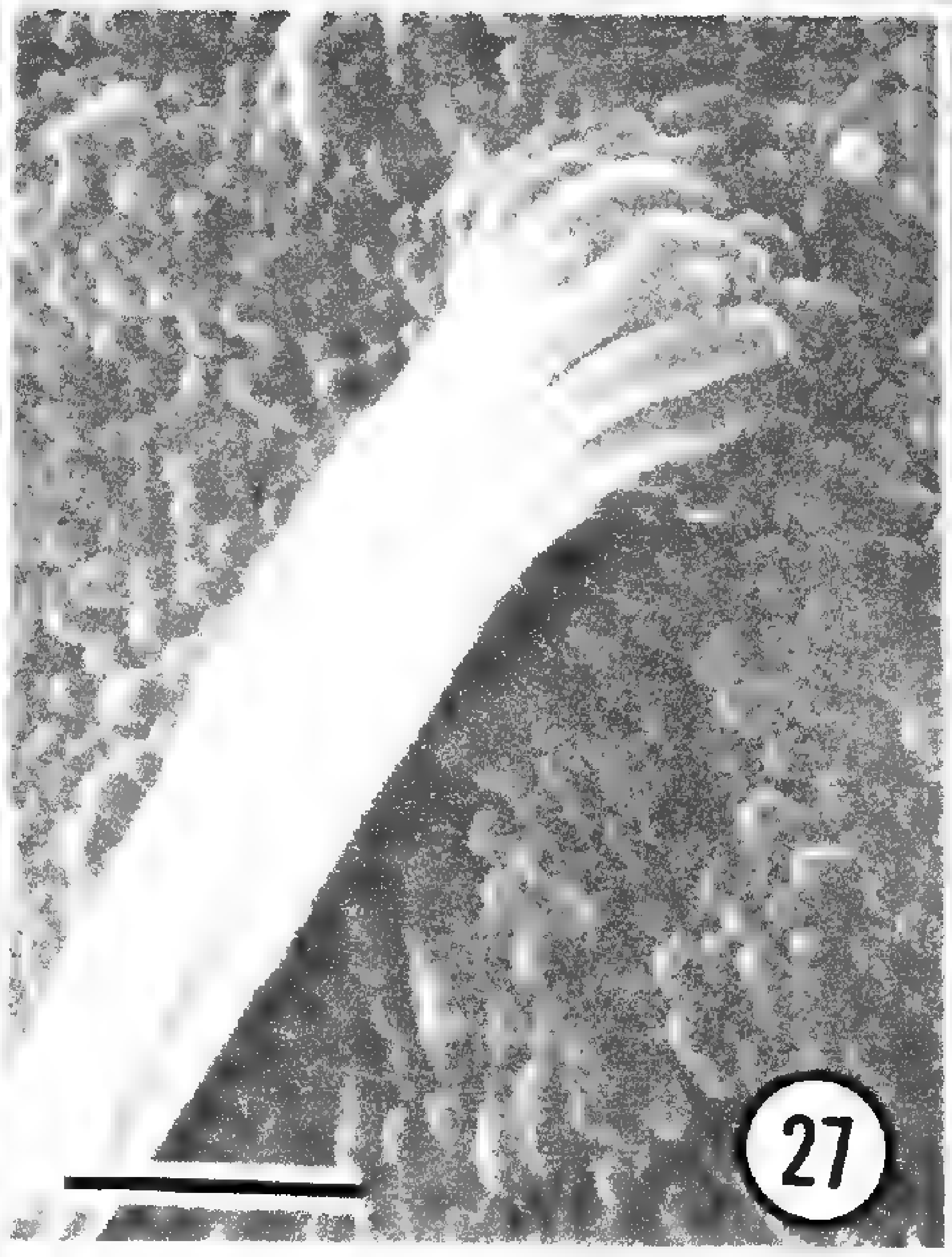
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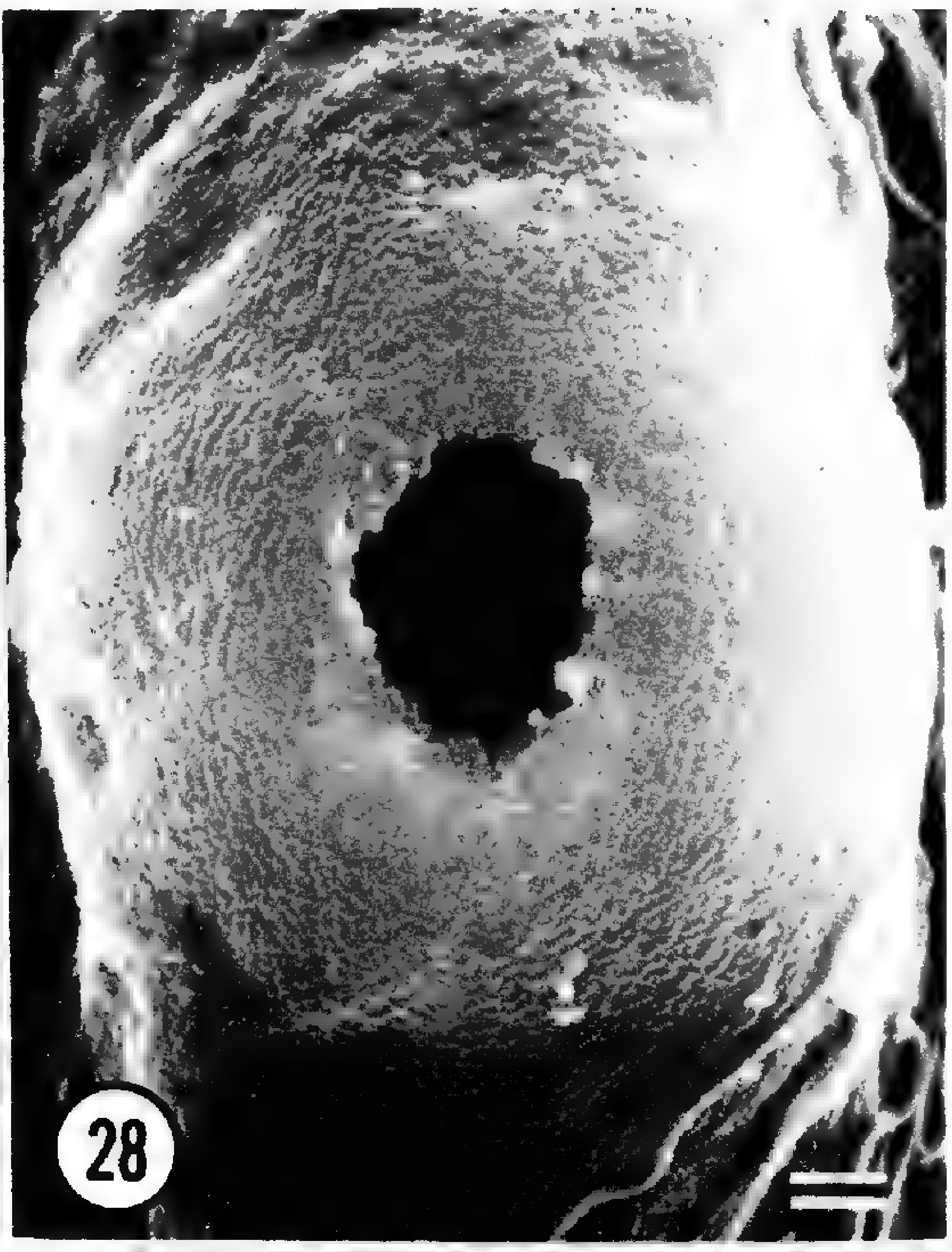
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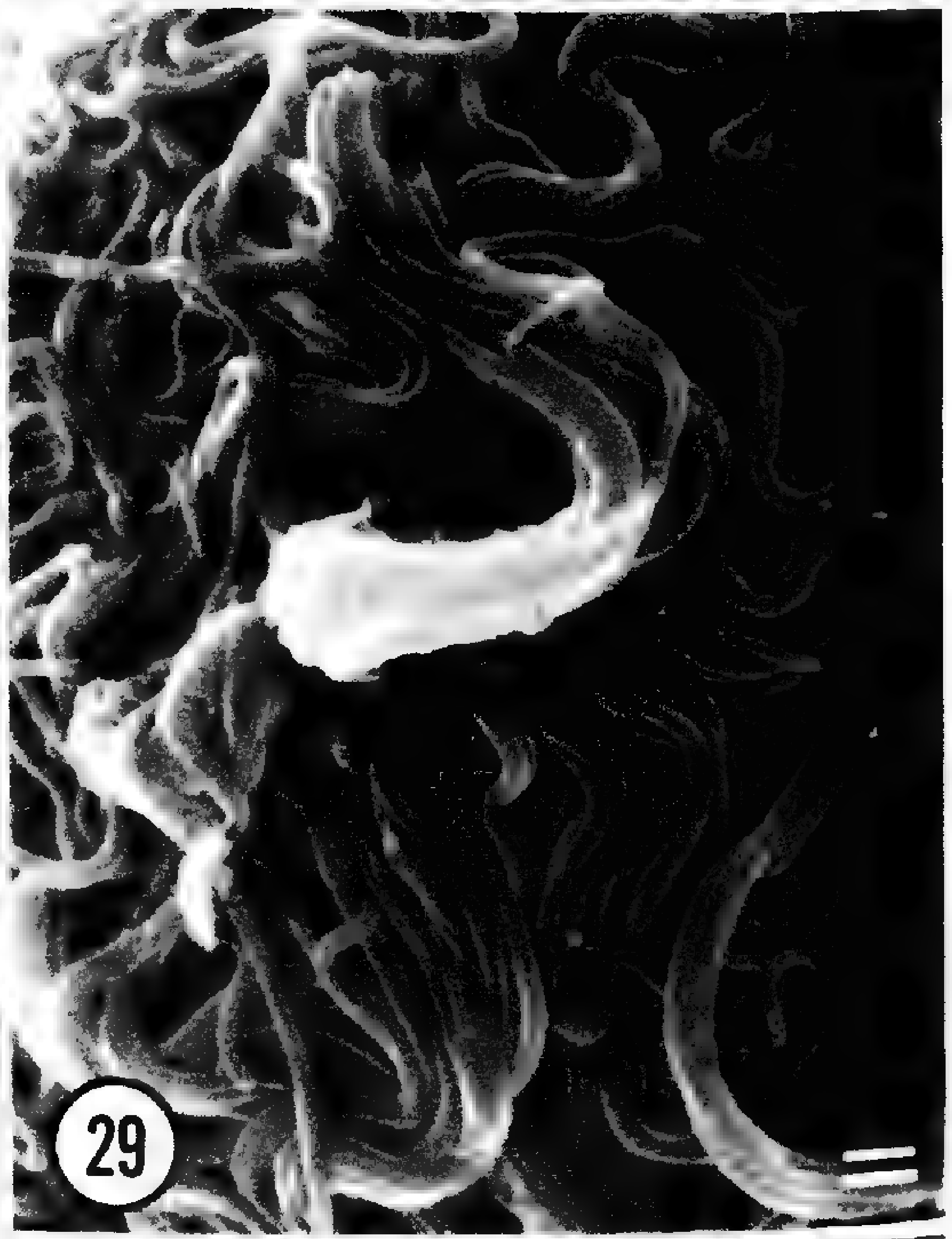
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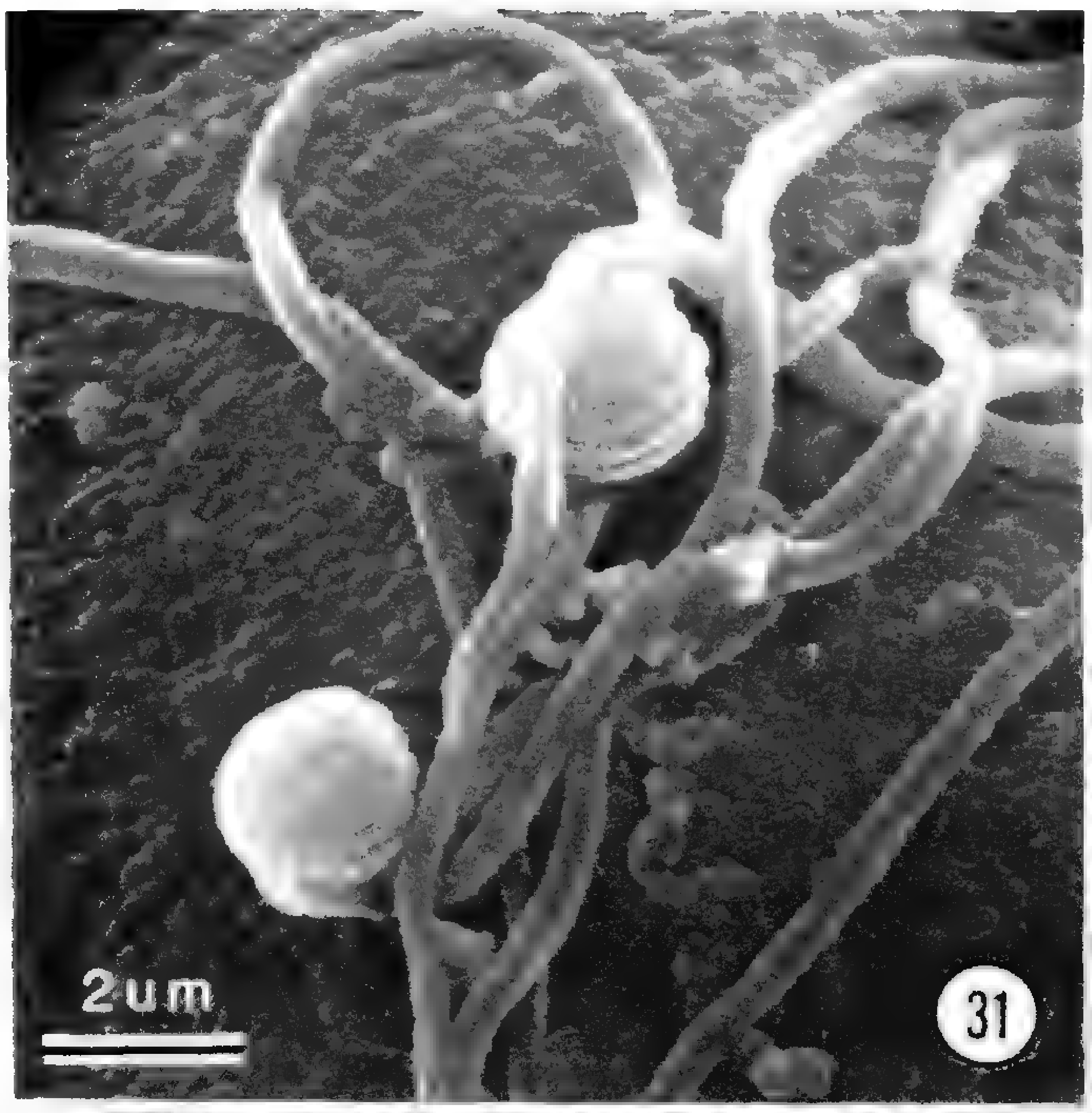

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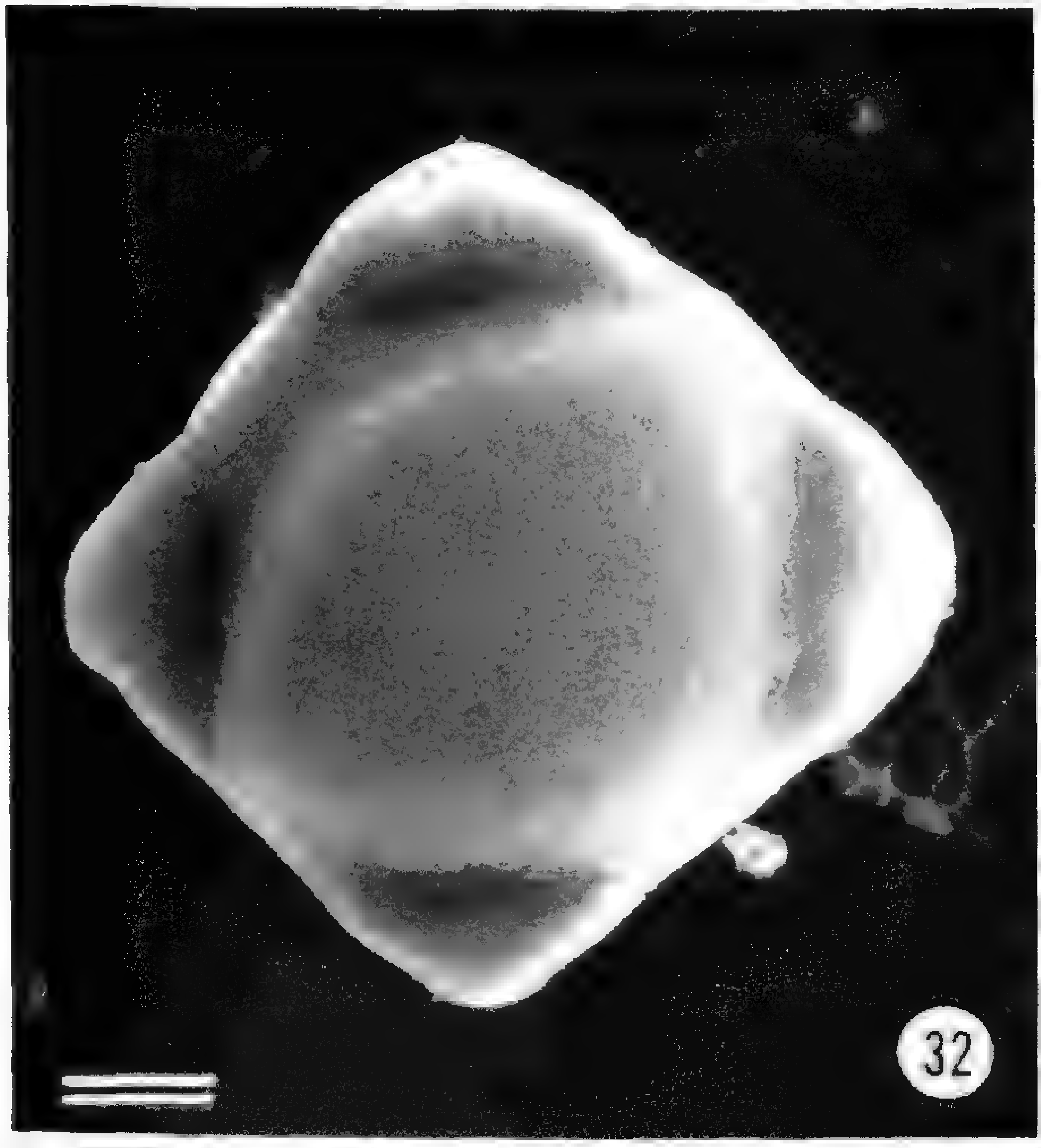

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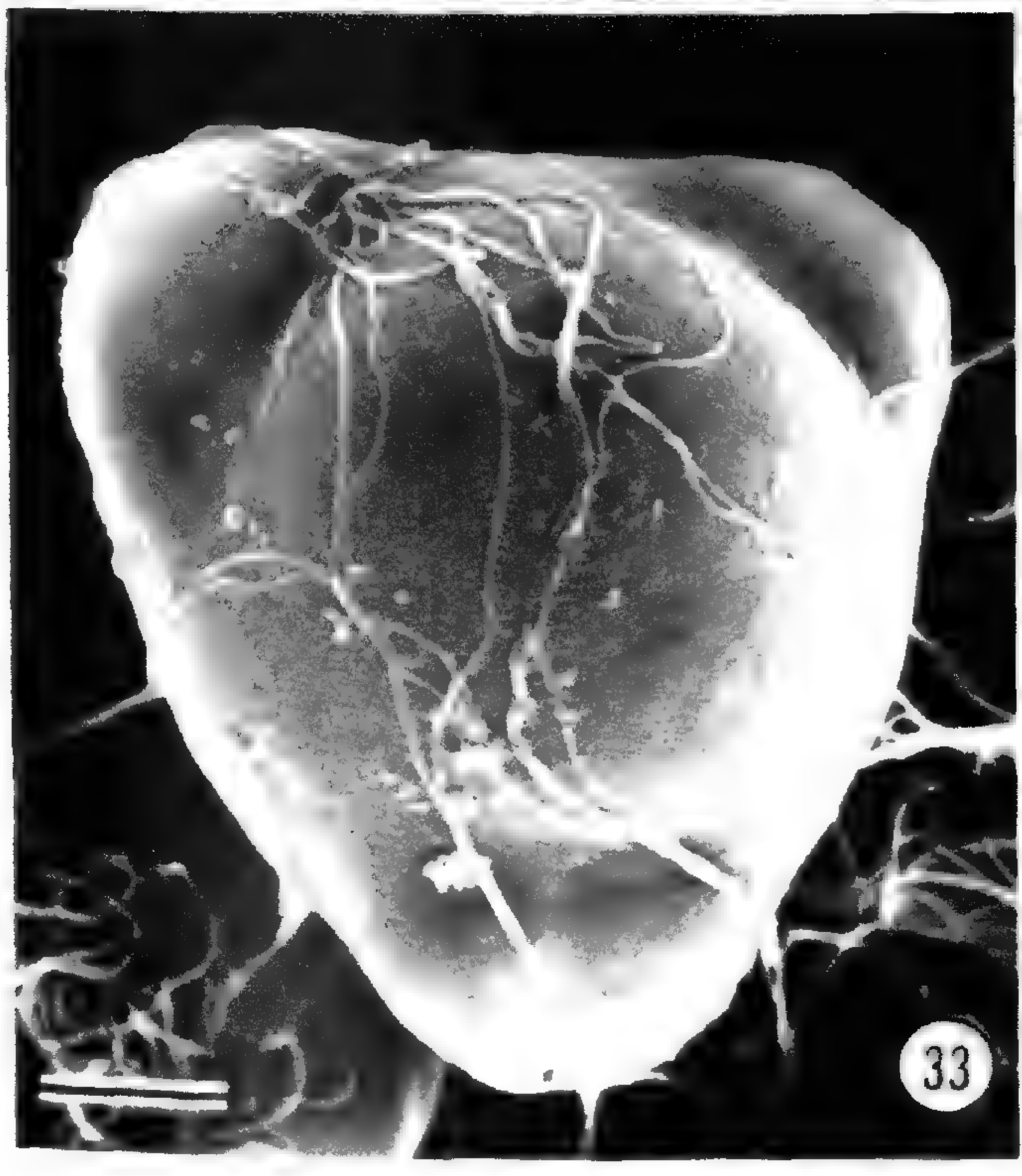

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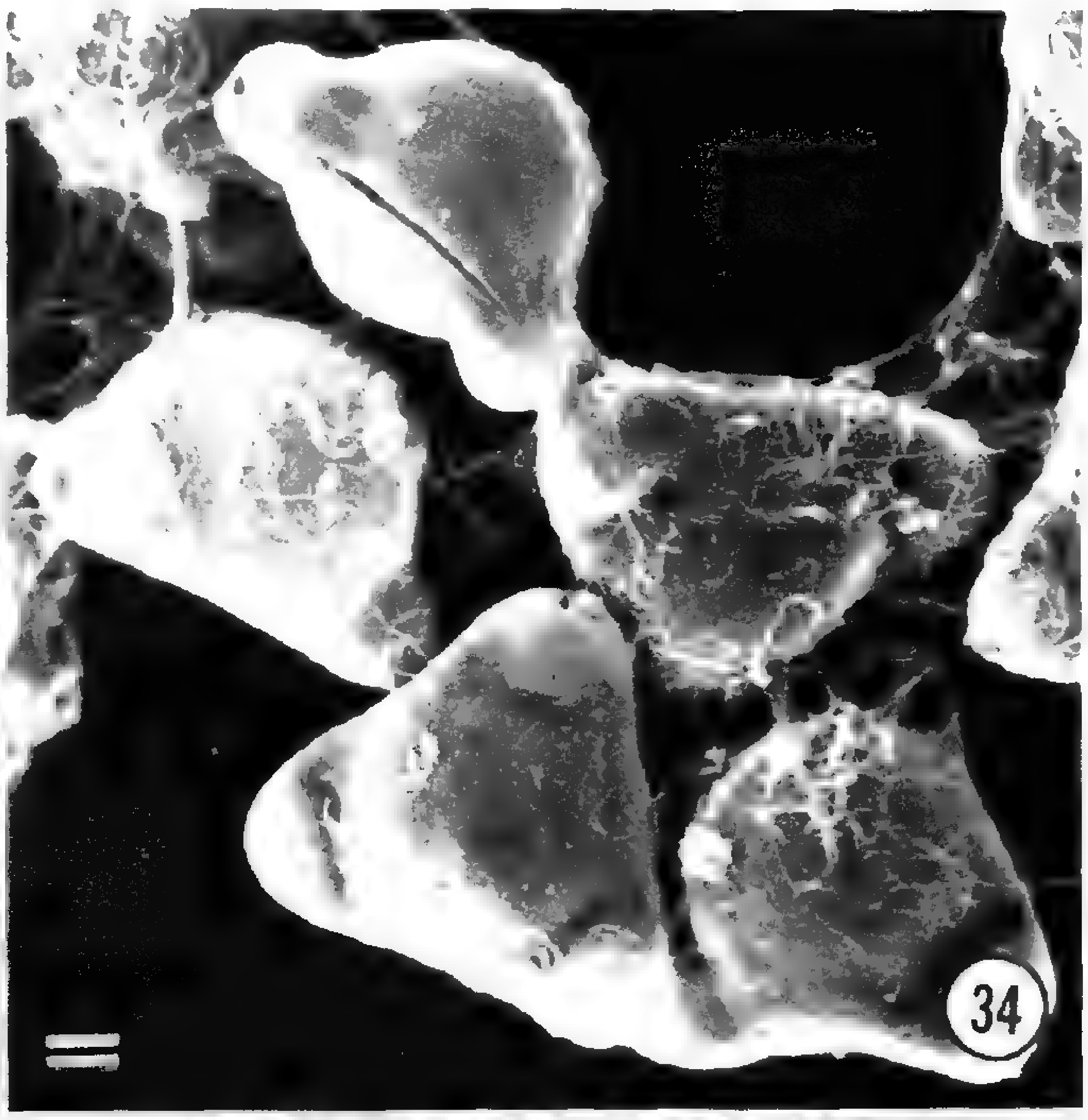

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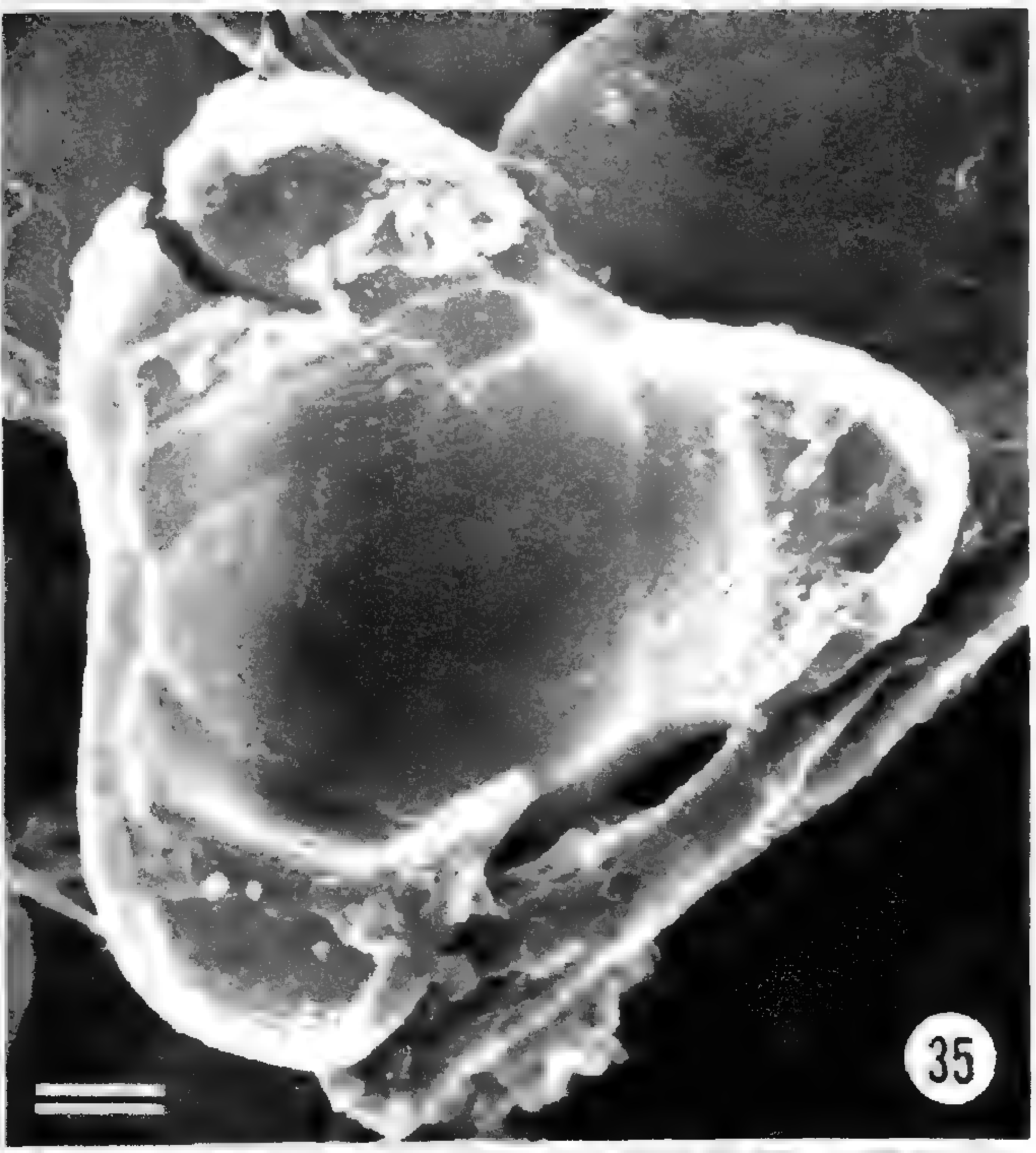

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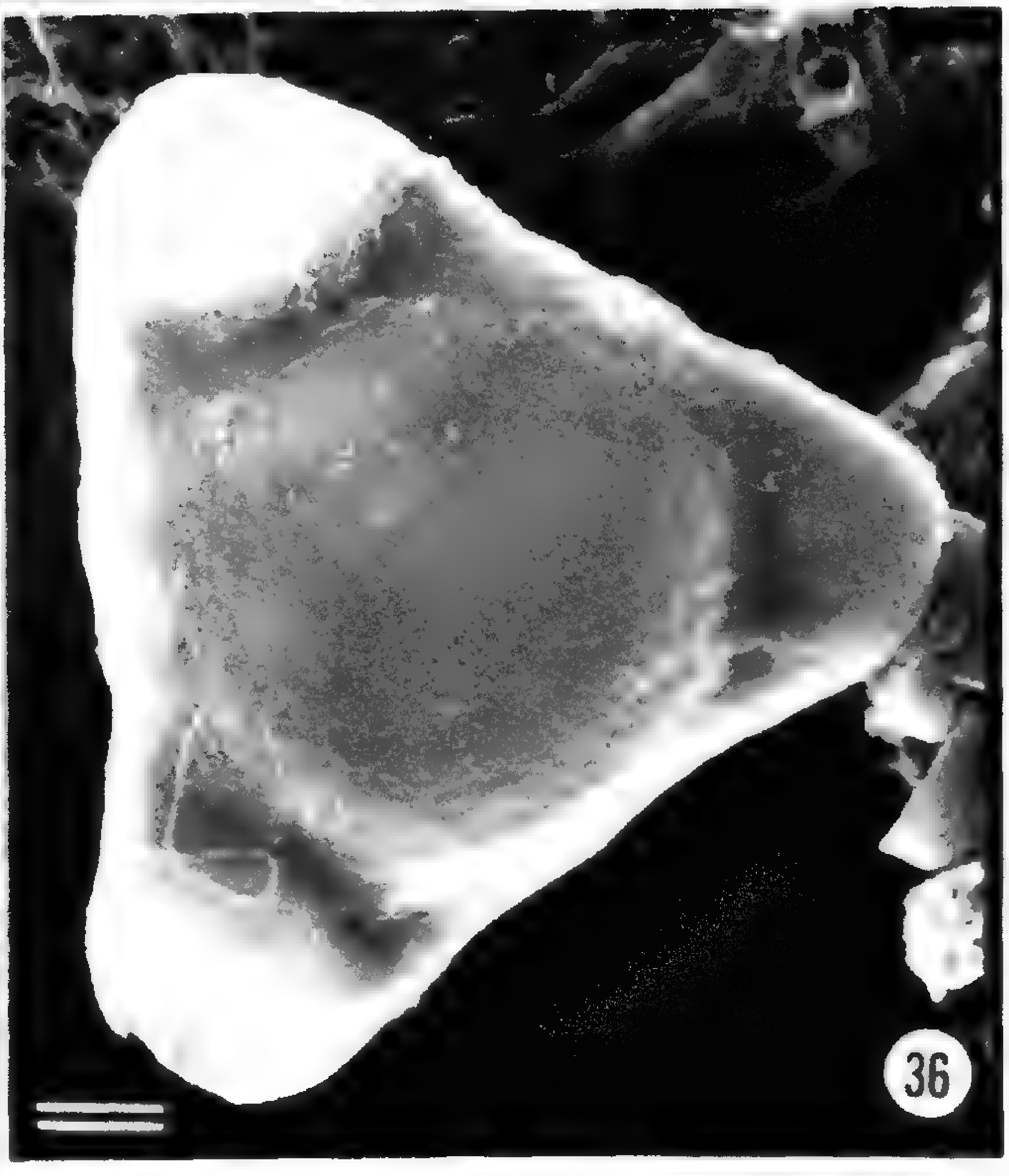

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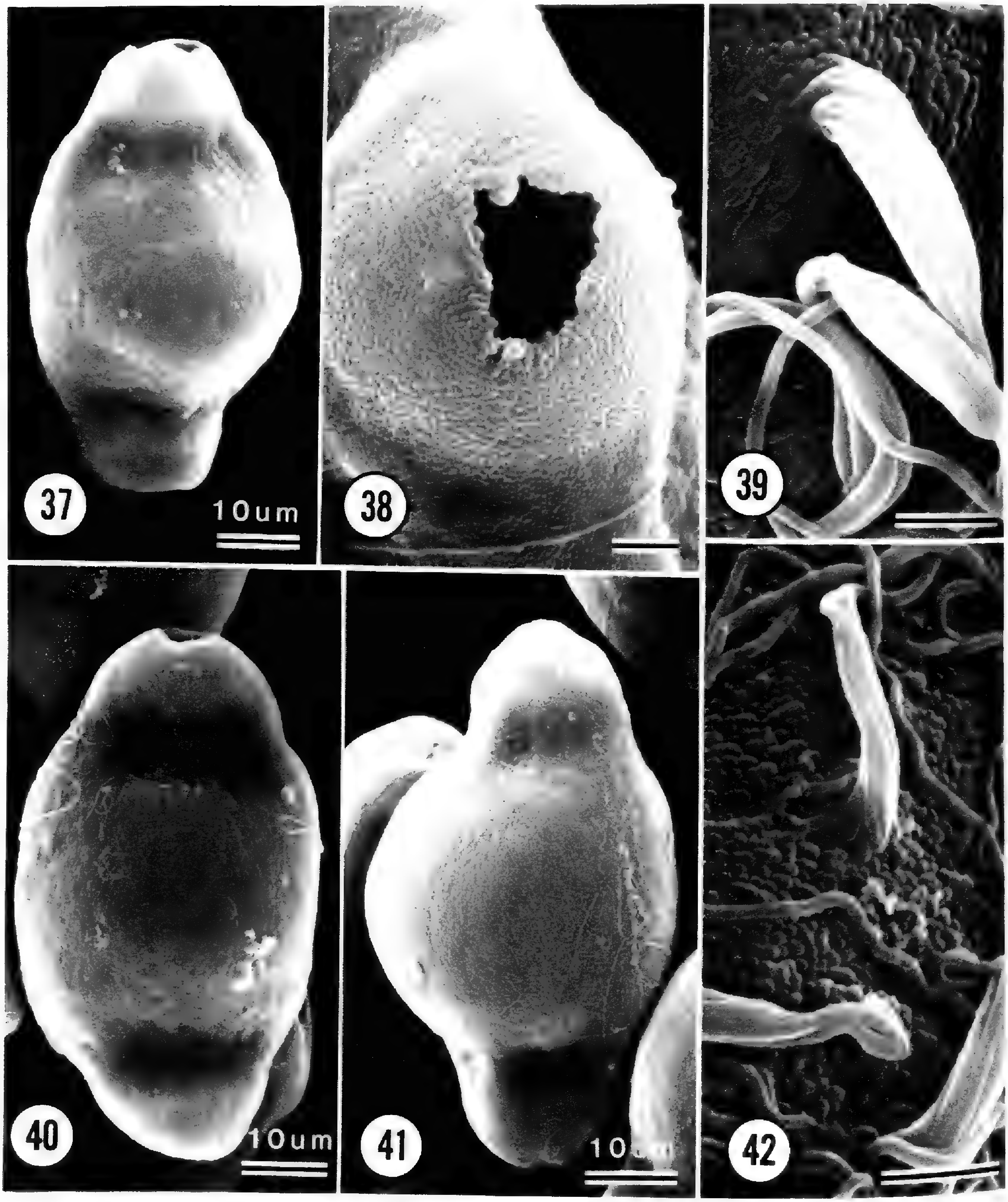

FIGURES 37–42. Scanning electron micrographs of *Fuchsia* sect. *Schufia*. 37–40. *F. arborescens.*—37. Slightly oblique polar view.—38. Pore with ragged margin.—39. Smooth to slightly segmented (?) viscin threads with an ektexine sculpture of both globular and elongated elements.—40. Polar view. 41, 42. *F. paniculata.*—41. Slightly oblique view.—42. See legend of Figure 39. The scale equals 2 μm, unless indicated.

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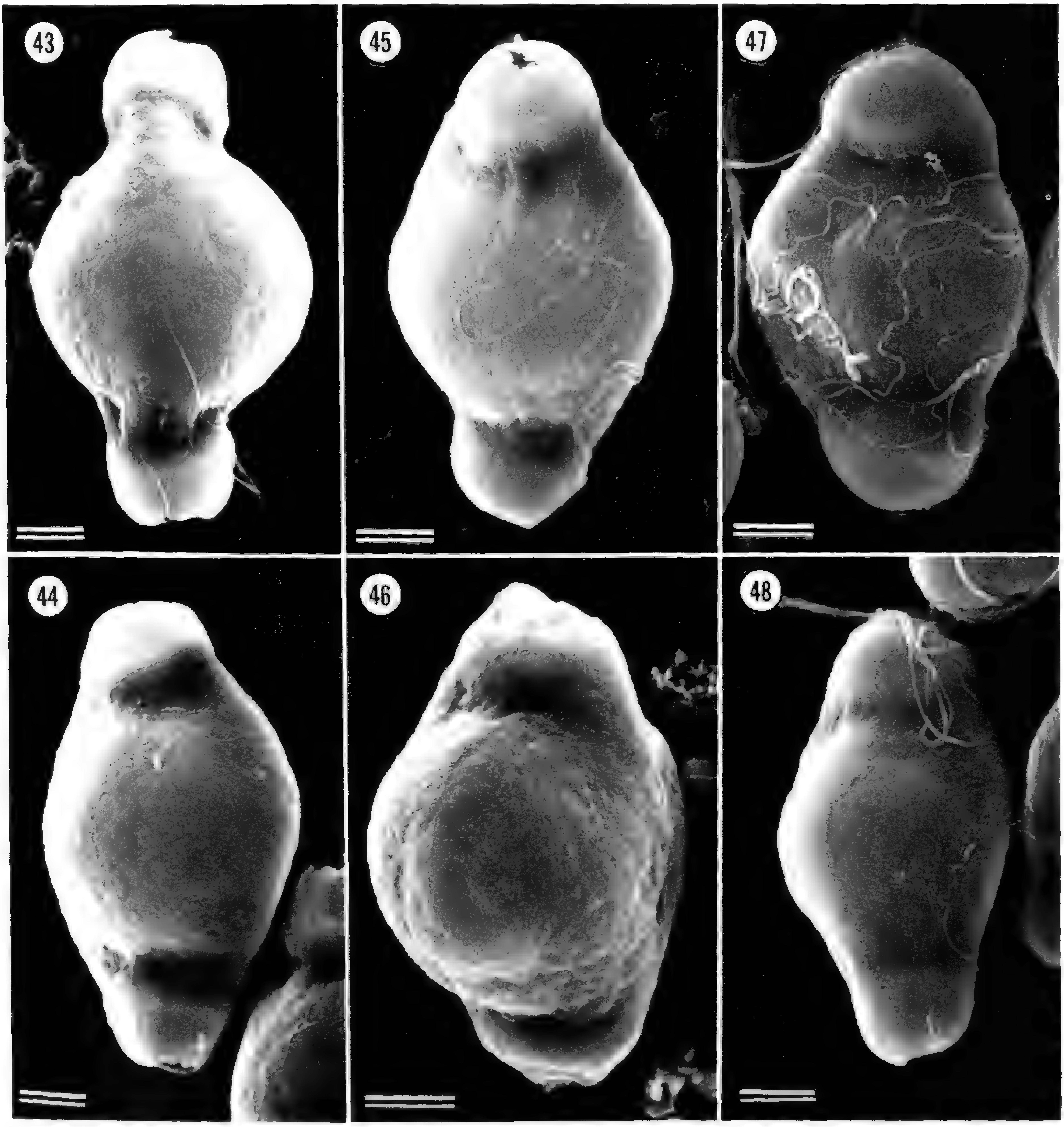
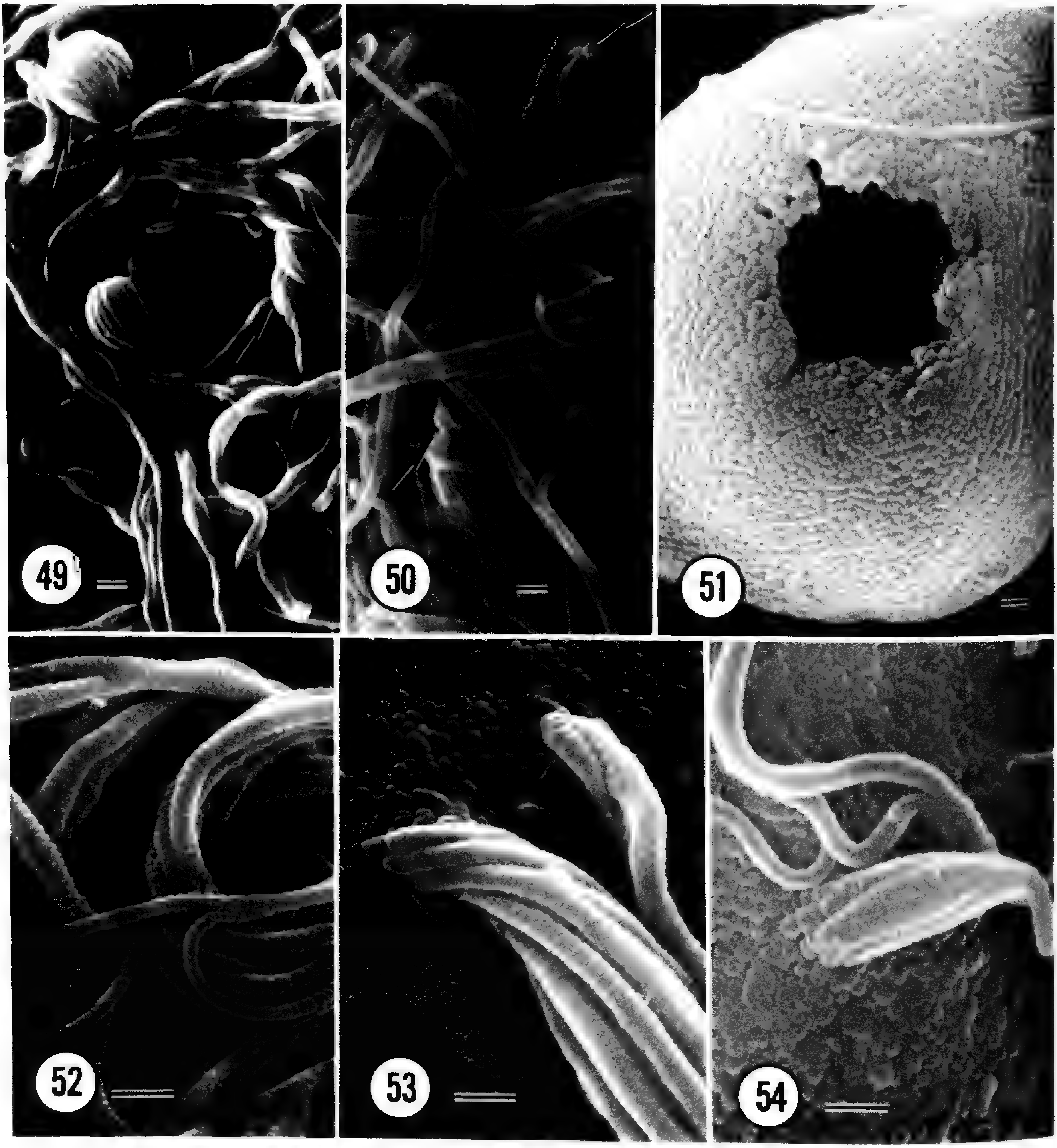
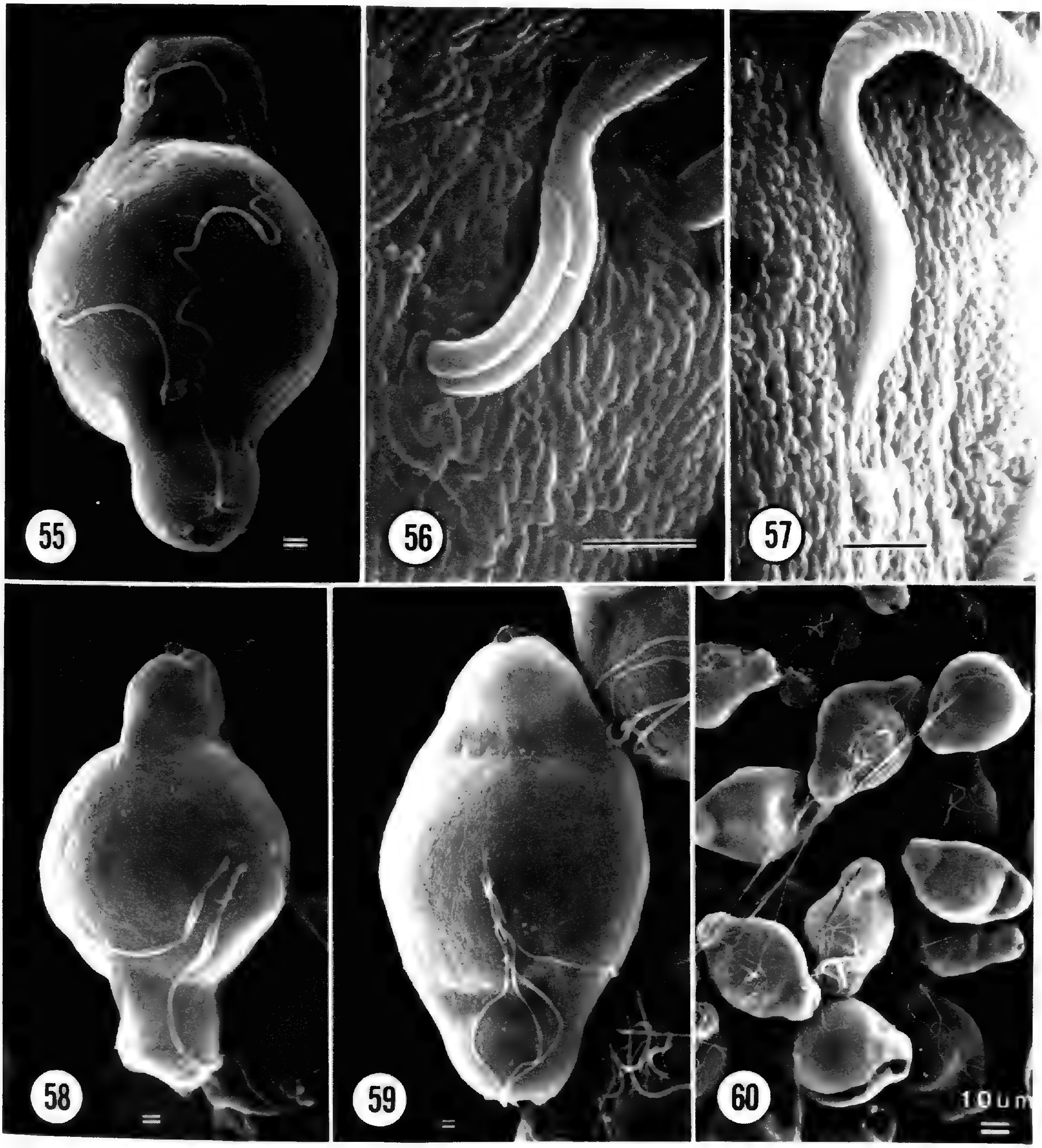
FIGURES 31–36. Scanning electron micrographs of *Fuchsia* sect. *Quelusia*. 31–33. *F. coccinea.*—31. Segmented viscin threads showing localized nodular distensions (see also Fig. 49).—32. A 4-aperturate grain, polar view.—33. Slightly oblique polar view. 34–36. *F. regia.*—34. Group of 3-aperturate grains.—35. Equatorial fracture, note thickened endexine around endoapertures.—36. Slightly oblique polar view. The scale equals 10 μm, unless indicated.



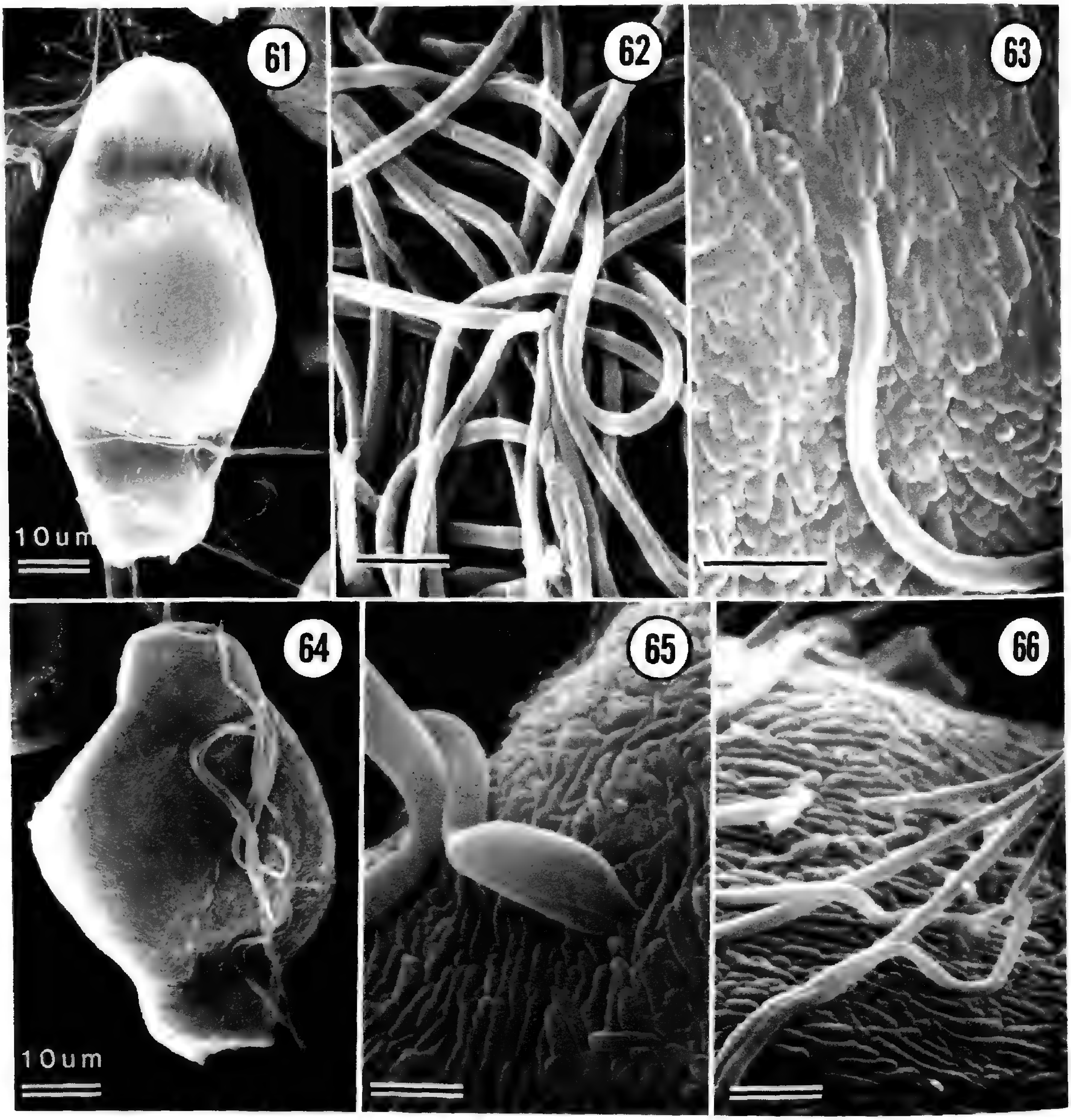
FIGURES 43–48. Scanning electron micrographs of *Fuchsia* sect. *Skinnera*. 43, 44. *F. excorticata*.—43. Mesocolpus-centered equatorial view.—44. Slightly oblique polar view.—45. *F. perscandens*, oblique polar view.—46. *F. cyrtandroides*, mesocolpus-centered equatorial view. 47, 48. *F. procumbens*.—47. Slightly oblique proximal polar view.—48. Slightly oblique polar view. The scale equals 10 μm.



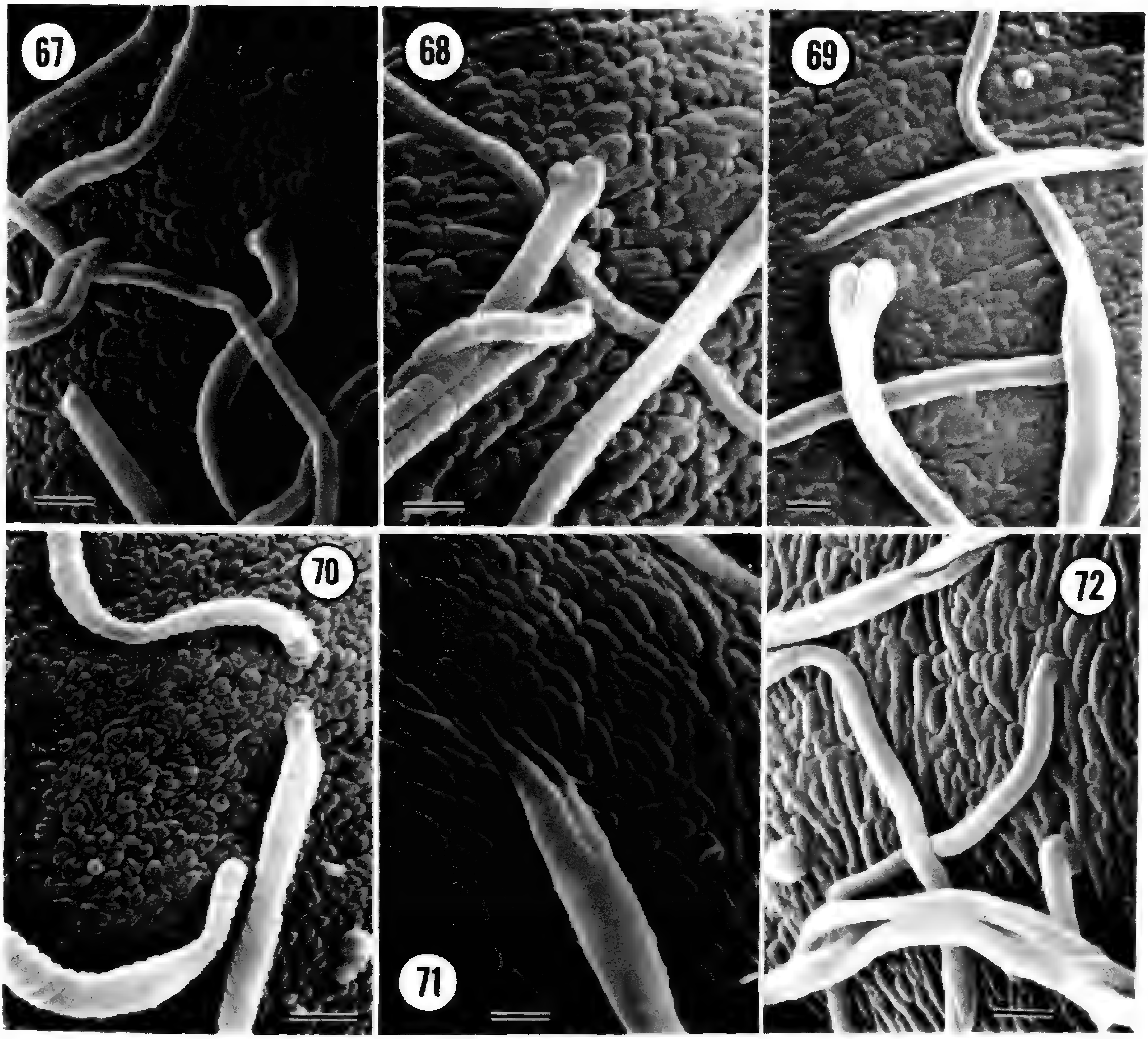
FIGURES 49–54. Scanning electron micrographs of *Fuchsia* sect. *Skinnera*. 49–50. *F. cyrtandroides.*—49. Viscin threads with various sized nodular distensions (arrows).—50. Ektexine at proximal pole with attachment of threads from inflated bases with somewhat elongated surface elements (arrows). Note that at this magnification (also Fig. 49) viscin threads appear to be mostly smooth with only rare suggestions of light segmentation; these should be compared with transmission electron micrographs (Figs. 183, 184) and companion high magnification scanning electron micrographs (Figs. 182, 185).—51. *F. excorticata*, pore with thin, ragged margin.—52. *F. procumbens*, segmented viscin threads.—53. *F. perscandens*, attachment of multiple-stranded, segmented viscin threads with globular element sculpture.—54. *F. excorticata*, see legend of Figure 53. The scale equals 1 μm.



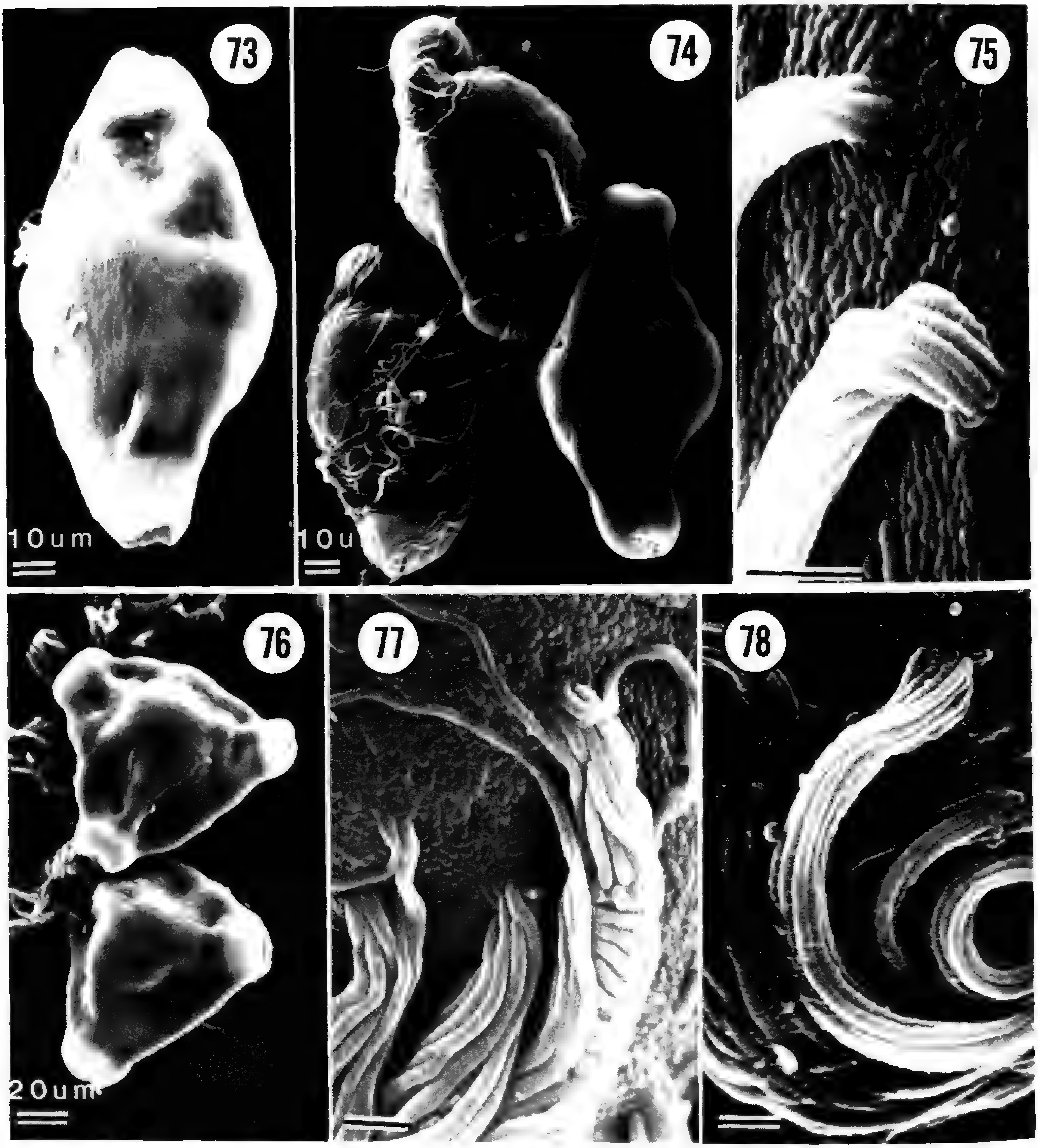
FIGURES 55–60. Scanning electron micrographs of *Fuchsia* sect. *Encliandra*. 55–57. *F. thymifolia* subsp. *thymifolia*.—55. Oblique view.—56. Ektexine with elongated element sculpture and sparsely segmented viscin threads.—57. Ektexine with globular element sculpture and segmented-ropy viscin thread (see also Fig. 147 of *F. thymifolia* subsp. *minimiflora*).—58. *F. obconica*, slightly oblique equatorial view. 59, 60, *F. encliandra* subsp. *encliandra*.—59. Proximal polar view.—60. Low magnification of group of pollen grains. The scale equals 2 μm, unless indicated.



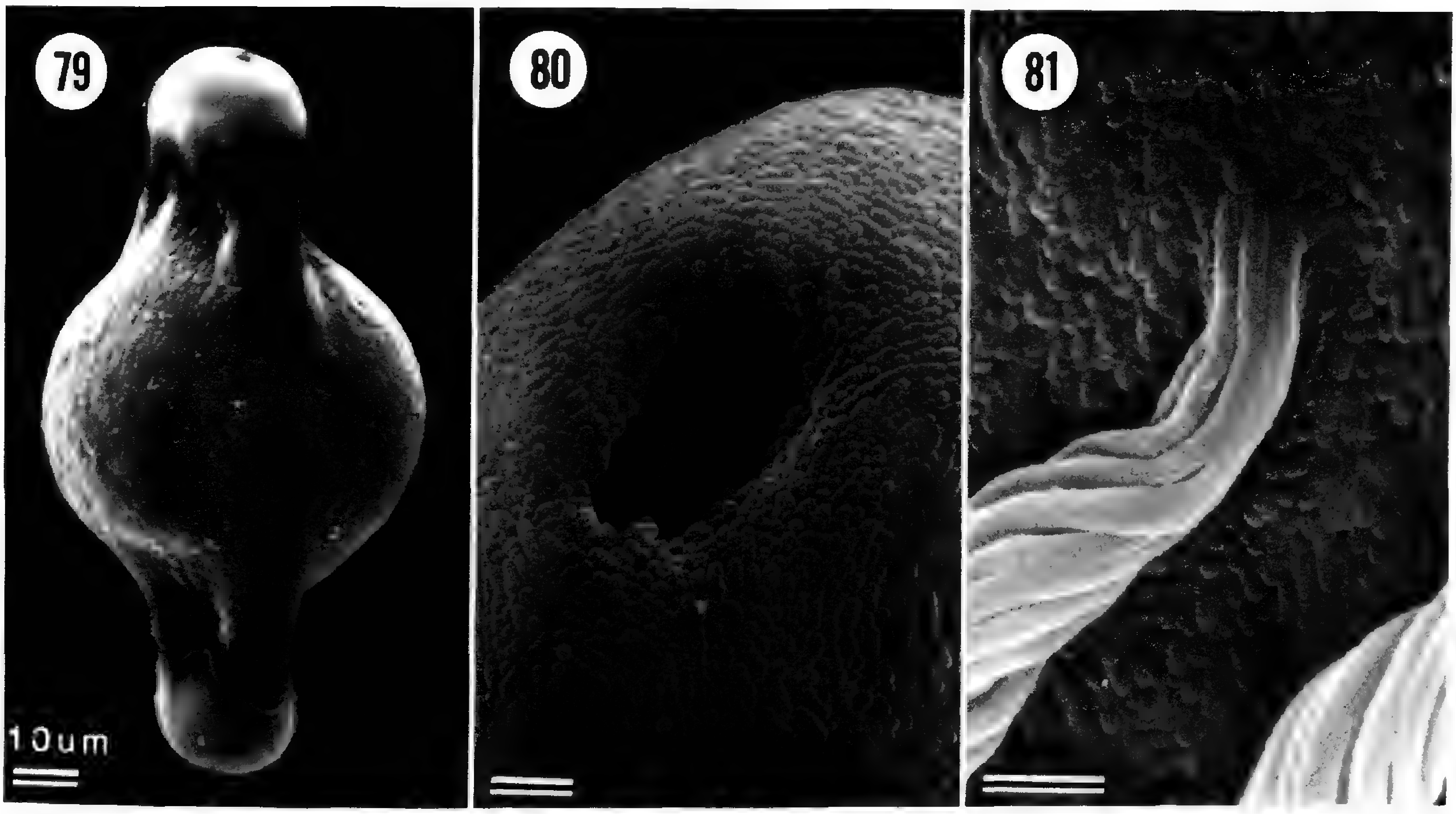
FIGURES 61–66. Scanning electron micrographs of *Fuchsia* sect. *Encliandra*. 61–63. *F. ravenii*.—61. Slightly oblique polar view.—62. Sparsely segmented threads.—63. Ektexine with elongated elements and smooth threads. 64, 65. *F. microphylla* subsp. *hemsleyana*.—64. Slightly oblique proximal polar view.—65. Ektexine with elongated elements and smooth threads.—66. *F. microphylla* subsp. *microphylla*, see legend of Figure 65. The scale equals 2 μm, unless indicated.



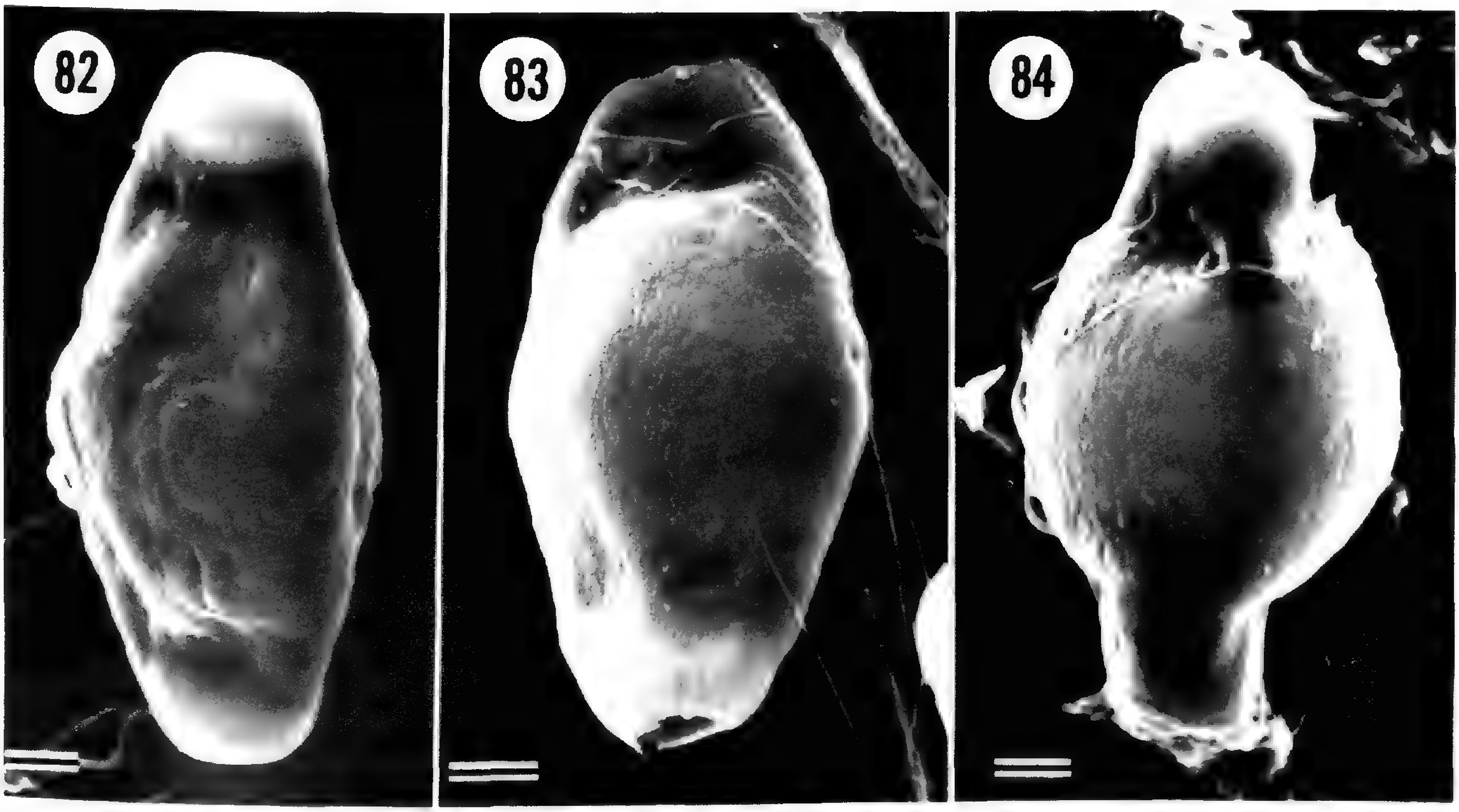
FIGURES 67–72. Scanning electron micrographs of *Fuchsia* sect. *Encliandra.* Viscin threads.—67. *F. cylindracea,* very sparsely segmented threads, with globular-elongated element sculpture.—68. *F. thymifolia* subsp. *thymifolia,* very sparsely segmented threads, with globular-elongated element sculpture.—69. *F. encliandra* subsp. *encliandra,* smooth threads.—70. *F. obconica,* segmented viscin threads, ektexine with globular element sculpture.—71. *F. ravenii,* viscin thread forked at exine surface and then inflated and smooth in area immediately adjacent; other parts of thread are segmented-ropy (upper right corner).—72. *F. cylindracea,* sparsely segmented threads with elongated element sculpture. The scale equals 1 μm.



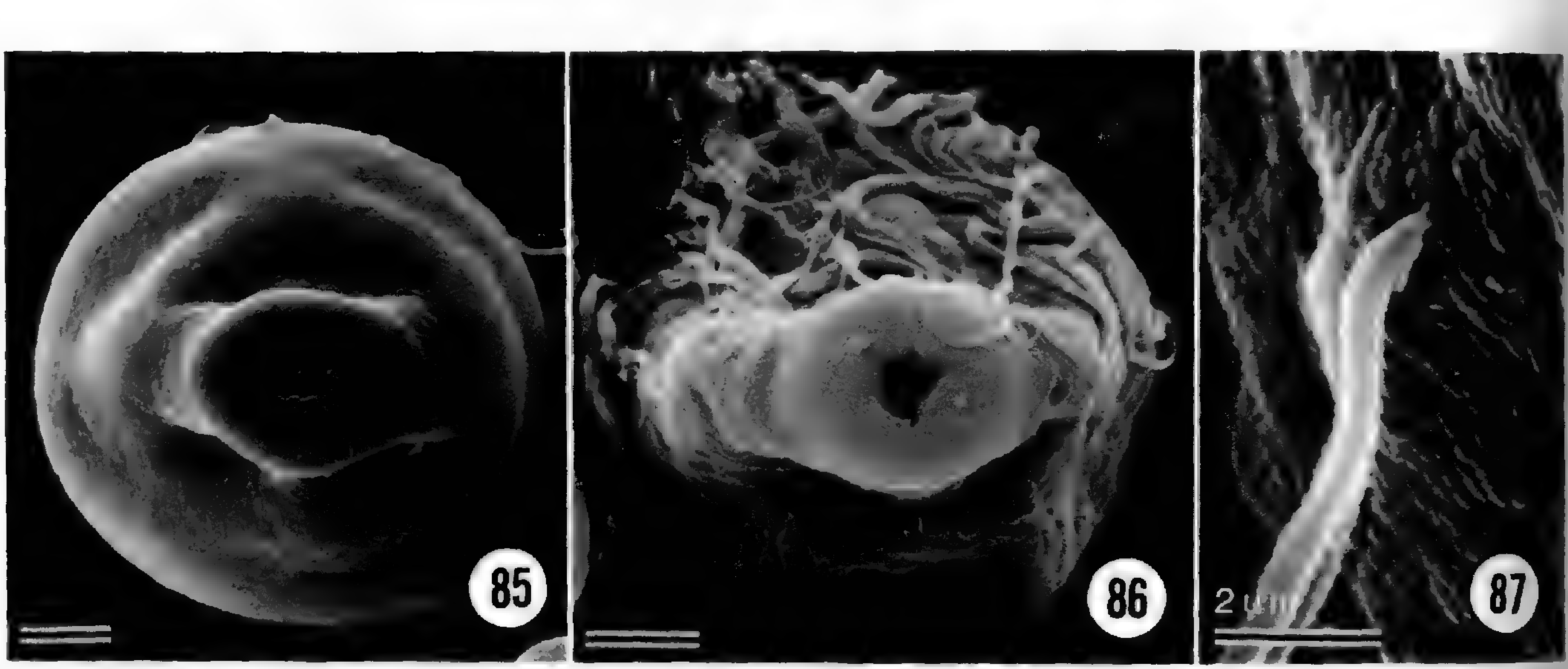
FIGURES 73–78. Scanning electron micrographs of *Fuchsia* sect. *Hemsleyella*. 73–75. *F. apetala*.—73. Oblique view.—74. Low magnification of group.—75. Ektexine with globular element sculpture and segmented viscin threads.—76. *F. inflata*, this collection (*Berry & Aronson 3012*) had grains that were predominantly 3-aperturate; a second collection (*Berry 3038*) was predominantly 2-aperturate. In Figure 76, and to some extent those in Figures 73 and 74, the partially collapsed condition indicates a thickening around the equator of the grain.—77. *F. tillettiana*, see description of Figure 75.—78. *F. apetala*, see description of Figure 75. The scale equals 2 μm, unless indicated.



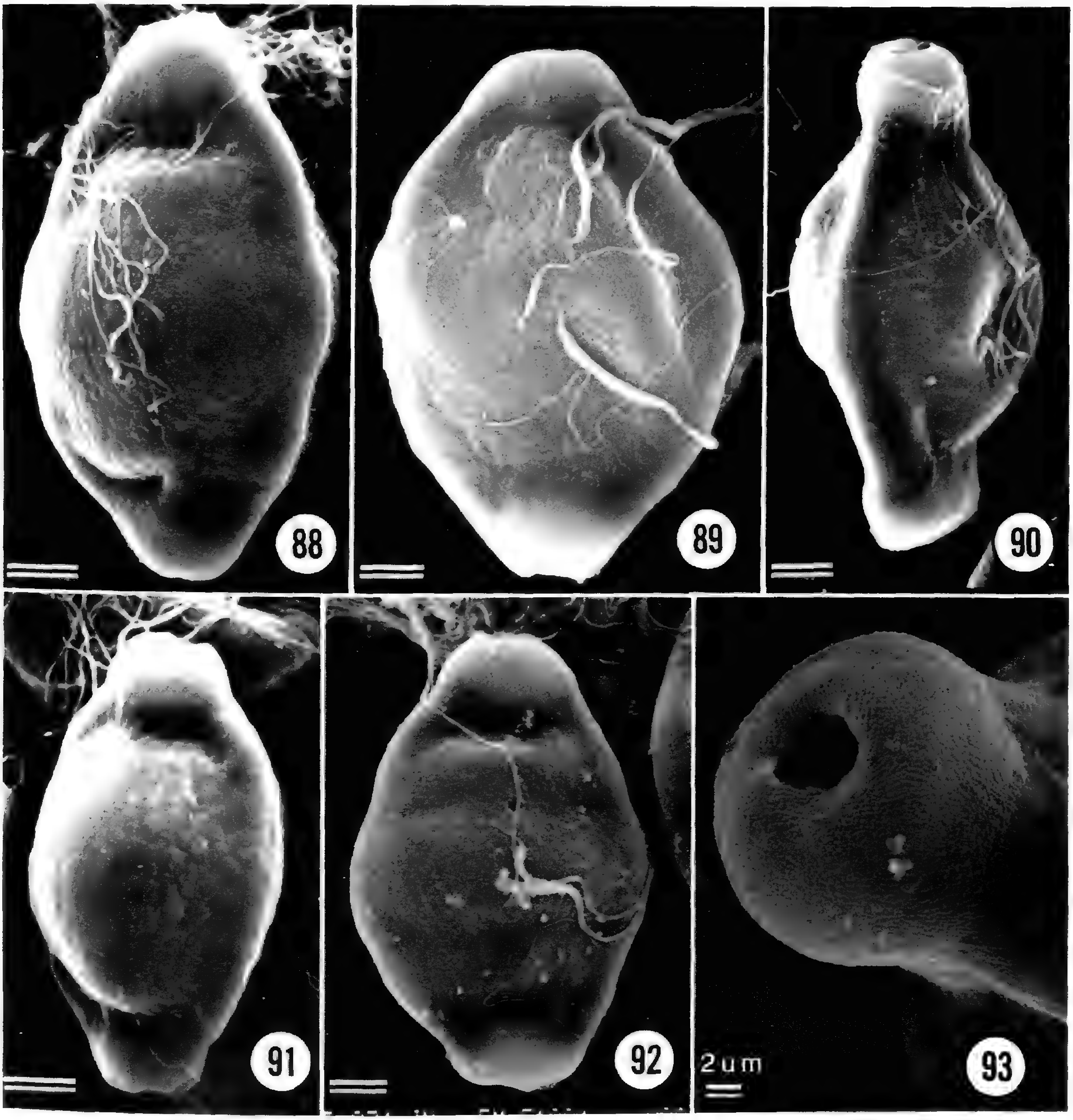
FIGURES 79–81. Scanning electron micrographs of *Fuchsia* sect. *Hemsleyella, F. tillettiana.*—79. Slightly oblique mesocolpus-centered equatorial view, equatorial thickening (see also Figs. 73, 74, 76) is very prominent.—80. Pore.—81. Ektexine with globular sculpture element and segmented threads. The scale equals 2 μm, unless indicated.



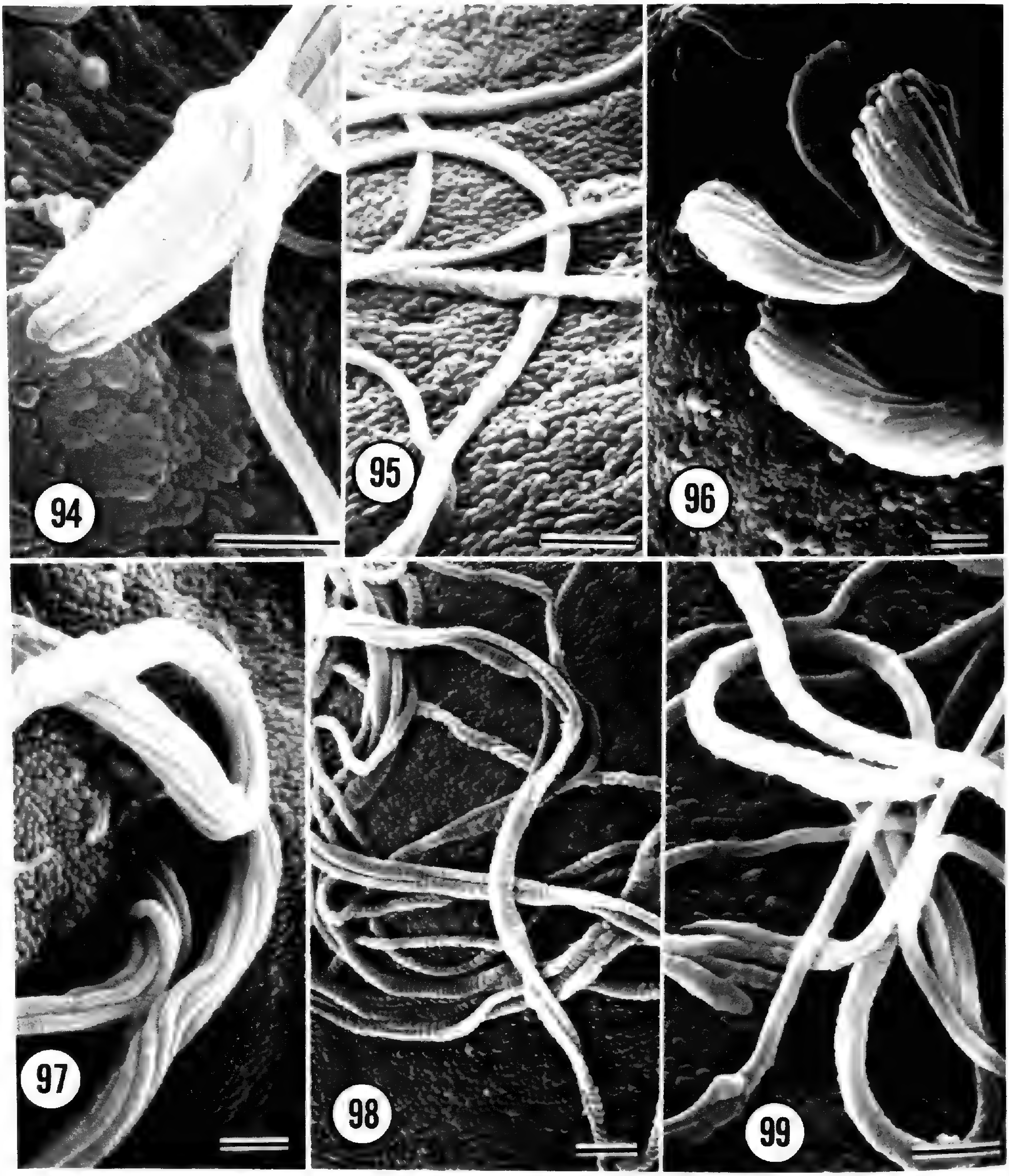
FIGURES 82–84. Scanning electron micrographs of *Fuchsia* sect. *Hemsleyella.*—82. *F. chloroloba,* oblique view.—83. *F. juntasensis,* oblique view.—84. *F. apetala,* mesocolpus-centered equatorial view. The scale equals 10 μm.



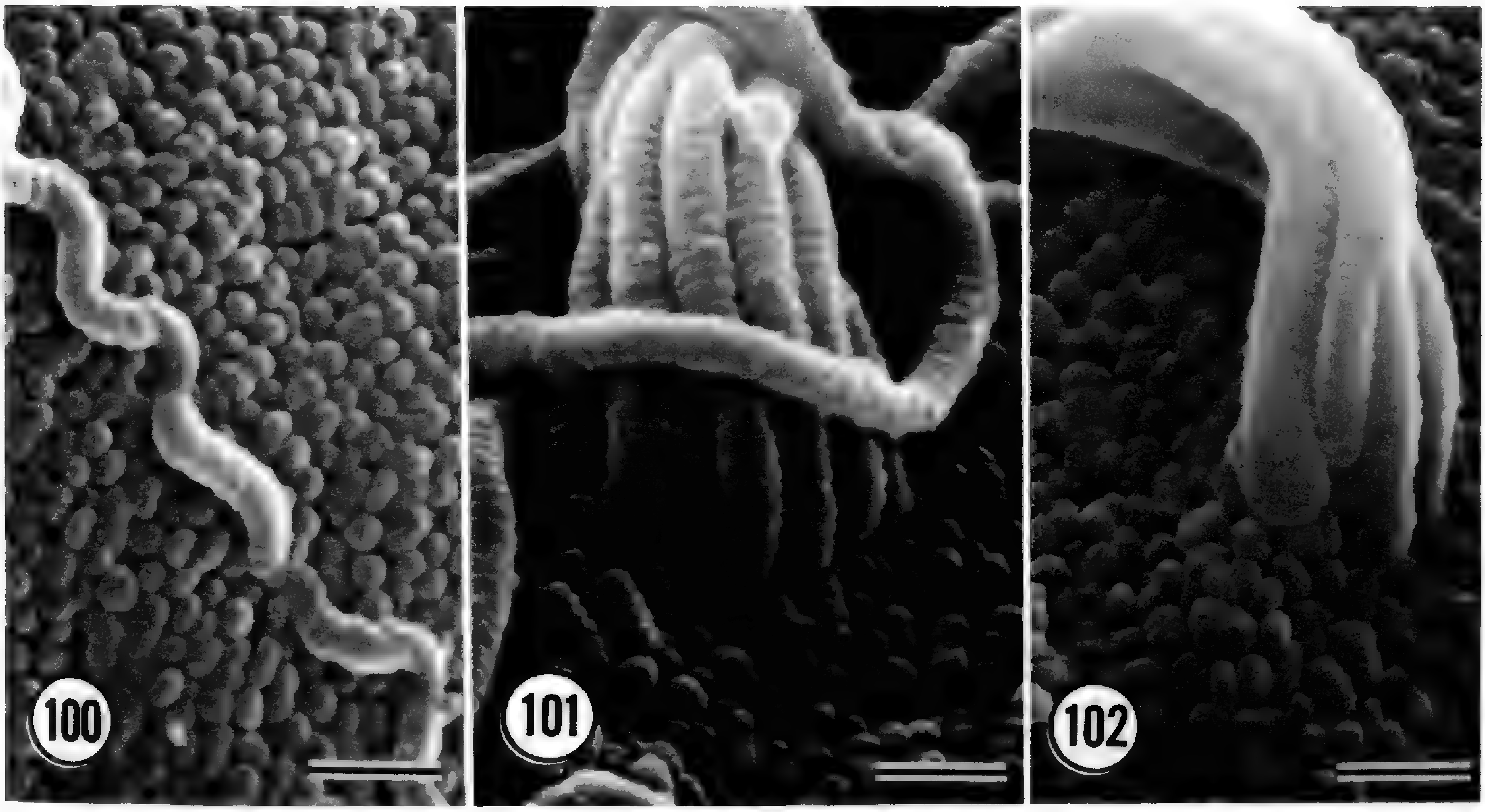
FIGURES 85–87. Scanning electron micrographs of *Fuchsia* sect. *Hemsleyella*.—85. *F. membranacea,* aperture-centered equatorial view, note elliptical shape of vestibulum. 86, 87. *F. chloroloba*.—86. Aperture-centered equatorial view.—87. Ektexine with globular element sculpture and segmented viscin threads. The scale equals 10 µm, unless indicated.



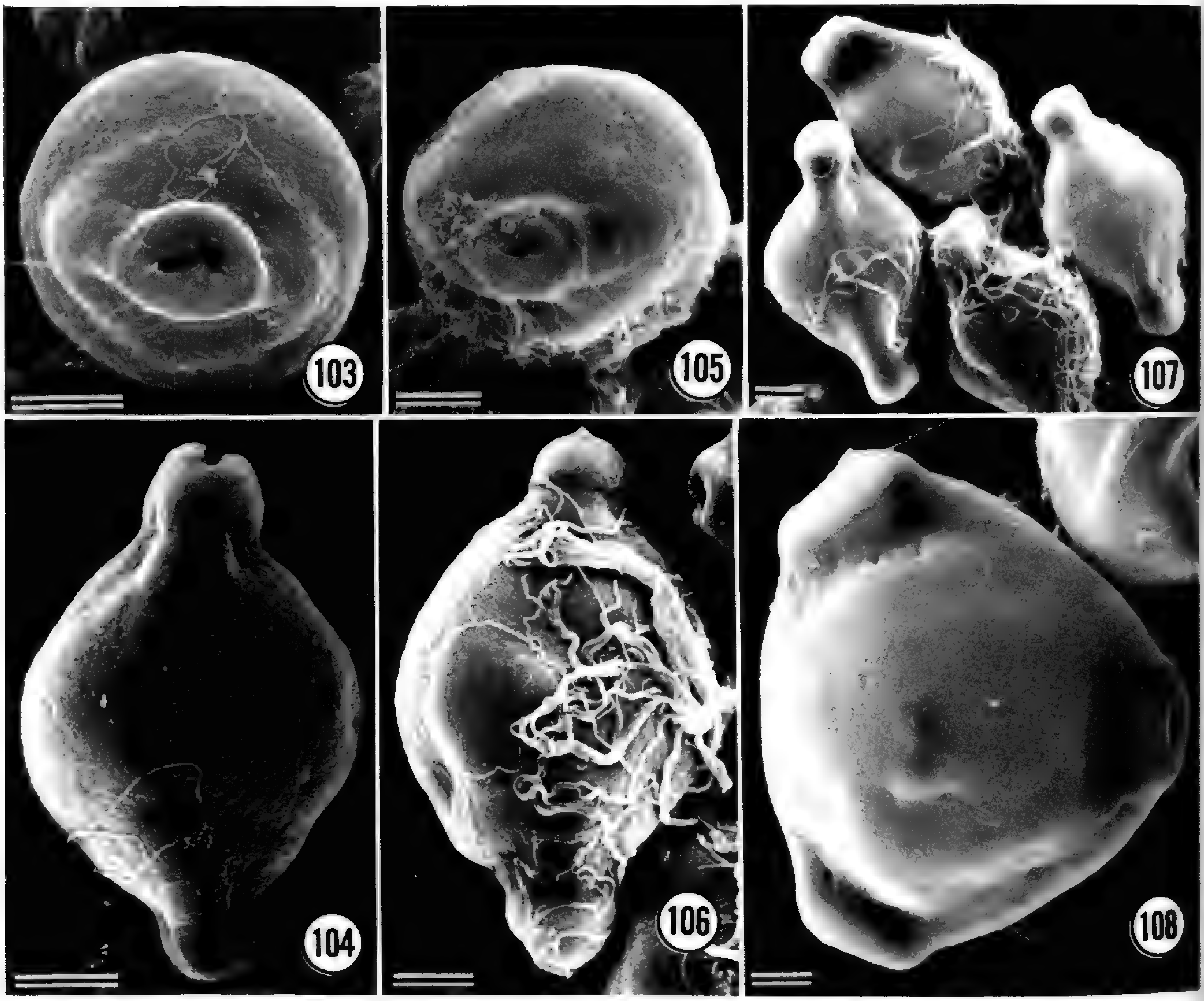
FIGURES 88–93. Scanning electron micrographs of *Fuchsia* sect. *Fuchsia.*—88. *F. triphylla,* slightly oblique proximal polar view.—89. *F. pringsheimii,* proximal polar view.—90. *F. gehrigeri,* oblique view.—91. *F. ayavacensis,* oblique distal view. 92, 93. *F. macrostigma.*—92. Proximal polar view.—93. Aperture, oblique view. The scale equals 10 μm, unless indicated.



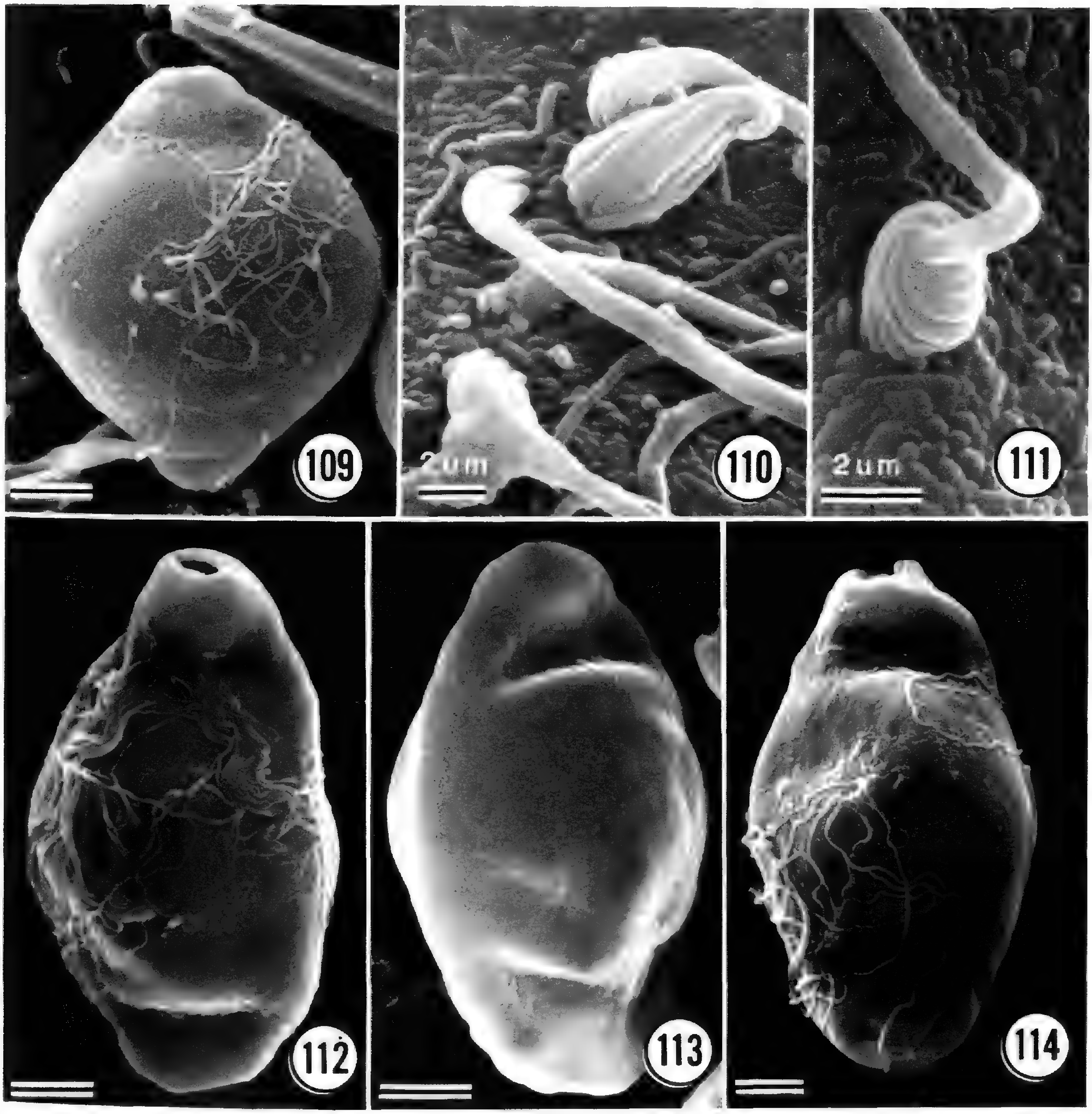
FIGURES 94–99. Scanning electron micrographs of *Fuchsia* sect. *Fuchsia*. Globular element sculpture with segmented viscin threads.—94. *F. triphylla*.—95. *F. hirtella*.—96. *F. gehrigeri*.—97. *F. cuatrecasasii*.—98. *F. pallescens*.—99. *F. petiolaris*. The scale equals 2 μm.



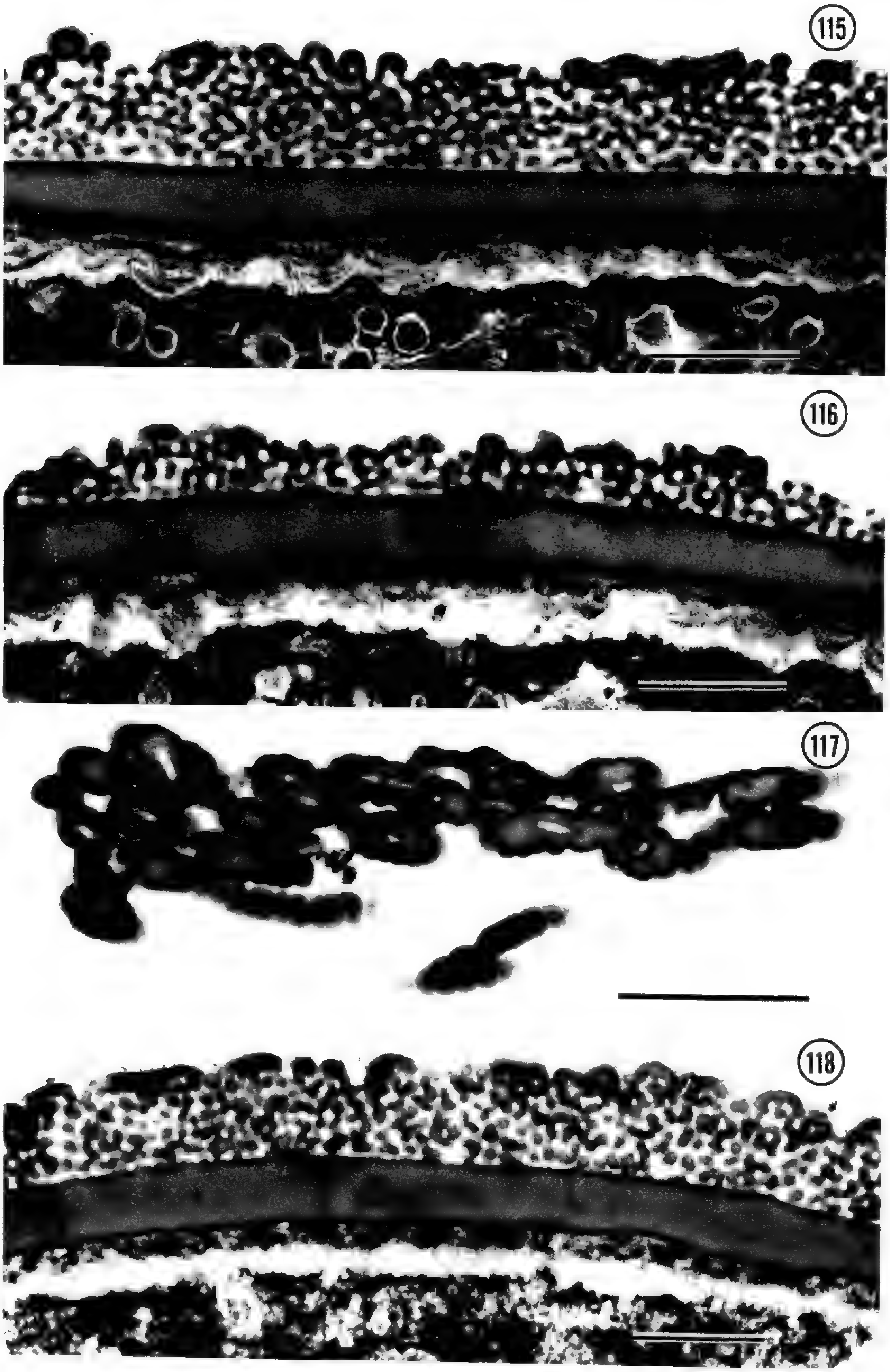
FIGURES 100–102. Scanning electron micrographs of *Fuchsia* sect. *Fuchsia*. Globular element sculpture with segmented viscin threads.—100. *F. tincta*.—101. *F. boliviana*.—102. *F. putumayensis*. The scale equals 1 μm.



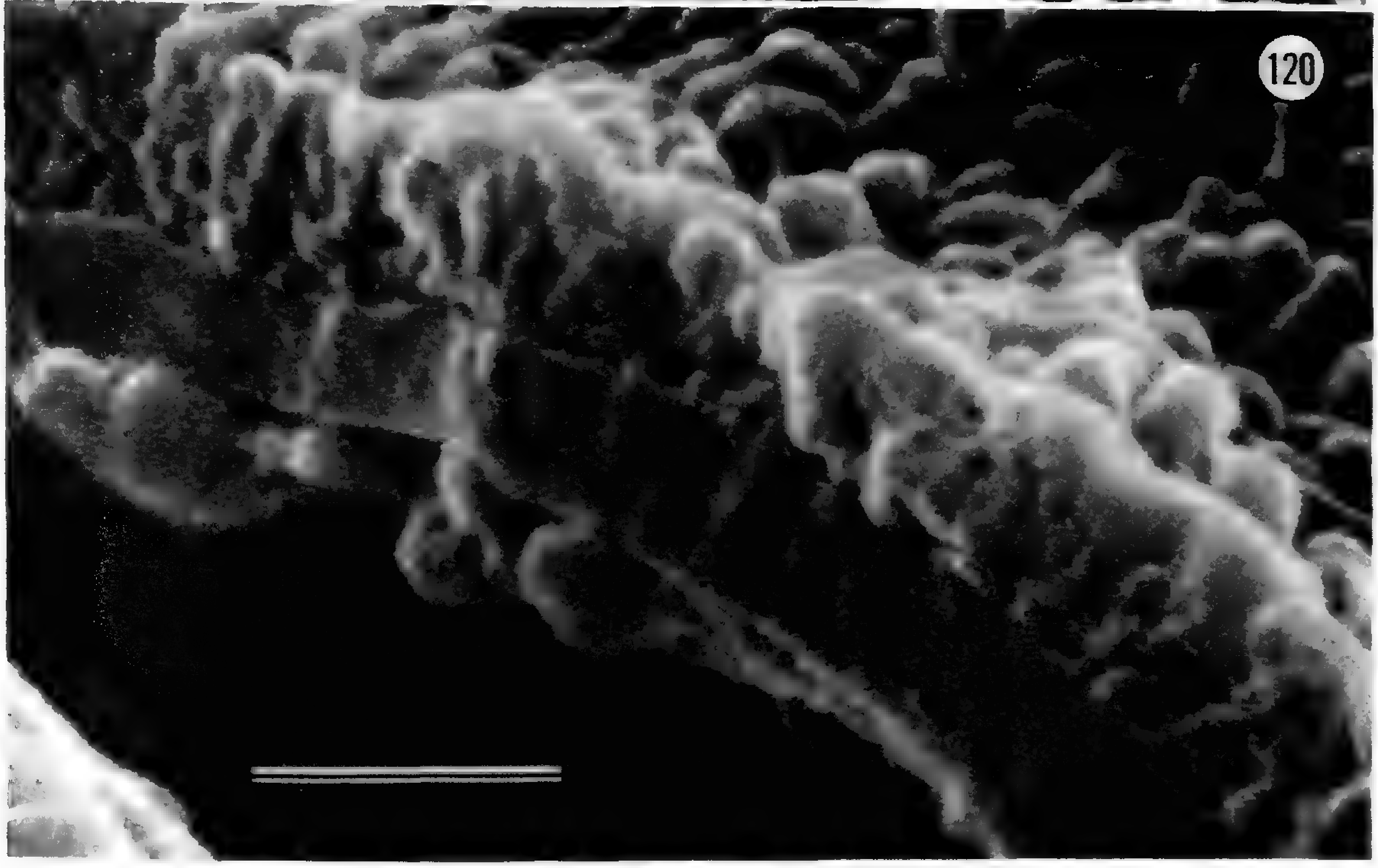
FIGURES 103–108. Scanning electron micrographs of *Fuchsia* sect. *Fuchsia*. 103–104. *F. macrophylla*.—103. Aperture-centered equatorial view, colpus slightly distorted.—104. Mesocolpus-centered equatorial view. 105, 106. *F. tincta*.—105. Aperture-centered equatorial view.—106. Mesocolpus-centered equatorial view.—107. *F. scabriuscula*, four grains held together by threads.—108. *F. corollata*, a 3-aperturate grain. The scale equals 10 μm.



FIGURES 109–114. Scanning electron micrographs of *Fuchsia* sect. *Fuchsia*. 109–111. *F. verrucosa*.—109. Proximal polar view.—110. Smooth viscin threads with irregular sculpture.—111. See legend of Figure 110.—112. *F. hartwegii*, oblique polar view.—113. *F. mathewsii*, distal polar view.—114. *F. petiolaris*, proximal polar view. Unless indicated, the scale equals 10 μm.



FIGURES 115–118. Transmission electron micrographs of *Fuchsia* pollen, sect. *Ellobium* (Figs. 115–117) and sect. *Encliandra* (Fig. 118). All pollen rehydrated. 115–117. *F. splendens.*—115. Section from approximately the middle of the distal polar face (at right) to the junction of the central body and apertural protrusion (tapered part of the endexine at left).—116. Same pollen grain as in Figure 115 but section from directly opposite polar face (i.e., proximal). Note the comparatively thinner ektexine.—117. Section through numerous viscin threads.—118. *F. ravenii*, section through middle of central body. In contrast to Figures 115 and 116 the granular basal component of the endexine forms a fairly uniform zone or layer, being clearly demarcated from the above massive endexine and below intine. The scale equals 1 μm.

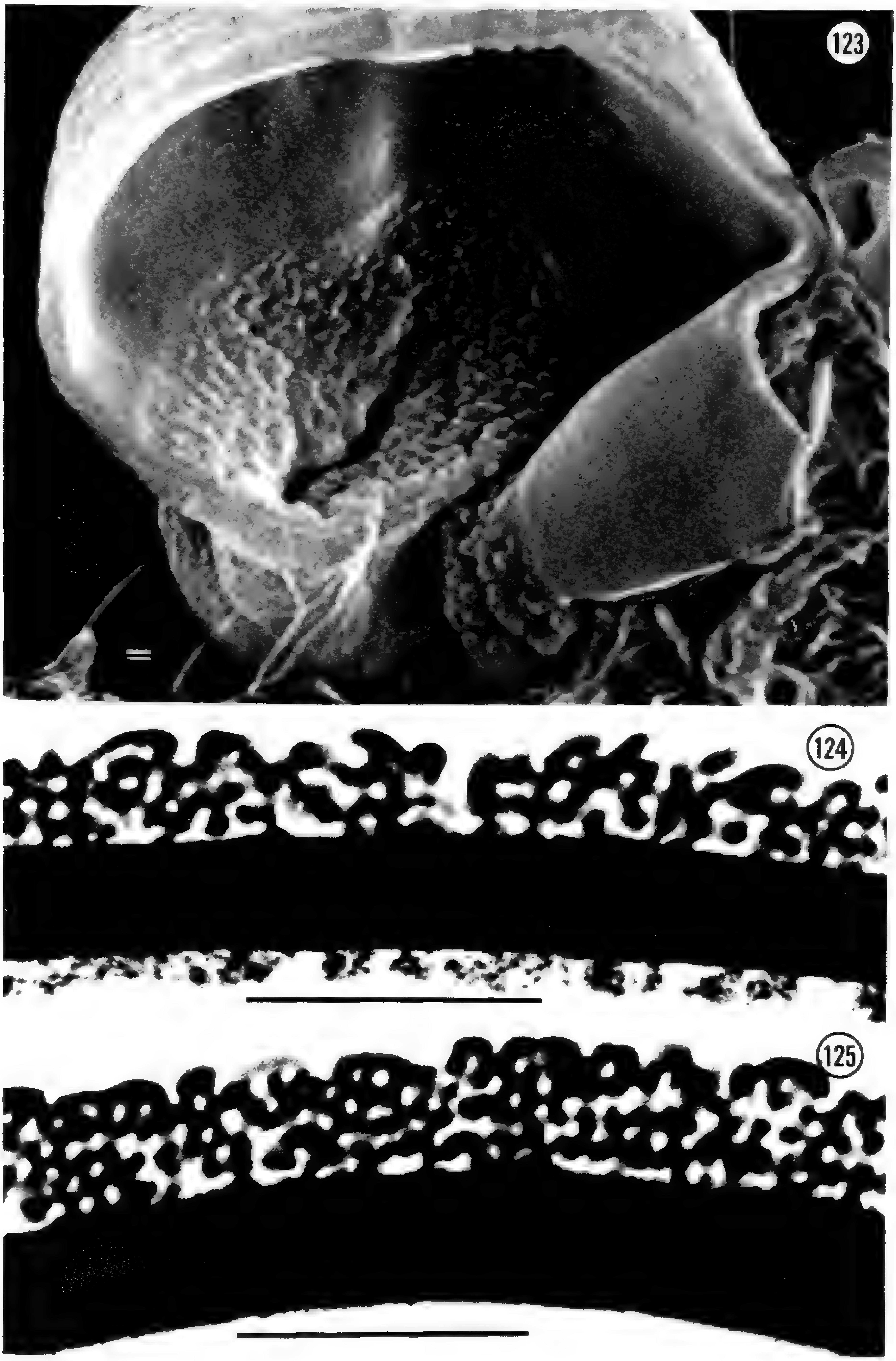


FIGURES 119, 120. Transmission (Fig. 119) and scanning (Fig. 120) electron micrographs of *Fuchsia* pollen, sect. *Encliandra*. Rehydrated (Fig. 119) and acetolyzed (Fig. 120) pollen.—119. *F. ravenii*, section through portion of central body and apertural protrusion.—120. *F. microphylla* subsp. *aprica*, view of fracture at the approximate junction of apertural protrusion with the central body. Note the lack of traditional structure to the ektexine, the thick and massive-homogeneous-uniform part of the endexine, and the highly irregular lower granular endexine which is roughly equivalent to the large endexine granules in Figures 119 and 122. The scale equals 1 μm.

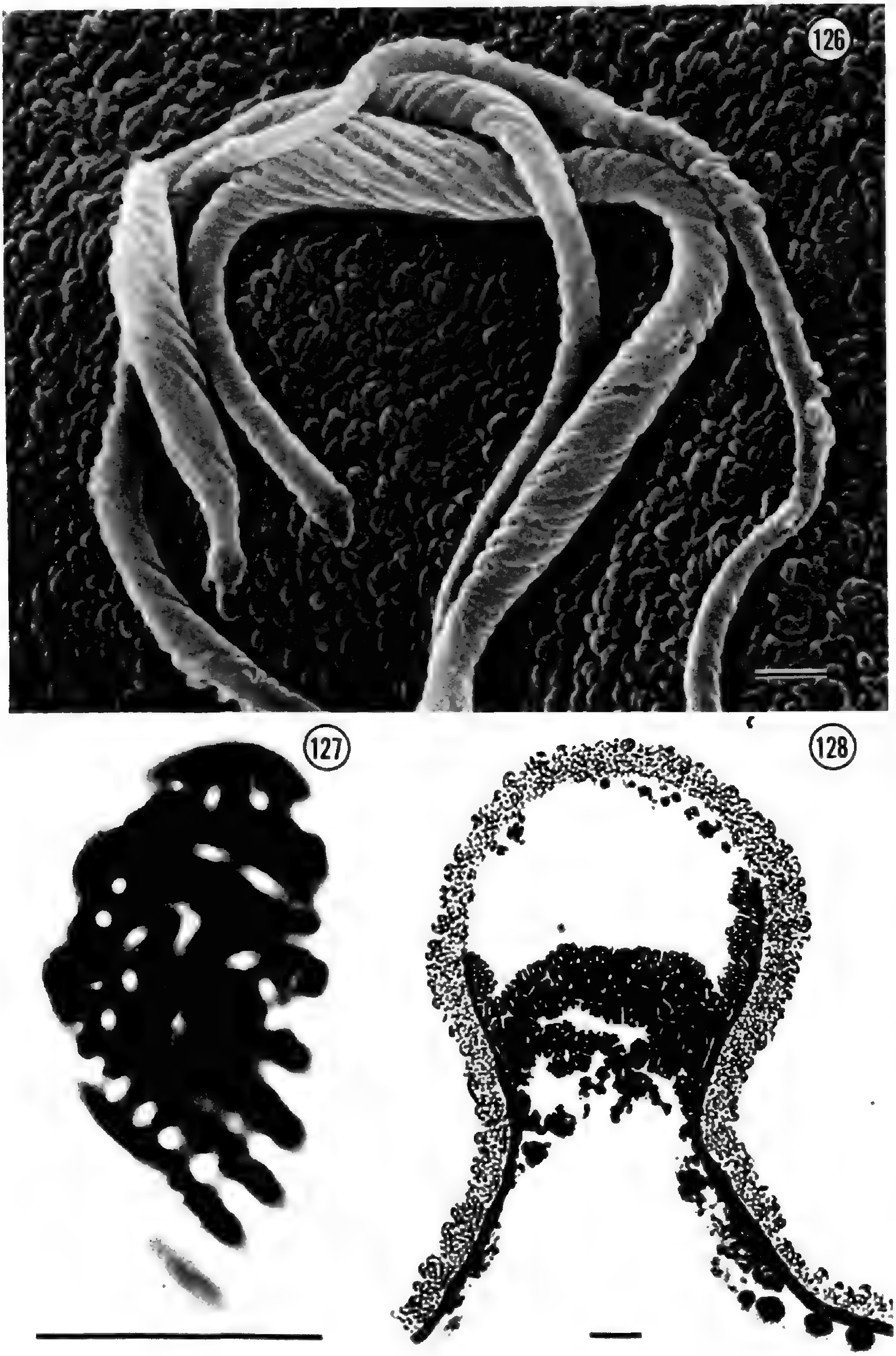
(121)

(122)

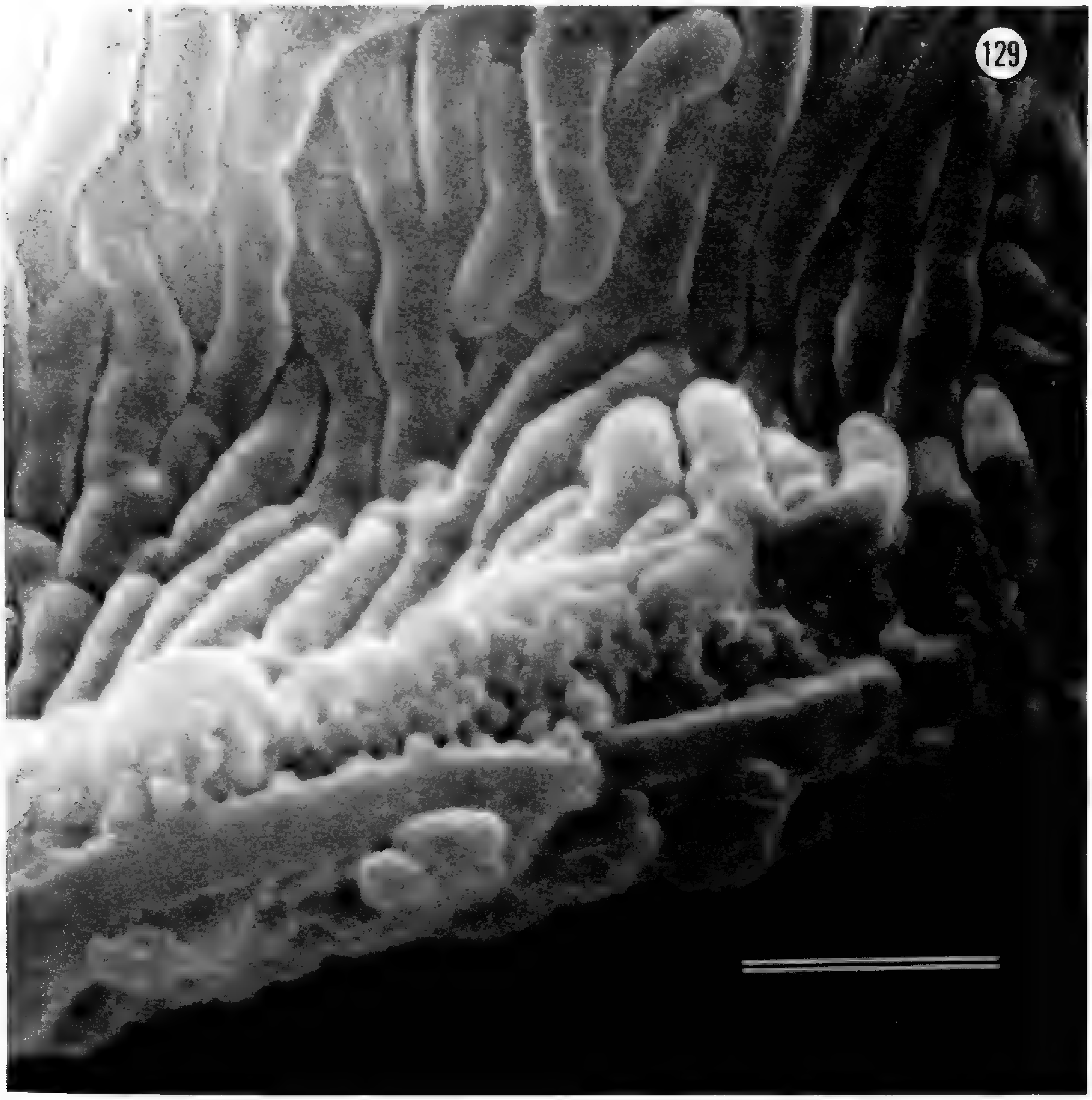
FIGURES 121, 122. Transmission electron micrographs of *Fuchsia* pollen, sect. *Encliandra, F. microphylla* subsp. *aprica*. Pollen acetolyzed.—121. Section slightly off middle of central body and approaching an apertural protrusion. The acetolyzed exines of *Fuchsia* (Figs. 124, 125, 133–135, 137, 158–162, 174, 179, 194) always appear extremely opaque with both ektexine and endexine approximately of equal electron density. In contrast, the rehydrated exines (Figs. 115, 116, 118, 119, 151–154, 164–173, 175, 178, 191) with the possible exception of *F. verrucosa* (Figs. 155, 156) are considerably less dense.—122. Section of apertural protrusion, including apertural channel. Comparison of apertural protrusions in the acetolyzed (Figs. 128, 132, 136, 163, 174, 176, 177, 193) and unacetolyzed (Figs. 119, 155, 171, 191) conditions indicates direct morphological correspondences in all structural features, although the highly channeled or honeycombed endexine is more clearly distinguished after acetolysis. The scale equals 1 μm.



FIGURES 123–125. Scanning (Fig. 123) and transmission (Figs. 124, 125) electron micrographs of *Fuchsia* pollen, sect. *Encliandra*. Pollen acetolyzed.—123. *F. microphylla* subsp. *aprica*, the internal view of this fractured pollen grain shows coarse globular elements of the apertural protrusion (see Figs. 119, 120) outlined by the relatively smooth endexine of the central body. 124, 125. *F. microphylla* subsp. *hidalgensis*.—124. Section near middle of the central body.—125. Same pollen grain as in Figure 124 but section from opposite face (either polar or lateral). Note absence of granular endexine component as well as slightly thicker ektexine. The scale equals 1 μm.

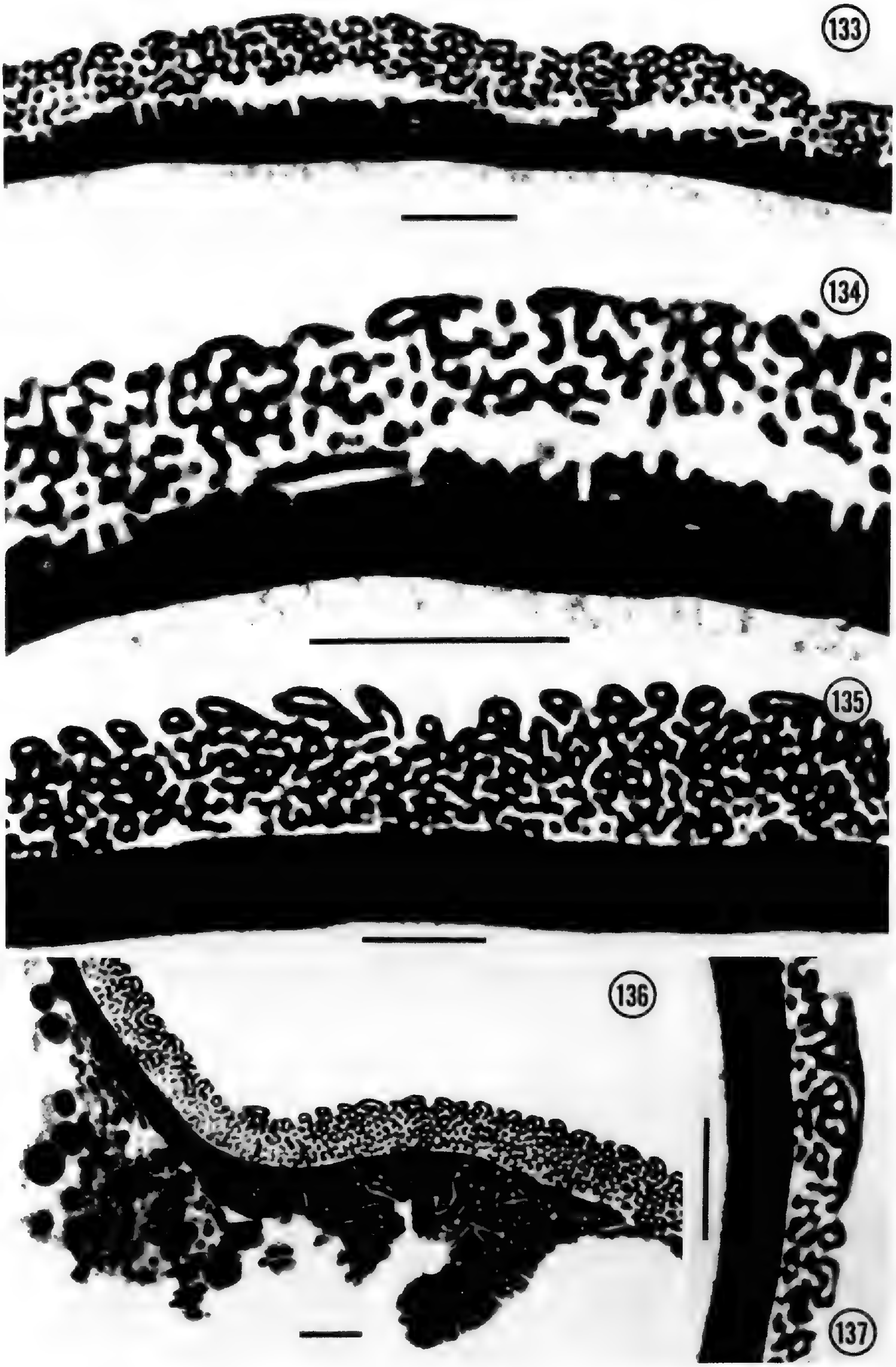


FIGURES 126–128. Scanning (Fig. 126) and transmission (Figs. 127, 128) electron micrographs of *Fuchsia* pollen, sect. *Encliandra, F. microphylla* subsp. *hidalgensis.* Pollen acetolyzed.—126. Scanning electron micrographs of groups of twisted, segmented-ropy viscin threads similar to those observed for *F. thymifolia* subsp. *thymifolia* (see Figs. 56, 57 and Pl. 5, Fig. 1 of Skvarla et al., 1978) and *F. thymifolia* subsp. *minimiflora* (Fig. 147) and which contrast with the smooth (Fig. 131) or beaded threads more typical of *Fuchsia.*—127. Section through a group of threads.—128. Section through apertural protrusion but not including pore or aperture channel. The channeled endexine clearly underlies the vestibulum or aperture chamber. The scale equals 1 μm.



FIGURES 129, 130. Scanning (Fig. 129) and transmission (Fig. 130) electron micrographs of *Fuchsia* pollen, sect. *Encliandra, F. microphylla* subsp. *hemsleyana.* Pollen acetolyzed.—129. Portion of a broken pollen grain showing the spongy undifferentiated ektexine with a surface sculpture of elongate elements. The massive endexine has a highly irregular lower margin.—130. Section through proximal surface including an oblique view of a smooth viscin thread connected with the ektexine surface. The scale equals 1 μm.

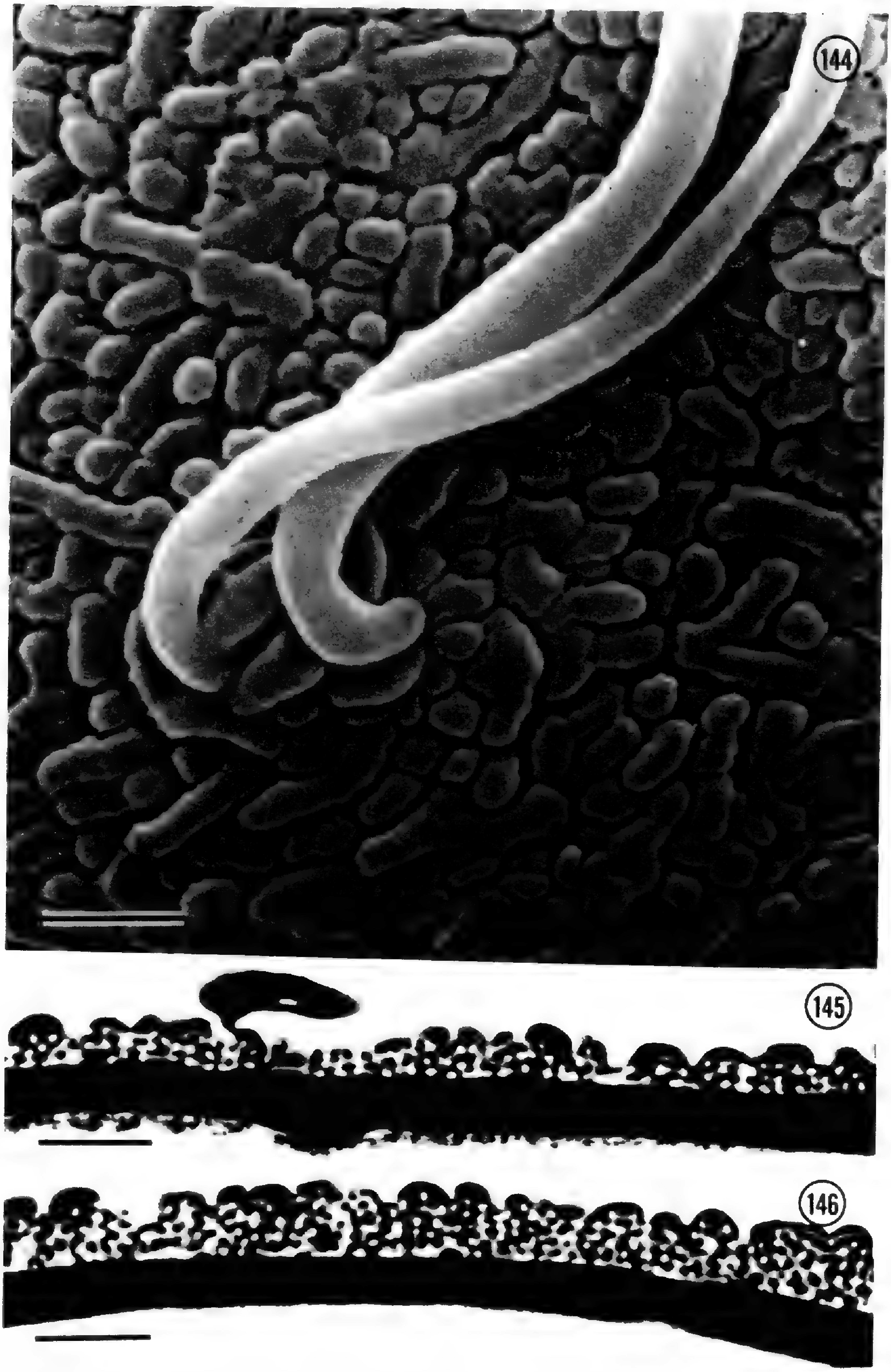
FIGURES 131, 132. Scanning (Fig. 131) and transmission (Fig. 132) electron micrographs of *Fuchsia* pollen, sect. *Encliandra, F. microphylla* subsp. *quercetorum*. Pollen acetolyzed.—131. Scanning electron micrograph of a great mass of smooth viscin threads.—132. Somewhat oblique section through apertural protrusion. The scale equals 1 μm.



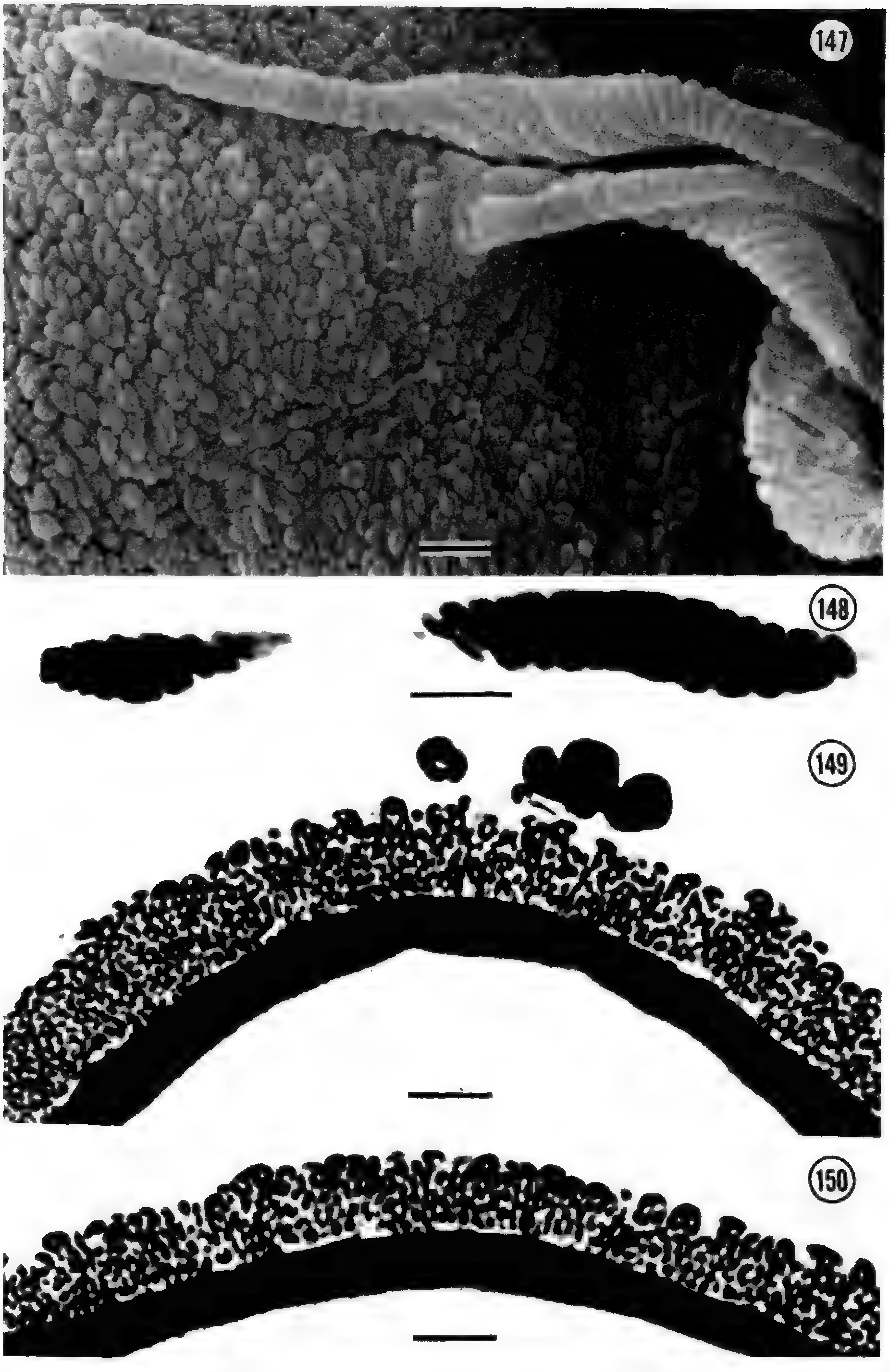
FIGURES 133–137. Transmission electron micrographs of *Fuchsia* pollen, sect. *Encliandra*. Pollen acetolyzed. 133, 134. *F. microphylla* subsp. *quercetorum*.—133. Section through middle of central body. Although the ektexine appears to be composed of a spongy-paracrystalline-beaded tectum separated from an irregular foot layer by occasional columellae, it seems more likely that the entire ektexine has been fractured basally. This appears to be common for this taxon (see also Pl. 1, Skvarla et al., 1976). The lower granular portion of the endexine is extensive, but in this print the fractured ektexine was emphasized at the expense of the granular endexine.—134. The same comments apply as discussed in Figure 135. 135–137. *F. encliandra* subsp. *tetradactyla*.—135. Section through middle of central body and somewhat oblique to the surface.—136. Section through portion of the central body and apertural protrusion.—137. Section near middle of central body. The structure of the ektexine (at the top) contrasts with the section in Figure 135. The scale equals 1 μm.

FIGURES 138–141. Transmission electron micrographs of *Fuchsia* pollen sect. *Encliandra, F. encliandra* subsp. *encliandra*. Pollen acetolyzed.—138. Section through proximal surface.—139. Longitudinal section through parts of two smooth viscin threads.—140. Section through a cluster of viscin threads with various orientations.—141. Somewhat oblique section through proximal surface near region of aperture protrusion. The scale equals 1 μm.

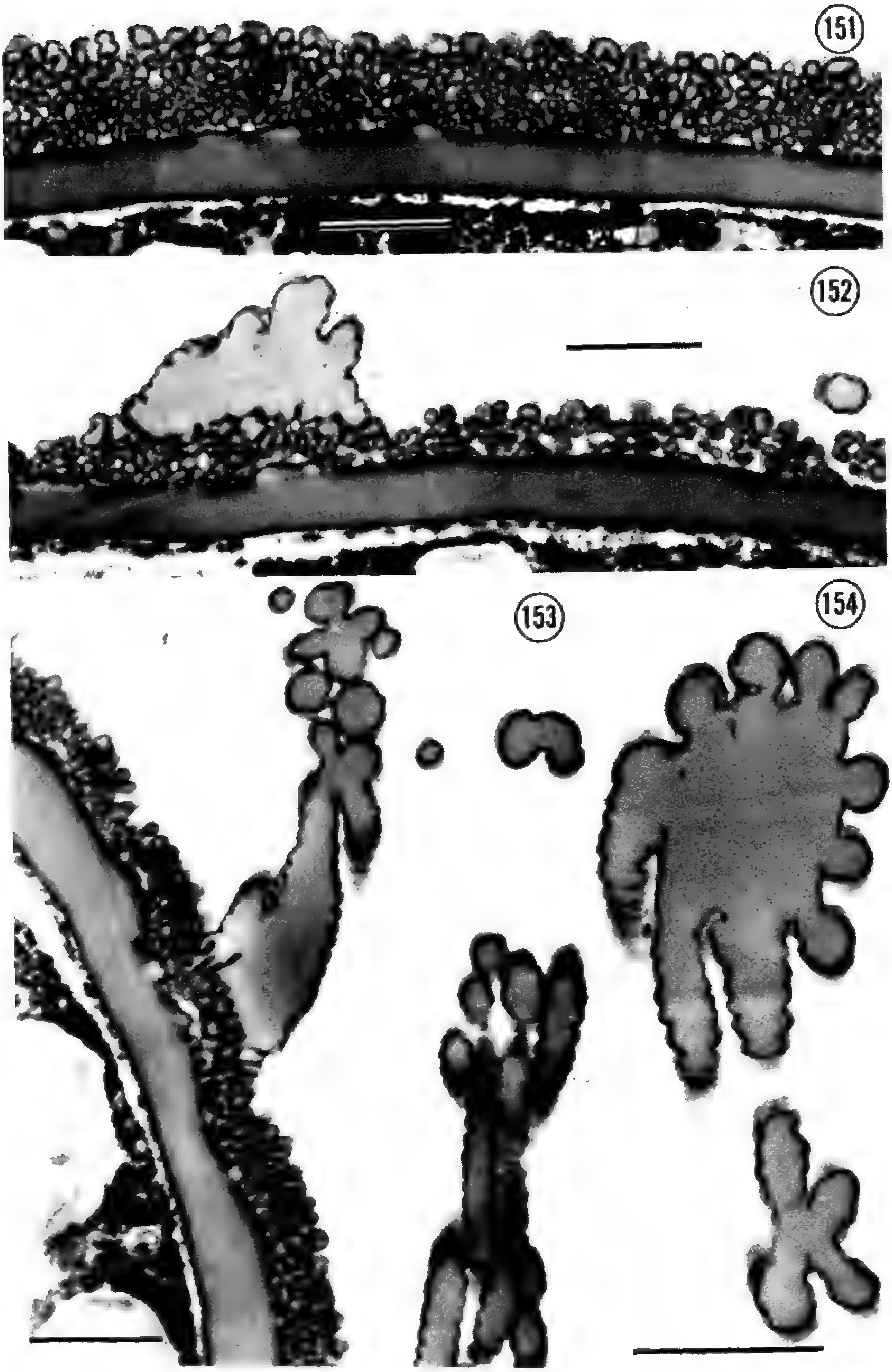
FIGURES 142, 143. Transmission electron micrographs of *Fuchsia* pollen, sect. *Encliandra, F. obconica.* Pollen acetolyzed.—142. View at proximal surface with prominently segmented viscin threads attached to exine surface.—143. Section through apertural protrusion and vestibulum but not including pore or aperture channel. The scale equals 1 μm.



FIGURES 144–146. Scanning (Fig. 144) and transmission (Figs. 145, 146) electron micrographs of *Fuchsia* pollen, sect. *Encliandra, F. cylindracea.* Pollen acetolyzed.—144. Smooth viscin threads are attached to the exine surface consisting mostly of slightly elongate sculpture elements.—145. Oblique view of proximal surface toward aperture protrusion with portion of a smooth viscin thread.—146. Same pollen grain section as Figure 145 but of directly opposite distal surface. The scale equals 1 μm.

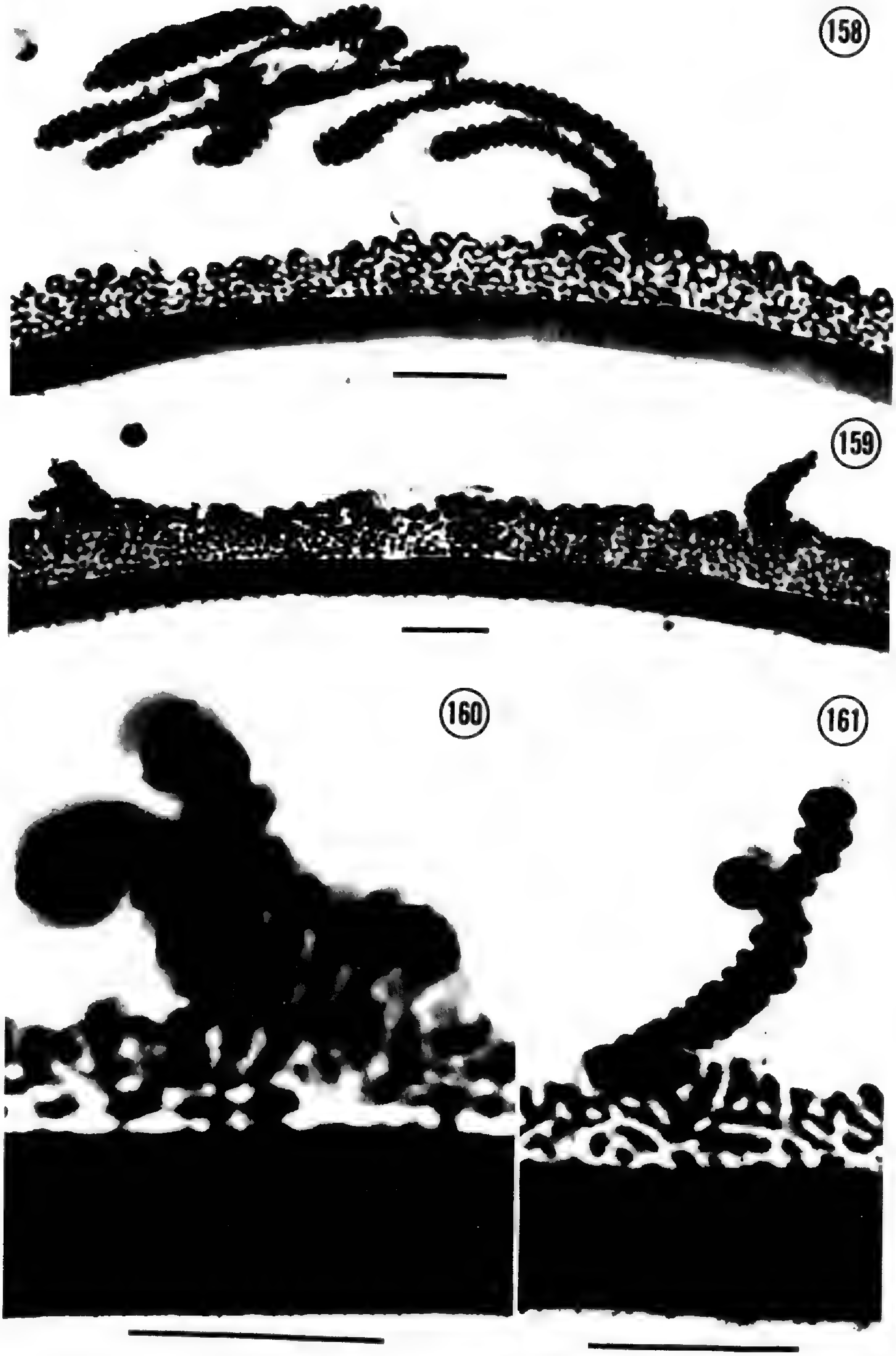


FIGURES 147–150. Scanning (Fig. 147) and transmission (Figs. 148–150) of *Fuchsia* pollen, sect. *Encliandra*, *F. thymifolia* subsp. *minimiflora*. Pollen acetolyzed.—147. The segmented-ropy viscin threads and a coarsely globular surface are similar to *F. thymifolia* subsp. *thymifolia* (Figs. 56, 57).—148. Longitudinal section through segmented thread.—149. Center of the proximal polar face.—150. Same pollen section as Figure 149 but directly opposite distal polar face. The scale equals 1 μm.



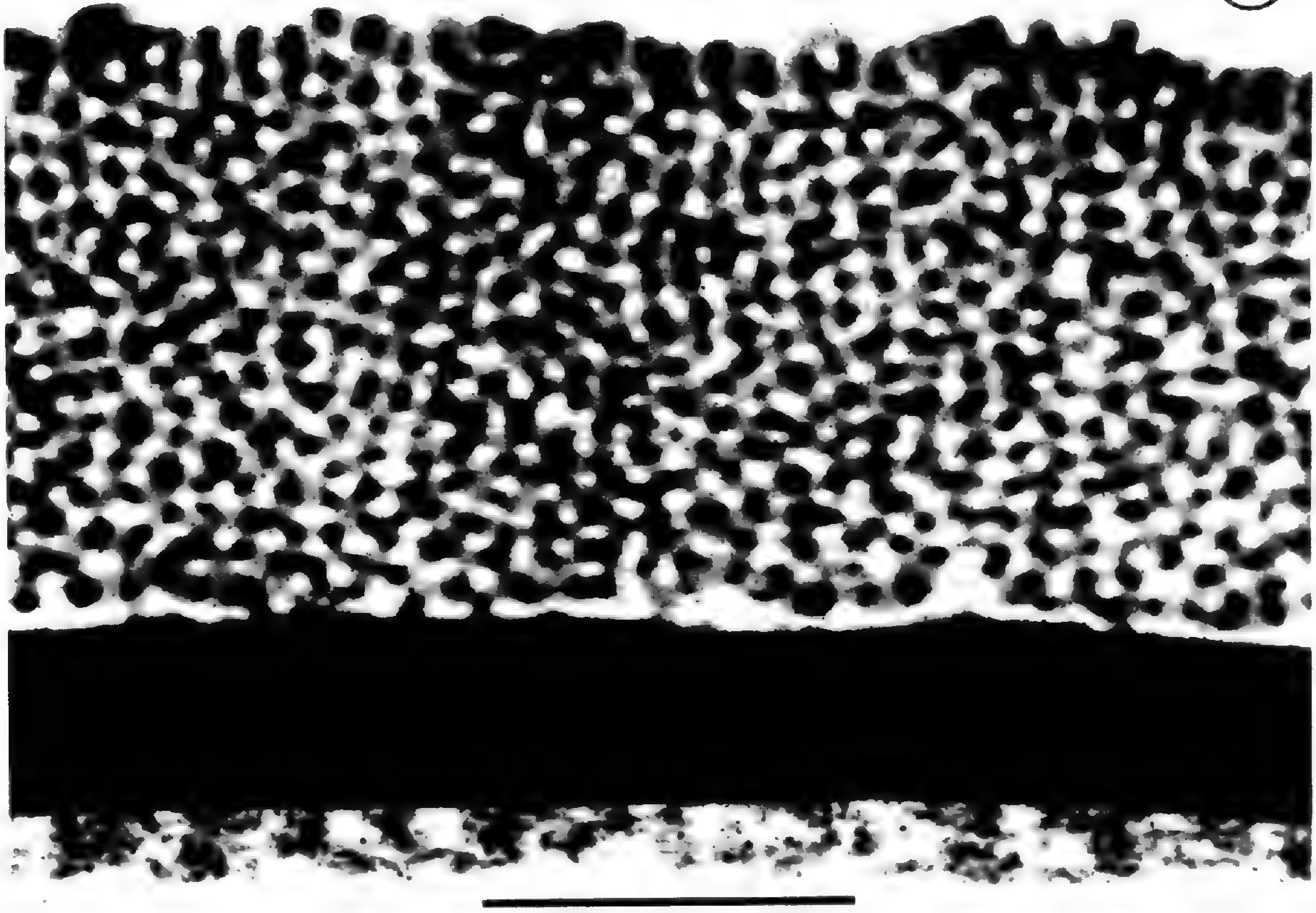
FIGURES 151–154. Transmission electron micrographs of *Fuchsia* pollen, sect. *Fuchsia*, *F. boliviana*. All pollen rehydrated.—151. Section through middle of distal polar face.—152. Same pollen grain as in Figure 151 but section from center of proximal polar face. In contrast to Figure 151, the ektexine is somewhat thinner.—153. Section at proximal polar face primarily to show relationship of viscin threads to the ektexine, as well as their appearance in different sectional views.—154. Section through a group(s) of viscin threads. The major distinction between acetolyzed and unacetolyzed viscin threads, apart from electron density, is that the latter always appear to be enclosed by a membrane (Figs. 152–154, 157, 164–167, 173, 178, 192) while the former are not (Figs. 117, 127, 158–161, 163, 179). The scale equals 1 μm.

FIGURES 155–157. Transmission electron micrographs of *Fuchsia* pollen, sect. *Fuchsia*, *F. verrucosa*. All pollen rehydrated.—155. Oblique section to include just one apertural protrusion.—156. Section through parts of two pollen grains bound together by pollenkitt or some other extra-exinous substance. Note the thicker concentration of granular endexine in the lower exine.—157. Longitudinal section through a smooth viscin thread. The scale equals 1 μm.



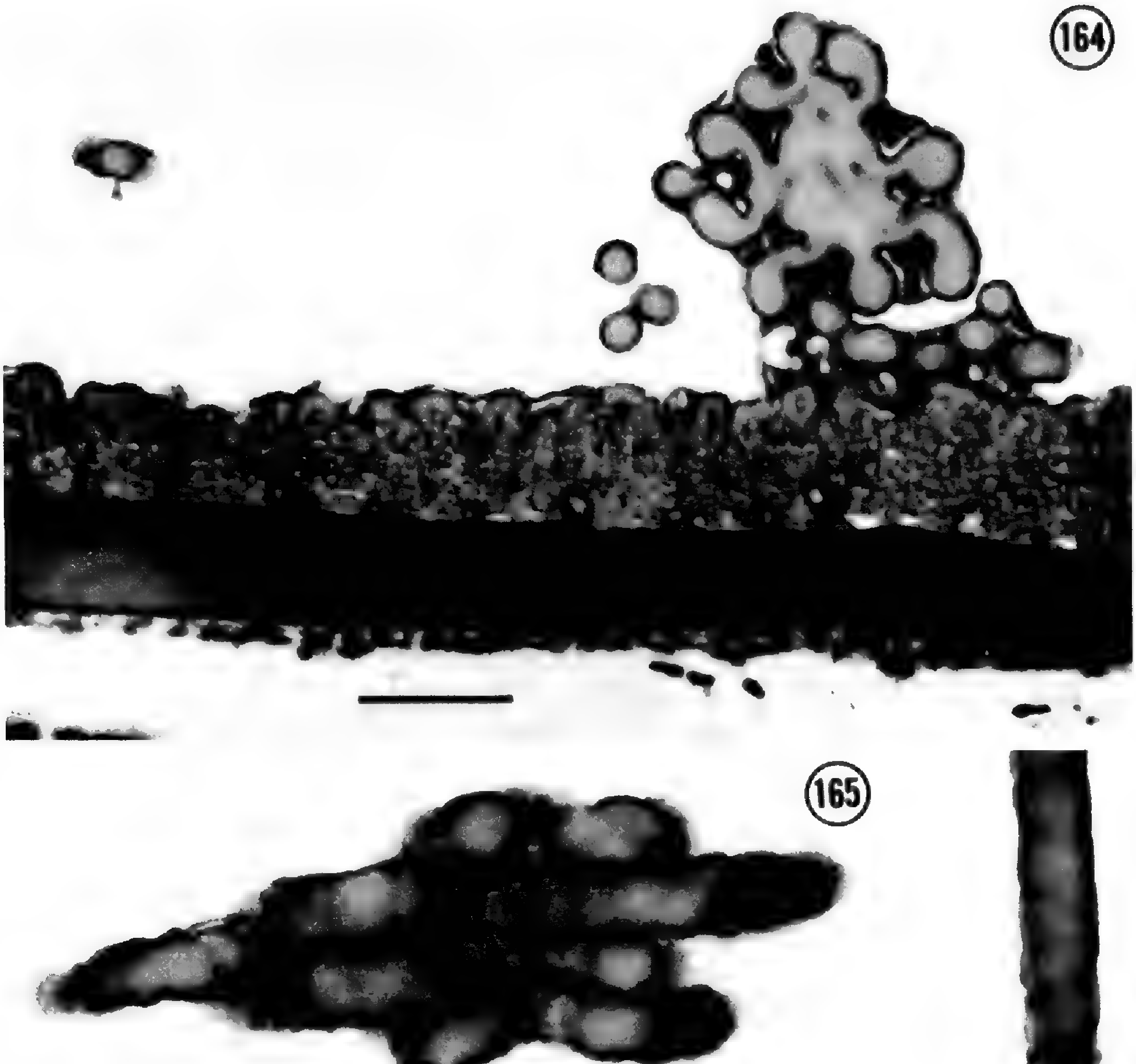
FIGURES 158–161. Transmission electron micrographs of *Fuchsia* pollen, sect. *Fuchsia* (Figs. 158, 159) and sect. *Hemsleyella* (Figs. 160, 161). Pollen acetolyzed. 158, 159. *F. hartwegii.*—158. Section along proximal face illustrating relationship between viscin threads and ektexine surface.—159. This section along the proximal surface is somewhat unique in that it includes at least two attachment areas of viscin threads with the ektexine. A thin basal granular endexine component is common. 160, 161. *F. garleppiana.*—160. In this section the ektexine is clearly seen to be an integral part of the viscin threads.—161. Similar to Figure 160. The scale equals 1 μm.

(162)

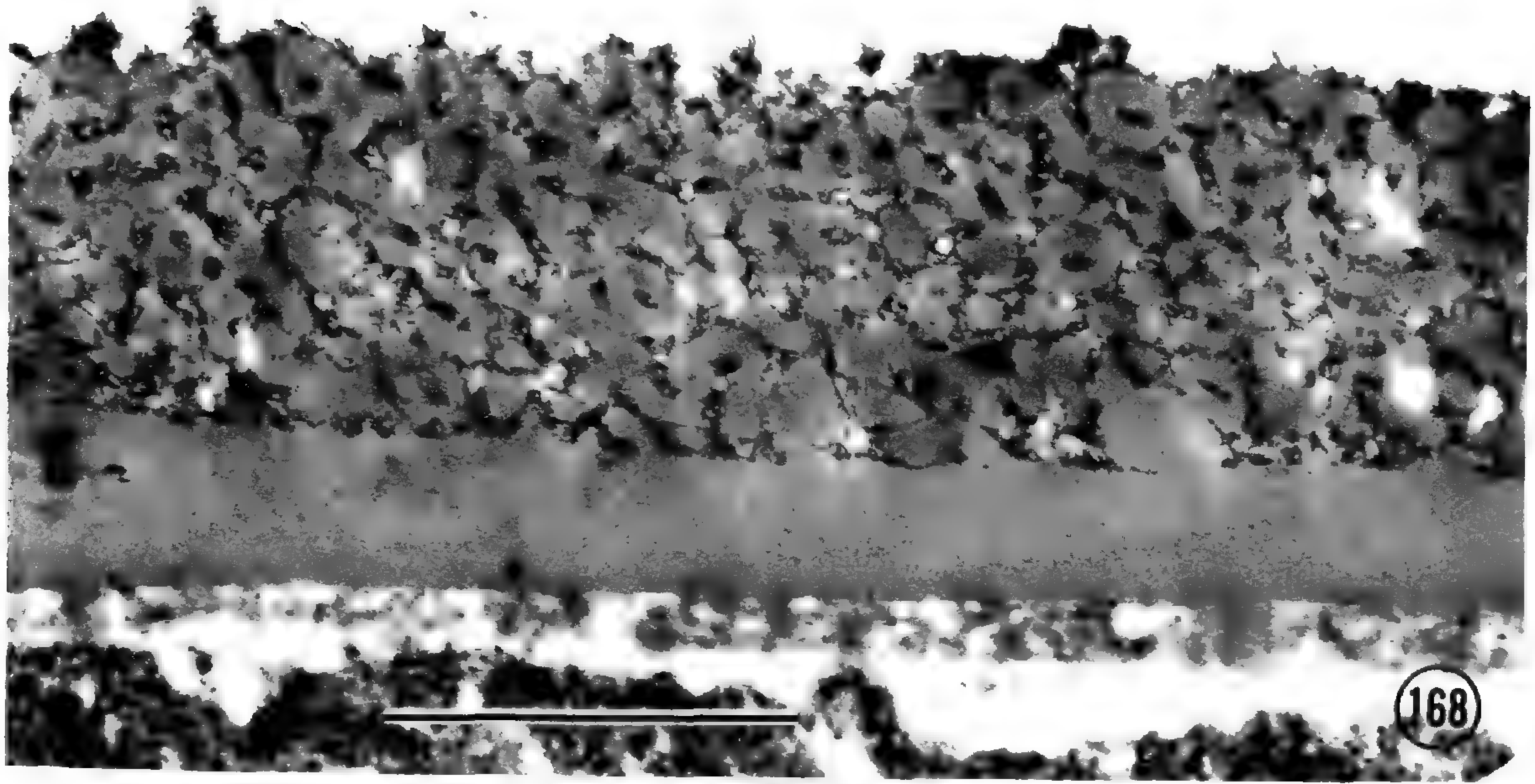


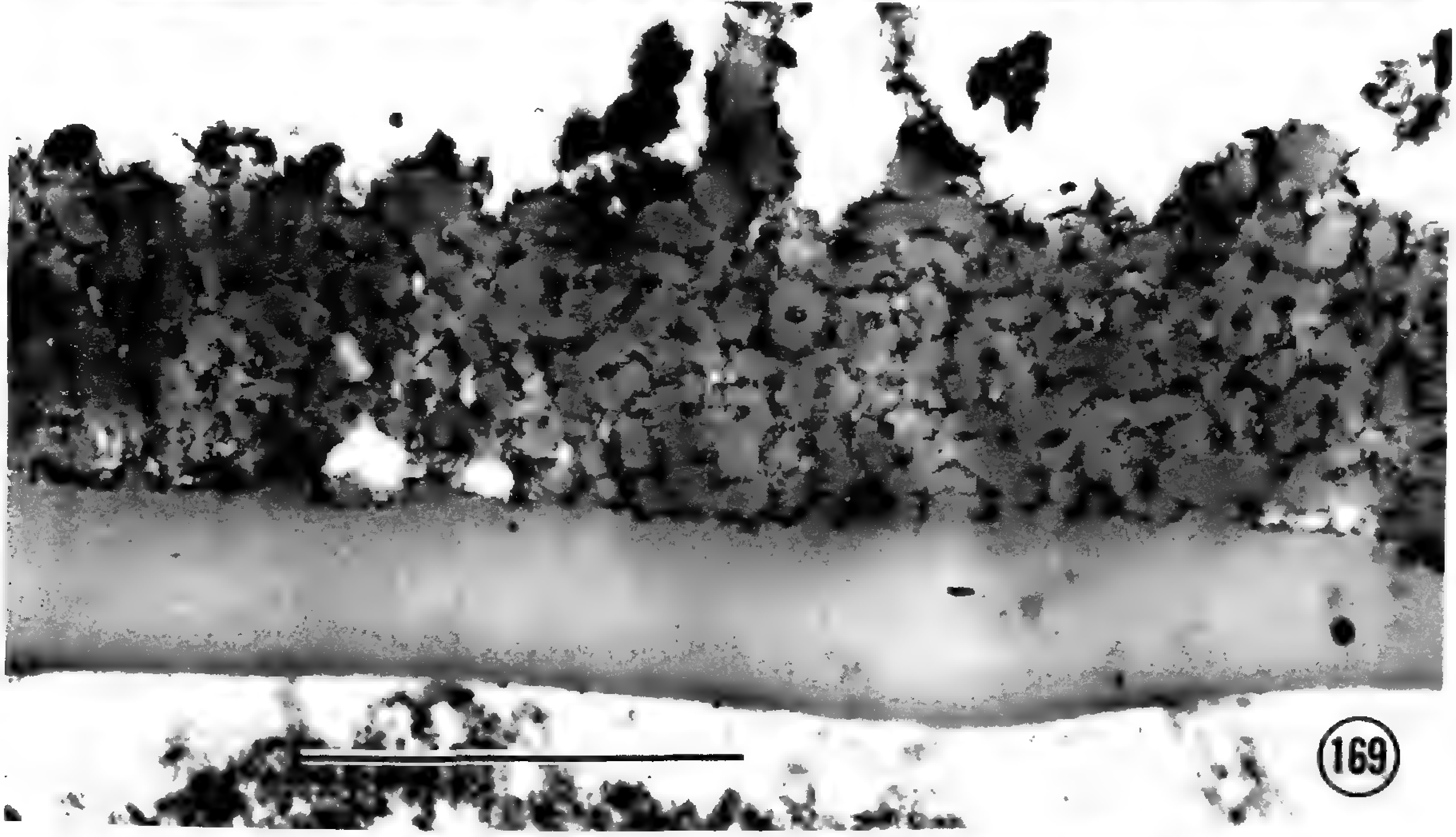
(163)

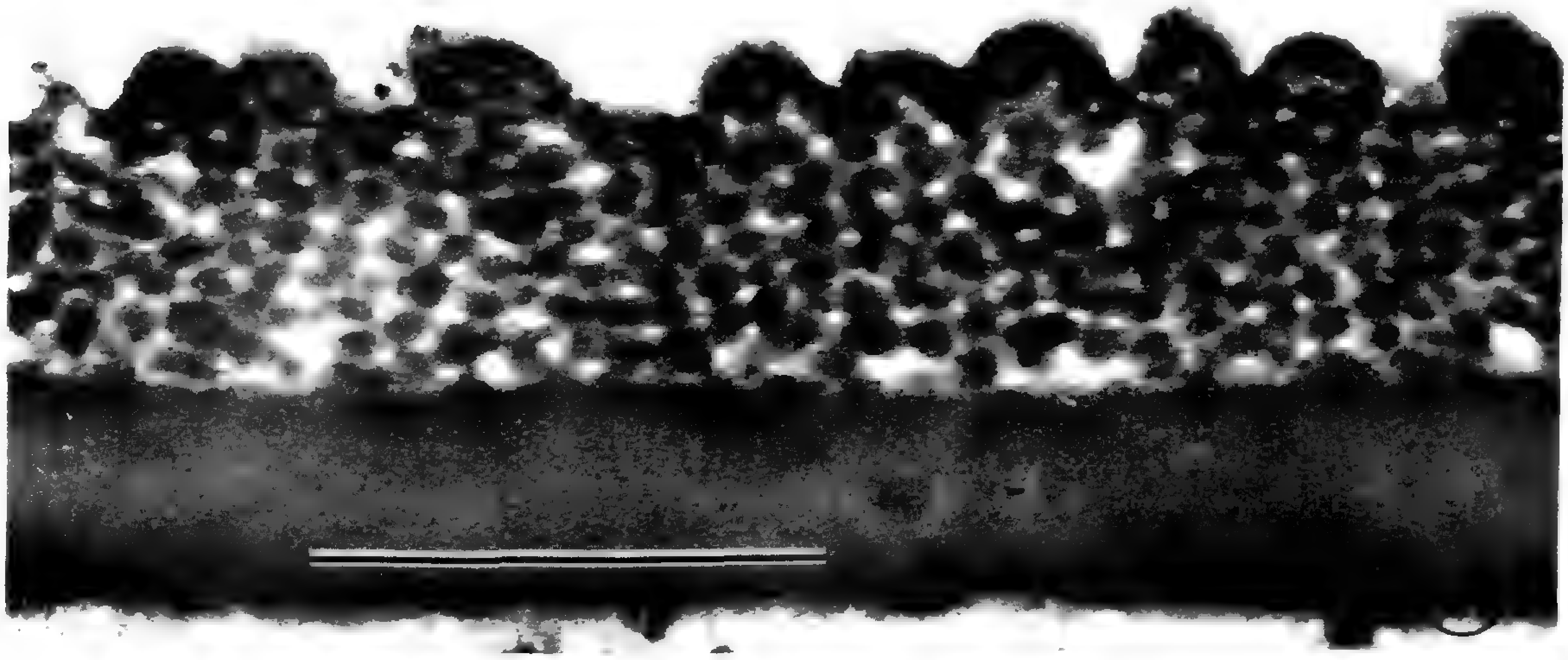
FIGURES 162, 163. Transmission electron micrographs of *Fuchsia* pollen, sect. *Hemsleyella, F. garleppiana.* Pollen acetolyzed.—162. High magnification of section through central body.—163. Portion of apertural protrusion. The scale equals 1 μm.



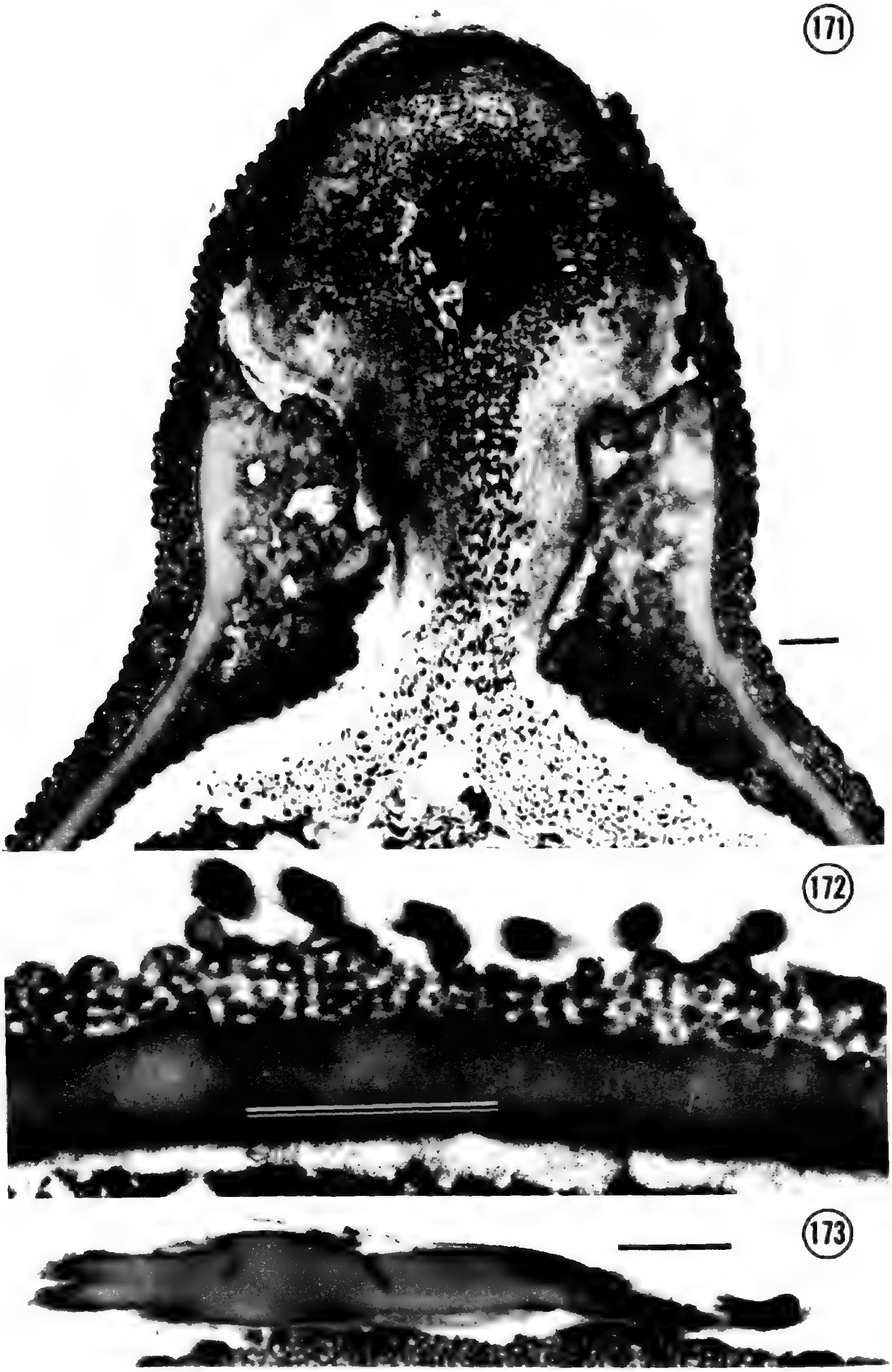
FIGURES 164–167. Transmission electron micrographs of *Fuchsia* pollen, sect. *Hemsleyella, F. tillettiana.* All pollen rehydrated.—164. Section at proximal polar surface. Note conspicuous membrane around threads in all figures in this plate.—165. Longitudinal section through four viscin threads.—166. Cross section through a group of viscin threads.—167. Longitudinal section through a single thread clearly showing the segmented-beaded nature. The scale equals 1 μm.



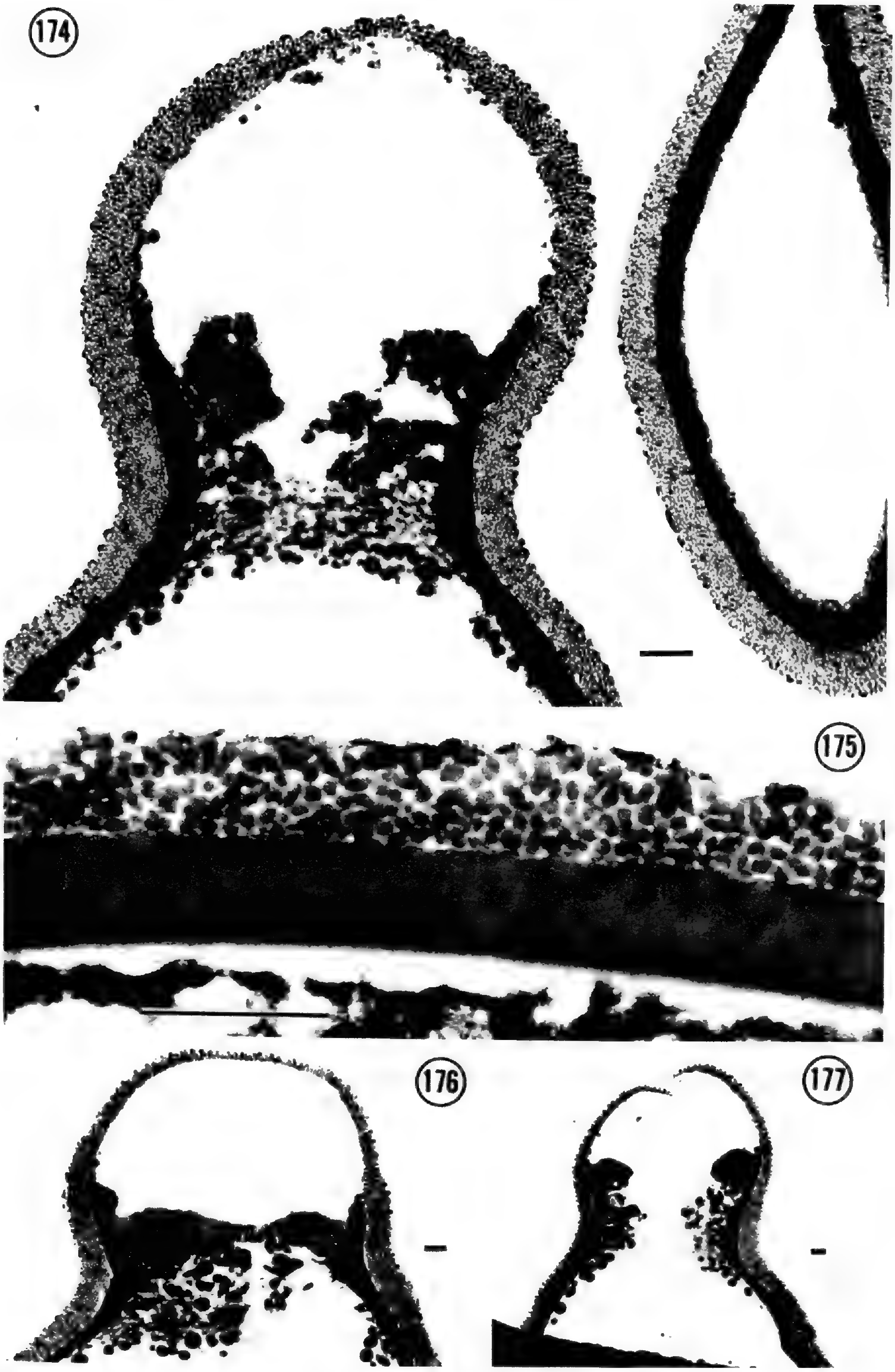




FIGURES 168–170. Transmission electron micrographs of *Fuchsia* pollen, sect. *Jimenezia* (Figs. 168, 169) and sect. *Kierschlegeria* (Fig. 170). All pollen rehydrated. 168, 169. *F. jimenezii.*—168. Section through middle of central body. Note the loosely formed granular endexine. The dense fibrous material on the ektexine surface is a precipitate from staining.—169. Section similar to Figure 115 in that the endexine is tapered at the junction of the apertural protrusion and central body. In this section the granular endexine component is not evident.—170. *F. lycioides*, section at middle of central body. The scale equals 1 μm.

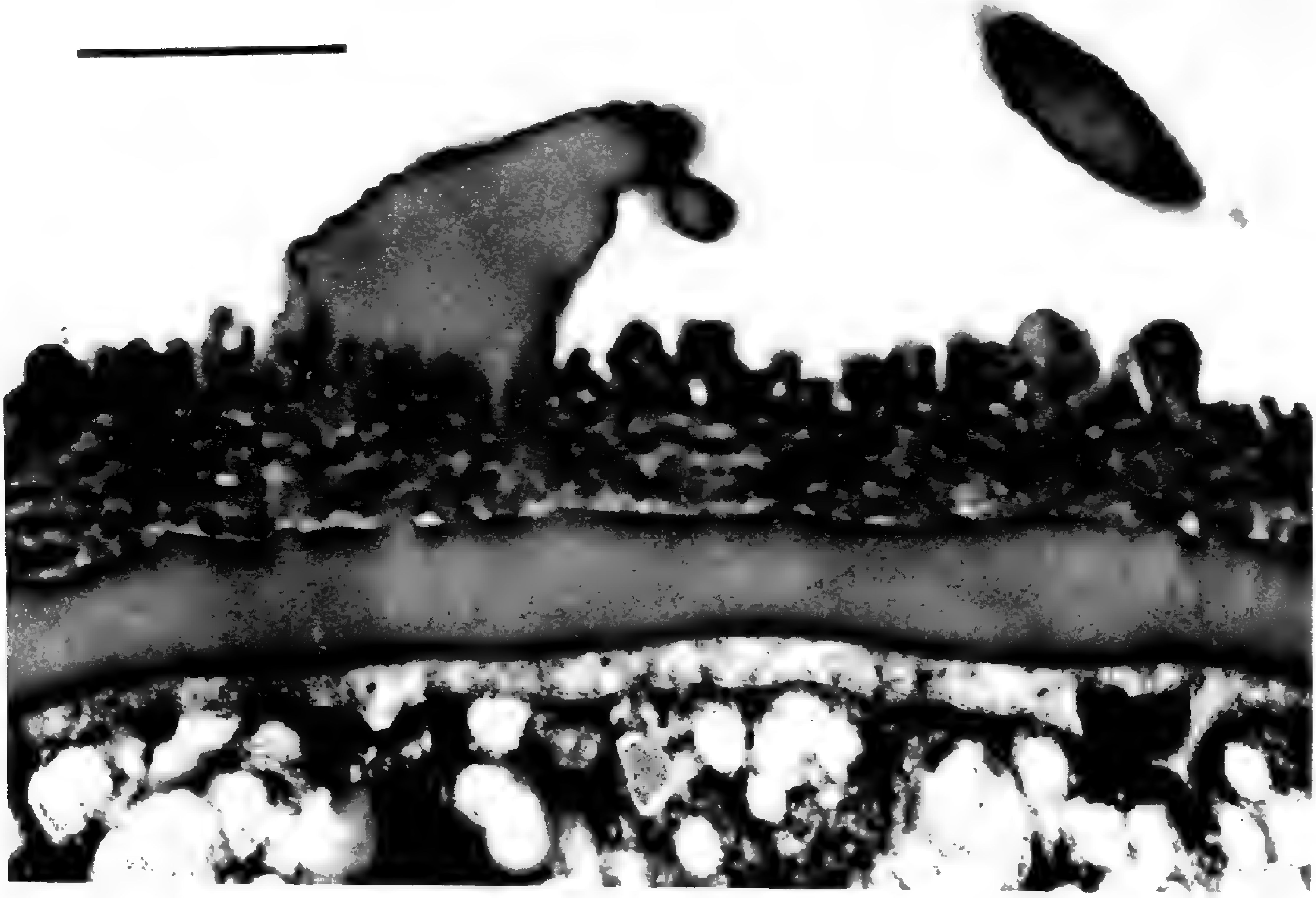


FIGURES 171–173. Transmission electron micrographs of *Fuchsia* pollen, sect. *Kierschlegeria, F. lycioides.* All pollen rehydrated.—171. Section through apertural protrusion with cytoplasm extending from the central body (at bottom) through aperture channel and into the vestibulum or aperture chamber.—172. Section at proximal polar surface showing at least six viscin threads in cross sectional view.—173. Longitudinal section of smooth viscin thread group along surface of the ektexine. The scale equals 1 μm.

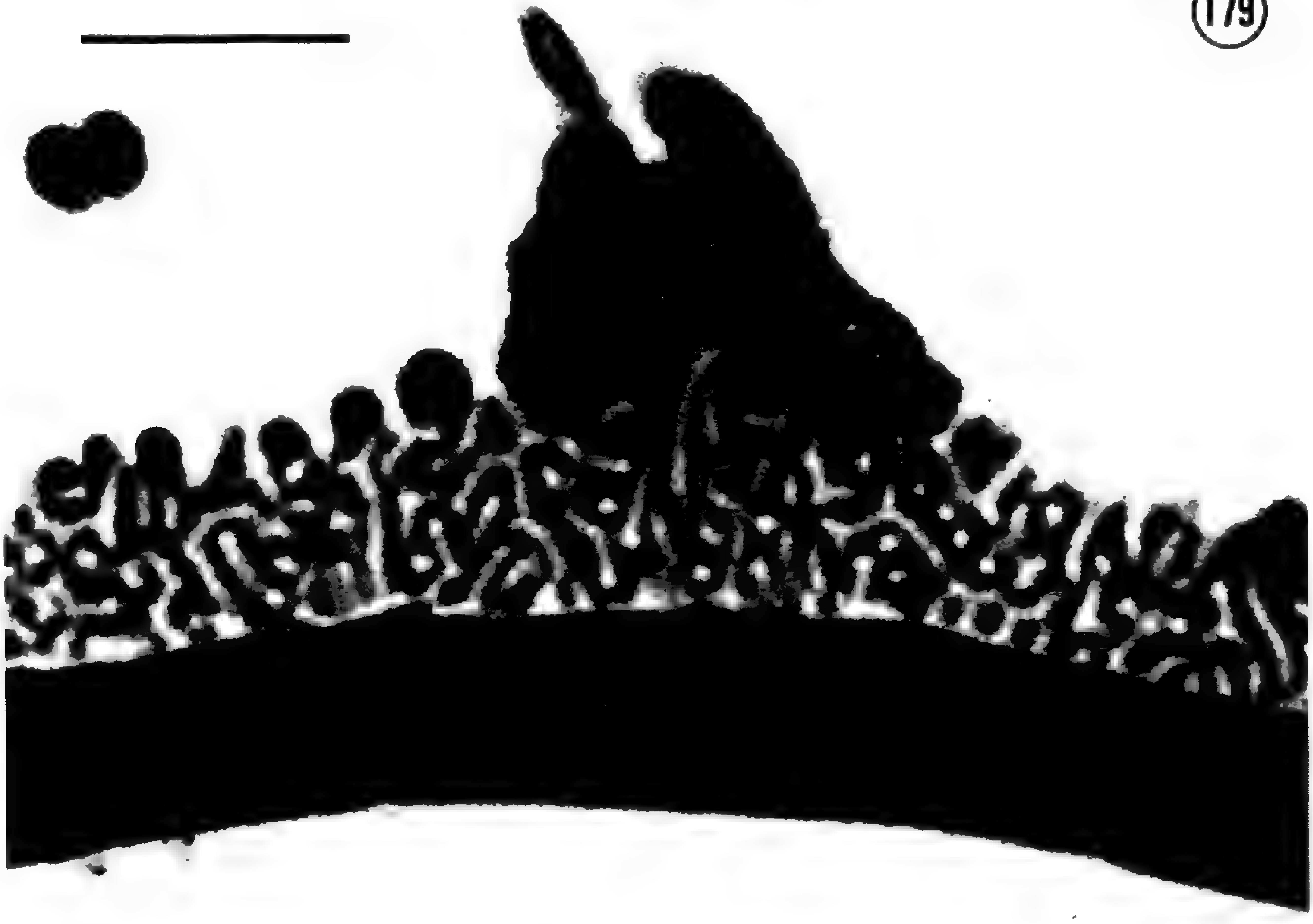


FIGURES 174–177. Transmission electron micrographs of *Fuchsia* pollen, sect. *Quelusia* (Figs. 174, 175) and sect. *Skinnera* (Figs. 176, 177). Acetolyzed (Figs. 174, 176, 177) and rehydrated (Fig. 175) pollen. 174, 175. *F. magellanica.*—174. Section of apertural protrusion (at left) and central body (at right).—175. This rehydrated pollen grain is similar to the acetolyzed grain in Figure 174 except that the ektexine appears to be partially enclosed by a membrane (as noted for the viscin thread) and does not show any granular endexine. 176, 177. *F. excorticata.*—176. This figure and the following (Fig. 177) are sections of the apertural protrusion at different levels. In Figure 176 the honeycombed endexine appears to line the aperture chamber, at least in part.—177. In this figure the section is essentially at mid-level through the center of the apertural protrusion and shows the pore area at the ektexine surface and the apertural channel through the endexine. Note apertural protrusion-central body junction (at right; also see Figs. 115, 169). The scale equals 1 μm.

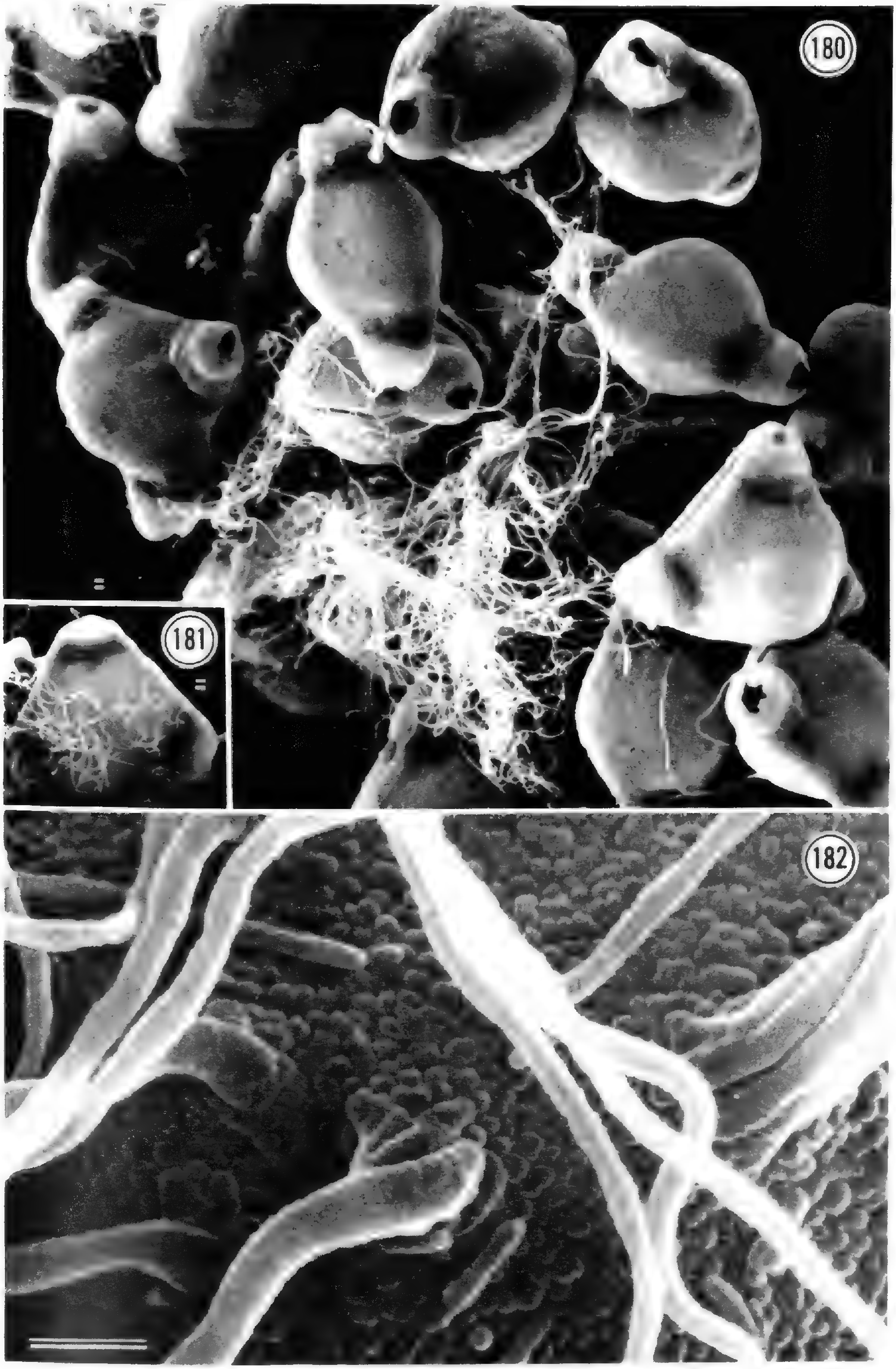
178



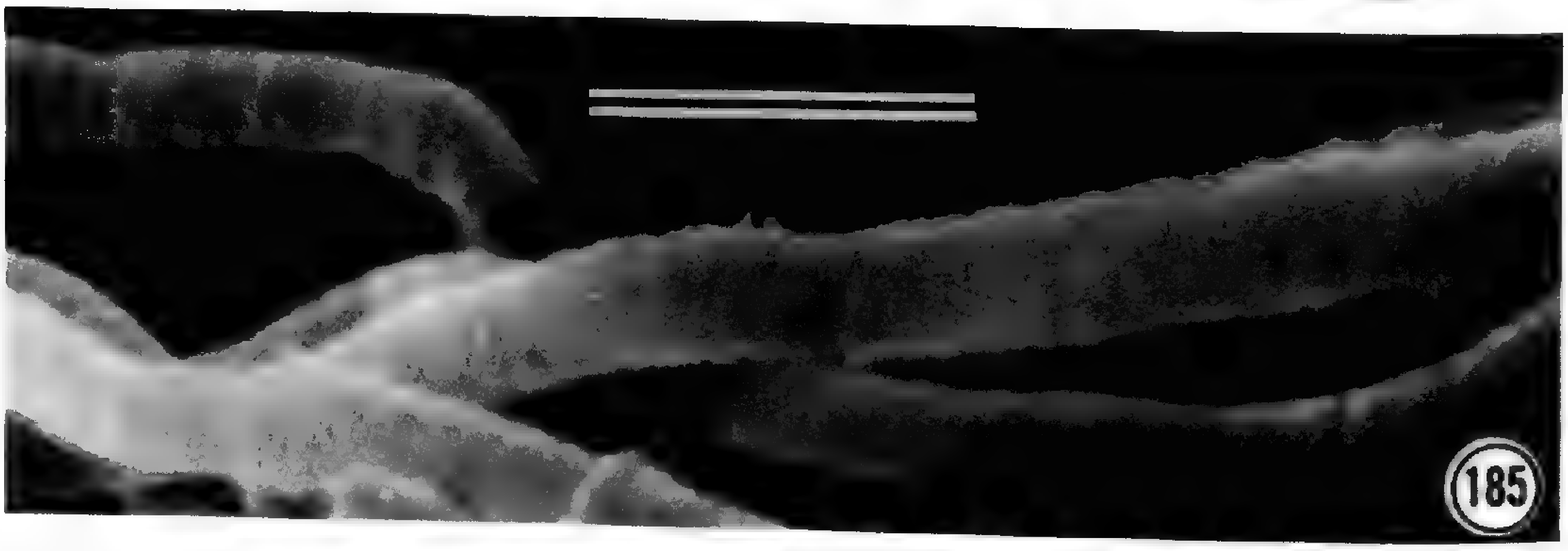
179



FIGURES 178, 179. Transmission electron micrographs of *Fuchsia* pollen, sect. *Skinnera, F. excorticata.* Rehydrated (Fig. 178) and acetolyzed (Fig. 179) pollen.—178. Section through proximal polar face showing viscin thread attachment with ektexine.—179. Section similar to Figure 178 and included for purpose of comparing acetolyzed and unacetolyzed pollen. The very fine dense granules are probably precipitated from osmic acid stain. The scale equals 1 μm.

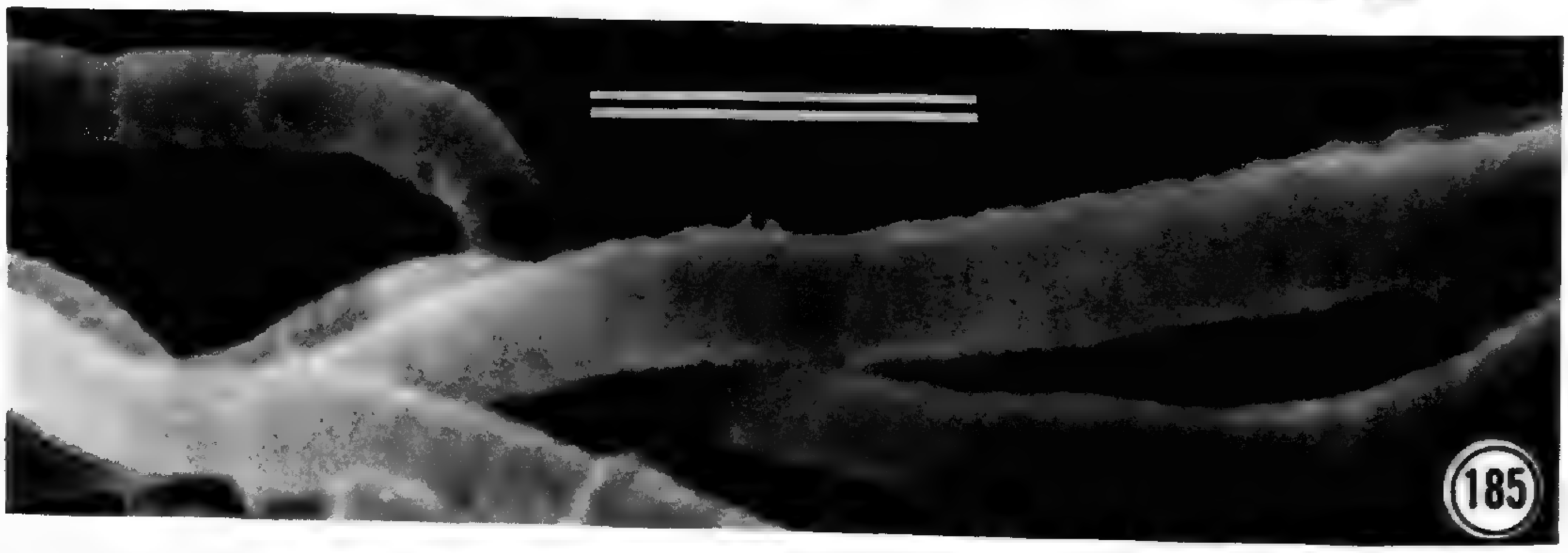


FIGURES 180–182. Scanning electron micrographs of *Fuchsia* pollen, sect. *Skinnera*. Pollen acetolyzed.—180. *F. excorticata*, a few 3-aperturate grains are interspersed with the predominant 2-aperturate grains. 181, 182. *F. cyrtandroides*.—181. A 3-aperturate grain (compare with more common 2-aperturate grains in Figs. 46, 49, 50).—182. Enlargement of proximal surface of Figure 181. Note faint but distinct lightly segmented nature of viscin threads. In Figures 180, 181 the scale equals 2 μm; in Figure 182 the scale equals 1 μm.



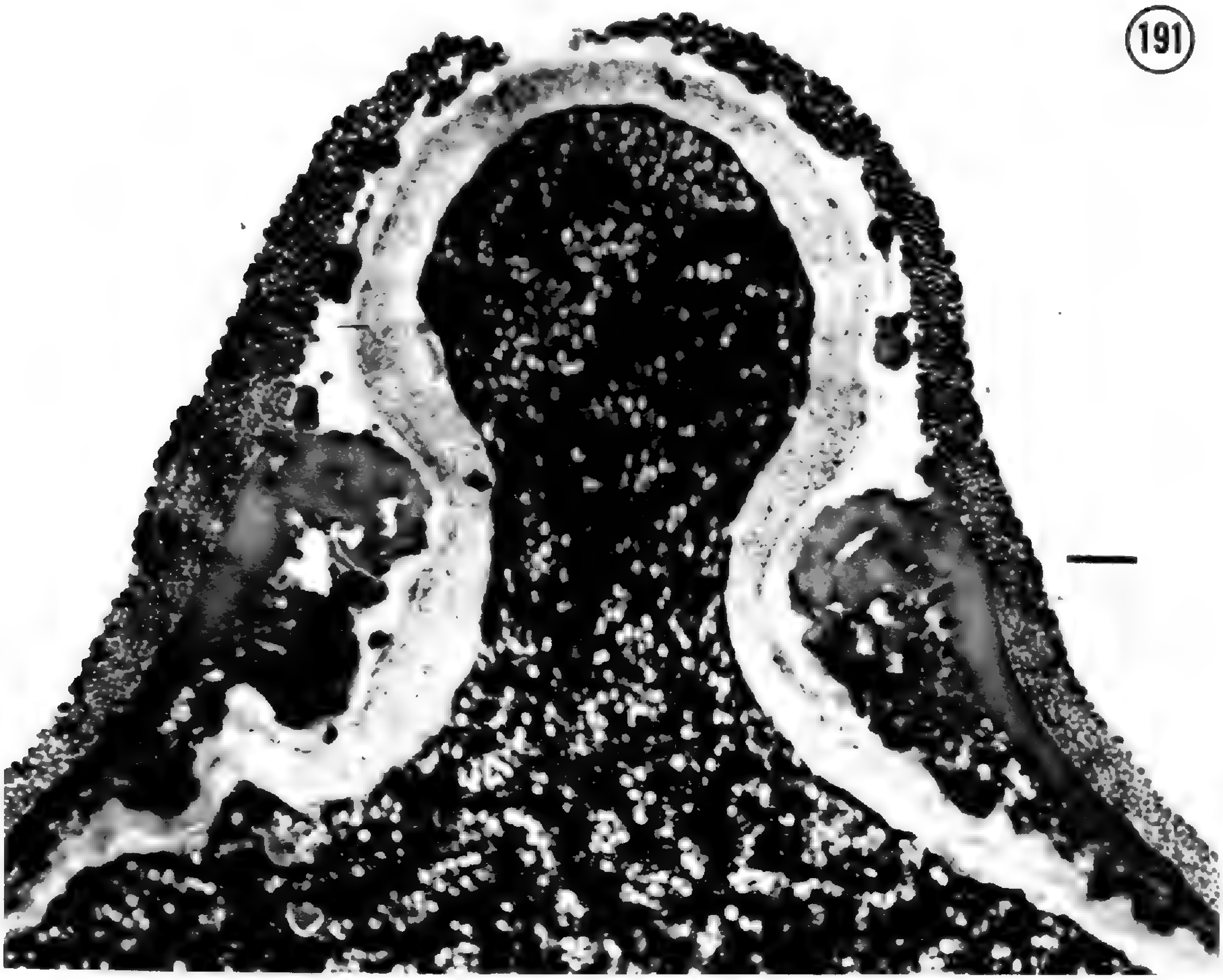
FIGURES 183–185. Scanning (Fig. 183) and transmission (Figs. 184, 185) electron micrographs of *Fuchsia* pollen, sect. *Skinnera, F. cyrtandroides*. Pollen acetolyzed.—183. Section includes exine on distal (at bottom) and proximal (at top) polar faces. Note that they are approximately equal. The lightly segmented nature of the viscin threads is evident in some of the threads in the group attached to the ektexine (at right). In the cross section of the thread cluster (at left) the segmented nature of the individual threads is not apparent.—184. Longitudinal section clearly indicating segmented nature of thread.—185. Group of threads from typical 2-aperturate grain showing their lightly segmented nature (compare with Figs. 49, 50, 182). The scale equals 1 μm.

FIGURES 186, 187. Transmission (Fig. 186) and scanning (Fig. 187) electron micrographs of *Fuchsia* pollen, sect. *Skinnera, F. perscandens.* Pollen acetolyzed.—186. Section through proximal face. The longitudinal section through the viscin threads indicates their light segmentation (see also Figs. 183, 184).—187. A cluster of threads (approximately equivalent in section view to cross section of thread cluster in Fig. 183). Segmentation of the threads is extremely light. The scale equals 1 μm.



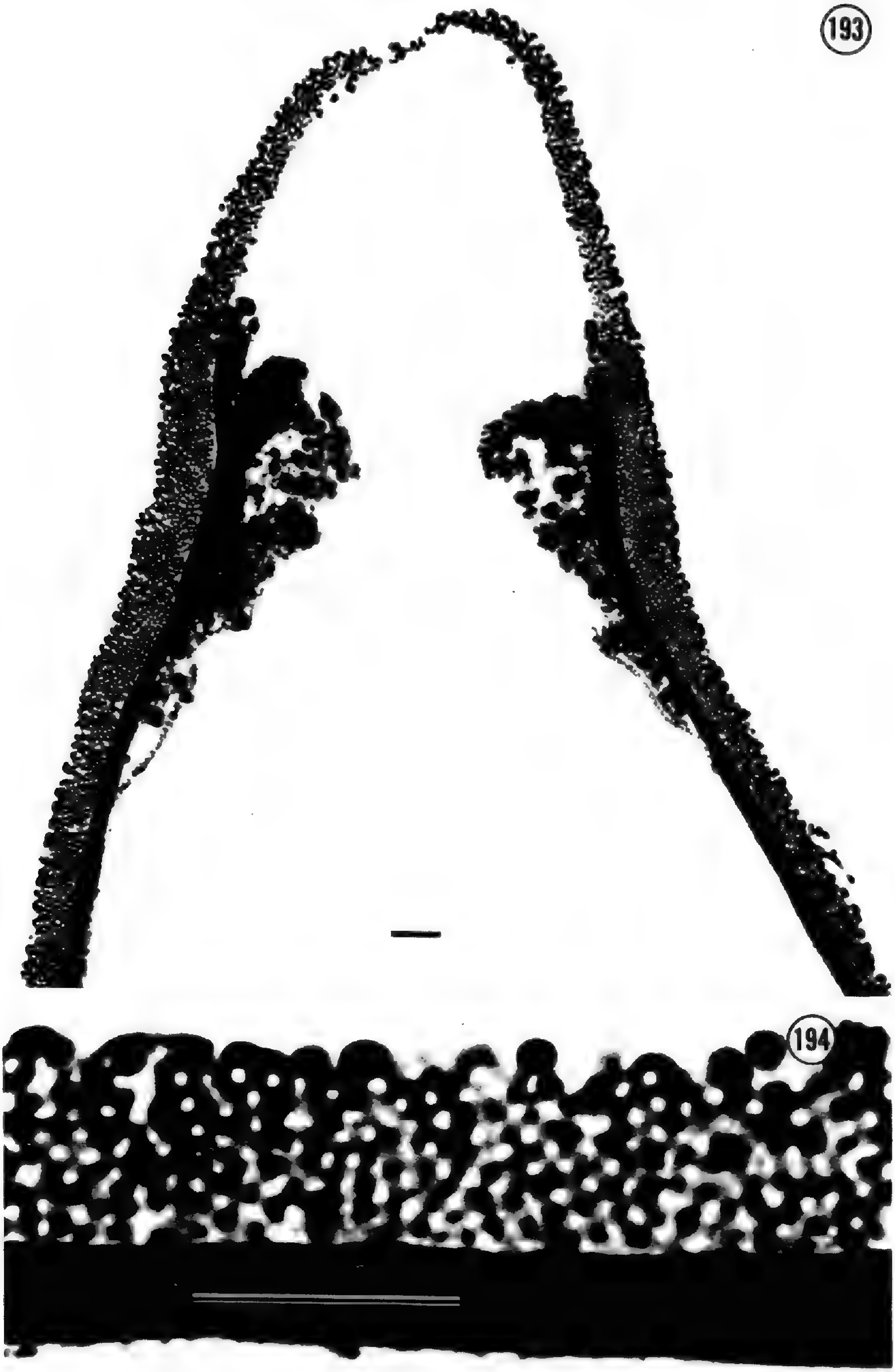
FIGURES 183–185. Scanning (Fig. 183) and transmission (Figs. 184, 185) electron micrographs of *Fuchsia* pollen, sect. *Skinnera, F. cyrtandroides.* Pollen acetolyzed.—183. Section includes exine on distal (at bottom) and proximal (at top) polar faces. Note that they are approximately equal. The lightly segmented nature of the viscin threads is evident in some of the threads in the group attached to the ektexine (at right). In the cross section of the thread cluster (at left) the segmented nature of the individual threads is not apparent.—184. Longitudinal section clearly indicating segmented nature of thread.—185. Group of threads from typical 2-aperturate grain showing their lightly segmented nature (compare with Figs. 49, 50, 182). The scale equals 1 μm.

(191)



(192)

FIGURES 191, 192. Transmission electron micrographs of *Fuchsia* pollen, sect. *Schufia*, *F. arborescens*. All pollen rehydrated.—191. Section through apertural protrusion showing cytoplasm from central body extending through the aperture channel and into the aperture chamber. Note well-defined intine.—192. Section at proximal polar face showing viscin thread attachment with ektexine. The scale equals 1 μm.



FIGURES 193, 194. Transmission electron micrographs of *Fuchsia* pollen, sect. *Schufia, F. paniculata.* Pollen acetolyzed.—193. View of apertural protrusion and a portion of the central body.—194. Section through central body. The scale equals 1 μm.

clearly have taxonomic value, aperture number (two versus three) and viscin thread morphology (smooth versus segmented). By using a combination of these features, most sections can be distinguished. Table 2 attempts to correlate these at the sectional level.

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THE SIMPLE LEAVED LUPINES AND THEIR RELATIVES IN ARGENTINA[1]

ANA MARIA PLANCHUELO AND DAVID B. DUNN[2]

ABSTRACT

Arguments are presented to support the thesis that leaves of lupines with a single blade are simple rather than unifoliolate. Three species in Argentina have all or some of their leaves simple. *Lupinus guaraniticus* and *L. sellowianus* have only simple leaves, whereas *L. paraguariensis* has simple leaves at the base of the plant and the first leaf of each lateral branch but the others are palmately compound. Three related species with palmately compound leaves are treated in this paper: *L. albescens, L. aureonitens,* and *L. multiflorus.*

The species of *Lupinus* are restricted to the New World, with the exception of a limited number in the Mediterranean region, and a few in Africa, reviewed by Gladstone (1974), and Plitmann (1981). The major speciation centers are in the montane western area of North America, Mexico, and in the Andean region of South America. The simple-leaved lupines occur mainly in the central and southeastern region of Brazil. Four species were treated by Small (1933) as the *Simplicifolii* in Florida. Dunn (1971) contended that the four taxa of the complex originated in Brazil and reached Florida by long range dispersal.

The species treated in this paper are the only known biennial or perennial lupines in northeastern Argentina that are related to lupines of Brazil, Paraguay, and Uruguay. Their floral or vegetative characteristics are not remotely similar to those of Andean lupines. The other three native species that grow in the area are annuals.

DISCUSSION OF LEAF CHARACTERISTICS IN *LUPINUS*

Different terminology has been used to describe the simple-blade leaf of lupines. Whether they should be considered simple-leaved or unifoliolate has been an unresolved question.

Bentham (1859), in his treatment of *Lupinus* in "Flora Brasiliensis," used the characteristics "leaves simple or unifoliolate" in the same statement of the key, without any subsequent separation or explanation about the difference. However, in the following genus, *Crotalaria,* he clearly separated simple-leaved species from unifoliolate species. He defined "Simplicifoliae" as those having leaves with one blade sessile or with a narrow petiole without articulation. In contrast, the "Foliolatae" are defined as having leaves with one to three leaflets, with the petiole articulate at the apex.

Smith (1945) recognized 21 simple-leaved lupines for Brazil and referred to them as unifoliate. Burkart (1952, 1967) also used the term unifoliolate in his description of *Lupinus.*

Hutchinson (1964), in the key to the tribe Lupineae, separated *Lupinus* by the characters "leaves simple, digitately several to many-foliolate or 1-foliolate." Later in the description of the genus he stated "very rarely digitately 3-foliolate or 1-foliolate."

Polhill (1976) considered the leaves of *Lupinus* "5–11(–17)-foliolate or less often (in Central and South America) 1–3-foliolate." However, Bisby (1981) described the subtribe Lupininae (with only one genus, *Lupinus*) with "leaves 5–17-foliolate, palmate, rarely simple."

This literature review shows that there is not an unanimous opinion in the use of appropriate terminology to describe the simple-blade leaves of *Lupinus.* To resolve the problem, we studied the morphology of the leaves using the same criteria of the articulation or abscission of the petiole introduced by Bentham (1859) in *Crotalaria.* The position of the abscission layer can readily be determined from old leaves of preceding years.

The perennial species of *Lupinus* with digi-

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[1] The work was a portion of the problems encountered by A. M. Planchuelo (1978) in her doctoral dissertation under the direction of D. B. Dunn at the University of Missouri–Columbia.

[2] Division of Biological Sciences, University of Missouri–Columbia, 202 Tucker Hall, Columbia, Missouri 65211. The authors wish to express their appreciation to the curators of the herbaria that were cited in the distributions. Without the study of the type material and the illustrations, the work would not have been possible.

ANN. MISSOURI BOT. GARD. 71: 92–103. 1984.

tately compound leaves commonly have the abscission layer at each petiolule or base of each leaflet, at the top of the petiole. In many species the petioles remain attached to the plant at least one year before finally weathering away. In other species the petiole is lost shortly after the fall of the leaflets, by a later abscission at the base of the petiole. In contrast, in the simple-leaved species of *Lupinus,* abscission occurs only at the base of the petiole or where the petiole becomes free from the fusion of the stipules. After abscission there is often a flange-like remnant remaining at the node where the leaves from the previous year were attached. However, there is no visible indication of an abscission zone at the top of the petioles of the 18 species of simple-leaved lupines that we have been able to study from Brazil, Paraguay, and Argentina. There are several species that have completely lost the entire petiole, in which case there is an abscission below the sessile blade.

We concluded from this study that the term unifoliolate is not appropriate for the genus *Lupinus,* hence, we considered the simple-blade leaves as truly simple.

An interesting condition in *L. paraguariensis* shows a transitional stage between simple and compound leaves. The juvenile basal leaves from the caudex, and the first leaf produced on the lateral branches, are simple. The other leaves of the main stems and branches are digitately compound with three to five leaflets. The compound leaves do not show any sign of abscission zone at the base of the leaflet or at the top of the petiole, and the petioles do not remain attached to the plant as in other species. *Lupinus paraguariensis* is the only known species with the combination of simple and compound leaves in mature plants.

We were able to obtain some viable seeds of *L. albescens,* and all of the seedlings in the colony we planted produced one simple elliptical leaf blade on the first leaf above the cotyledons. The second leaf had three leaflets, the third had five leaflets, and the number of leaflets increasd as the vigor of the seedling increased, until the typical number of the mature plants developed, as cited in the section on taxonomy. We are confident that the same situation will occur in *L. aureonitens* and *L. multiflorus,* because they are morphologically closely related to *L. paraguariensis.* None of the North American lupines that we have grown experimentally have germinated with the first leaf simple.

TAXONOMY

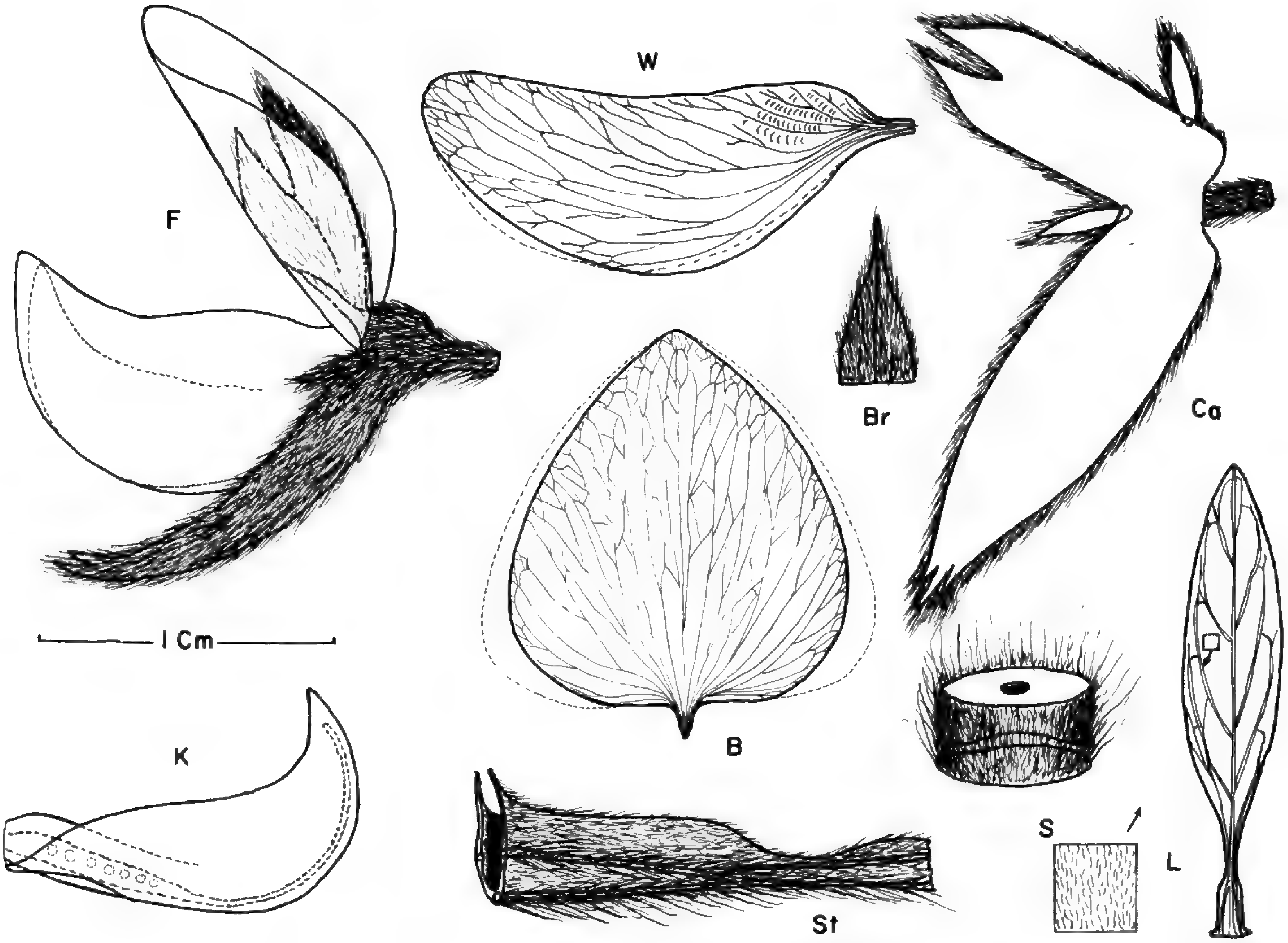
Only the perennial or biennial species of northeastern Argentina, adjacent Brazil, Paraguay, and Uruguay are treated in this paper (Fig. 1). There are three native annual species (*L. bracteolaris* Desr., *L. linearis* Desr., *L. gibertianus* C. P. Smith) and three annuals sometimes cultivated (*L. albus* L., *L. angustifolius* L., *L. luteus* L.) in this area that are not included. The leaves in this group are simple or compound with well-developed pinnate lateral venation. The plants are herbaceous and generally die back to a perennial caudex, with the exception of *L. guaraniticus* (Hassl.) C. P. Smith, which may become sprawling and suffruticose. The stipules are well developed in all of the species except *L. guaraniticus,* in which the free tips are absent. The tapered base, as well as the absence of a gibbous base of the upper-lip of the calyx, is very similar in all of the species of this group, and sets them apart from the Andean lupines, in which the gibbous base is often well developed. The tooth-like tip of the wings and the conformation of the banner also suggest that the species in the group are closely related.

KEY TO THE SPECIES

1a. Leaves all or some simple.
  2a. Leaves all simple.
    3a. Stipules with free tips absent; stems ligneous or herbaceous, appressed sericeous; petioles 8–13 mm long; flowers 13–16 mm long ________ 1. *L. guaraniticus*
    3b. Stipules with free tips present; stems herbaceous, shaggy-lanate; petioles 20–60 mm long; flowers 10–12 mm long ________ 2. *L. sellowianus*
  2b. Leaves simple at the base of the plant and the first leaf of each lateral branch, the others palmately compound ________ 3. *L. paraguariensis*
1b. Leaves all compound.
  4a. Wing tips rounded, without a tooth-like tip; keel angle over 90° ____ 5. *L. multiflorus*
  4b. Wing tips with an upturned tooth-like tip; keel angle 90° or less.
    5a. Leaves primarily basal; stems with branches primarily basal; lower leaves generally with three leaflets; leaflets complanate ____ 4. *L. aureonitens*
    5b. Leaves primarily cauline; stems erect, branching above; all leaves of mature plants with 5–12 leaflets, conduplicate ________ 6. *L. albescens*

1. Lupinus guaraniticus (Hassl.) C. P. Smith, Sp. Lup. 325. 1943. (Fig. 2). *L. attenuatus* Gardn.

FIGURE 1. Distribution of the simple leaved lupines of Argentina and their relatives as listed in the legend.



Lupinus guaraniticus (Hassler) C.P. Smith

FIGURE 2. Illustration of typical structures of *Lupinus guaraniticus.* The floral and vegetative parts, with the exception of the leaf, are drawn to the scale shown from the mean values of a set of multiple specimen dissections. B = banner petal flattened, dorsal view; Br = bract, dorsal surface; Ca = calyx, cut at the left lateral sinus and opened so that the inside surface shows; F = lateral view of the left side of the flower; K = keel petals, enclosing the staminal tube and the pistil, with the mean number of ovules drawn; L = typical leaf (not to scale), the lateral veins drawn from the lower surface view; inset illustrates the thinly strigose hairs of upper surface; S = stem structure showing the flange left after abscission of the leaf; St = stipular portion fused to the petiole with no free portion present; W = wing petal.

var. *guaraniticus* Hassler in Fedde, Repert. Spec. Nov. Regni Veg. 16: 158. 1919. TYPE: Paraguay. In fields, Alto Paraná, *Fiebrig 5681* (holotype, G; isotype, SI; photo, UMO).

Plants perennial, 3–7 dm tall, several stems from a branched caudex; *stems* herbaceous, or becoming ligneous, suffruticose, hollow, 3–6 mm diam., sericeous, hairs of several sizes, tawny in age, the longest hairs 2–3 mm long, internodes 2–4 cm long; stipules with the free tip absent, connate portion sheathing half of the diameter of the stem; *petioles* 8–13 mm long; *leaves* simple, entire, lance-elliptic, complanate at maturity, minutely strigose to thinly sericeous above, finely to densely sericeous below, the largest blades 7–9.5 cm long, 1.7–3 cm wide with 4–6 lateral veins on each side arcing forward, tips acute to obtuse, the base as a narrow wing along the entire petiole, abscission of the leaf near the base of the petiole; *peduncles* 3.5–6.5 cm long at anthesis, sericeous; *racemes* 7–11 cm long, flowers scattered; *bracts* caducous, ovate, sericeous dorsally, 4–6 mm long, 2–2.8 mm wide at the base, tips attenuate; *pedicels* 2.5–3 mm long at anthesis, 5–6 mm long in fruit, sericeous; *calyces* sericeous outside, glabrous within, the base slightly or not gibbous above, lower-lip lanceolate, 12–17 mm long, 3–5 mm wide, the tip trifid, central tooth ca. 2 mm long, 1 mm wide, the lateral teeth much shorter and curved outward, upper-lip 8–12 mm long, 3–4 mm wide below, bifid, the notch 2–3.5 mm deep, the lobes 1.5 mm wide, lips connate 1.5–2.5 mm, bracteoles lanceolate, 2–3.5 mm long, 0.7–1 mm wide, attached 0.3–0.6 mm below the lips of the lateral sinuses; *corolla* glabrous; *banner* oval-ovate with a short claw, 12–15 mm long, 10–13 mm wide, appressed 2–4 mm, reflexed 10–13 mm, reflexed/appressed ratio 3–5, the blade arching out and upward with the sides hardly reflexed; *wings* arcuate, 13–16 mm long, 5–6 mm wide, the claw 1.5–2 mm long, the lobe above the claw poorly developed; *keel* arcuate, 3.5–5 mm wide in the middle, tip acute, curved backward; *ovules* 6–8; *legumes* 5.5–6.5 cm long, 9–10 mm wide, ascending lanate; *seeds* 6–6.5 mm long, 4–5 mm wide, dark brown mottling and speckles on tan, funicular pit elongate, 2 mm long.

The species is reported from grassy areas in open places or slopes from Paraguay, southern Brazil, and Misiones and Corrientes in Argentina. It is viewed as the most primitive species of those treated in this paper, due to the ligneous sprawling stems, which often persist more than one year: other species die back to a woody caudex or function as biennials. The lack of the free tips of the stipules places it out of the direct lineage to the other species treated here.

Representative specimens. ARGENTINA. CORRIENTES: Santo Tomé, Ruta 40 y Arroyo Chimiray, *Schinini & Canevali 10323* (CTES, MO, UC), *Quarin 3402* (CTES). MISIONES: San Pedro, En la picada a La Celulosa, *Perrone s.n.* (BA #54259, SI); San Pedro, *Niederlein 1129* (SI).

BRASIL. PARANA: Arapati, Fda. do Tigre, *Hatschbach 7206* (US); Castro, Carambei, *Hatschbach 35482* (BH, CTES); Guarapuara, Aeroporto, *Hatschbach 30851* (UC); Laranjeiras do Sul, *Hatschbach 4238, 4239* (US); *Hatschbach 35213* (BH, CTES, MO, UC); Tibagi, Fda. Mt. Alegre, Invernada Miranda, *Hatschbach 2822* (US). RIO GRANDE DO SUL: Canabara, S Fr. de Paula, *Rambo 36207* (MO); Caxias do Sul, no Strede Caxias—V. Oliva, *Valls 1431* (CTES); St. Loureuro Gomez, *Bornmuller 325* (GH); S Angelo, S João Velho, *Pedersen 11949* (CTES, SI). SANTA CATARINA: Agua Doce, Campos de Palmas, *Smith & Klein 13612* (US); Curitibanos, Campo 11 km SE of Marombas, *Smith & Klein 12202* (US); Campo Alegre, *Reitz & Klein 5267, 6165* (US).

PARAGUAY. Itaqugry, alto Paraná, *Fiebrig 5881* (SI); Regione fluminis, alto Paraná, *Fiebrig 5681* (G, SI).

2. **Lupinus sellowianus** Harms in Fedde, Repert Spec. Nov. Regni Veg. 17: 5. 1921. TYPE: Brazil. Location unknown, *Sello 4866* (holotype, B, not seen) (Fig. 3).

Plants perennial, herbaceous, seasonal stems arising from a subsurface root-stalk; *stems* 2.5–4.5 dm tall, hollow, slightly fistulose, loosely shaggy-lanate, lower internodes very short, upper 2–3 cm long, ridged from the veins of the petioles, 3–6 mm diam.; *stipules* 2–4 cm long, free tips 1.5–2 cm long, caudate-attenuate to subulate, occasionally foliaceous; *petioles* 2–6 cm long, longer ones below, lanate as stems; *leaves* simple, lanate on both sides, the blades of the largest leaves 8–11 cm long, 1–2 cm wide, smaller above, not abscissing from the petioles, withering in age and the petioles breaking near the base, without a clear-cut abscission layer, prominent lateral veins raised below, arcing out and toward the tip, 5–8 pairs; *peduncles* 4–6.5 cm long, lanate as stems, hairs 4–7 mm long; *racemes* 10–20 cm long, flowers scattered to subverticillate; *bracts* lance-shaped, tips attenuate, caducous, 8–10 mm long, 2–2.8 mm wide below; *pedicels* 1–2 mm long, densely appressed lanate; *calyces* densely lanate outside, glabrous within except the margins of the lips, upper-lip bifid, 6–8 mm long, the notch 2.8–3.5 mm deep, lower-lip tridentate to trifid, 8–10 mm long, the teeth 1.5–2.5 mm long, lips connate 2 mm, bracteoles lanceolate, 2–3 mm long, 0.6–1 mm wide; *corolla* glabrous; *banner* ovate to oval, slightly emarginate at the tip, with a short claw at the base, 9.8–11.6 mm long, 6.4–8 mm wide, reflexed 6–7 mm, appressed 4.3–5.5 mm, reflexed/appressed ratio 1.3, the angle 120–135°; *wings* narrow, lower margin arcuate, tip pointed, weakly fused distally below the tip, 10.5–11.5 mm long, 3.3–4.7 mm wide, claw 1.5–1.8 mm long, tooth above the claw 1.4–2 mm wide; *keel* 2.5–3.4 mm wide in the middle, the angle 85–90°; *ovules* 4; *legumes* immature, 25 mm long, 6 mm wide, shaggy-lanate.

The floral parts are remarkably similar to those of *L. multiflorus* as well as the leaf venation and indument of vegetative parts. This species is reported for the first time for Argentina.

Smith (1945: 492) cited three specimens of *L. sellowianus* from the Berlin herbarium. One is the type specimen *Sello 4966,* from Brazilia; the second is *Dusen 13173,* from Parana; the third is *Dusen 7261,* from Espirito Santo, which was photographed by mistake as the type specimen, and the picture is filed in the New York herbarium. These three specimens were apparently destroyed by fire in Berlin in WWII.

Representative specimens. ARGENTINA. MISIONES: Bernardo de Irigoyen, 7 km en camino a San Pedro, *Krapovickas et al. 23381* (CTES).

BRAZIL. ESPIRITO SANTO: Villa Velha, *Dusen 7261* (photo NY); Laranjeiras do Sul, *Hatschbach 35218* (UC); Ponta Grossa, *Hatschbach 17390* (UC). SAO PAULO: S Pedra Campos, *Lofgren 319* (RB).

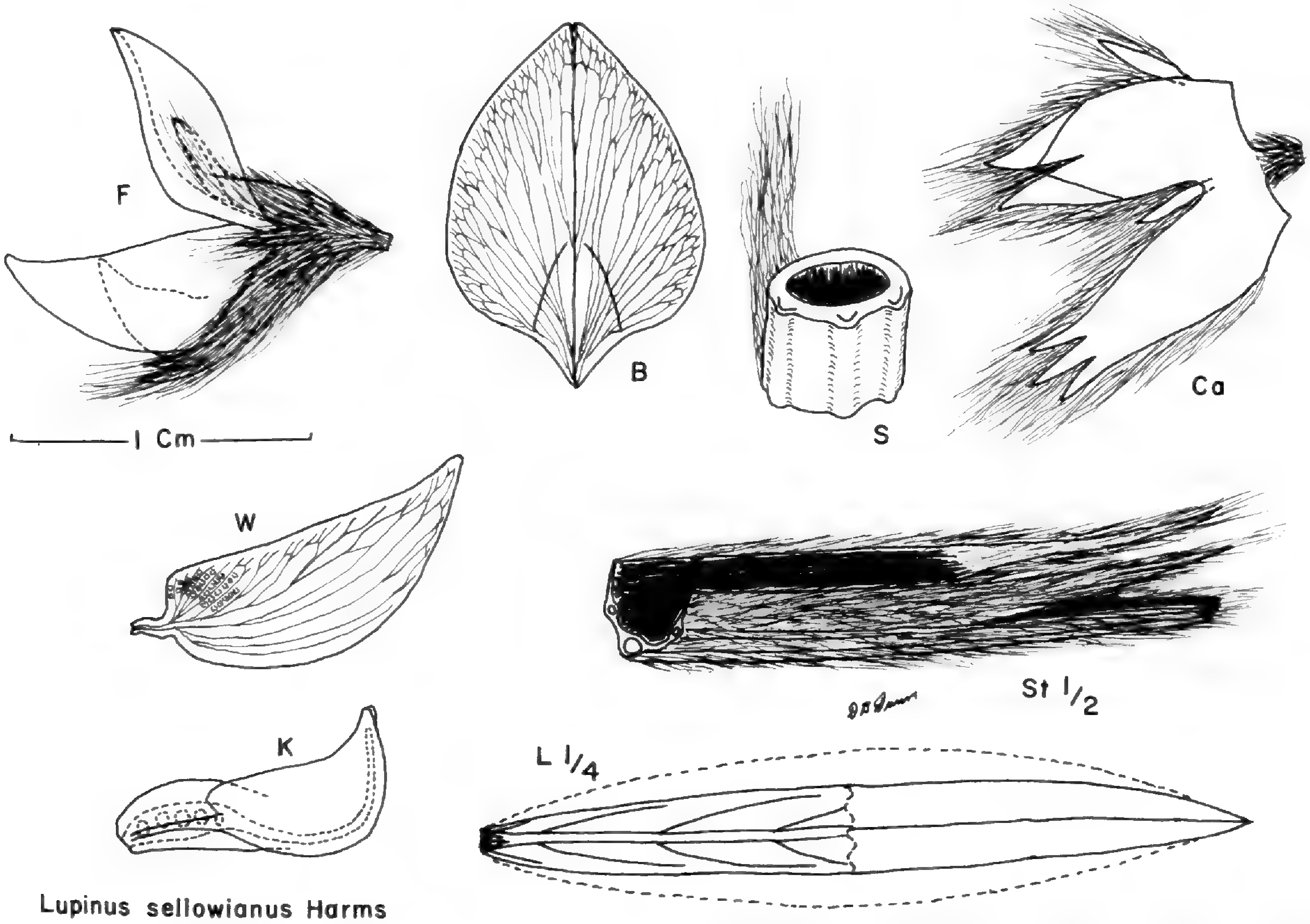


FIGURE 3. Illustration of typical structures of *Lupinus sellowianus.* The floral parts and the section of the stem are drawn to the scale shown from the mean values from dissections of specimens cited. B = banner petal flattened, dorsal view; Ca = calyx, cut at the left lateral sinus and opened to show the inside surface; F = lateral view of the left side of the flower; K = keel petals, enclosing the staminal tube and the pistil, with the mean number of ovules drawn; L = average largest leaf (drawn to ¼ of the scale shown), lateral veins of the lower surface drawn on the lower half; S = stem structure, first year growth, vascular traces from petiole above; St = stipules, detached at the node (drawn to ½ of the scale shown); W = wing petal.

3. **Lupinus paraguariensis** Chodet & Hassler, Bull. Herb. Boissier, Ser. 2, 4: 836. 1904. TYPE: Paraguay. Regione fluminis, Capibary, *Hassler 4430* (holotype, G; isotypes, GH, LIL, MO, NY, UC; photos, F, GH, UMO) (Fig. 4).

L. paraguariensis var. *missionum* Hassler in Fedde, Repert. Spec. Nov. Regni Veg. 16: 159. 1919. TYPE: Argentina. Misiones: fields near San Ignacio, *Hassler 445* (holotype, G).

L. missionum (Hassler) C. P. Smith, Sp. Lup. 325. 1943.

Plants perennial, possibly biennial, 4–8 dm tall; *stems* fistulose, 6–8 mm diam., appressed woolly pubescence to 5 mm long, with an undercoat of shorter hairs, internodes 2–8 cm long; *stipules* 2–5.5 cm long, the free tips slender, 1.5–4.5 cm long, lanate; longer *petioles* 6–12 cm long, lanate; *leaves* simple at the base of the plant and the first leaf on each branch, the others 3–5 palmately compound, leaflets broadly elliptical to elliptical-oblanceolate, complanate at maturity, appressed lanate on both surfaces, the largest 10–13 cm long, 1.8–4.5 cm wide, midribs and pinnate lateral veins conspicuous, tips obtuse, mucronate; abscises near the base of the petiole or at the point where the stipules become free; *peduncles* 4–7 cm long, lanate; *racemes* 12–30 cm long or little longer after fully developed, flowers scattered or subverticillate; *bracts* deciduous, narrow, lanceolate, 8–15 mm long, 1–2.5 mm wide below, lanate dorsally, tips long-attenuate; *pedicels* 2–4 mm long at anthesis, 6–7 mm long in fruit, lanate; *calyces* appressed lanate outside, glabrous within, except the tips and margins of the lips, lower-lip oblong, arcuate, 13–18 mm long, 4–6 mm wide, tips trifid, the teeth similar, 1–3 mm long, 0.4–0.8 mm wide, upper-lip 9–13

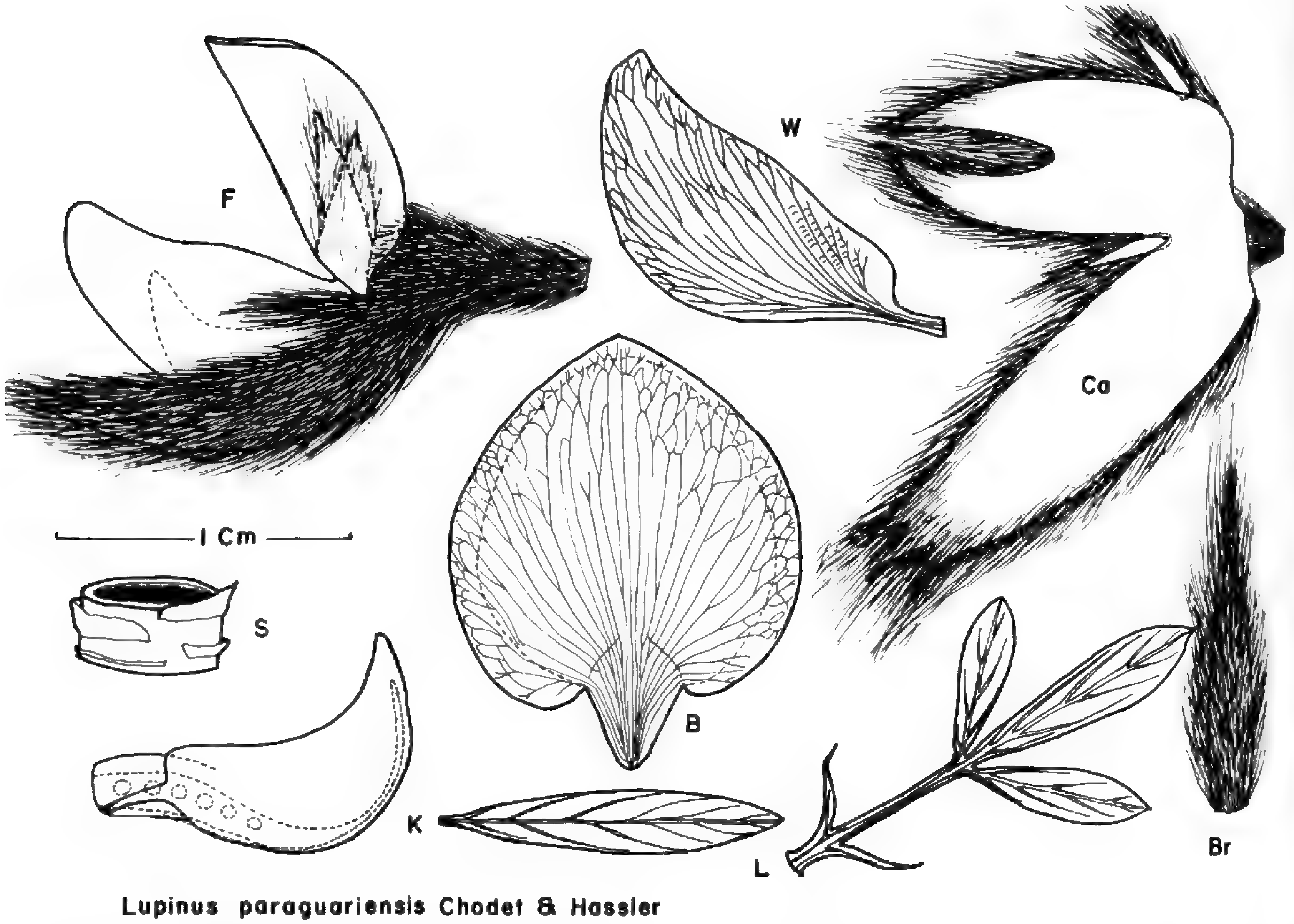


FIGURE 4. Illustration of the typical structures of *Lupinus paraguariensis*. The floral and vegetative parts, except the leaves, are drawn to the scale shown, from the mean values of a set of multiple dissections, from the geographic range of the species from specimens cited. B = banner petal flattened, dorsal view; Br = bract, dorsal view; Ca = calyx, cut at the left lateral sinus and opened to show the inside surface; F = lateral view of the left side of the flower; K = keel petals enclosing the staminal tube and pistil, with the mean number of ovules drawn; L = leaflet and trifoliolate leaf (not drawn to scale), note leaflets often connected by lamina at base, petiole often with a wing; S = stems fistulose, with flanges left where leaves abscissed, in some areas they weather away; W = wing petal.

mm long, bifid, the notch 3.5–6 mm deep, each lobe 2 mm wide, lips connate 2.5–3.5 mm, bracteoles lanceolate, tips attenuate, 2.5–4 mm long, 0.4–0.7 mm wide, attached at the lips of the lateral sinuses, both lips elongating after fertilization; *corolla* glabrous; *banner* oval, 14–15 mm long, 10–13 mm wide, appressed 4.5–5.5 mm, reflexed 8–9 mm, reflexed/appressed ratio 1.8, the angle 113°, the top part arcing forward; *wings* 13–15 mm long, 5–6 mm wide, the claws 2–3 mm long, the lobe above the claws poorly developed, the blade arcing upward distally as a broad blunt tip; *keel* 3.5–4.5 mm wide in the middle, the tip strongly hooked backward; *ovules* 6–7; immature *legumes* to 4 cm long, 8 mm wide, densely shaggy-lanate; *seeds* not seen.

The species occurs in southern Brazil, Paraguay, and Argentina. It is found in open areas or along river banks, and flowers in early spring. The similarity of floral traits to those of *L. guaraniticus* and *L. velutinus* of Brazil clearly suggests that they are all related. The variety *missionum*, named by Hassler, represents only younger plants or those in less favorable ecological situations. Field studies are needed to verify this.

Representative specimens. ARGENTINA. CORRIENTES: Candelaria, entre San Ignacio y Santa Ana, *Cabrera et al. 29362* (SI, UMO); Capital, Riachuelo, arenal alto de Yatay-pony, *Schinini & Ahumada 12368* (CTES); Empedrado, Río Empedrado, ruta 12, *Krapovickas et al. 19961* (CTES); Esquina, Estancia Santa Bárbara, *Carnevalli 3368* (CTES); Ituzaingó, Isla Apipé Grande, *Schinini & Vanni 15784* (CTES); Lavalle, ruta 12, 7 km N de Enpalme con ruta 120, *Tressens et al. 651* (CTES); Santo Tomé, Estancia San Juan Bautista, *Krapovickas et al. 26015* (CTES). MISIONES: Apóstoles, Pueblo Apóstoles, *Ibarrola 1091* (GH); cruces rutas 201–203, 30 km NE of Apóstoles, *Krapovickas et al. 15470* (CTES, UC); Loreto, Loreto, *Burkart 4586* (GH), *Gruner 1028* (BAF); San Ignacio, Alrededores, *Pfeiffer 111* (CTES); Posadas alrededores, *Spegazzini 10811* (BAF); San Ignacio, *Hassler 445* (G, type of var. *missionum*), *Muniez 114* (BAF); 5 km de San Ignacio, camino al Teyu-Cuare, *Quarin 3477* (CTES); San Ja-

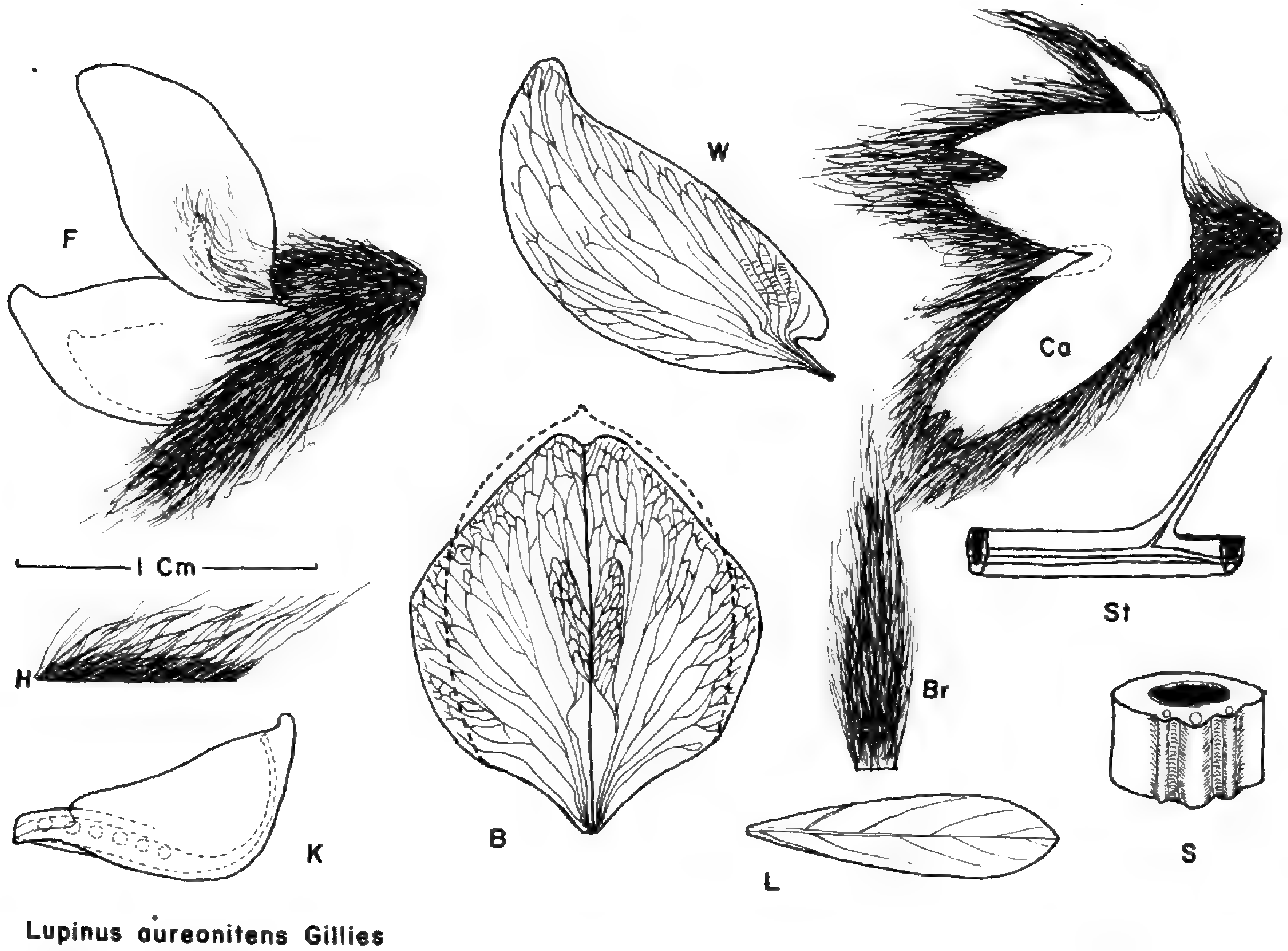


FIGURE 5. Illustration of the typical structures of *Lupinus aureonitens.* The floral and vegetative parts are drawn to the scale shown from the mean values of the limited number of specimens cited. B = banner petal flattened, dorsal view; Br = bract, dorsal surface; Ca = calyx, cut at the left lateral sinus and opened so that the inside surface shows; F = flower, left lateral view; H = stem hairs, multiple sizes; K = keel petals, enclosing the staminal tube and pistil, with the average number of ovules drawn; L = average largest leaflet (not drawn to scale), lateral veins of lower surface shown; S = stem structure, first year, varies to fistulose, vascular traces show on the internodes from the petiole above; St = stipule, detached at the node, not abscissing; W = wing petal.

vier, 11 km NE de San Javier, *Krapovickas & Cristobal 28870* (CTES).

BRAZIL. PARANA: Entrada Curitiba, Ponta Grossa, Proxima Rio Papagaio, *Pereira 6112* (RB); Ponta Grossa, Parque Villa Velha, *Hatschbach 8752* (RB). RIO GRANDE DO SUL: Sao Lepoldo, *Leite 553* (NY).

PARAGUAY. Condillere de Peribebui, *Balansa 3109* (BAF); Regione Fluminis, Yhu, *Hassler 9498* (F, NY, UC); Sierra de Maracayú, regione fluminis, Capibary, *Hassler 4430* (F, GH, LIL, MO, NY, UC); Valenzuela, *Rojas 12841* (BAF).

4. **Lupinus aureonitens** Gilles in Hooker, Bot. Misc. 3: 201. 1833. TYPE: Argentina. Buenos Aires: Pampas near Cabeza del Tigre (K, not seen) (Fig. 5).

L. purolantus C. P. Smith, Sp. Lup. 343. 1944. TYPE: Argentina. Buenos Aires: Sierra Tampé, Sierra de la Ventana, *Lorentz 3* (holotype, US; isotypes, CORD, F).

Plants biennial, or possibly sometimes annual, or a short lived perennial, 15–20 cm tall in fruit, branches mostly basal; *stems* ligneous and hollow, 6–10 mm diam., densely soft subappressed to spreading lanate throughout all vegetative parts, tawny in age, longer hairs 5–7 mm long, with a dense undercoat of kinky hairs 2.5–4 mm long, upper internodes 1.8–3 cm long at fruiting, the lower not elongated; *stipules* 2.5–4 cm long, free tips 1.5–2 cm long, the lower ones imbricated for ca. 7 cm; *petioles* 5–8 cm long, persistent long after the leaflets drop; *leaflets* 3–6, oblanceolate, mostly complanate, 4–6 lateral veins on each side of the midrib, hidden in the dense lanate hairs, largest leaflets 4–6 cm long, 8–18 mm wide, tips obtuse, mucronate; *peduncles* 2–4 cm long; *racemes* 12–20 cm long in fruit, flowers scattered; *bracts* deciduous, densely lanate dorsally, lanceolate, tips caudate, 6 mm long, 2 mm wide below; *pedicels* 2–5 mm long at anthesis, 6–8 mm long in fruit; *calyces* densely lanate outside, glabrous within except at the tips of the lips, lower-lip lance-oblong, 9–10 mm long, 3–4 mm wide, tridentate, the central tooth 1.5 mm long, 0.5 mm wide, the lateral teeth shorter, upper-lip 7–8 mm long, 4–5 mm wide, bifid, the notch 1.5–2 mm deep, the lobes 1.5–2 mm wide, lips connate 2.5–3 mm, bracteoles lance-attenuate, 3–4 mm long, 0.7–1 mm wide, attached 0.5 mm below the lips of the lateral sinuses; *corolla* glabrous; *banner* oval-obovate, 10–13 mm long, 8–12 mm wide, appressed 6–6.5 mm, reflexed 7 mm, reflexed/appressed ratio 1.1, the angle 120–135°, the tip bilobed, or entire, the teeth 0.5 mm long, 1 mm wide; *wings* 12–14 mm long, 5.5–6 mm wide, the tip ending as a lobe or tooth-like, the claw 2–2.5 mm long, the lobe above the claw 1.5–2 mm wide; *keel* 3.5–4 mm wide in the middle, the angle 85–88°; *ovules* 6; *legumes* 4–5 cm long, 8–9 mm wide, densely shaggy-lanate; *seeds* light tan, much dark mottling, 5 mm long, 4 mm wide, the funicular pit 1.3–1.5 mm diam., angle mark not observed.

The species appears more similar morphologically to *L. paraguariensis* in many traits but has the vegetative habit similar to *L. multiflorus.* The leaflet venation and indument are more like *L. paraguariensis.* The distribution is primarily south of Buenos Aires. The leaves with three leaflets are generally basal or the first leaves on the lateral branches. The reduction in the number of the leaflets in the basal leaves suggests relationship with *L. paraguariensis.*

Representative specimens. ARGENTINA. BUENOS AIRES: Tandil, Cerros, *Grondona 8016* (BAA); Cerros Heusser y Clavez, *Hicken s.n.* (SI #5883); General Villegas, *Parodi 13385* (BAA, SI); *Cabera 5694* (SI); Sierra Tampé, Sierra de la Ventana, *Lorentz 3* (CORD, F, US), *Hauman s.n.* (BAA #2285, SI), *Hicken s.n.* (SE #5882); Saavedra, Sierra de Bravard, Abra Hinojo, *Gomez et al. s.n.* (BAA #11346).

5. **Lupinus multiflorus** Desr. in Lam., Encyclopedia 3: 624. 1789. TYPE: Uruguay. Montevideo, *Commerson* (holotype, P; flowers and leaflets loaned) (Fig. 6).

L. multiflorus Desr. *β. grandiflorus* Benth. in Mart., Fl. Brasil. 1: 16. 1859. TYPE: Unknown.
L. multiflorus Desr. *γ. paucifoliatus* Benth. in Mart., Fl. Brasil. 1: 16. 1859 (holotype, K; photo, UMO).

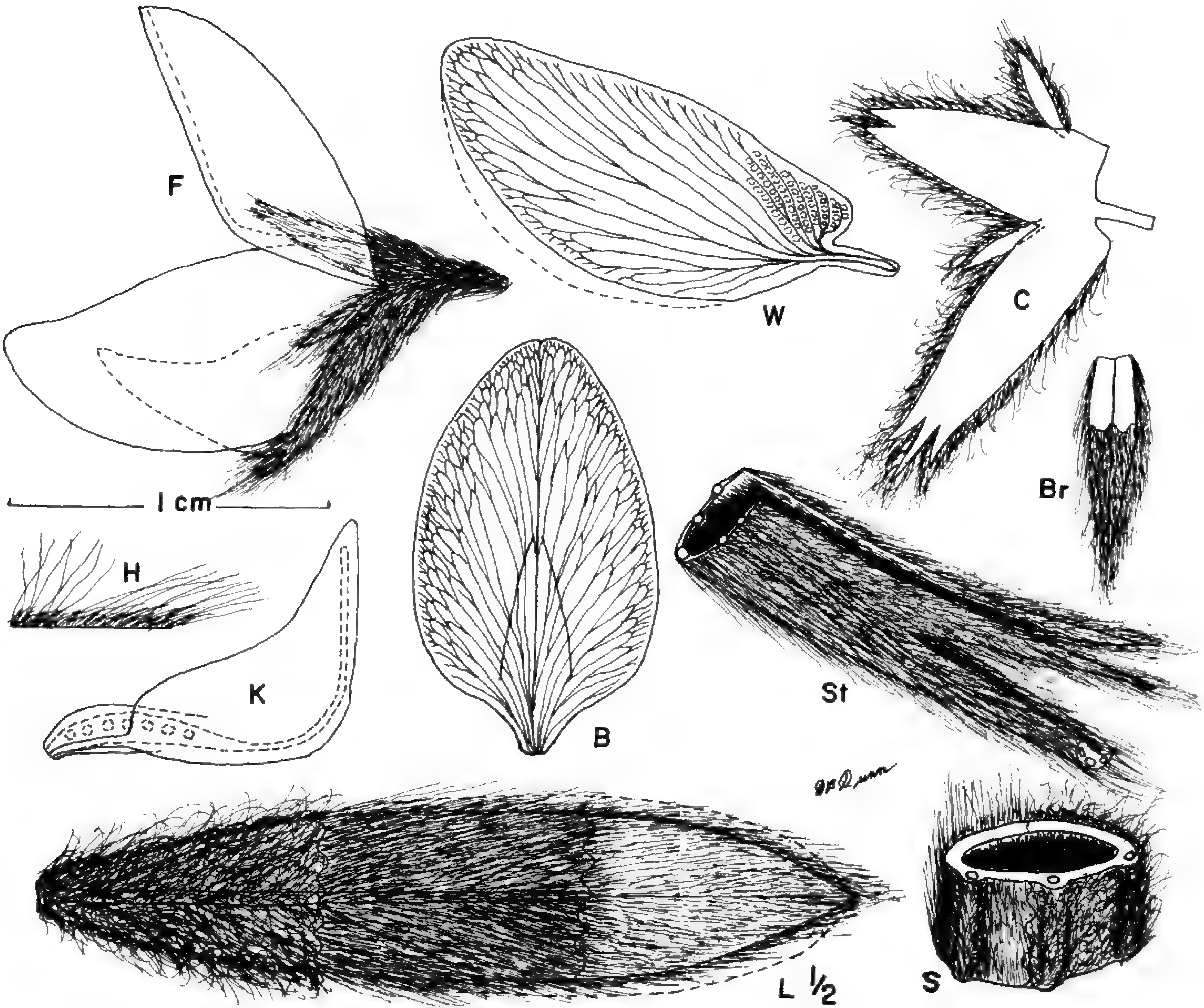
Plants perennial, short lived, branching basal, with the leaves primarily basal, rosette at ground level when the primary raceme reaches anthesis; *stems* elongate some by fruiting, usually only the upper 2–4 internodes, 5–7 mm diam., hollow, somewhat ligneous in age, pubescence tawny in age, the longer hairs 2–4 mm long, appressed sericeous to lanate, with an undercoat of shorter kinky hairs, lower internodes hidden by the imbricated stipules, upper internodes 1.5–2 cm at anthesis, 2.5–3.5 cm in fruit, three ridged from the veins of the petioles; *stipules* densely pubescent dorsally, sparsely pilose ventrally, 15–26 mm long, free tips narrowly triangular-subulate, 8–15 mm long, 2 mm wide, the lower ones imbricate; longest *petioles* 8–11 cm long, persisting into the second season after the leaflets abscise; *leaflets* 5–8, elliptic-oblanceolate, conduplicate but complanate in age, strigose to sericeous above, appressed sericeous to sublanate below, with 4–6 lateral veins on each side of the midrib, visible after removing the hairs below, the largest 4–7 cm long, 6–15 mm wide, tips acute, mucronate; *peduncles* 3–8 cm long, sericeous; *racemes* 8–25 cm long, flowers scattered; *bracts* deciduous, lance-caudate, 6–7 mm long, 1.5–2 mm wide, sericeous dorsally; *pedicels* 2 mm long at anthesis, 5–8 mm long in fruit, densely sericeous; *calyces* densely appressed sericeous outside, glabrous within, the base tapering into the pedicel, not gibbous, lower-lip lance-shaped, 8–11 mm long, 2–3 mm wide, tridentate, the teeth 1.5–2 mm long, central largest, upper-lip 6–8 mm long, 3 mm wide, bifid, the notch 1–1.5 mm deep, lobes 1–1.5 mm wide, lips connate 2 mm, bracteoles lanceolate, 2.5–3 mm long, 0.5–0.8 mm wide, attached close to the margins of the lateral sinuses; *corolla* glabrous; *banner* oblong-ovate, 12–16 mm long, 7.5–10 mm wide, appressed 6–7.5 mm, reflexed 5.5–7 mm, reflexed/appressed ratio 0.88–0.92, the angle 120–130°; *wings* 12–16 mm long, 5–7 mm wide, the claw 2–2.5 mm long, lobe above the claw ca. 2 mm wide; *keel* 2.5–3.5 mm wide in the middle, the angle 95–105°; *ovules* 6–8; *legumes* 4–5.5 cm long, 7–8 mm wide, subapressed sericeous to lanate; *seeds* 5–6 mm long, 4–5 mm wide, tan with brown mottling, funicular pit 1.5 mm diam.

The species occurs in Uruguay and Corrientes, Argentina, growing in sandy or gravelly soils. Only one specimen has been seen from Brazil. The sublanate hairs are sometimes present in this species, which is mostly sericeous.

Representative specimens. ARGENTINA. CORRIENTES: La Cruz, *Burkart 8189* (SE), *Parodi 12548* (BAA, GH).

BRAZIL. SANTA CATARINA: Laguna, *Hatschbach 27205* (NY).

URUGUAY. Colonia, Coll. unknown (BAA #1047);



Lupinus multiflorus Desr.

FIGURE 6. Illustration of the typical structures of *Lupinus multiflorus*. The floral and vegetative parts are drawn to the scale shown from the mean values of a set of several dissections, from the geographic range of the specimens cited. B = banner petal flattened, dorsal view; Br = bract, dorsal surface; Ca = calyx, cut at the left lateral sinus and opened to show the inside surface; F = lateral view of the left side of the flower; K = keel petals, enclosing the staminal tube and pistil, with the mean number of ovules drawn; L = average largest leaflet (drawn at ½ the scale shown), lower portion—lower surface sublanate, middle portion—lower surface sericeous, lateral veins prominent, distal third—upper surface; S = stem structure, first year growth, vascular traces from petiole forming ridges on the internode below; St = stipules, detached at the nodes; W = wing petal.

Florida, Cerro Colorado, Ea. San Pedro, *Gallinal et al. s.n.* (SE# PE 3509); La Valleja, Nico Pérez, *Herter 99791* (MO); Montevideo, *Commerson s.n.* (P); Montevideo, *Barattini s.n.* (MO #1224502), *Berro 1902* (BAF); Independencia, *Osten 5632* (SE), *Isabelle s.n.* (F #153885, NY).

6. **Lupinus albescens** Hooker & Arnott, Bot. Misc. 3: 201. April 1833. TYPE: Uruguay. Unknown, *Baird s.n.* (holotype, K; H-82/77-7, only the two plants on the right side of the herbarium sheet) (Fig. 7).

L. incanus Graham, Edin. Phil. Jour. 16: 178–179. Dec. 1833.

L. parodianus C. P. Smith, Sp. Lup. 208. 1940. TYPE: Argentina. Buenos Aires: Isla Martin Garcia, *Parodi 2530* (holotype, GH; isotype, BAA).

Plants perennial, herbaceous 3–6 dm tall, erect, ramose above; *stems* hollow, ligneous to fistulose, angular, 5–10 mm diam., the hairs yellowish brown, appressed sericeous to sublanate, felt-like mat, longer hairs 2–3 mm long, with a dense undercoat of shorter hairs, upper internodes 2–7 cm long; *stipules* 10–30 mm long, shortest above, both surfaces densely pubescent, subulate-caudate free tips 7–15 mm long, 1.5 mm wide below; *leaves* primarily cauline; *petioles* 7–

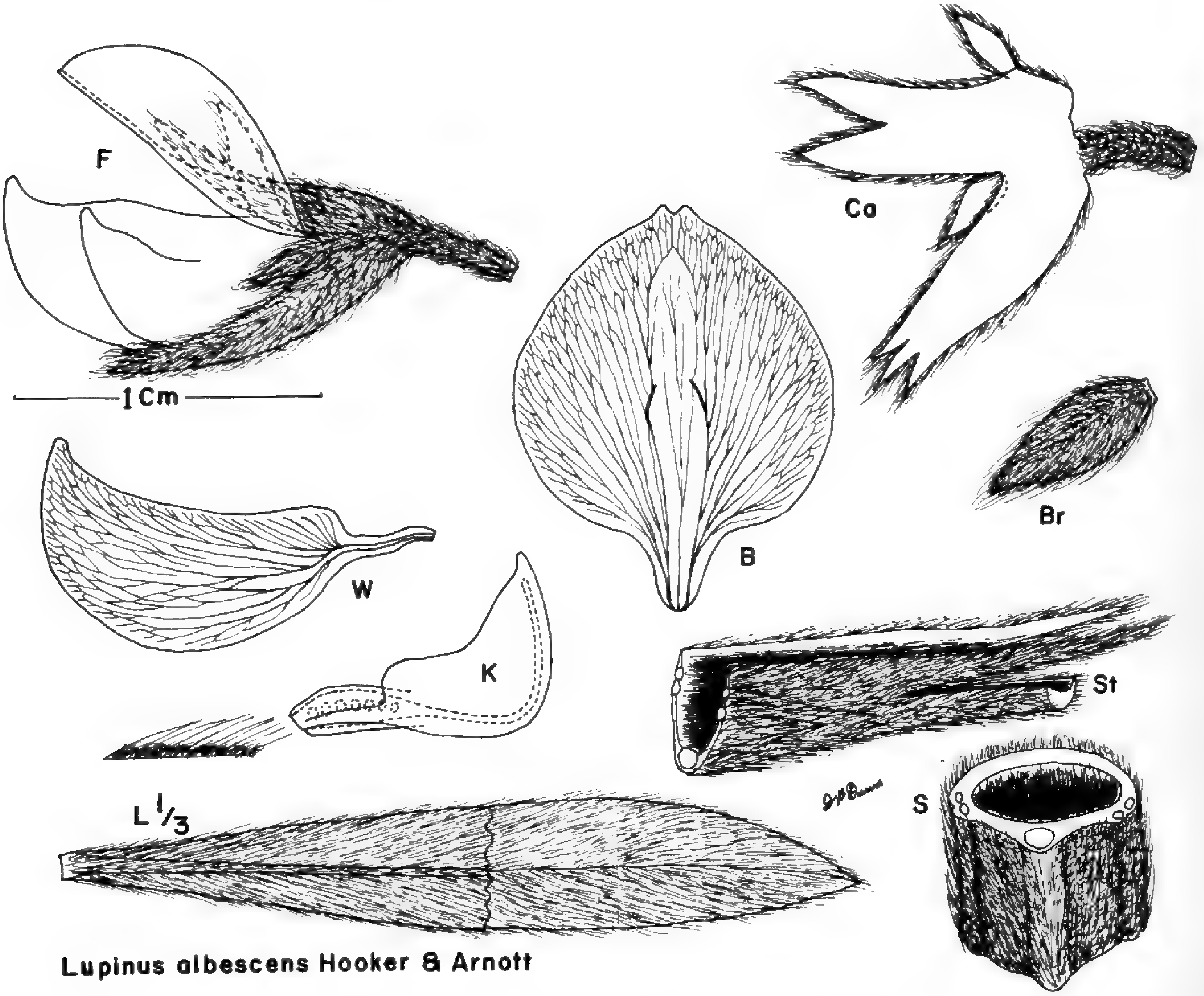


FIGURE 7. Illustration of the typical structures of *Lupinus albescens*. The floral and vegetative parts are drawn to the scale shown, from the mean values of select specimens dissected from within the geographic distribution of the species. B = banner petal flattened, dorsal view; Br = bract, dorsal surface; Ca = calyx, cut at the left lateral sinus and opened to show the inside surface; F = lateral view of the left side of the flower; H = hairs of several sizes; K = keel petals, enclosing staminal tube and pistil, with the mean number of ovules shown; L = average largest leaflet (drawn to ⅓ scale shown), lower half—lower surface, upper half—upper surface; S = stem structure, first year growth, vascular traces form ridges on the internodes below the petioles; St = stipule, detached at the node; W = wing petal.

16 cm long, pubescent, persisting into the second season after the leaflets abscise; *leaflets* 5–12, oblanceolate, conduplicate or complanate in age, densely sericeous to sublanate on both surfaces, the lateral veins 4–6 pairs, visible below after removing the hairs, the abscission occurs at the base of each leaflet and the petioles persist into the second season; *peduncles* 4–8 cm long; *racemes* 9–40 cm long, flowers verticillate to scattered; *bracts* caducous, ovate-caudate, 6–10 mm long, 2–2.4 mm wide, densely sericeous to lanate dorsally; *pedicels* 4–6 mm long at anthesis, 8–10 mm long in fruit; *calyces* densely sericeous to lanate outside, glabrous within, the base not gibbous above, lower-lip lanceolate, 7–10 mm long, 2.5–4.5 mm wide, tip tridentate, the central tooth 2 mm long, 0.6 mm wide, lateral teeth shorter, upper-lip 6–9 mm long, bifid, the notch 1.5–3.5 mm deep, lips connate 1.5–2.5 mm, bracteoles lanceolate, 2–3 mm long, 0.8–1 mm wide, attached from near the lip to ca. 1 mm below the lips of the lateral sinuses; *corolla* glabrous; *banner* obovate, 9–14 mm long, 8–11 mm wide, tip bidentate, the teeth 0.5 mm long, 0.8 mm wide, the angle 130–150°; *wings* 9.5–14.5 mm long, 4.5–6.5 mm wide, the tip with a small tooth-like lobe, the claw 2–3 mm long, lobe above the claw 1.5–2 mm wide; *keel* 3–4 mm wide in the middle,

the angle 80–88°; *ovules* 7–8; *legumes* 6–8 cm long, 8–10 mm wide, densely sericeous; *seeds* 5.8–6.5 mm long, 4.5–5.7 mm wide, sides convex but seeds rather flat, generally dark brown to blackish, stippled and mottled with areas, occasionally more tan and buff than darker colors, funicular pit with large projecting rim, the pit oval 1.2–1.6 mm long.

The species occurs in Uruguay and northeastern Argentina, where it grows in sandy soils and dunes. It is common near Paraná River and on islands. It appears to be the most common perennial species in eastern Argentina. The erect habit clearly separates it from *L. aureonitens,* which also has a tooth at the tip of the wings.

The Hooker Herbarium at Kew has three herbarium sheets (H82/77–6; H82/77–7; H82/77–8) with plants labeled as *L. albescens* Hook. Only the H82/77–7 can be considered the holotype of the species because it specified "Banda Oriental, Baird," as Hooker and Arnott cited in the original description. The two plants and the leaves on that herbarium sheet are *L. albescens,* but the inflorescence in the left upper corner belongs to another species.

Representative specimens. ARGENTINA. BUENOS AIRES: Isla Martín Garcia, *Cabrera 2874* (SI), *Parodi 2526* (CTES), *2530* (BAA, GH). CHACO: San Fernardo, Antequera, *Krapovickas & Cristobal 20066* (CTES, GH); Isla Soto, *Burkart 30853* (CTES, SE), *Schinini 16157* (CTES); Acceso al puente Manuel Belgrano, *Schinini 16024* (CTES). CORRIENTES: Capital, Alrededores de la Ciudad de Corrientes, *Alboff s.n.* (NY); Puente Pesoa, *Fernandez 205* (CTES); Río Riachuelo, *Crovetto 11116* (CTES); Bella Vista, 10 km S of Bella Vista, *Schinini & Ahumada 15918* (CTES, MO); Empedrado, "Las Tres Marias," Rio Paraná, *Pedersen 3049* (GH, MO); Río Empedrado, ruta 12, *Krapovickas et al. 19959* (CTES); Esquina, Isla frente a Esquina, *Krapovickas et al. 26899* (BAA, CTES, MO); Ituzaingó, Ituzaingó, *Arbo et al. 2129* (CTES), *Daciuk 4* (CTES), *Holmberg 219* (SI), *Krapovickas et al. 24471, 24472* (CTES), *Meyer 6038* (GH, U), *Spegazzini 10057* (SI); Villa Olivari, *Schinini & Vanni 15663* (CTES); Paso de los Libres, Paso de los Libres, *Burkart et al. 29917* (CTES, SI); Laguna Mansa, *Schinini 7604* (CTES, MO), *7730* (CTES), *Faggi et al. s.n.* (BAA #13983, CTES); Goya, Goya, *Boelcke 1510* (SI). ENTRE RIOS: Federacion, Santa Ana, *Burkart 28652* (SI), *29337* (CTES); 8 km N, *Burkart 22588* (SI). SANTA FE: Capital, San José del Rincón, *Burkart 9056* (SI), *Ragonese 2441b, 3617* (SI); Altoverde, *Donnet 2088* (SI); Isla Timbó, en el cruce de balsa de Santa Fe a Paraná, *Burkart et al. 23699* (SI, UC); Isla Pacará, frente a la capital, *Boelcke & Correa 9103* (BAA, CTES); Rosario, Rosario, *Burkart 8774* (F).

PARAGUAY. Puerto Bartoni, alto Paraná, *Jimenez 7884* (SI).

URUGUAY. Colonia, Riachuelo, *Cabrera 3938* (F); San José, Arazoti, *LeGrand 1697* (SI); Soriano, Arenal Grande, *Cabrera 2571* (NY); unknown, *Baird s.n.* (K, #82/77–7, specimen on right only).

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SYSTEMATICS AND REPRODUCTIVE BIOLOGY OF THE CENTRAL AMERICAN SPECIES OF THE *APHELANDRA PULCHERRIMA* COMPLEX (ACANTHACEAE)[1]

LUCINDA A. MCDADE[2]

ABSTRACT

Aphelandra (Acanthaceae) is a neotropical genus of about 170 species of herbs, shrubs, and small trees. The *A. pulcherrima* complex is a monophyletic group of about 40 species distinguished by the presence of bracteal nectaries and a unique corolla morphology. Thirteen Central American species belonging to this complex are recognized based on herbarium, field, and greenhouse studies; pollen morphology; and artificial hybridizations. The genus *Aphelandra* and the *A. pulcherrima* complex probably originated in South America. Central American species have evolved from South American or intermediate Central American ancestors. The species treated here are diffusely branched shrubs or sparsely branched, monocaulous plants. They are found in primary forest to disturbed secondary and edge habitats, and from low to middle elevations. Field observations indicate that all species produce odorless flowers that last a single day, produce copious, rather dilute nectar, and are hummingbird pollinated. All but *A. deppeana* are pollinated by large hermit hummingbirds (Trochilidae: Phaethorninae) or hermit-like species. The long, decurved bills and traplining foraging habits of these birds correspond to the floral morphology and spatial distribution of the plants. Chromosome data are not systematically useful within the group studied. All 12 species for which counts were obtained have $n = 14$ chromosomes. The 13 species are variable palynologically, showing three distinct pollen types, as well as significant variability in pollen size (length and width). Pollen characters resolve all but two species and provide evidence for patterns of phylogenetic relationships among the species. Although hybrids between many species pairs can be readily synthesized, hybrids in nature are rare. Four isolating mechanisms in addition to allopatry and intersterility are identified as potentially important among Central American Aphelandras. The paucity of naturally occurring hybrids is in most cases due to more than one type of barrier. Putative hybrids between *A. sinclairiana* and *A. gracilis,* and between *A. sinclairiana* and *A. golfodulcensis* have been found in the field. Artificial disturbance has apparently been important in creating situations favorable for hybridization between at least one of these pairs of species. Phylogenetic analysis identifies two main lineages within the group: Group I (*A. terryae, A. sinclairiana, A. storkii, A. gracilis, A. golfodulcensis, A. panamensis,* and *A. deppeana*) and Group II (*A. lingua-bovis, A. leonardii, A. laxa, A. campanensis, A. hartwegiana,* and *A. darienensis*). These results are in accord with data from artificial hybridizations, except that phylogenetic analysis indicates that the species of Group II are as closely interrelated as those of Group I, whereas crossability indices suggest that these species are much more distantly related. Genetic incompatibility may be an important barrier to interbreeding between species of Group II such that the results of artificial hybridizations do not provide reliable estimates of the degree of relationship among these species.

Aphelandra (Acanthaceae) is a morphologically diverse genus traditionally distinguished by its lack of cystoliths and possession of four monothecous anthers, bilabiate corollas, and elongate, tricolpate pollen grains. The more than 160 species are confined to the New World tropics, ranging from northern Argentina and Bolivia to northern Mexico. Over two-thirds of the taxa are confined to South America with notable concentrations of species in southeastern Brazil, Co-

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lombia, and Peru (Wasshausen, 1975). Thirty to 40 species are found in Central America and Mexico.

Aphelandra has been treated in several regional floras (Leonard, 1938, 1953, 1954; Gibson, 1974; Durkee, 1978), and in a recent monograph (Wasshausen, 1975). Knowledge of many of the species and of phylogenetic relationships among species, however, remains fragmentary. Many taxa are known only from one or very few, frequently incomplete specimens, and data from field and experimental studies are essentially lacking.

This study is a systematic investigation of the Central American species of the *Aphelandra pulcherrima* complex. The complex is an apparently monophyletic assemblage of about 40 species. As treated here, 13 of these species occur in Central America. New data from several sources have been gathered: comparative morphology of living plants, field observations, chromosome counts, palynology, studies of floral biology, and artificial hybridizations. The taxonomic treatment is based on these data and portrays the best hypothesis for the phylogenetic relationships among these species.

SYSTEMATIC POSITION AND TAXONOMIC HISTORY

The Acanthaceae are a large, predominantly tropical family with about 250 genera and 2,600 species (Long, 1970; Heywood, 1978). The family is pantropical with four centers of distribution: Indomalaysia, Africa, Brazil, and Central America (Long, 1970). Whereas most acanth genera are restricted to one continent, a few are pantropical (e.g., *Justicia, Ruellia*).

Taxonomists have almost unanimously considered Acanthaceae to be closely related to Scrophulariaceae. These two families, along with Bignoniaceae, Lentibulariaceae, Gesneriaceae, Pedaliaceae, several other small families, and a varying group of families of disputed affinities, have usually been classified together at the ordinal level (e.g., Scrophulariales: Stebbins, 1974; Takhtajan, 1969; Cronquist, 1968, 1981; Bignoniales: Thorne, 1976; Tubiflorae: Engler, 1964; Personales: Hutchinson, 1973). Although the phylogenetic relationships of all of these families have not yet been fully studied, it is likely that several families are not strictly monophyletic (sensu Hennig, 1966: strictly monophyletic taxa must include all and only the descendants of a common ancestral species). For example, because Orobanchaceae are probably derived from within Scrophulariaceae, the latter family is not strictly monophyletic. Confident recognition of strictly monophyletic families and placement of disputed groups must await phylogenetic analysis at the ordinal level.

Acanthaceae provide an excellent example of the unresolved relationships encountered in the order. Considerable disagreement exists as to the taxonomic placement of the groups recognized by Lindau (1895) as subfamilies of Acanthaceae: Nelsonioideae, Thunbergioideae, Mendoncioideae, and Acanthoideae. Bremekamp (1953, 1965) systematically reviewed the evidence for taxonomic placement of these groups and concluded that Nelsonioideae should be transferred to Scrophulariaceae (near Rhinantheae) and that the remaining three subfamilies should be recognized at the familial level. Mohan Ram and Wadhi (1964, 1965) favored retention of Nelsonioideae in Acanthaceae on the basis of embryological characters, and emphasized similarities between this group and Andrographideae. Thunbergioideae are embryologically distinct from Acanthaceae, justifying, in their view, Bremekamp's recognition of the group as a family. Embryological data are lacking for Mendoncioideae. After morphological and anatomical study of the genera comprising Nelsonioideae (sensu Lindau), Hossain (1971) returned this group to Acanthaceae as a tribe (Nelsonieae) near Andrographideae. Hossain also took exception to Bremekamp's removal and elevation to familial status of Mendoncioideae and Thunbergioideae, but presented no new evidence. Cuticular studies demonstrate that all four of Lindau's subfamilies share diacytic stomates (Ahmad, 1974a, 1974b). This evidence suggests recognition of a monophyletic taxon composed of the four groups, but diacytic stomates occur sporadically throughout the Scrophulariales (Metcalfe & Chalk, 1950). Shared possession of odd panduriform trichomes suggests a relationship between Thunbergioideae and Nelsonioideae (Ahmad, 1978). Based on a study of epidermal hairs of 109 species in 39 genera from all subfamilies, Ahmad (1978) favored retention of Lindau's subfamilies within Acanthaceae. There is thus considerable disagreement as to the exact familial limits of Acanthaceae, as well as lack of consensus regarding relationships among the four clearly circumscribed groups.

There is little doubt, however, that Acantha-

TABLE 1. Characters distinguishing Bremekamp's subfamilies of Acanthaceae.

Character	Acanthoideae	Ruellioideae
Shoots	Never articulated	Always articulated
Cystoliths	Absent	Present[a]
Stamens	4	2 or 4
Anthers	Monothecous[a]	At least 2 bithecous
Pollen	Colpate	Colporate or porate[a]
Tribes included	Hasselhoffieae Rhombochlamydeae Stenandriopsideae Aphelandreae Acantheae	Trichanthereae Whitfieldieae Louterideae Ruellieae Lepidagathideae Andrographideae Justiceae

[a] Hypothesized derived character states.

ceae (sensu Bremekamp, Lindau's Acanthoideae) are a closely related group sharing several derived characters: ovary bilocular with two longitudinal rows of ovules in each locule, capsule loculicidal and explosively dehiscent with the exalbuminous seeds supported by well-developed retinacula. Whether Acanthaceae thus delimited are strictly monophyletic will be determined only by analysis of sister group relationships at the family level within the order.

Several systems of classification for subdivision of Acanthaceae (sensu Bremekamp) have been proposed, with emphasis on pollen characters. Nees von Esenbeck (1847a) recognized 11 tribes within his "suborder" Echmatacantheae, which included the genera currently placed in Acanthaceae sensu stricto. Bentham and Hooker (1876) divided these genera among three tribes: Ruellieae, Acantheae, and Justiceae. Lindau's (1895) Acanthoideae was divided into two "series" (= supertribes): Contortae (corolla aestivation usually convolute) with seven tribes, and Imbricatae (corolla aestivation usually imbricate) with ten tribes. More recently, Bremekamp (1965) recognized two subfamilies, Acanthoideae and Ruellioideae, that are distinguished by differences in several characters (Table 1), and comprise five and seven tribes, respectively. Although intrafamilial classification of Acanthaceae has not been a major aspect of this study, I provisionally accept Bremekamp's system as best representing the probable phylogenetic relationships among genera in this family. Both subfamilies are distinguished by apparently derived character states (e.g., monothecous anthers in Acanthoideae, cystoliths and colporate or porate pollen in Ruellioideae).

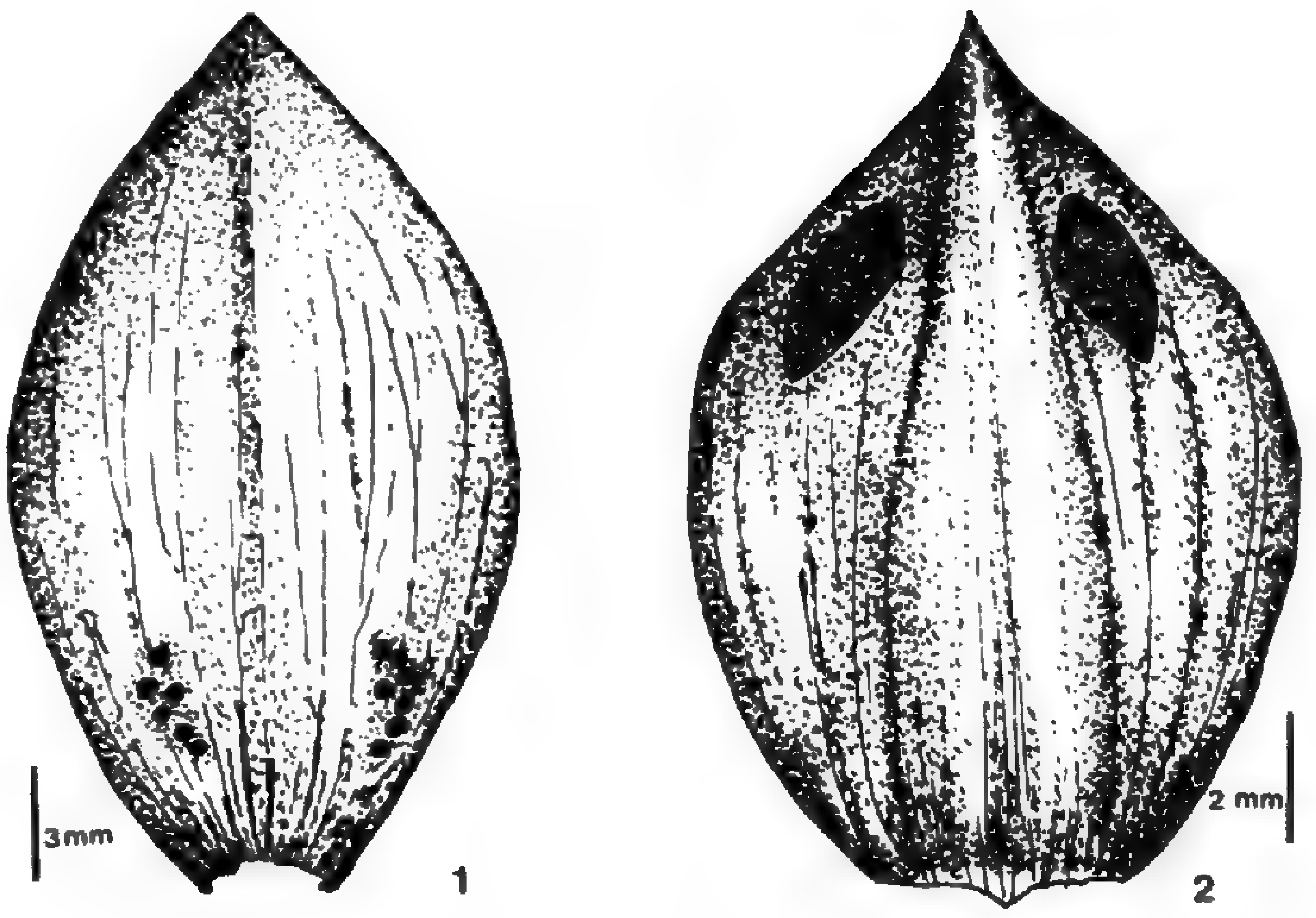
Of the tribes comprising Bremekamp's Acanthoideae, the Acantheae and Aphelandreae are well-defined groups of genera that share one or more derived character states (Bremekamp, 1965) and are probably monophyletic. The remaining tribes, however, bear further investigation. All three resemble either Acantheae or Aphelandreae and are separated from these only by one or a few character states that appear to be primitive within the subfamily. Stenandriopsideae, for example, are separated from Aphelandreae by possession of a subactinomorphic corolla (versus a strongly zygomorphic corolla in the latter tribe), and from Acantheae by lack of the characteristic incision at the adaxial side of the corolla. Further study of these small, geographically restricted groups might provide evidence that they are relatively primitive members of either Acantheae or Aphelandreae. These latter two tribes are probably sister groups (sensu Hennig, 1966), but the phylogenetic relationships within the subfamily bear further study.

There is little disagreement as to taxonomic placement of *Aphelandra*. It is related to the Old World genus *Acanthus* and these, together with a group of allied genera, have been placed in the single tribe Acantheae (Bentham & Hooker, 1876) or segregated into two related tribes. Nees von Esenbeck (1847a) recognized two adjacent tribes, Aphelandreae and Acantheae, in his "series" (= supertribe) Imbricatae. Bremekamp (1965) follows this alignment, placing both tribes in his subfamily Acanthoideae as discussed above (Table 1). Neotropical genera allied with *Aphelandra* in Aphelandreae include *Cyphacanthus, Neriacanthus, Encephalosphaera, Stenandrium,* and *Holographis*. The phylogenetic relationships among these genera, however, have yet to be rigorously investigated and one or more might be more correctly placed within *Aphelandra*. *Encephalosphaera,* for example, has been distinguished from *Aphelandra* only on the basis of pollen characters. A broader palynological survey of *Aphelandra* (Wasshausen, 1975; McDade, unpubl. data) indicates that pollen variability is much greater than was known to Lindau when he described *Encephalosphaera*.

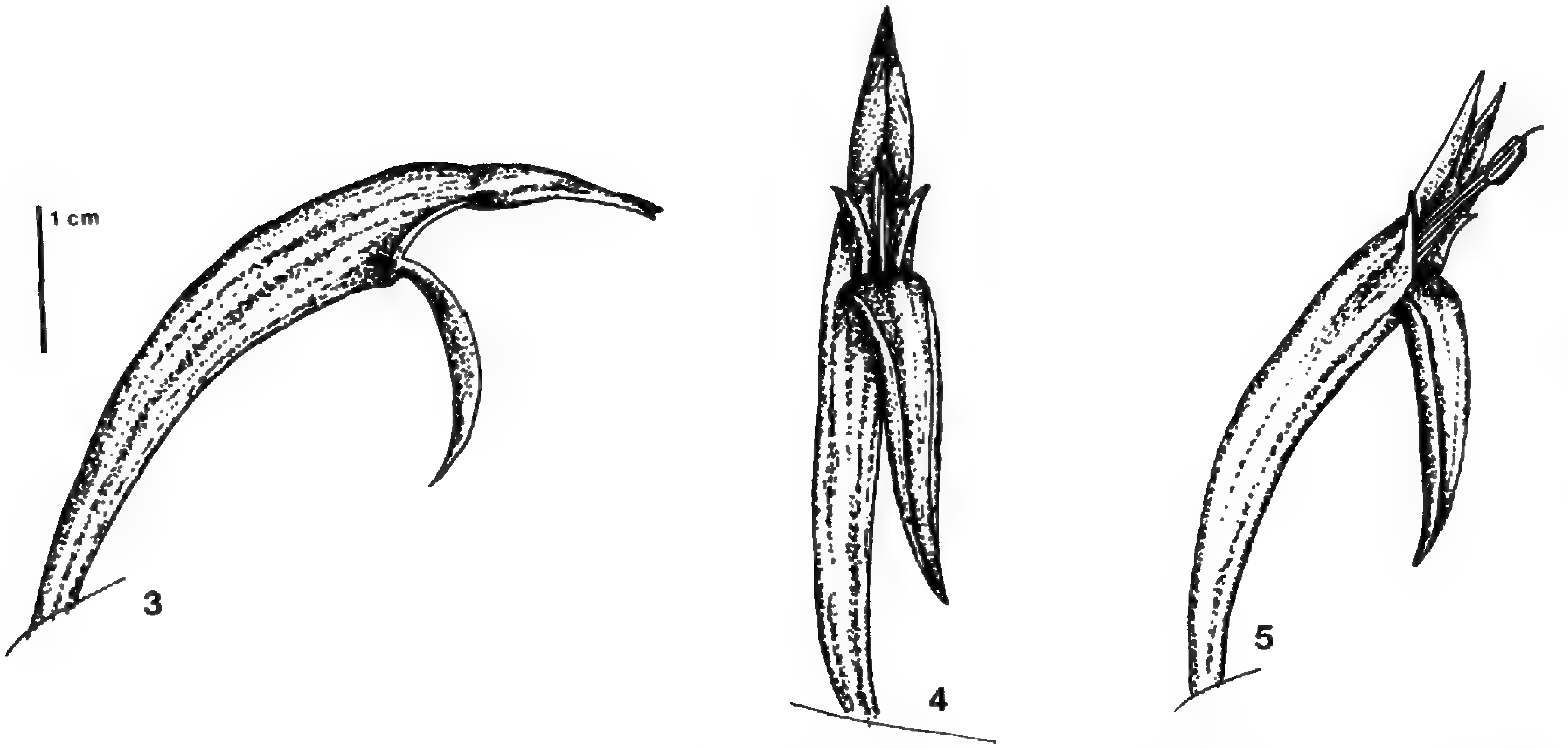
Plants currently placed in *Aphelandra* were first described in *Justicia* by Jacquin in 1762 and Vahl in 1794 (Wasshausen, 1975). *Aphelandra* was first proposed as a distinct genus by Robert Brown (1810) to include *J. pulcherrima* Jacq., *J. scabra* Vahl, and *J. cristata* Jacq. These species were distinguished from *Justicia* by their four unilocular anthers and calyx of five unequal segments. Rafinesque (1838) appears to have recognized the same differences when he erected the genus *Amathea* based on *J. pulcherrima* Jacq. In the first half of the nineteenth century, five additional genera were described that have since been considered congeneric with *Aphelandra*: *Synandra* Schrader (1821), *Strobilorhachis* Klotzsch (1839), *Hydromestus* Scheidweiler (1842a), *Hemisandra* Scheidweiler (1842b), and *Lagochilium* Nees von Esenbeck (1847a). A more detailed discussion of these segregate genera and relevant taxonomic decisions is found in Wasshausen (1975).

Many species have been described in *Aphelandra,* with notable contributions by Nees von Esenbeck (1847a, 1847b), Lindau (1893, 1895, 1904), Leonard (1938, 1953, 1961), and Wasshausen (1973a, 1973b, 1975). A recent revision of the entire genus (Wasshausen, 1975) recognized 165 species and two varieties. Two additional species were described by Durkee (1978). Three new species were recognized in the course of this study (McDade, 1982) and a previously recognized species is reduced to synonymy herein. Several regional treatments of the genus are available, including those for Costa Rica (Leonard, 1938), Colombia (Leonard, 1953), Guatemala (Gibson, 1974), and Panama (Durkee, 1978).

In the only published supraspecific classification of this large and variable genus, Nees von Esenbeck (1847a) recognized two sections based on relative length of the middle and lateral lobes of the lower corolla lip. In *Stenochila,* the lateral lobes were less than one-fourth as long as the middle lobe. Section *Platychila* included species with lower corolla lobes more nearly equal. The latter section was divided further into two subsections, *Genuinae* and *Acanthoideae,* with entire and serrate or pinnately lobed leaves, respectively. Although Lindau (1895) followed Nees von Esenbeck's system in his treatment of the genus, subsequent systematists have not. It is apparent that there are several monophyletic groups within the genus, each of which can be recognized by several derived character states [e.g., the *A. pulcherrima* complex referred to by Leonard (1953) and treated in part here]. Several difficulties, however, have thus far frustrated attempts to devise a valid infrageneric classification of the genus. Many species are poorly known and are represented in herbaria by one or few specimens, which frequently lack mature inflorescences and flowers. In addition, several aspects of corolla morphology (including relative size and degree of fusion of the lobes, morphology of the upper lip at anthesis, and position of the anthers in relation to the corolla) are poorly preserved in most herbarium specimens and difficult to observe. Establishment of a natural supraspecific classification of the genus *Aphelandra*



FIGURES 1, 2. Floral bracts and bracteal nectaries in the *Aphelandra pulcherrima* complex.—1. Few (1–10), individually large, circular to oval glands characteristic of species of Group I: (1) *A. terryae,* (2) *A. sinclairiana,* (3) *A. storkii* (figured), (4) *A. gracilis,* (5) *A. golfodulcensis,* (6) *A. panamensis,* and (7) *A. deppeana.*—2. Oblong patches composed of many (>100) minute glands characteristic of species of Group II: (8) *A. lingua-bovis,* (9) *A. leonardii,* (10) *A. laxa,* (11) *A. campanensis,* (12) *A. hartwegiana* (figured), and (13) *A. darienensis.*



Figures 3–5. Corolla morphology in the *Aphelandra pulcherrima* complex.—3. Lateral view, anthers and stigma concealed within folded lobes of upper lip.—4. Frontal view, note reduction of lateral lobes of lower lip, and anther pocket formed by folding of lobes of upper lip.—5. Anther pocket opened to reveal anthers and exserted stigma, note bilobed upper lip.

will be a valuable contribution to systematic knowledge of Acanthaceae.

Delimitation of the *Aphelandra pulcherrima* Species Complex

This group of about 40 species forms a morphologically well-defined, monophyletic complex, with all members sharing several derived features including extrafloral nectaries on the bracts and a distinctive floral morphology. Nectaries are borne laterally and usually medially along both margins of the abaxial surface of the floral bracts, and are of two distinct types: clumps of 1–10 relatively large (0.5–1.25 mm diam.) glands, or oblong patches (several mm diam.) of many (>100) extremely minute glands (Figs. 1, 2, respectively). Nectar production begins soon after the inflorescences are initiated and continues throughout the flowering period. Nectar is consumed by ants of many species and ants are rarely absent from inflorescences. Several unusual features of the corolla result in a very distinctive structure: the edges of the bilobed upper lip are laterally folded to form a pocket that par-

Table 2. Central American members of the *Aphelandra pulcherrima* species complex.

Species (Abbreviation)	Range
1. *A. terryae* Standley (TE)	E Panama and Colombia
2. *A. sinclairiana* Nees (SI)	Central Panama
3. *A. storkii* Leonard (ST)	Limón and Heredia, Costa Rica
4. *A. gracilis* Leonard (GR)	Central Panama
5. *A. golfodulcensis* McDade (GO)	SW Costa Rica and adjacent Panama
6. *A. panamensis* McDade (PA)	Central Panama
7. *A. deppeana* Schldl. & Cham. (DE)	S Mexico to N South America
A. dukei Wassh. (= *A. deppeana* Schldl. & Cham.)	
8. *A. lingua-bovis* Leonard (LB)	SW Costa Rica, Panama, and Colombia
9. *A. leonardii* McDade (LE)	Costa Rica and Panama
10. *A. laxa* Durkee (LA)	San Blas, Panama
11. *A. campanensis* Durkee (CA)	Central Panama
12. *A. hartwegiana* Nees ex Benth. (HA)	E Panama and Colombia
13. *A. darienensis* Wassh. (DA)	Darién, Panama

tially or completely conceals the anthers at anthesis, and the lateral lobes of the lower corolla lip are extremely reduced (to only 1–2 mm long) and flattened in a plane perpendicular to the tube so that they almost contact one another across the mouth of the tube (Figs. 3–5). This closed-mouth, concealed-anther morphology functions in pollination. A hummingbird inserts its bill into the corolla by using the tip of the bill to force apart the lateral corolla lobes. As the broadest, basal portion of the bill enters the corolla, the upper lip opens, bringing the anthers and exserted stigma into contact with the bird's head.

No other species of *Aphelandra* have both bracteal nectaries and the distinctive corolla morphology that characterize this complex. Shared possession of these derived morphological features provides strong evidence for a monophyletic origin of this group of species. Three South American species outside this complex possess bracteal nectaries: *A. lamprantha* Leonard, *A. impressa* Lindau, and *A. hylaea* Leonard. These species are probably the closest living relatives of the *A. pulcherrima* group, with one or more constituting the sister group of the *A. pulcherrima* complex.

The species belonging to this complex are identified in Appendix A. Nine species restricted to Central America and four found both in Central and northern South America are recognized as belonging to the *A. pulcherrima* complex (Table 2). The comparatively recent origin of the Central American isthmus compared to the older continent of South America, along with the clear Gondwana distribution pattern of Acanthaceae and the presence of close relatives of *Aphelandra* in Africa suggest a South American origin of the genus and of this species complex. The wholly Central American species are thus derived directly or through intermediate Central American ancestors from South American ancestors. Species found in both areas probably represent extensions of older South American ranges to include adjacent eastern Central America.

COMPARATIVE MORPHOLOGY

Habit and branching. The species of *Aphelandra* treated here have two distinct growth forms that are associated with distinctive arrangements of the inflorescences. Individuals of six species are relatively low plants characterized by a very soft-wooded central axis that branches only after differentiation of the growing point into an inflorescence (Fig. 6). The one or two lateral branches subsequently formed are equal and, again, branch only after flowering. This pattern has been described by Troll (1935) as dichasial sympodial branching. Because the stems are soft-wooded (sometimes rather succulent), the branches invariably break after at most three branching points. As a consequence, individuals of species with this monocaulous growth form are mostly 1–2.5 m tall and very rarely larger than 3 m. The remaining seven species form true shrubs with generally profuse lateral branching (Fig. 7). Individuals of four species are soft-wooded shrubs that attain heights of 4–5 m. *Aphelandra gracilis* and *A. panamensis* are small trees to 7 m tall and 12 cm DBH. Individuals of *A. deppeana* tend to sprawl, forming horizontal branches close to the ground, and reach heights of 3–4 m. Plants of all species retained their characteristic habits when grown in greenhouses and

FIGURE 6. Monocaulous habit characteristic of six Central American species of the *Aphelandra pulcherrima* complex: (3) *A. storkii*, (8) *A. lingua-bovis*, (10) *A. laxa*, (11) *A. campanensis*, (12) *A. hartwegiana*, and (13) *A. darienensis*. (*Aphelandra storkii*, Finca La Selva, Heredia, Costa Rica.)

Figure 7. Shrubby habit characteristic of seven Central American species of the *Aphelandra pulcherrima* complex: (1) *A. terryae,* (2) *A. sinclairiana,* (4) *A. gracilis,* (5) *A. golfodulcensis,* (6) *A. panamensis,* (7) *A. deppeana,* and (9) *A. leonardii.* (*Aphelandra panamensis,* Cerro Jefe, Panamá, Panama.)

were unusual only in their tendency to flower profusely while very small.

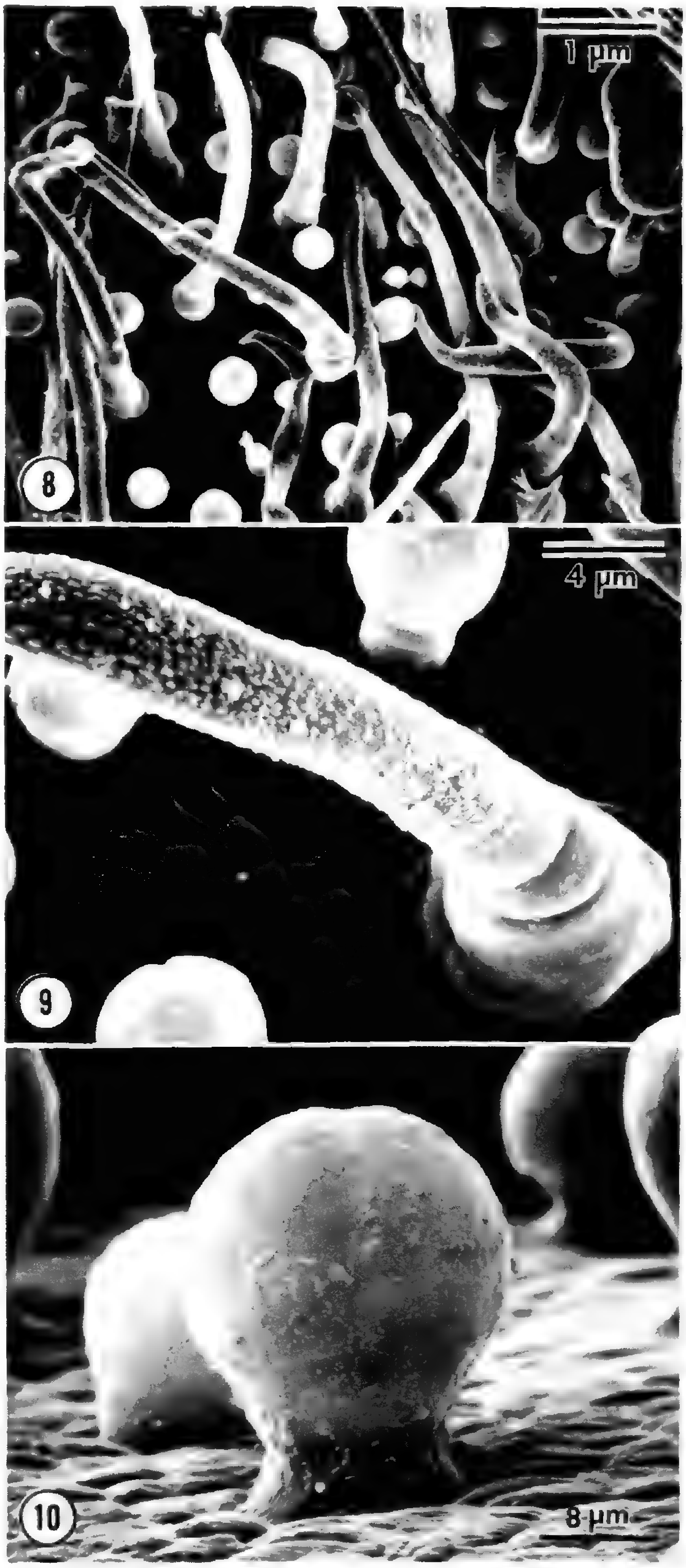
Leaves. All species treated here have opposite, isophyllous leaves, with the exception of infrequent alternate-leaved individuals (or branches of individuals) of *A. terryae* and *A. golfodulcensis.* The leaves of most species have a well-differentiated blade and petiole, but those of *A. panamensis* and occasionally *A. deppeana* are sessile. Petioles are slender and similar in vestiture to the veins of the abaxial leaf surface. Leaves are simple, with entire, undulate or crenulate margins, and range from linear (in occasional plants of *A. deppeana*) through elliptic (most species) to obovate. Texture of the blades ranges from membranous to coriaceous to very slightly succulent, and from glabrous through moderately scabrous to densely pubescent. Trichomes of the adaxial and abaxial leaf surfaces are generally identical in type and length, but differ in density. Venation is pinnate with the costa generally depressed below the adaxial surface and protruding on the abaxial surface. Leaf surfaces are generally plane, but are slightly bullate in *A. storkii* and occasional individuals of *A. sinclairiana.* Except for variability in size, leaf variation over the range of each species appears to be minimal. However, Costa Rican plants of *A. leonardii* have leaves that differ from those of Panamanian plants in shape (narrower), vestiture (trichomes more dense), and texture (membranous rather than slightly succulent).

Vestiture. Two types of trichomes occur in the species treated here. Simple, uniseriate trichomes composed of 1–3 thin-walled basal cells, and a long (rarely septate), thick-walled terminal cell(s) are found in all species on at least some structures (Figs. 8, 9). The terminal cells are usually smooth, but may be short barbellate. In addition, multicellular, capitate to turbinate, presumably glandular trichomes are found in many species (Fig. 10). Trichomes of both types are widely distributed in Acanthaceae (Ahmad, 1978; Singh & Jain, 1975). Of taxonomic significance in the species treated here are the density, length and posture of simple trichomes on different plant structures, as well as the presence or absence of glandular trichomes.

Inflorescences. *Aphelandra* has spicate inflorescences with distichously arranged flowers, each subtended by a floral bract and two bracteoles. In the species treated here, two distinct arrangements of spikes are found that are correlated with plant habit. Species that branch freely to form true shrubs produce many spikes in a terminal, paniculate inflorescence. In species that branch rarely or not at all, inflorescences are simple or rarely composed of up to five spikes. Individual spikes of shrubby species are relatively short (10–20 cm) and few-flowered (12–40 per spike). Those of sparsely branched species are much longer (to 70 cm) and have many more flowers (to over 200 per spike). The arrangement of flowering spikes is of taxonomic significance and may have important implications for plant breeding systems as it relates to the number of flowers open daily per plant.

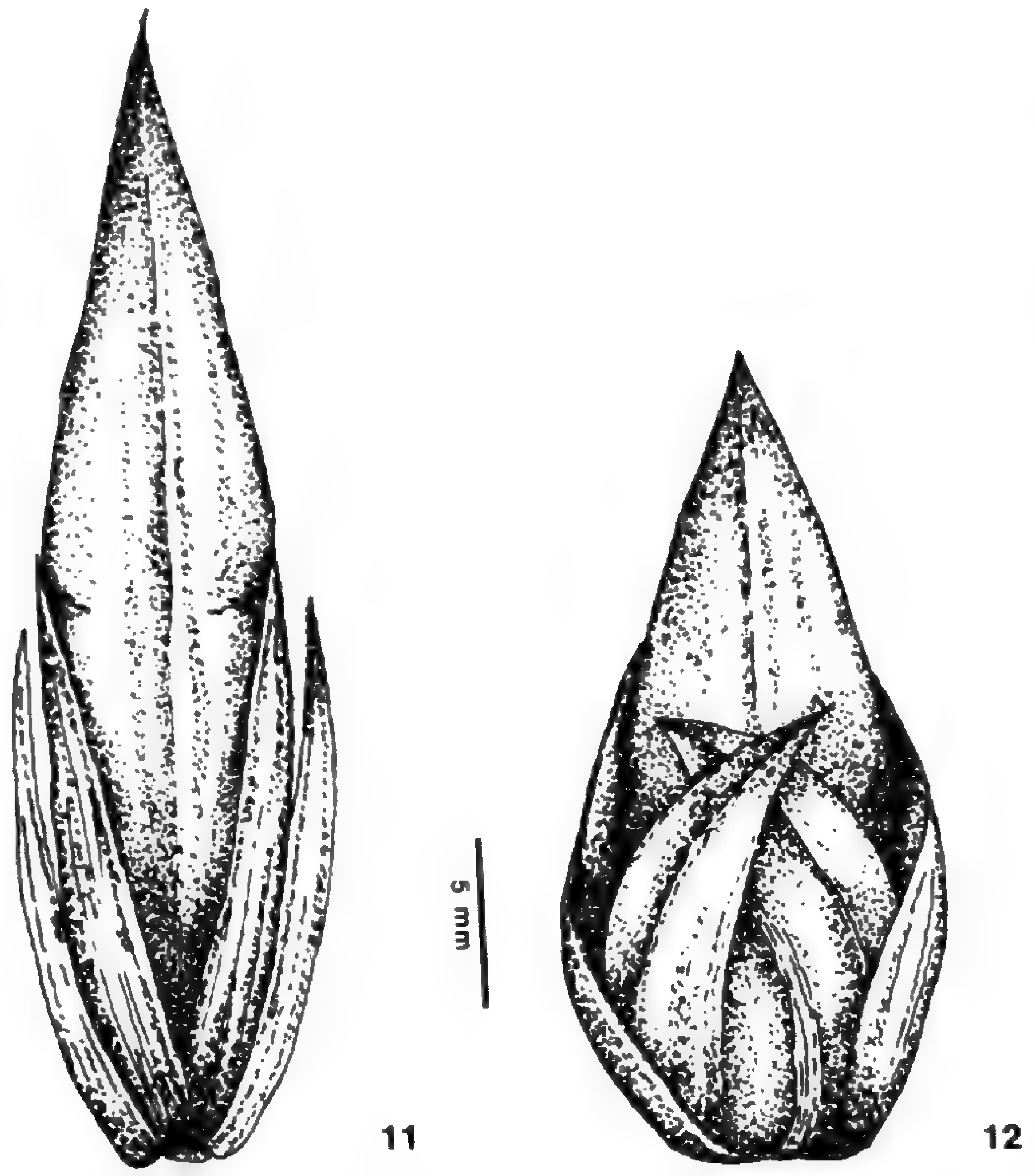
Floral bracts. The usually large and conspicuous bracts that subtend flowers of *Aphelandra* are highly variable among species and are traditionally important in identification systematics (Leonard, 1953; Wasshausen, 1975). All species treated here have extrafloral nectaries located laterally and usually medially along both margins of the floral bracts. As described above, two distinct types of nectaries occur (Figs. 1, 2). Additional taxonomically significant features of floral bracts are size, texture, color, apical shape, position of the nectaries and disposition along the rachis.

Species with nectaries composed of a few, large glands have bracts that are membranous and divergent from the rachis. *Aphelandra panamensis* and *A. deppeana* share imbricate bracts that are green and marginally toothed. *Aphelandra gracilis* and *A. golfodulcensis* have entire, green to dull orange, rather small and narrowly ovate bracts that are barely imbricate in the latter and quite lax in the former. The remaining species, *A. terryae, A. sinclairiana,* and *A. storkii,* have orange bracts that are closely imbricate. Bracts of *A. sinclairiana* and *A. terryae* are obtuse at the apex whereas those of the remaining species are acute. Bract size is an important character among these species, ranging from 5 mm long in *A. gracilis* to 25–30 mm long in *A. storkii. Aphelandra storkii* differs from the other species sharing large glands in having bracts that are coriaceous.



FIGURES 8–10. Trichomes of Central American species of the *Aphelandra pulcherrima* complex (scanning electron photomicrographs, *A. hartwegiana, McDade 425,* DUKE).—8. Uniseriate and glandular trichomes of adaxial leaf surface.—9. Uniseriate trichomes showing basal cells and part of barbellate terminal cell, adaxial leaf surface.—10. Glandular turbinate trichome, abaxial leaf surface.

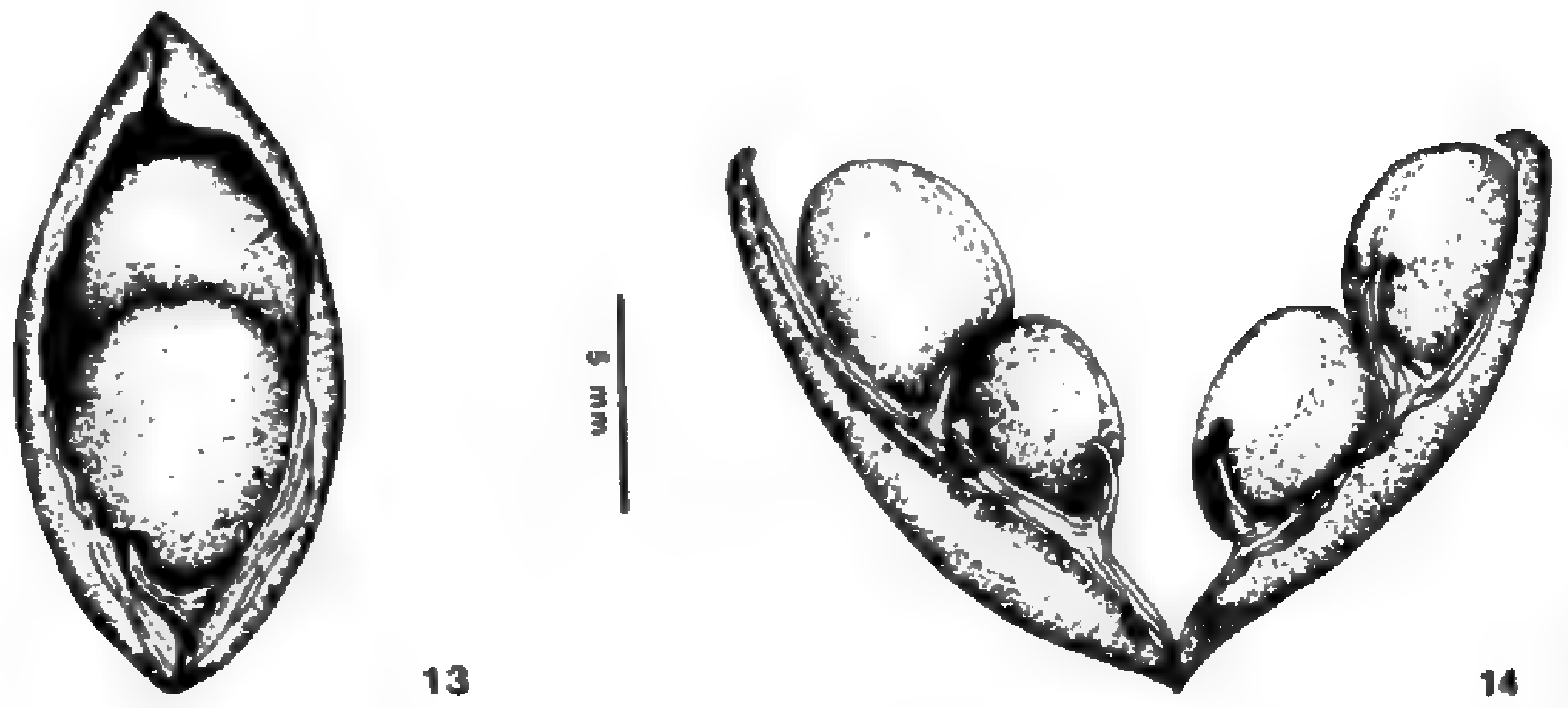
The floral bracts of species with minute glands are characteristically entire and leathery in texture. Among these species, *A. lingua-bovis, A. leonardii,* and *A. campanensis* have rhombic-ovate bracts that are appressed to the rachis and nested among adjacent bracts, overlapping only



Figures 11, 12. Bracteoles of the *Aphelandra pulcherrima* complex.—11. Lanceolate, apically acute, sepal-like bracteoles most common in the group.—12. Falcate, keeled bracteoles found only in (11) *A. campanensis,* (12) *A. hartwegiana* (figured), and (13) *A. darienensis.*

slightly. *Aphelandra laxa* shares this pattern except that the bracts are laxly disposed. Flowers of these species wither and dry before falling from the plant because they are held tightly between the rachis and the close-fitting bracts. *Aphelandra hartwegiana* is similar but the bracts are broadly ovate and diverge from the rachis. Although it shares the glandular morphology of the above species, *A. darienensis* has bracts that are ovate, densely imbricate and apically arched away from the rachis.

Bracteoles. A pair of conspicuous lateral bracteoles subtend each flower in nearly all species of *Aphelandra* [in the remaining species, these structures are rudimentary (Leonard, 1953; Wasshausen, 1975)]. With three exceptions, bracteoles of the species treated here are lanceolate to narrowly ovate and are similar to the sepals in texture and apical shape (Fig. 11). In *A. hartwegiana,* the bracteoles are falcate and cross apically on the adaxial side of the corolla (Fig. 12). The bracteoles of *A. campanensis* and *A. darienensis* are similarly falcate, but do not overlap.

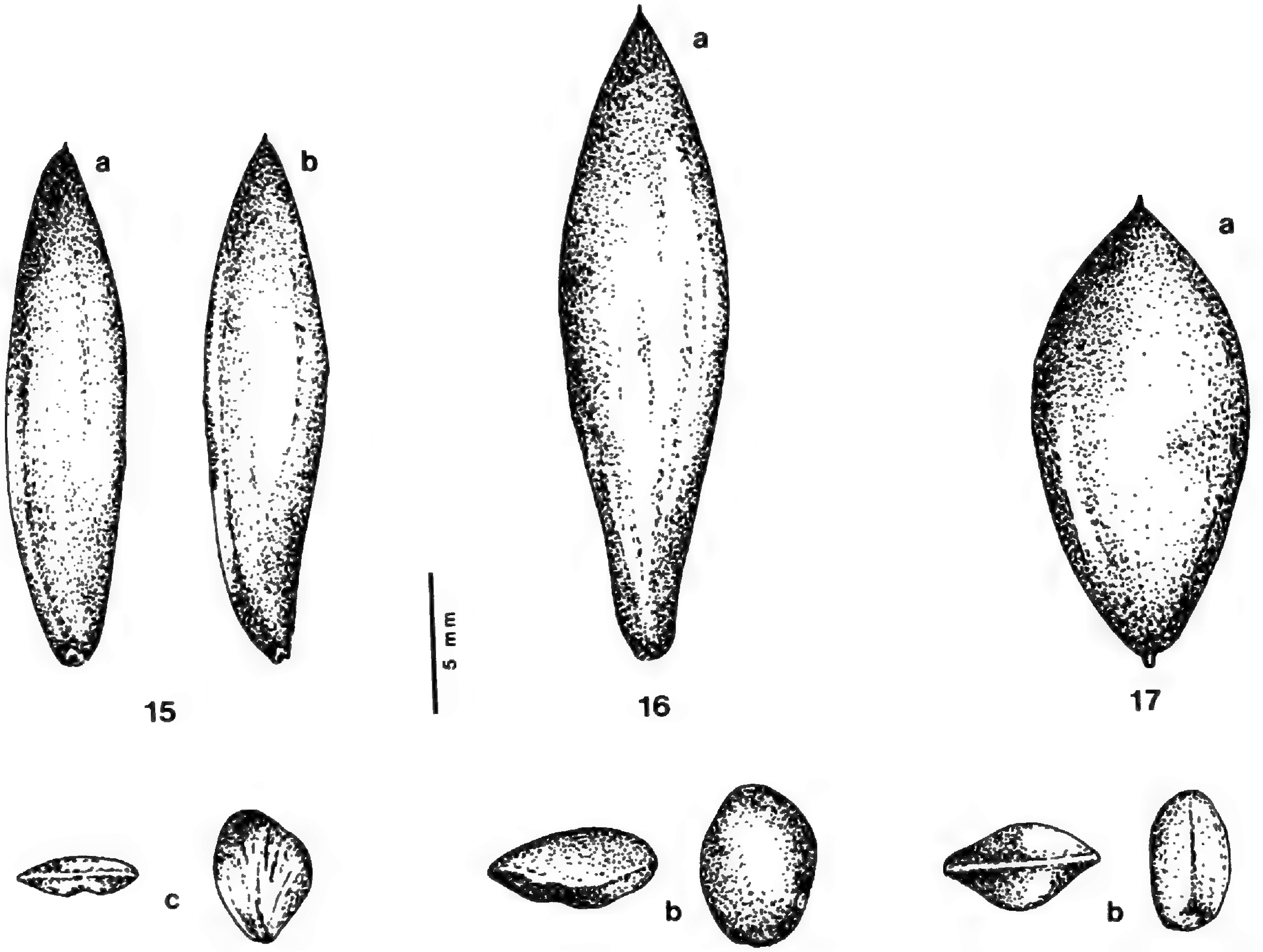


Figures 13, 14. Capsule morphology and dehiscence in *Aphelandra.*—13. Immature fruit opened to show one of two rows of two superposed seeds.—14. Dehiscent capsule with seeds held by woody retinacula (*A. deppeana* figured).

Calyx. Species of *Aphelandra* have a five-parted, polysepalous calyx with a wide adaxial segment, narrower paired abaxial segments and narrowest paired lateral segments. The species treated here are variable in calyx length, width, shape (oblong or lanceolate), shape at the apex (acute or obtuse and apiculate), and color (green to brightly colored).

Corolla. As described above, species of the *A. pulcherrima* complex share a unique and derived morphology of the upper and lower corolla lips (Figs. 3–5). The corolla tube in these species is constricted to 1–2 mm in diam. just above the ovary, which may protect the nectaries and ovary from sharp, probing bills of pollinating hummingbirds. This narrowed section is further congested and strengthened by the bases of the filaments, which are inserted in the tube just above the narrowest point. In five of the species treated here (*A. leonardii, A. laxa, A. campanensis, A. hartwegiana, A. darienensis*), corollas open by an abrupt downward movement of the lower lip. The lower lip remains plane and is strongly reflexed to lie parallel to the corolla tube. In the remaining eight species, the corolla lobes are more tightly imbricate in the bud and flowers open gradually or when visited by a pollinator. Additional corolla characters of taxonomic importance in this group of species include total length (36–75 mm), color, pubescence (glabrous to pilose), texture (membranous to quite coriaceous), and dimensions of the upper lip.

Androecium. All species of *Aphelandra* possess four monothecate, epipetalous stamens. The anthers are basifixed, erect and held parallel to

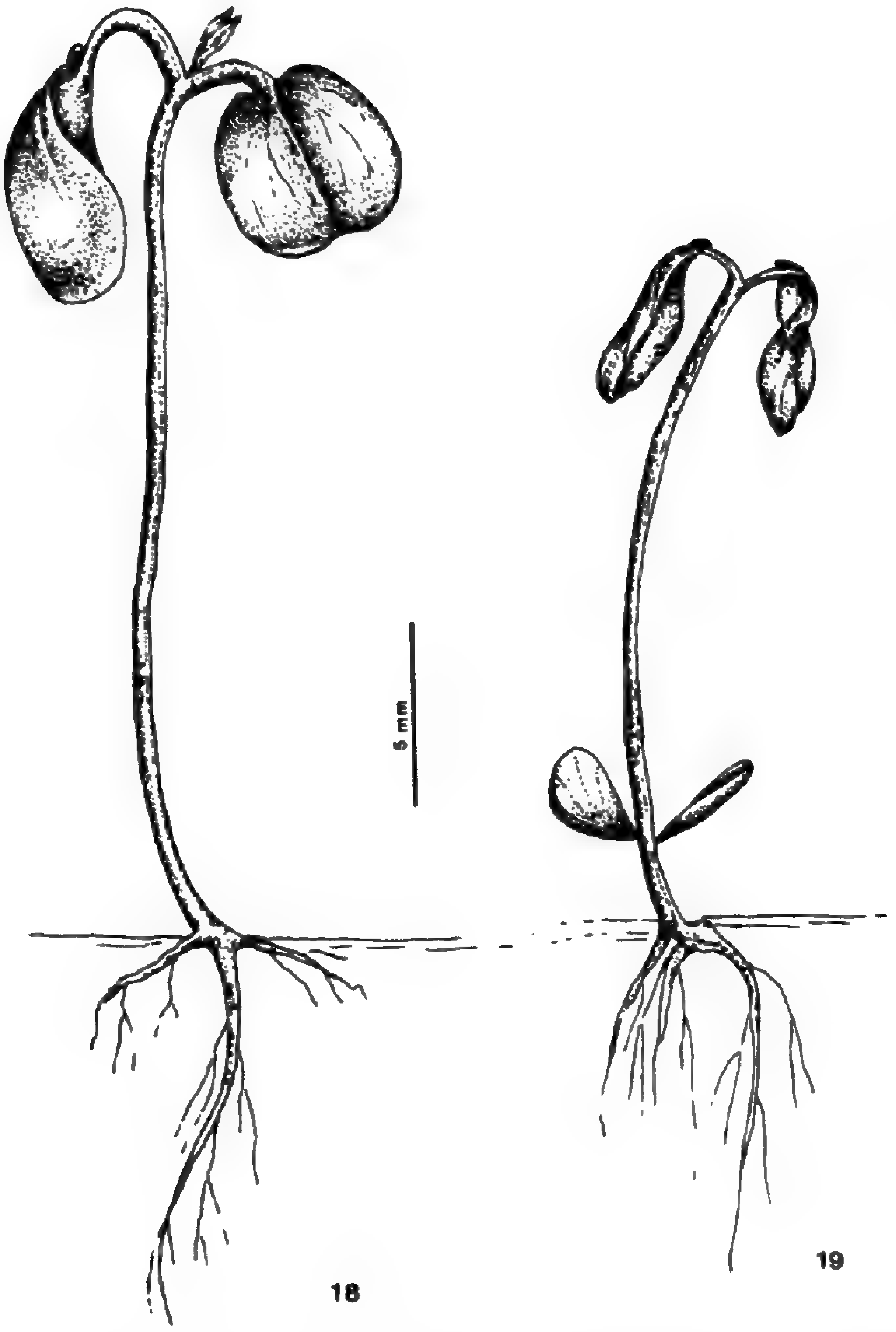


FIGURES 15–17. Capsule and seed variability in the *Aphelandra pulcherrima* complex.—15. Dorsiventrally flattened, stipitate capsule (a, frontal view; b, lateral view) and flattened seeds (c) characteristic of species of Group II: (8) *A. lingua-bovis,* (9) *A. leonardii* (figured), (10) *A. laxa,* (11) *A. campanensis,* (12) *A. hartwegiana,* and (13) *A. darienensis.*—16. Stipitate, terete capsule (a) and sub-globose seeds (b) characteristic of: (1) *A. terryae,* (2) *A. sinclairiana,* (3) *A. storkii* (figured), (4) *A. gracilis,* and (5) *A. golfodulcensis.*—17. Sub-globose, terete capsule lacking a distinct stipe (a) and sub-globose seeds (b) characteristic of (6) *A. panamensis* and (7) *A. deppeana* (figured).

the adaxial side of the corolla tube. In the *A. pulcherrima* complex, the anthers are concealed within the folded lobes of the upper lip at anthesis and emerge only when the flower is visited by a pollinator. Within the group, anther length, which ranges from 3 mm in *A. deppeana* to 10 mm in *A. hartwegiana,* is taxonomically useful, as is pollen color, which varies from cream (e.g., *A. gracilis*) to yellow (e.g., *A. leonardii*) and orange (e.g., *A. sinclairiana*).

Gynoecium. Species of *Aphelandra* characteristically have a bilocular ovary with four ovules. In the Central American group dealt with here, the ovary is uniformly green and glabrous, except that occasional individuals of *A. terryae* have red-tipped ovaries. The style is filiform and extends to, and usually slightly beyond, the adaxial pair of anthers (Fig. 5). Most species have shallowly bilobed stigmas that may be red or pink. *Aphelandra deppeana* and *A. panamensis,* however, have oblique stigmas that appear to be hollow and are not distinctively colored.

Fruits. *Aphelandra* has explosively dehiscent capsules in which the four (or fewer) seeds are borne on membranous to woody, hook-like retinacula (Lindau, 1895; Long, 1970; Figs. 13, 14). In six of the species treated here, the capsules are clavate with a narrowed stipe below the seed-bearing portion of the fruit. They are dorsiventrally flattened and thus oval in cross-section (Fig. 15a, 15b). Five species have capsules that are stipitate and terete (Fig. 16a). In *A. deppeana*



FIGURES 18, 19. Seed germination patterns in the *Aphelandra pulcherrima* complex.—18. Epigeal germination characteristic of species of Group II: (8) *A. lingua-bovis,* (9) *A. leonardii,* (10) *A. laxa,* (11) *A. campanensis,* (12) *A. hartwegiana,* and (13) *A. darienensis.*—19. Semi-hypogeal germination, with only slight elongation of the hypocotyl, characteristic of species of Group I: (1) *A. terryae,* (2) *A. sinclairiana,* (3) *A. storkii,* (4) *A. gracilis,* (5) *A. golfodulcensis,* (6) *A. panamensis,* and (7) *A. deppeana.*

and *A. panamensis,* fruits are sub-globose, lack a distinct stipe, and are terete (Fig. 17a). All species have capsules that are elliptic in outline, except *A. sinclairiana* has capsules that are laterally narrowed between the pairs of seeds and are sinuate in outline. Capsules of most species are green when immature, but those of *A. sinclairiana* are black, and those of *A. panamensis* and *A. lingua-bovis* are dull orange-brown. Among species, capsule length ranges from 13 mm (*A. deppeana*) to 35 mm (*A. darienensis*).

Seed and seed germination patterns. As is characteristic of Acanthaceae, *Aphelandra* seeds are exalbuminous (Bremekamp, 1965). Mature seeds are various shades of brown, glabrous and orbicular to irregularly angular in outline (Figs. 15c, 16b, 17b). Of the 13 species treated here, seven have seeds that are only slightly flattened (diameter/width ratio < 2) and six have strongly flattened seeds (diameter/width ratio > 2). Relative seed width is associated with fruit morphology: sub-globose seeds occur in species with terete fruits (Figs. 16, 17), and strongly flattened seeds occur in species with similarly flattened fruits (Fig. 15).

Epigeal and semi-hypogeal germination patterns are found among the species studied here. In epigeal germination, the cotyledons are raised above the surface by elongation of the hypocotyl (Fig. 18). In semi-hypogeal germination, the cotyledons emerge from the seed but remain at the level of the substrate because no (or very little) elongation of the hypocotyl occurs (Ng, 1978; Fig. 19). Seed morphology is correlated with germination pattern: flattened seeds germinate epigeally (six species), and sub-globose seeds germinate semi-hypogeally (seven species).

SYSTEMATIC IMPLICATIONS

Comparative morphology provides evidence for the four taxonomic changes resulting from this study. *Aphelandra dukei* is considered conspecific with *A. deppeana* and three new species were described (McDade, 1982): *A. panamensis, A. golfodulcensis,* and *A. leonardii.* Detailed justification for these changes is provided in the taxonomic treatment. Comparative morphology also provides characters for reconstructing phylogenetic relationships among these species. The results of phylogenetic analysis are previewed here in summary form to facilitate discussion of interrelationships in subsequent sections. The Central American species treated here belong to two lineages, referred to hereafter as Groups I (species 1–7) and II (8–13) (Table 3). Species of each lineage share several derived character states (see Phylogenetic Analysis) and may be readily recognized by suites of distinguishing features (Table 3).

CHROMOSOME DATA

In the most thorough cytogenetic survey of Acanthaceae to date, Grant (1955) reported approximately 100 new chromosome counts for the family and suggested that chromosome data would be useful in studying interrelationships within the group, especially at lower taxonomic levels. Although many new counts have been reported subsequently, systematic applications

TABLE 3. Morphological characters distinguishing groups of species within the Central American members of the *Aphelandra pulcherrima* complex. NA denotes data not available.

Species	Bracteal Nectaries	Capsule	Seed	Germination Pattern	Habit
Group I					
1. *A. terryae* (TE)	Large	Terete	Sub-globose	Semi-hypogeal	Shrub
2. *A. sinclairiana* (SI)	Large	Terete	Sub-globose	Semi-hypogeal	Shrub
3. *A. storkii* (ST)	Large	Terete	Sub-globose	Semi-hypogeal	Monocaulous
4. *A. gracilis* (GR)	Large	Terete	Sub-globose	Semi-hypogeal	Shrub
5. *A. golfodulcensis* (GO)	Large	Terete	Sub-globose	Semi-hypogeal	Shrub
6. *A. panamensis* (PA)	Large	Sub-globose, terete	Sub-globose	Semi-hypogeal	Shrub
7. *A. deppeana* (DE)	Large	Sub-globose, terete	Sub-globose	Semi-hypogeal	Shrub
Group II					
8. *A. lingua-bovis* (LB)	Minute	Flattened	Flattened	Epigeal	Monocaulous
9. *A. leonardii* (LE)	Minute	Flattened	Flattened	Epigeal	Shrub
10. *A. laxa* (LA)	Minute	Flattened	Flattened	NA	Monocaulous
11. *A. campanensis* (CA)	Minute	Flattened	Flattened	Epigeal	Monocaulous
12. *A. hartwegiana* (HA)	Minute	Flattened	Flattened	Epigeal	Monocaulous
13. *A. darienensis* (DA)	Minute	Flattened	Flattened	Epigeal	Monocaulous

of cytological data are essentially lacking. The chromosome numbers reported previous to this study for four species of *Aphelandra* ($n = 14, 14, 28, 34$; Table 4) suggested that cytology might be valuable in elucidating relationships within the group treated here.

MATERIALS AND METHODS

Flower buds were collected from both field populations and greenhouse plants (grown from cuttings taken from field populations) for study of meiotic chromosomes. Root tips from cuttings and from young seedlings were used to determine mitotic chromosome numbers. Suitable cytological material was obtained from at least one locality of all species except *A. laxa*. Chromosome vouchers are deposited at DUKE. All materials were fixed in Carnoy's solution (3 absolute alcohol: 1 glacial acetic acid) for 24 hours at room temperature or for four hours at 60°C. Material not processed immediately was stored in 70% ethanol and kept refrigerated when possible.

Anthers or root tips were gently boiled for about five minutes in acetocarmine (saturated solution of carmine in 45% acetic acid). A single anther or root tip was then transferred to a drop of 45% acetic acid. The root cap was removed and the distal 1–2 mm of the meristem was excised. The root tip or anther was then placed in a small drop of Hoyer's solution (Anderson, 1954; Beeks, 1955) on a clean slide. The tissue was gently broken apart using a dissecting needle or flat scalpel edge, a cover glass was added and pressure applied to spread and flatten the preparation.

RESULTS

The haploid number of all 12 species is 14 (Table 5). Karyotype analysis proved impossible due to the small size of the chromosomes (2–3 μm) and their tendency to clump in metaphase cells. The same difficulties were reported by Grant (1955) in his work with the closely related tribe Acantheae.

The previously reported meiotic count of $n =$

TABLE 4. Published reports of chromosome numbers of species of *Aphelandra*.

Species	*n*	Source
A. aurantiaca	14	Takizawa, 1957
A. chamissoniana	14	Takizawa, 1957
A. fulgens (= *A. deppeana*)[a]	28	Pal, 1964
A. cristata (= *A. tetragona*)[b]	34	Narayanan, 1951

[a] Species included in this study.

[b] South American member of the *A. pulcherrima* complex.

TABLE 5. Chromosome numbers of Central American species of the *Aphelandra pulcherrima* complex. NA denotes data not available.

Species	*n*	2*n*	Voucher
1. *A. terryae* Standley	NA	28	Panama. Darién: along Río Pirre ca. 10 km S of El Real, *McDade 431.*
2. *A. sinclairiana* Nees	14	NA	Panama. Colón: ca. 14 km from Colón along hwy. to Panamá, *McDade 384.*
	14	NA	Panama. Colón: along Pipeline Rd., *McDade 280.*
3. *A. storkii* Leonard	14	NA	Costa Rica. Heredia: Finca La Selva, near Pto. Viejo, *McDade 350.*
4. *A. gracilis* Leonard	NA	28	Panama. Panamá: slopes of Cerro Jefe, *McDade 420.*
5. *A. golfodulcensis* McDade	14	NA	Costa Rica. Puntarenas: San Vito de Java, *McDade 251.*
	14	28	Costa Rica. Puntarenas: Corcovado National Park, *McDade 401.*
6. *A. panamensis* McDade	NA	28	Panama. Colón: Sta. Rita Ridge, ca. 7 km from hwy. between Panamá and Colón, *McDade 388.*
	14	NA	Panama. Darién: slopes of Cerro Pirre, *McDade 428.*
7. *A. deppeana* Schldl. & Cham.	NA	28	Costa Rica. Puntarenas: ca. 18 km SE of Palmar N., *McDade 290.*
8. *A. lingua-bovis* Leonard	14	NA	Costa Rica. Puntarenas: Corcovado National Park, *McDade 402.*
	NA	28	Panama. Darién: summit and upper slopes of Cerro Pirre, *McDade 429.*
9. *A. leonardii* McDade	14	28	Costa Rica. San José: Río Tarrazú near Frailes, *McDade 310.*
11. *A. campanensis* Durkee	NA	28	Costa Rica. Limón: ca. 5 km N of Bribri, *McDade 242.*
12. *A. hartwegiana* Nees ex Benth.	NA	28	Panama. Darién: along trail between El Real and Pirre, *McDade 425.*
13. *A. darienensis* Wassh.	NA	28	Panama. Darién: upper slopes of Cerro Pirre, *McDade 430.*

28 for *A. fulgens* (= *A. deppeana*) (Pal, 1964) is in conflict with my determination of $2n = 28$ for both meiotic and mitotic cells of the same species from Costa Rica. Pal does not indicate the source of the plant(s) from which the count was obtained, but the species was apparently cultivated in a botanical garden. Study of this species throughout its extensive range will be required to document and described this possible variation in chromosome number. The $2n = 68$ report for *A. tetragona* (Narayanan, 1951), a Venezuelan species belonging to the *A. pulcherrima* complex, suggests that chromosomal differentiation has occurred at least to some extent in the South American members of the complex and that further cytological work is warranted.

Although chromosome numbers have been determined for a small proportion of *Aphelandra* species (15 of about 170), counts of $n = 14$ for representatives of three distantly related species groups [*A. aurantiaca* (Scheidw.) Lindl., *A. chamissoniana* Nees, *A. pulcherrima* group] suggest that 14 is the base number of the genus. This same number has been reported for species belonging to most other tribes within Acanthaceae (Grant, 1955).

POLLEN

The diversity of pollen morphology in Acanthaceae is well-known (Erdtman, 1966) and its taxonomic importance has long been emphasized (Radlkofer, 1883; Lindau, 1895; Bremekamp, 1944; Raj, 1961). Although the results of a somewhat restricted survey of pollen morphology served as the basis of Lindau's (1895) classification of the family at the suprageneric level, more recent and complete studies using both light and electron microscopy have revealed considerable variation within Lindau's supposedly uniform groupings (Bremekamp, 1944; Raj, 1961; Gibson, 1972; Wasshausen, 1975). To assess accurately the systematic value of pollen morphology at higher taxonomic levels, knowledge of the infrageneric range of pollen variability is necessary. Unfortunately, complete palynological surveys have been made of only a few small genera of Acanthaceae. Partial surveys of several large genera have indicated extensive infrageneric variability (e.g., *Aphelandra*: Wasshausen, 1975; *Justicia*: Raj, 1961; *Ruellia*: Chaubal, 1966).

Variability in pollen size among taxa in Acanthaceae has received little systematic attention. Even among species with morphologically indistinguishable pollen, significant differences in grain size may exist. Pollen size is readily determined and is commonly reported in palynological descriptions.

In an SEM survey of pollen of 60 species of *Aphelandra,* Wasshausen (1975) found considerable diversity in shape (spheroidal to perprolate) and sculpturing (verrucose, reticulate, psilate). Although indicating that pollen characters should be useful in classification of *Aphelandra* at the species level, Wasshausen found that evidence from pollen analysis conflicted with his interpretation of the affinities of several species based on morphological studies. Resolution of these possible discordances will require thorough analysis of the relationships within *Aphelandra,* as well as a complete palynological survey of the genus. For the 13 species treated here, analysis of pollen size, shape, and ultrasculpturing using both light and scanning electron microscopy was conducted.

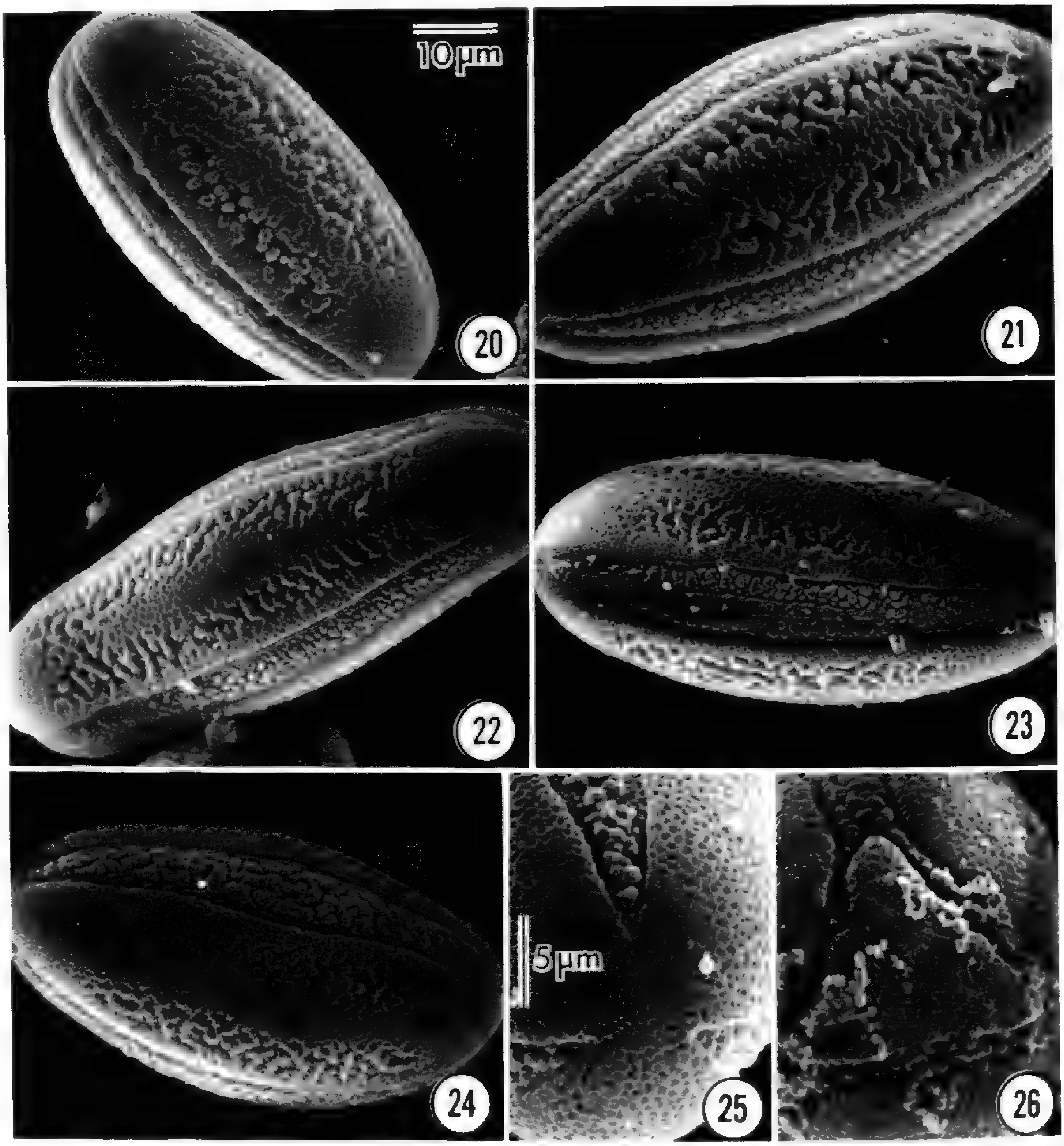
MATERIALS AND METHODS

For scanning electron microscopic study (SEM), pollen was obtained from two or more plants from each of one to five populations that spanned the geographic range of each species (Appendix B). Anthers were collected from field and greenhouse plants from flower buds one to three days prior to anthesis and fixed initially in FAA (formalin: acetic acid: alcohol). Fresh or fixed pollen of *A. laxa* was not available and thus dried anthers were removed from herbarium specimens and rehydrated for 24 hours in Aerosol OT solution. Following a dehydration series through 100% ethanol to 100% freon, the anthers were dried using carbon dioxide as a transitional fluid in a BOMAR SPC-900/EX critical point dryer. To minimize charging, a small piece of glass coated with polyvinyl chloride (in methyl ethyl ketone solution) was attached to the stub surface using low resistance cement. Pollen grains were extracted by slicing a dried anther and gently tapping it over a prepared stub. Stubs were then coated with a 250 angstrom layer of gold-palladium using a sputter coater. The samples were viewed and photomicrographs taken using a JEOL JSM-T20 scanning electron microscope.

Pollen samples to be measured for size analysis were collected from several sources including dried herbarium specimens, field populations, and greenhouse plants (Appendix B). One to seven localities from throughout the range of each species were sampled. Fresh specimens were fixed initially in FAA and stored for varying lengths of time. Both dried and FAA-fixed anthers were acetolyzed by boiling in 9:1 acetic anhydride: sulfuric acid, straining to remove anther debris, boiling in 10% KOH, and eventual storing in 70% ethanol (Livingstone, pers. comm.). Two sub-samples of at least 25 grains were taken from each sample and mounted in aniline blue in lactophenol solution. Length and width of each grain were measured under high dry magnification of 400 × (bright field light microscopy). These data were analyzed by Analysis of Variance (ANOVA), followed by Duncan Multiple Range a posteriori test for significant differences among species means (Sokal & Rohlf, 1969; SAS User's Guide, 1979).

RESULTS

Pollen of all 13 *Aphelandra* species studied is isopolar, radiosymmetric, tricolpate, and prolate (*A. panamensis*) to perprolate (remaining 12 species). With few exceptions as noted below, there is little variability at either the individual or population level among grains of the same



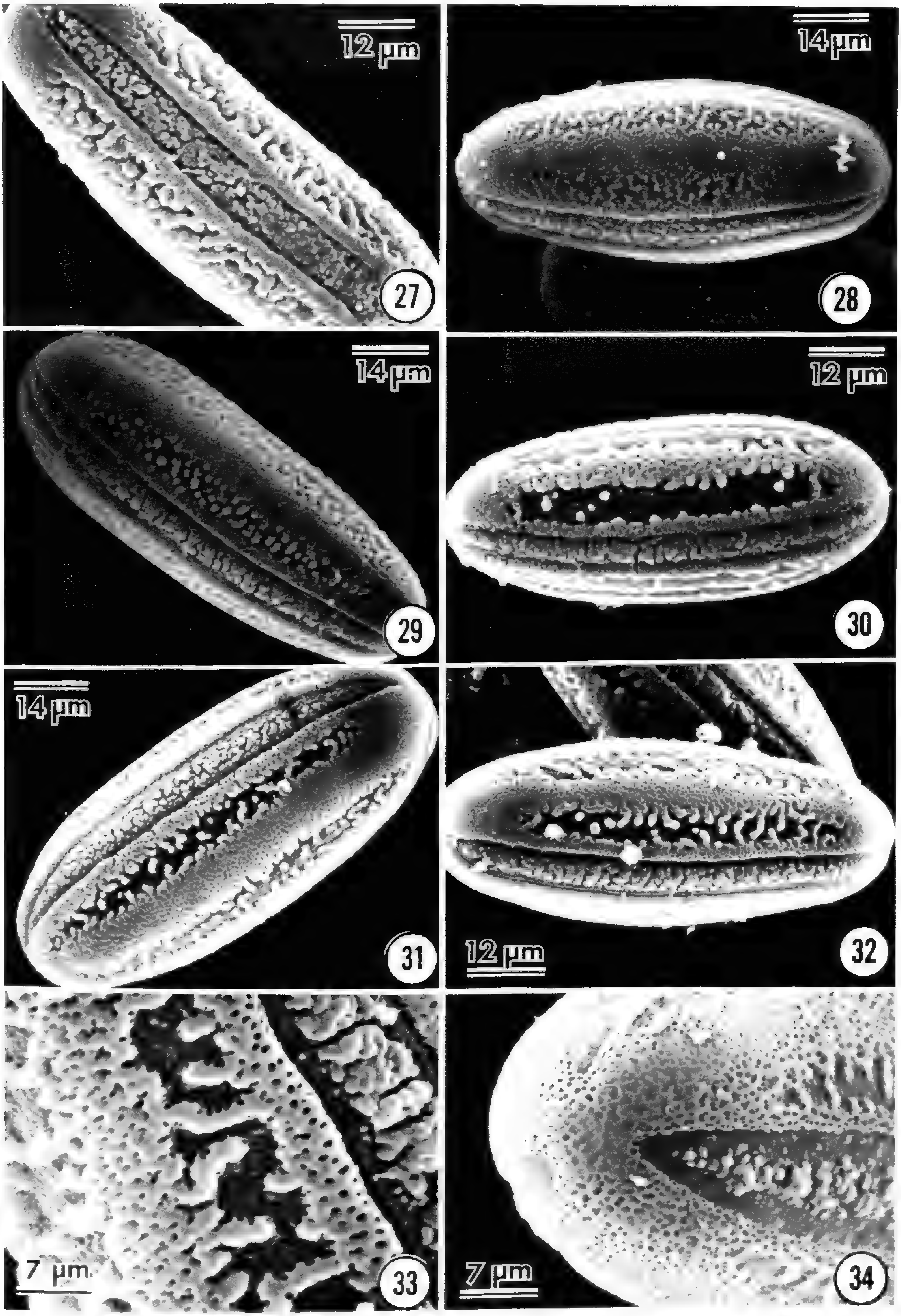
Figures 20–26. *Aphelandra* pollen of Type I (scanning electron photomicrographs).—20. (3) *A. storkii, McDade 350* (DUKE).—21. (1) *A. terryae, McDade 431* (DUKE).—22. (4) *A. gracilis, McDade 529* (DUKE).—23. (5) *A. golfodulcensis, McDade 401* (DUKE).—24. (2) *A. sinclairiana, McDade 389* (DUKE).—25. (3) *A. storkii*, polar view, *McDade 350* (DUKE).—26. (5) *A. golfodulcensis*, polar view, *McDade 251* (DUKE).

species. Three pollen types are distinguished on the basis of morphology (shape and sculpturing).

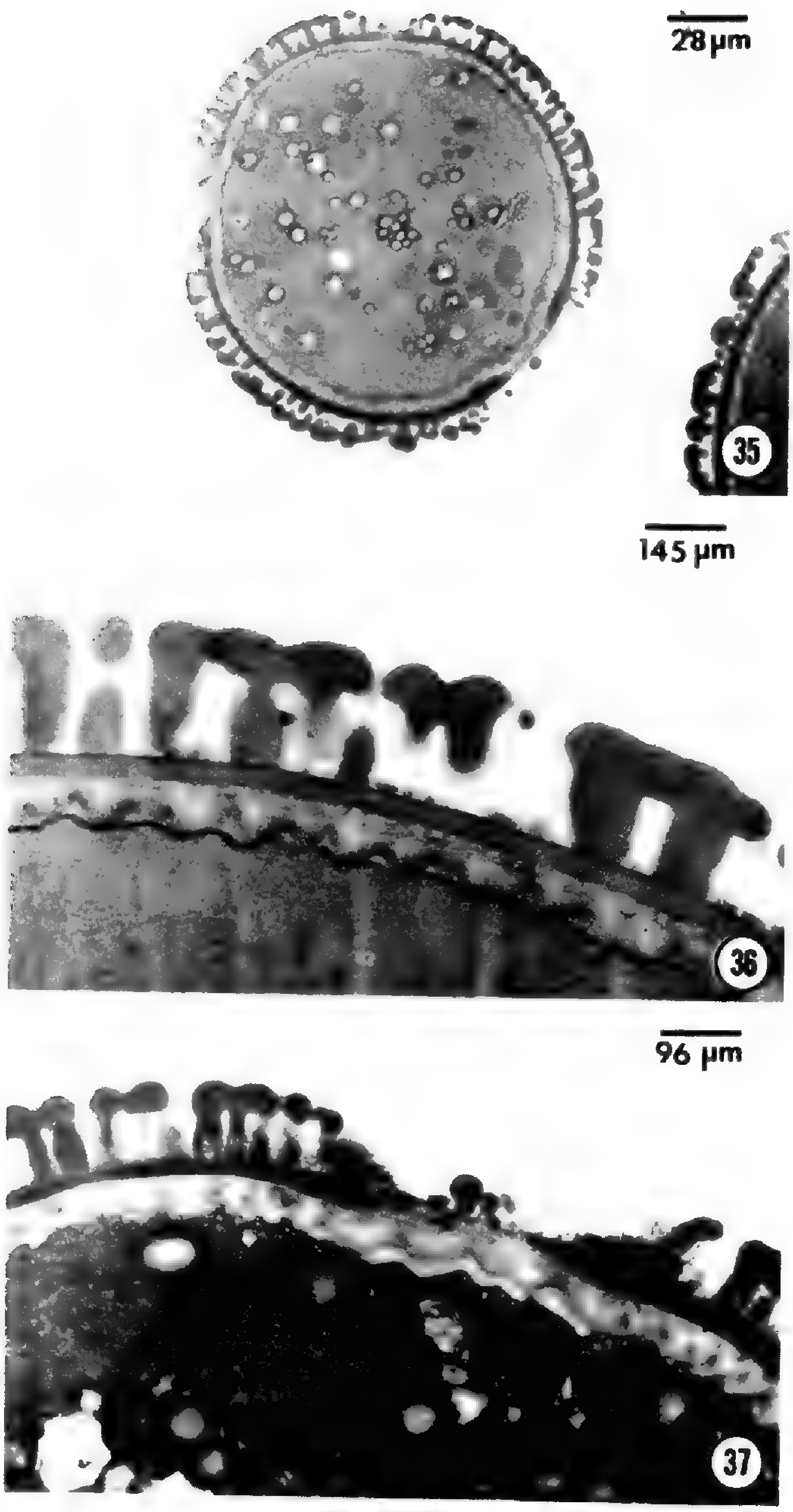
Type I (Figs. 20–26). Pollen perprolate and tapering to the poles, colpi not meeting at the poles (Fig. 25). Sculpturing gemmate to verrucose over colpi, finely reticulate elsewhere with the exception of longitudinal bands of vermiculate sculpturing along both edges of each colpus, these extending from the equator about halfway to each pole.

Aphelandra terryae, A. sinclairiana, A. storkii, A. golfodulcensis, and *A. gracilis* (species 1–5, Figs. 20–26) have pollen of Type I. Among these species, there is little difference in pollen morphology although grain size differs markedly (see below). A few individuals of *A. golfodulcensis* show unusual colpi that bifurcate near the poles and meet, leaving a triangular shield of typical finely reticulate exine at the pole (Fig. 26).

Type II (Figs. 27–34). Grains similar to Type I in shape (perprolate and tapering to the poles) and morphology of the colpi. Exine sculpturing gemmate to verrucose over colpi, finely reticulate elsewhere, except longitudinal bands devoid of sculpturing along both edges of each colpus. These bands interlaced and bordered with regions of



FIGURES 27–34. *Aphelandra* pollen of Type II (scanning electron photomicrographs).—27. (10) *A. laxa, Mori et al. 6854* (MO).—28. (9) *A. leonardii, McDade 310* (DUKE).—29. (9) *A. leonardii, McDade 432* (DUKE).—30. (11) *A. campanensis, McDade 273* (DUKE).—31. (12) *A. hartwegiana, McDade 425* (DUKE).—32. (13) *A. darienensis, McDade 430* (DUKE).—33. (11) *A. campanensis, McDade 273* (DUKE).—34. (11) *A. campanensis, McDade 242* (DUKE).



FIGURES 35–37. Ultrastructure of *Aphelandra* pollen (transmission electron photomicrographs, preparation after Stone et al., 1979).—35. Cross-section, note three colpi with reduced exine.—36. Structure of wall, well-developed intine and exine (composed of foot-layer, columellae and tectum).—37. Reduction of wall (particularly of exine layers) over colpus. (*Aphelandra storkii, McDade 350.*)

vermiculate exine (Fig. 33) and extending from the equator approximately half the distance to each pole.

Aphelandra leonardii, A. laxa, A. campanensis, A. hartwegiana, and *A. darienensis* (species 9–13, Figs. 27–34) have pollen of Type II. Among these species, there are differences with respect to width of unsculptured bands (narrow in *A. leonardii* and *A. laxa,* quite broad in *A. darienensis*), as well as in size (see below). Structurally, the unsculptured regions probably are the exposed foot layer of the exine, with the columellae and tectum lacking (Figs. 35–37).

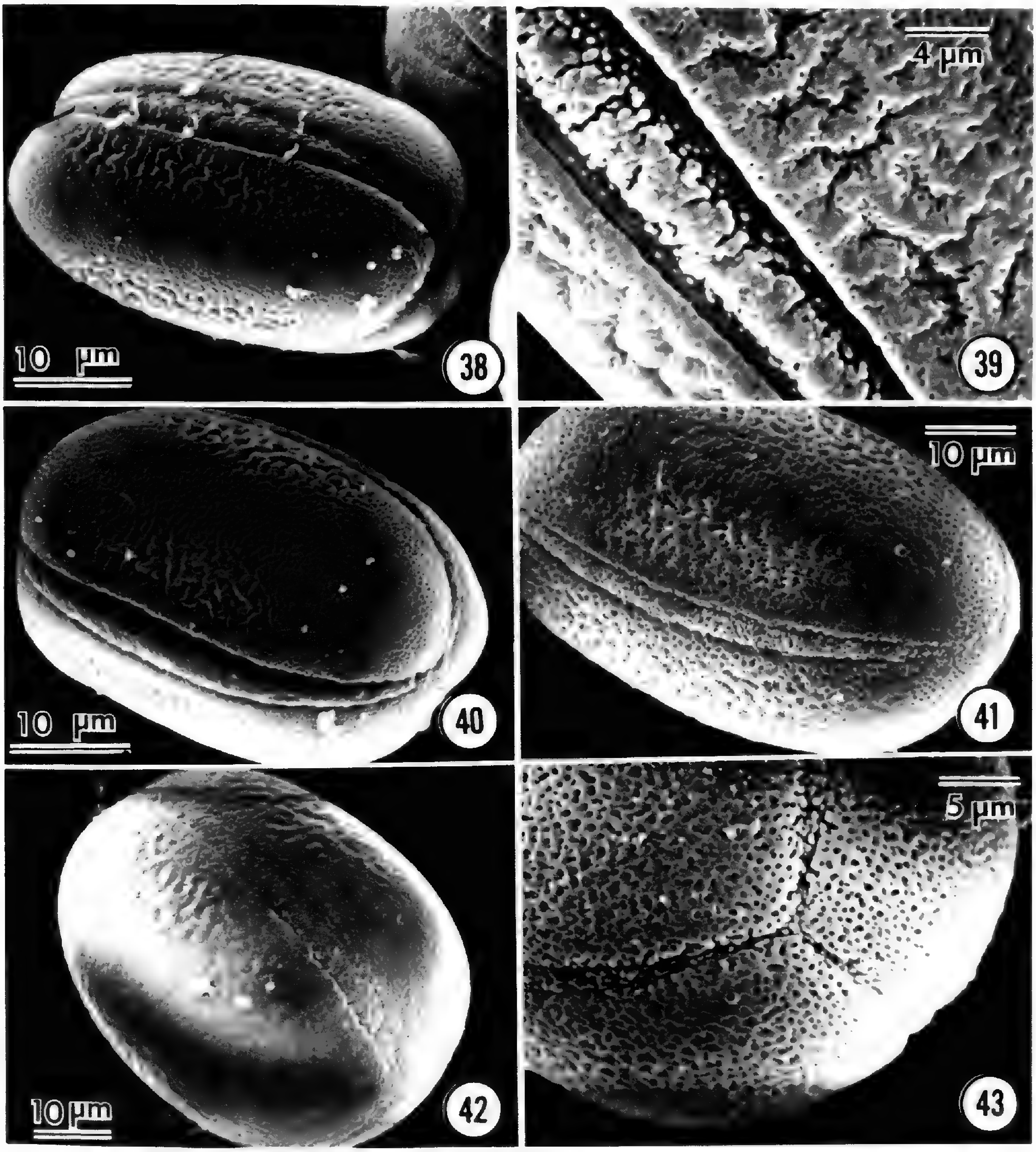
Type III (Figs. 38–43). Pollen prolate to barely perprolate, tapering very little from equator to the poles so that grains are somewhat rectangular, syntricolpate (colpi meeting at the poles: Figs. 40, 43). Exine finely reticulate to vermiculate over colpi, elsewhere finely reticulate. Longitudinal bands along colpi may be quite indistinct (Fig. 42) or may be well-defined regions bearing vermiculate sculpturing (Figs. 40, 41).

Aphelandra deppeana, A. panamensis, and *A. lingua-bovis* (species 6–8; Figs. 38–43) have pollen of Type III. Pollen of the last species is somewhat variable among populations with respect to degree of sculpturing relief (from quite smooth, extremely finely reticulate grains with ill-defined colpi, to rather coarsely reticulate grains with vermiculate colpi; i.e., contrast Figs. 41, 42). Although grains of these species are quite similar in shape, there is significant size disparity between *A. lingua-bovis* and the other species.

Pollen grains of the 13 species range in length from 45.6 µm (*A. panamensis*) to 88.6 µm (*A. hartwegiana*), and in width from 24.8 µm (*A. deppeana*) to 40.0 µm (*A. lingua-bovis*). Analysis of variance revealed significant differences among species in both length ($F_s = 375.83$; 13,3083 df; $P < 0.00001$), and width ($F_s = 321.00$; 13,3083 df; $P < 0.0001$). Duncan Multiple Range test for differences among means permitted further resolution of these data into statistically distinguishable groups of means (Tables 6, 7). All species can be distinguished on the basis of pollen length, width, or both, with the exception of two species pairs: *A. darienensis–A. lingua-bovis,* and *A. golfodulcensis–A. sinclairiana.* When both morphology and size of pollen are considered, only *A. golfodulcensis* and *A. sinclairiana* remain indistinguishable.

SYSTEMATIC IMPLICATIONS

Pollen characters support three of four taxonomic changes made in this treatment. Pollen morphology separates *A. leonardii,* with pollen of Type II, from *A. pulcherrima* which has pollen of Type I (Figs. 44, 45). Although grains of *A. deppeana* and *A. panamensis* are not distinguishable by shape and sculpturing, pollen length and width differ (Tables 6, 7). The results of pollen



FIGURES 38–43. *Aphelandra* pollen of Type III (scanning electron photomicrographs).—38. (7) *A. deppeana, McDade 533* (DUKE).—39. (7) *A. deppeana, McDade 396* (DUKE).—40. (6) *A. panamensis, McDade 428* (DUKE).—41. (8) *A. lingua-bovis, McDade 399* (DUKE).—42. (8) *A. lingua-bovis, McDade 380* (DUKE).—43. (8) *A. lingua-bovis*, polar view, *McDade 399* (DUKE).

analysis also support the inclusion of *A. dukei* within *A. deppeana*: the grains are indistinguishable both morphologically (Figs. 46, 47) and in length and width (Tables 6, 7). However, pollen characters provide no additional basis for the recognition of *A. golfodulcensis* as distinct from *A. sinclairiana*.

Pollen morphology also provides evidence for the recognition of interrelated groups among these 13 species. With the exception of *A. lingua-bovis*, the species of Group II (9–13) share pollen of Type II. Species 1–5 (Group I, excepting *A. deppeana* and *A. panamensis*) have Type I pollen. Of the three remaining species sharing pollen Type III, *A. deppeana* and *A. panamensis* are close relatives. The relationship of these two with *A. lingua-bovis* is less clear and is discussed in more detail subsequently.

Preliminary surveys of additional species of *Aphelandra* (Wasshausen, 1975; McDade, unpubl. data) suggest that pollen morphology, together with size analysis, has considerable sys-

TABLE 6. Pollen length variability among Central American species of the *Aphelandra pulcherrima* complex.

Species	N (Populations, Grains)	Pollen Length[a] (Mean ± 1 s.d.)	Pollen Type[b]
12. *A. hartwegiana*	4, 162	88.6 ± 10.59	II
10. *A. laxa*	1, 50	82.1 ± 4.36	II
13. *A. darienensis*	1, 65	80.9 ± 3.74	II
11. *A. campanensis*	4, 407	79.0 ± 9.04	II
9. *A. leonardii*	7, 344	78.7 ± 7.20	II
8. *A. lingua-bovis*	6, 273	78.5 ± 9.48	III
4. *A. gracilis*	5, 212	74.7 ± 7.44	I
1. *A. terryae*	5, 167	74.1 ± 10.53	I
5. *A. golfodulcensis*	7, 361	70.6 ± 7.94	I
2. *A. sinclairiana*	8, 451	69.5 ± 8.43	I
3. *A. storkii*	1, 93	61.1 ± 3.49	I
A. "*dukei*"	1, 34	49.8 ± 2.70	III
7. *A. deppeana*	7, 239	49.7 ± 7.22	III
6. *A. panamensis*	3, 138	45.6 ± 8.12	III

[a] Bars connect means not significantly different ($P > 0.05$).
[b] See text.

tematic potential. At least three additional morphological types are recognizable that may clarify relationships within the large and heterogeneous genus.

REPRODUCTIVE BIOLOGY

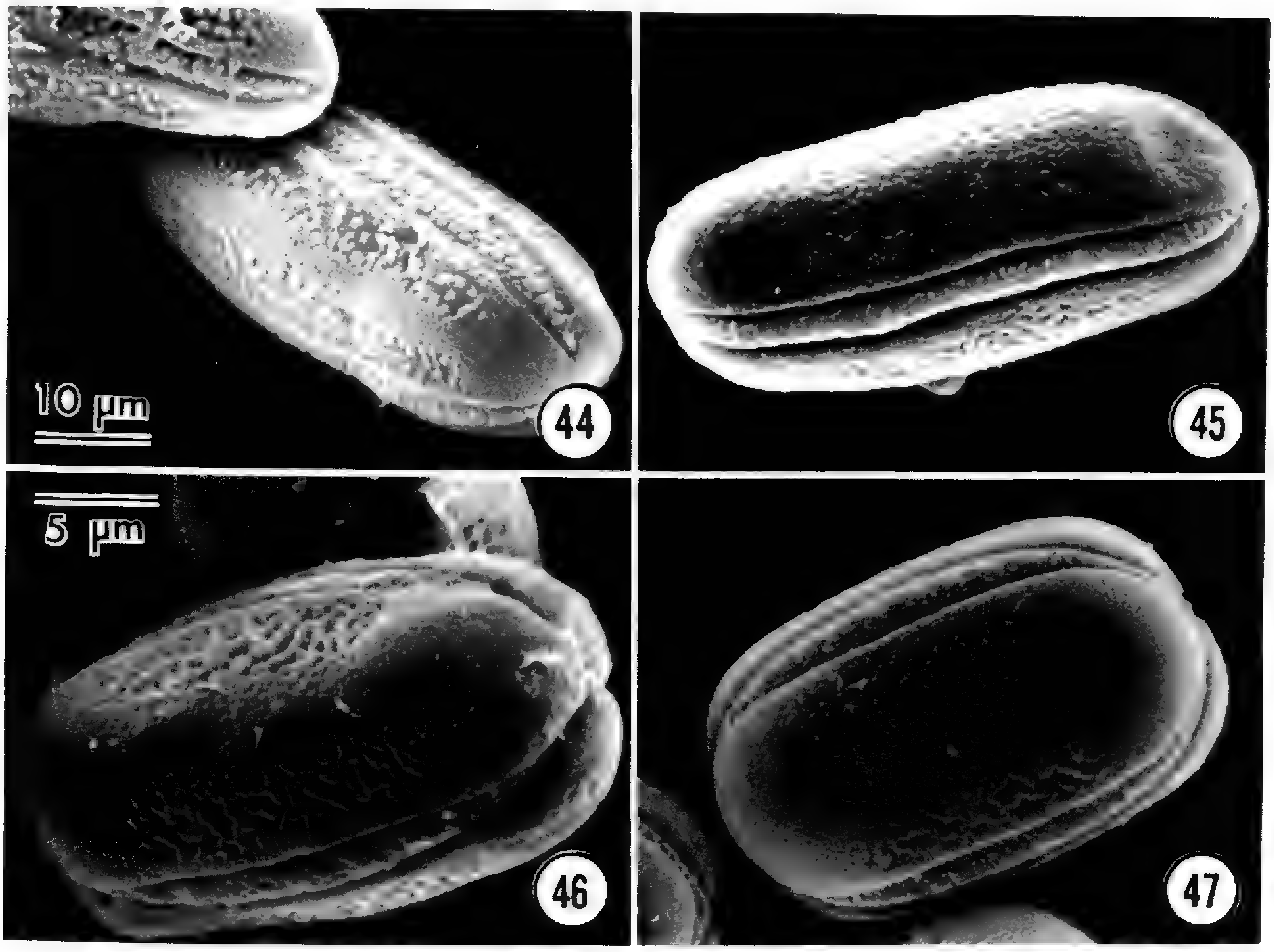
Field investigations were undertaken to characterize the floral biology of the Central American species of the *Aphelandra pulcherrima* complex (McDade, 1980). Aspects of particular systematic significance discussed here are seasonality and phenology of flowering, pollinator relationships, and seed dispersal.

Seasonality and phenology. Flowering seasonality was determined for 12 species of *Aphelandra* over the course of 18 months of field work, augmented by study of herbarium specimens. Four species flower during the Central American dry season (late Dec. through March or April), and eight flower during the wet season (April or May to Dec.) (Table 8). At least five of the wet season flowering species (*A. panamensis, A. stor-*

TABLE 7. Pollen width variability among Central American species of the *Aphelandra pulcherrima* complex.

Species	N (Populations, Grains)	Pollen Width[a] (Mean ± 1 s.d.)	Pollen Type[b]
8. *A. lingua-bovis*	6, 273	40.0 ± 5.76	III
13. *A. darienensis*	1, 65	38.7 ± 2.72	II
12. *A. hartwegiana*	4, 162	38.1 ± 4.79	II
11. *A. campanensis*	4, 407	35.4 ± 5.42	II
9. *A. leonardii*	7, 344	32.1 ± 4.24	II
10. *A. laxa*	1, 50	31.2 ± 2.54	II
4. *A. gracilis*	5, 212	29.7 ± 4.08	I
3. *A. storkii*	1, 93	29.6 ± 2.84	I
2. *A. sinclairiana*	8, 451	28.0 ± 7.96	I
1. *A. terryae*	5, 168	27.1 ± 3.31	I
5. *A. golfodulcensis*	7, 361	27.1 ± 3.16	I
6. *A. panamensis*	3, 138	27.1 ± 3.08	III
7. *A. deppeana*	7, 239	24.8 ± 3.01	III
A. "*dukei*"	1, 34	22.2 ± 1.43	III

[a] Bars connect means not significantly different ($P > 0.05$).
[b] See text.



FIGURES 44–47. Pollen morphology of two taxonomically difficult pairs of *Aphelandra* species (scanning electron photomicrographs).—44. (9) *A. leonardii, McDade 432* (DUKE).—45. *A. pulcherrima, Blum 3523* (US).—46. *A. dukei, Duke 14397* (US).—47. (7) *A. deppeana, McDade 290* (DUKE).

kii, A. lingua-bovis, A. leonardii, and *A. hartwegiana*) mature fruits during the following dry season. This fruiting pattern may have adaptive value since *Aphelandra* fruits must desiccate before dehiscence and seed dispersal can occur.

Field and greenhouse observations indicate that flowers open at or shortly after dawn and fall in the late afternoon or night of the same day. Release of pollen coincides with floral anthesis; by late afternoon, the anthers are empty and discolored. Controlled pollinations of greenhouse plants indicate that the stigma is receptive immediately following anthesis and that there is no temporal separation of male and female phases. There is, however, considerable spatial separation: the stigmas of all species are exserted 3–10 mm beyond the anthers. This separation effectively prevents autogamy (McDade, 1980).

Aphelandra flowers secrete nectar beginning just prior to anthesis and continuing until late afternoon (McDade, 1980; McDade & Kinsman, 1980). Sugar concentration in the nectar of six species ranged from 24% to 36% (McDade, 1980). Flowers of the species treated here are odorless, at least to human sensitivities. However, inflorescences of *A. sinclairiana* have a sweet, citrus-like aroma.

Flower visitors. Observations were made to identify animals that consume the floral resources (nectar and/or pollen) of *Aphelandra,* and to characterize the behavior of each species visiting the flowers. A visit was defined as actual physical contact of the animal with at least one flower. In a "legitimate" visit, an animal gained access to the nectar through the natural opening at the distal end of the corolla tube. All other means of extracting nectar or pollen were considered "illegitimate." Observation periods of 45 minutes or longer were scheduled to cover daylight hours as fully as possible, and were conducted at 14 localities of ten species (Table 9; Appendix C). Data were not obtained for *A. darienensis, A. terryae,* or *A. laxa.*

A summary of the observed animal visitors is presented by species of *Aphelandra* in Table 9. Flowers of all species observed were pollinated by hummingbirds. The complex and extremely consistent floral morphology and phenology of all 13 species treated here suggests that the three

TABLE 8. Flowering seasonality of Central American species of the *Aphelandra pulcherrima* complex.

Wet Season	Dry Season
3. *A. storkii*	1. *A. terryae*
6. *A. panamensis*	2. *A. sinclairiana*
7. *A. deppeana*	4. *A. gracilis*
8. *A. lingua-bovis*	5. *A. golfodulcensis*
9. *A. leonardii*	
11. *A. campanensis*	
12. *A. hartwegiana*	
13. *A. darienensis*	

species not studied in the field have the same pollinators. The distinctive morphology of the upper corolla lip restricts potential pollinators to animals with mouth parts sufficiently deep to open the upper lip and bring the anthers and stigma into contact with the visitor's body. Animals with narrow mouth parts (e.g., Lepidoptera, Hymenoptera) would never contact the functional floral organs and thus could not be effective pollinators.

With two exceptions, flowers were pollinated virtually exclusively by two species of large hermit hummingbirds (Trochilidae: Phaethorninae): *Phaethornis superciliosus* (long-tailed hermit) and *P. guy* (green hermit). These birds range from central Mexico to northern Bolivia and Amazonian Brazil (*P. superciliosus*), and from Costa Rica to northern Venezuela and southern Peru (*P. guy*). *Phaethornis superciliosus* occurs from sea level to about 900 m, and *P. guy* replaces it at mid-elevations (to about 1,700 m). Flowers of *A. lingua-bovis* and *A. campanensis*, which range from the lowlands to over 1,000 m, are pollinated by both birds. Most species, however, have more restricted elevational distributions and have only one pollinator. There is a close correspondence between the corolla tube length (35–45 mm above basal constriction) and curvature, and the bill length (35–44 mm) and curvature of both species of *Phaethornis*. Thus, these birds are able to gain access to nectar near the base of the corolla and to effect pollination in a "legitimate" visit (i.e., hovering in front of the flower and inserting the bill at the mouth of the corolla tube, causing the pocket-like corolla lip to open, thus bringing the anthers and stigma into contact with the bird's head). Three additional lines of evidence suggest that these birds are effective pollinators: (1) pollen of *A. storkii* was removed from the crown feathers of several individuals of *P. superciliosus* at La Selva, Costa Rica; (2) hummingbirds that visit *Aphelandra* usually have a clearly visible crown patch of pollen following flower probing; and (3) all of the species observed in the field set fruit and seed (McDade, 1980).

In addition to close morphological correspondence between flowers of *Aphelandra* and their pollinators, there is notable coincidence between hermit foraging behavior and the spatial distribution of the plants. In minimally disturbed areas, plants occur as isolated individuals or small clumps in natural openings of the forest canopy (e.g., tree falls, stream edges). Similarly, most hermit hummingbirds forage on established circuits (traplines) among dispersed individuals and small clumps of species with distinctive floral morphologies (Skutch, 1964; Snow & Snow, 1972; Stiles, 1975, 1977; Feinsinger & Colwell, 1978). My observations agree with this view of hermit foraging: there was none of the agressive behavior associated with defense of territories by other hummingbird species (Stiles, 1975, 1977; Feinsinger, 1976). Except for brief periods of resting and preening, hermit pollinators moved away from plants immediately after visiting the open flowers. Within a patch or individual, pollinators generally visited every accessible flower unless the patch was extremely large or the foraging bird was disturbed in some way.

Aphelandra leonardii was the only long-flowered species not visited by one or both species of large *Phaethornis* hummingbirds. Flowers of this species at Frailes, Costa Rica were visited by the violet sabrewing (*Campylopterus hemileucurus*). Individuals of this species have bills that coincide morphologically with size and structure of flowers of *Aphelandra*. Ridgely (1976) and Feinsinger (1976) have characterized this bird's foraging behavior as hermit-like. It is clear that pollen was transferred effectively at this site because high levels of fruit and seed set were observed (McDade, 1980).

Aphelandra deppeana, with corollas only 36–42 mm long, was pollinated by a different group of hummingbirds (Table 9). Although euglossine bees have been reported to pollinate flowers of this species (Deuth, 1977), hummingbirds of the subfamily Trochilinae were the most frequent flower visitors at my study site. Territorial behavior by male blue-tailed hummingbirds (*Amazilia cyanura*) foraging in large patches of *A. deppeana* was observed. More sporadic, non-territorial feeding by members of both this species and *A. rutila* (cinnamon hummingbird) occurred at small clumps and isolated plants. Bill length

TABLE 9. Animal visitors to flowers of Central American species of the *Aphelandra pulcherrima* complex. NA denotes data not available.

Species and Location (Total Hr. Observed)	Legitimate Visitors (Pollinators)	Illegitimate Visitors		
		Nectar Robbers		Pollen Robbers
		Birds	Insects	
1. *A. terryae*	NA	NA	NA	NA
2. *A. sinclairiana* Colón (23)	*Phaethornis superciliosus*	*P. longuemareus* *Chalybura buffoni*[a]	*Trigona* sp. *Xylocopa* sp.	*Trigona* sp.
3. *A. storkii* Pto. Viejo (31.5)	*P. superciliosus*	*P. longuemareus*	*Trigona* sp.	*Trigona* sp.
4. *A. gracilis* El Valle (3)	*P. guy*	*P. longuemareus*	—	—
5. *A. golfodulcensis* Corcovado (12)	*P. superciliosus*	*P. longuemareus*[a] *Heliothrix barroti*[a] *Thalurania furcata* *Amazilia tzacatl* *Coereba flaveola*	*Trigona* sp. *Xylocopa* sp.	*Trigona* sp.
San Vito (11.25)	*P. guy*	*P. longuemareus*	—	—
6. *A. panamensis* Cerro Pirre (2.5)	*P. guy*	*P. longuemareus*	—	—
7. *A. deppeana* Cañas (11.75)	*A. cyanura* *A. rutila*	*A. cyanura* *Chlorostilbon canivetii*	—	*Trigona* sp.
8. *A. lingua-bovis* Corcovado (6.75)	*P. superciliosus*	*P. longuemareus* *C. flaveola*	—	—
San Vito (8.75)	*P. guy*	*P. longuemareus*	—	—
9. *A. leonardii* Frailes (1.5)	*Campylopterus hemileucurus*	—	—	—
10. *A. laxa*	NA	NA	NA	NA
11. *A. campanensis* El Valle (4.75)	*P. guy*	*P. longuemareus*	—	—
El Copé (1)	*P. guy*	—	—	—
12. *A. hartwegiana* Río Pirre (4)	*P. superciliosus*	—	—	—
13. *A. darienensis*	NA	NA	NA	NA

[a] Primarily robbing species occasionally observed to visit legitimately.

of both species (17–23 mm) corresponds to corolla tube length in *A. deppeana* (22–24 mm above basal constriction). Observation of pollen on the crowns of foraging individuals, as well as high fruit and seed set (McDade, 1980), indicates that these birds are effective pollinators.

In addition to visits by pollinating hummingbirds, several other sorts of flower visits were observed (Table 9). Eight species were visited by birds with short bills that pierced or ripped holes near the base of the corolla tube to gain access to nectar. Birds visiting in this manner never contact the anthers or stigma and are not pollinators. Flowers of four species were also visited by bees, particularly *Trigona* spp. (Apidae: Meliponinae). These bees most frequently collected pollen from flowers, but also took nectar from two species (*A. golfodulcensis* and *A. storkii*). Individual bees typically settled on the upper corolla lip, chewed through the folded corolla lobes, and collected pollen from the concealed anthers. Because the stigma is exserted several mm beyond the anthers, bees are unlikely to contact the stigma while gathering pollen. In fact, these bees frequently severely damaged or severed the style at the level of the anthers, precluding seed set. *Trigona,* as well as occasional carpenter bees (Anthophoridae: Xylocopinae, *Xylocopa* sp.) ex-

TABLE 10. Comparison of seed set from inter- and intrapopulation crosses of *Aphelandra* species.

Species	Inter	Intra	t_s	df
5. *A. golfodulcensis*	0.590	0.490	3.478[a]	7
6. *A. panamensis*	0.448	0.210	257.089[b]	1
7. *A. deppeana*	0.636	0.535	9.528[b]	9
8. *A. lingua-bovis*	0.109	0.223	38.776[b]	3
9. *A. leonardii*	0.461	0.614	182.143[b]	5

[a] $P < 0.01$.

[b] $P < 0.001$.

tracted nectar through holes made near the base of the corolla tube.

Because they affect nectar and pollen resources available for pollinators, these non-pollinating bird and insect visitors are an important component of the floral biology of some populations of *Aphelandra* (McDade & Kinsman, 1980). The extent of their impact in terms of fruit and seed set, however, remains to be fully determined.

Seed dispersal. Seeds of *Aphelandra* are dispersed by explosive dehiscence of the capsules. The two woody lateral ribs are held together at the apex in immature fruits by hygroscopic cells. As capsules mature and dry, this tissue ruptures and dehiscence occurs as the ribs spring apart from the apex, arching outward from the rachis (Bremekamp, 1965; Sell, 1969; Figs. 13, 14). The retinacula, two of which are attached to each woody rib of the capsule, each hold one seed and insure that the seeds are propelled away from the parent plant rather than falling directly to the ground. Dispersal distances vary depending upon position of the fruit and plant, and surrounding vegetation. Limited observations of *A. sinclairiana* in Panama indicate that seeds can be thrown more than 10 m from the parent plant.

SYSTEMATIC IMPLICATIONS

Differences in flowering seasonality are an important isolating mechanism between several closely related pairs of *Aphelandra* species (Table 8). In addition, pollinator relationships of *A. deppeana* and *A. panamensis* provide support for recognizing them as distinct species. They are morphologically distinct, elevationally isolated and are pollinated by different species of hummingbirds (Table 9). These data indicate, however, that diversification of floral morphology and phenology in conjunction with pollination by different animals has not been a major feature in the radiation of this group of *Aphelandra*. Other factors must have spurred speciation and the subsequent evolution of isolating mechanisms in this group.

INTERPOPULATION CROSSES

Perhaps the most serious operational difficulty in applying the biological species concept is that of demonstrating reproductive continuity among the individuals and populations of a species. Even with plants that are readily cultivated and hand-pollinated, the logistics of carrying out the necessary crosses are prohibitive. Conducting interpopulation crosses to test for reproductive continuity within putative species must be regarded as sampling, and the results taken as evidence for or against, but not proving, potential reproductive continuity within species.

MATERIALS AND METHODS

Plants were grown in the greenhouse from cuttings or seeds taken from field populations. Crosses between sites were carried out for all species for which individuals from more than one population were available (Appendix C). Hand pollinations were made between 0730 and 0900 E.S.T., by placing an excess of pollen on the stigma of the ovulate parent. No emasculations were performed because selfing is prevented by exsertion of the stigma well beyond the anthers at anthesis. The floral bracts subtending all treated flowers were color-coded using acrylic paints and observed until just prior to dehiscence of fruits or until failure to set fruit was apparent. Any inflorescence that did not set fruit, as well as distal portions of inflorescences beyond fully formed fruits, were not included in the analysis because the cause of failure to fruit was not known. Fruits were collected as they began to desiccate, opened, and the number of fully filled seeds counted. At least 50 interpopulation pollinations were attempted between plants from each pair of sites.

Fruit set from each cross was calculated as the proportion of treated flowers that produced fruits. Seed set per fruit was expressed as a fraction of the maximum of four. These two indices were multiplied to yield percent seed set; that is, the proportion of ovules in each cross that developed into mature seeds.

RESULTS

Seed set from interpopulation crosses involving five species is compared with seed set data

TABLE 11. Crossability indices between Central American species of the *Aphelandra pulcherrima* complex. The larger of the paired indices from reciprocal crosses is presented as the most conservative estimate of degree of relationship. The full matrix is presented as Appendix D. NA denotes data not available. Species numbers and abbreviations as in Table 2.

Species	1. TE	2. SI	3. ST	4. GR	5. GO	6. PA	7. DE	8. LB	9. LE	11. CA	12. HA
2. SI	0.66										
3. ST	0.59	0.39									
4. GR	0.59	NA	0.62								
5. GO	0.86	0.98	0.51	0.51							
6. PA	0.80	0.99	0.58	0.37	0.64						
7. DE	0.11	0.13	0.29	0.05	0.17	0.89					
8. LB	0.03	0.07	0	0.45	0.04	0	0.08				
9. LE	0.11	0.16	0.12	0.49	0.27	0.90	0.15	0.12			
11. CA	NA	NA	0	0	0	0	0.07	0	0.17		
12. HA	NA	NA	0.03	NA	0	0	0	0	0.26	0.04	
13. DA	0.07	0.01	0	NA	0.03	0	0	0	0.39	NA	NA

from intrapopulation crosses [representing means of at least 100 attempted pollinations for each species (McDade, 1980)] in Table 10. Interpopulation crosses of *A. golfodulcensis, A. panamensis,* and *A. deppeana* produced significantly more seeds than did intrapopulation crosses. The reverse occurred in *A. lingua-bovis* and *A. leonardii.* In these last two species, however, seed set from interpopulation crosses was higher than from the most fertile interspecific pollinations (Appendix D).

These data provide no evidence that there are reproductive barriers between plants from different sites of the species tested. In the form of step-wise exchange of genes through both pollen flow and dispersal events, this lack of reproductive barriers may result in reproductive continuity within these species.

ARTIFICIAL HYBRIDIZATIONS

MATERIALS AND METHODS

Interspecific pollinations were carried out with all species treated here except *A. laxa,* using greenhouse grown plants from field populations. Three to eight individuals from one to three populations of each species were used in the artificial hybridizations. Except when the number of flowers and overlapping flowering periods were limiting, at least 50 crosses of each possible combination were attempted. Controlled pollinations were carried out as described above for interpopulation crosses. Hybrid seeds were germinated on filter paper and formed vigorous, rapidly growing seedlings. Representative seedlings of each successful cross were cultivated in the greenhouse for use in future studies.

Crossability indices for each cross attempted were calculated from percent seed set from each cross. For each ovulate species, percent seed set from interspecific crosses was divided by seed set from out-crosses within that species (McDade, 1980). This was done to avoid errors in comparing results among species due to differences in gamete viability, appropriate pollination conditions, etc. Crossability indices (CIs) thus can range from zero (for crosses yielding no seeds) to greater than one (if seed set from an artificial hybridization exceeds seed set from intrapopulation crosses).

RESULTS

Crossability indices for each cross attempted are presented in Appendix D. Considerable disparity exists between indices for some species pairs, depending upon which species was the ovulate parent. For instance, in the cross *A. panamensis* ♀ × *A. sinclairiana* ♂, seed set was 0.986, whereas in the reciprocal cross, seed set was only 0.042. Although there is a significant correlation ($r = 0.313$, 90 df, $P < 0.01$) between reciprocal crossabilities for each species pair, the disparity between indices is apparent, particularly when one cross of a reciprocal pair yielded very high seed set. Many factors beyond degree of relationship can influence seed set from experimental hybridizations (e.g., interspecific and intraspecific incompatibility barriers, pollen germinability, pollen tube growth, and harmonious growth and development of the hybrid embryo within the ovary). These may vary markedly in their influence on the success of hybridizations depending on whether a species is used as the ovule or pollen parent (Ornduff,

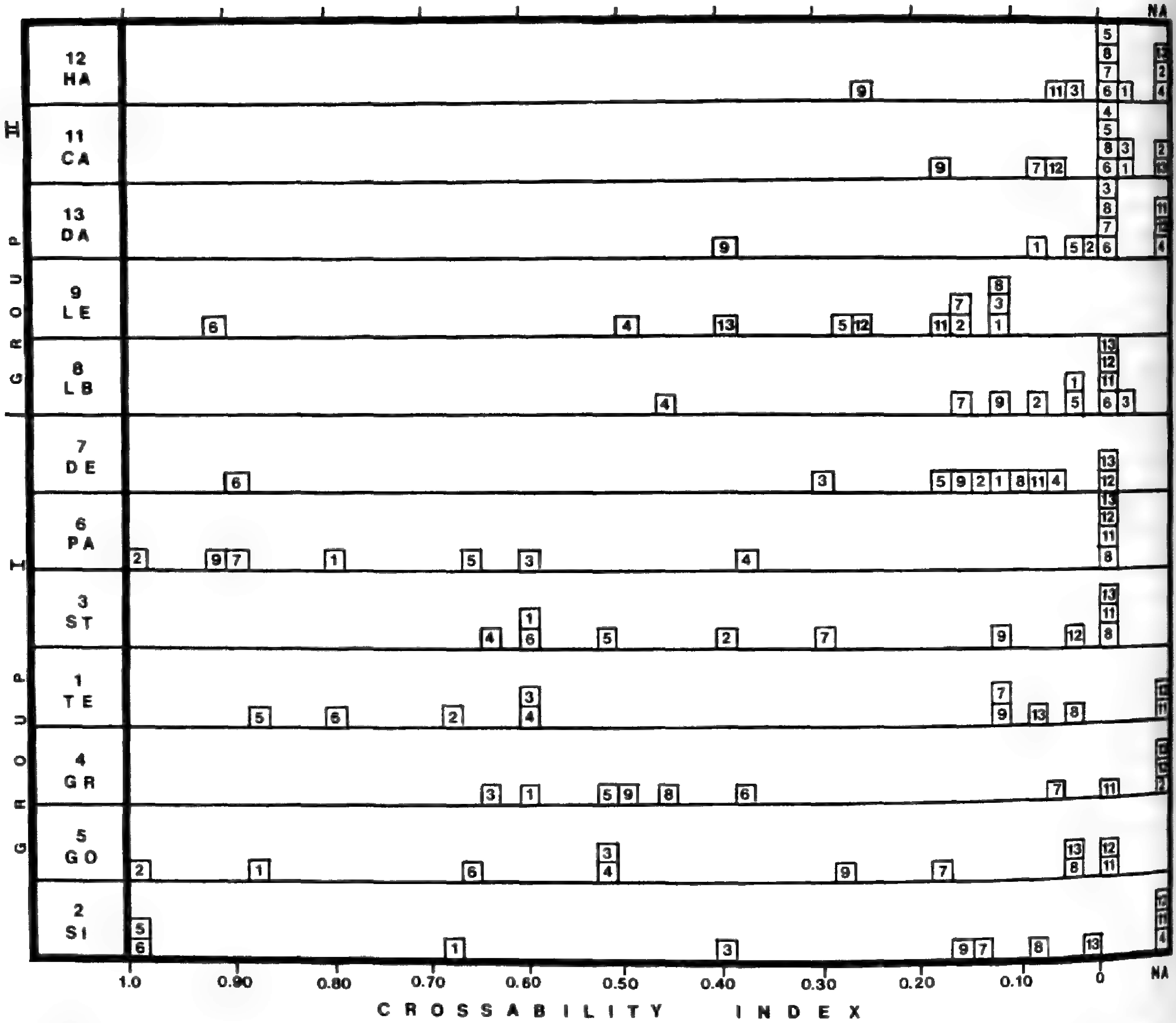


FIGURE 48. Frequency distribution table of crossability indices for 12 Central American species of the *Aphelandra pulcherrima* complex. Species are arranged in rows so that those crossing most readily are proximate. Each square is labelled with the appropriate species identification number. Data not available (NA) are indicated at the far right.

1969). For example, Lloyd (1965) crossed races of *Leavenworthia* and found that seed set was higher when the staminate parent was self-incompatible and the ovulate parent self-compatible, than when the reciprocal cross was made.

The goal of this study was to obtain estimates of the degree of relationship among the species of *Aphelandra* treated here. During the evolution of these species from a common ancestor, crossability has decreased from full interfertility to various degrees of incompatibility between each pair of species. The larger of the reciprocal CIs for each species pair thus represents the most conservative estimate of relationship. The smaller index may be a product of various aspects of incompatibility beyond degree of relationship, as described above, and would over-estimate divergence. The larger index for each species pair is, therefore, used in all further analyses (Table 11).

Crossability indices are presented in tabular and diagrammatic form as recommended by McDade and Lundberg (1982). The frequency distribution of crossability indices (Fig. 48) shows that, with the exception of a very high crossability between species 9 (*A. leonardii*) and 6 (*A. panamensis*), all of the CIs above 0.50 are among species 1–7 (Group I, Table 3). Crossabilities among species 8–13 (Group II), and between these and species 1–7 are mostly less than 0.20. Summarization of the crossability data by group (Fig. 49) emphasizes this pattern. Species 7 (*A. deppeana*) is apparently isolated within Group I. Although species 6 and 7 are highly interfertile

(CI = 0.89), of the CIs among species 1–7, all of those below 0.30 have species 7 as one member of the pair. Species 9 (*A. leonardii*) appears to be intermediate between the two groups. Of four crossability indices above 0.20, three involve species 9, as do six of seven CIs above 0.11.

Crossability maps, representing the best two dimensional configuration of species based on the matrix of crossability indices, were constructed using Multidimensional Scaling (Kruskal & Wish, 1978; McDade & Lundberg, 1982; Fig. 50). The locations and relative proximities of species on the map are indicative of their interrelationships based upon the results of artificial hybridizations. Subsequent maps display connections between species that cross at or above five selected crossability levels (Fig. 51–55). Crossability mapping emphasizes the close relationships among species 1–6 of Group I (*A. terryae, A. sinclairiana, A. storkii, A. gracilis, A. golfodulcensis, A. panamensis*). Species 7 (*A. deppeana*) is closely related to species 6 (*A. panamensis*), but is more distant from the remaining five species. Species 9 (*A. leonardii*) occupies an intermediate position between this interrelated group and the much less closely linked species 11, 12, 13, and 8 (*A. campanensis, A. hartwegiana, A. darienensis,* and *A. lingua-bovis*). The tentative position of species 8 merits further discussion. Whereas multidimensional scaling placed species 9 between species 1–7 and 8 based on all crossing relationships, the first connection of species 8 is with species 3 at CI = 0.45. No further connections are made until CI = 0.12 with species 9 (Fig. 55). It is possible that the crossability index between species 8 and 3 is the result of a sampling error due to the unusually small number of crosses attempted ($n = 10$). An initial connection of species 8 (*A. lingua-bovis*) with 9 (*A. leonardii*) would be more in accord with the pattern of crossabilities between species 8 and all other taxa.

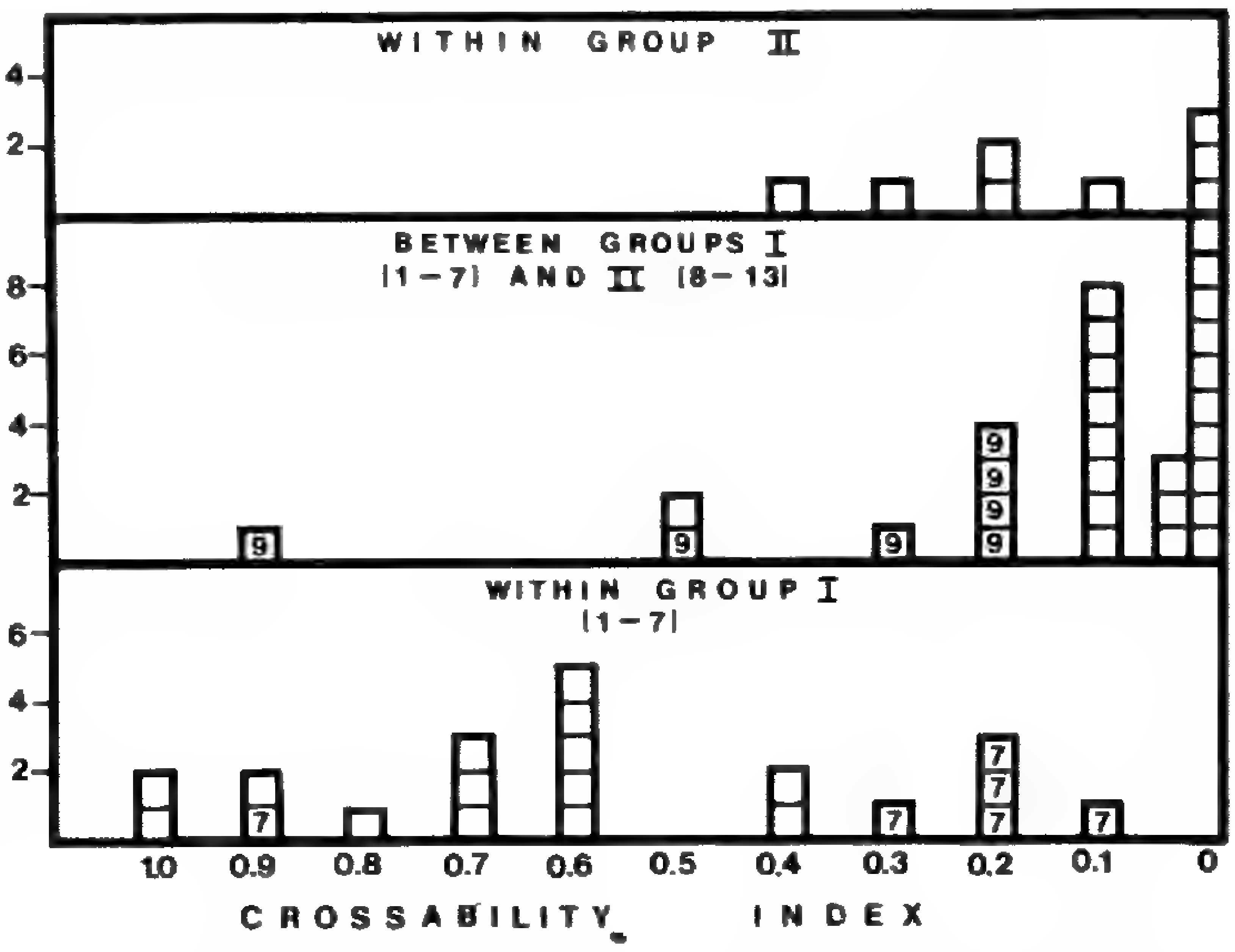
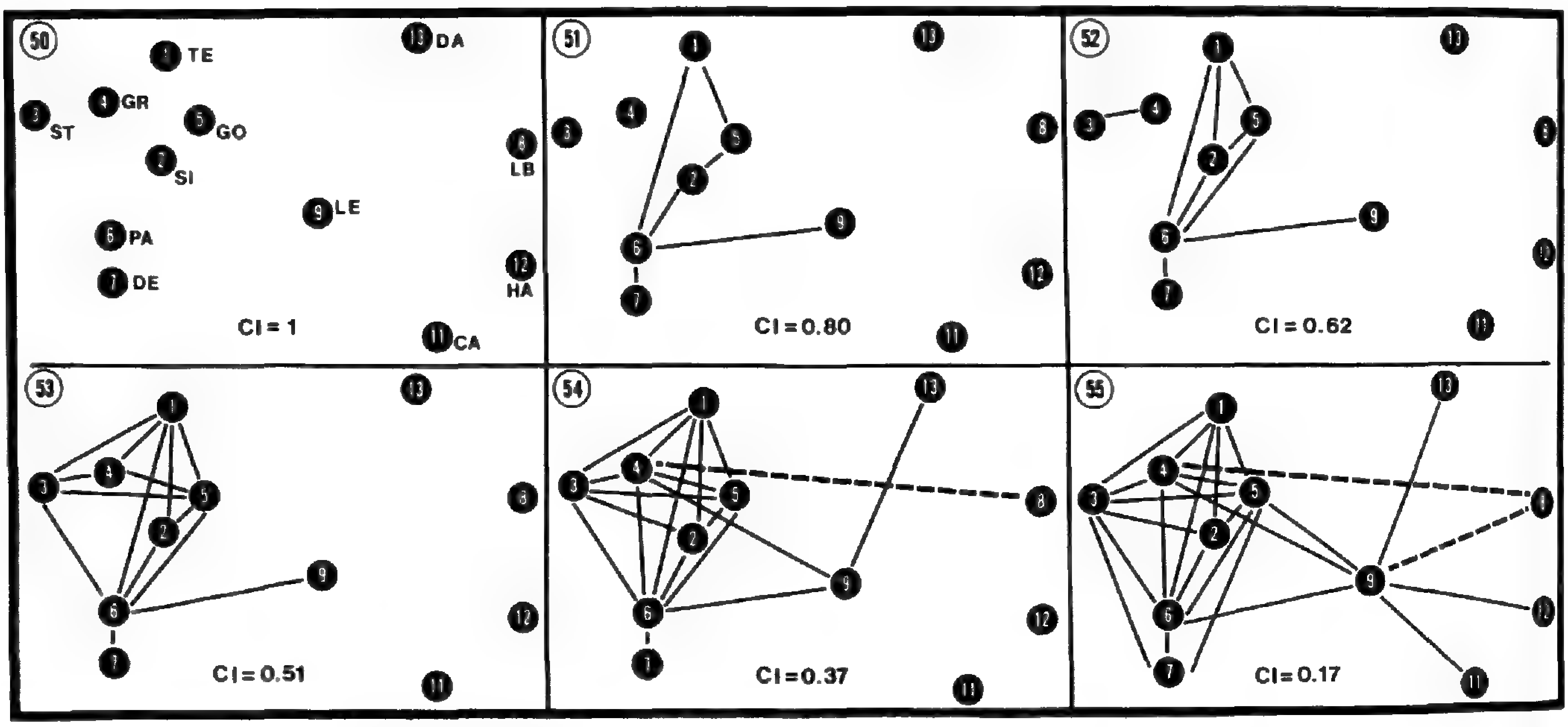


FIGURE 49. Summary frequency distribution of crossability indices within and between the species of Groups I and II. Numbered boxes illustrate points made in text.

NATURAL HYBRIDIZATION AND ISOLATING MECHANISMS

Only two combinations of parental species are suspected of producing naturally occurring hybrid offspring. Three Panamanian localities host putative hybrids between *A. sinclairiana* and *A. gracilis*. All three are mid-elevation sites where cloud forest habitat of *A. gracilis* has been disturbed and warmer and drier local climates result. *Aphelandra sinclairiana* usually occurs along edges and in gaps in primary lowland to premontane forest, and may also colonize extensively disturbed areas at higher elevations. Hybrid plants between these two species are found in disturbed areas near El Valle (Coclé), Cerro Jefe and El Llano (Panamá) (Fig. 56). They are distinctly intermediate in many characters and produce distorted, apparently sterile pollen. Unfortunately, I have not attempted this cross in the greenhouse.

Interspecific hybrids apparently between *A. sinclairiana* and *A. golfodulcensis* occur at various localities in the Caribbean lowlands of northeastern Costa Rica (Fig. 56). Although the ranges of the two parental species are separated by the central mountain range in Costa Rica, older collections indicate that the two may have occurred close together along either slope of the central plateau north of the high Talamanca range. These localities are mostly urban population centers at the present time. The putative hybrids are intermediate between the two parental species in many features and, though quite vigorous, are pollen sterile. Numerous self- and cross-pollinations between clumps of these plants were attempted without any successful seed set. Collection localities suggest that streams and rivers are important in the propogation of this sterile hybrid. Three clumps of the hybrid occur at La Selva in Heredia province, all of which are along the banks of the Río Puerto Viejo within the flood zone. Branches broken off upstream would root quite readily when lodged against the bank downstream, giving rise to new "individuals" of



FIGURES 50–55. Crossability mapping of Central American species of the *Aphelandra pulcherrima* complex, at six successive levels of crossability. All connections made at and above the indicated CI are presented in each map. Dashed lines indicate conflicting evidence for the position of species 8 as discussed in text.

the hybrid. Hybrids between *A. sinclairiana* and *A. golfodulcensis* have been made in the greenhouse, and these are indistinguishable from the putative hybrids from Costa Rica. Field studies and greenhouse hybridizations indicate that, if the ranges of the two parental species overlapped, compatibility of flowering times, identical pollinator species, and interfertility would result in the production of hybrids.

With these exceptions, reproductive isolation between Central American species of the *A. pulcherrima* complex is apparently complete. For species pairs that are fully allopatric and/or completely intersterile (Table 12), further discussion of isolating mechanisms is moot. The results of greenhouse crosses using plants from field populations, however, indicate that many species with adjacent or sympatric ranges are interfertile. Be-

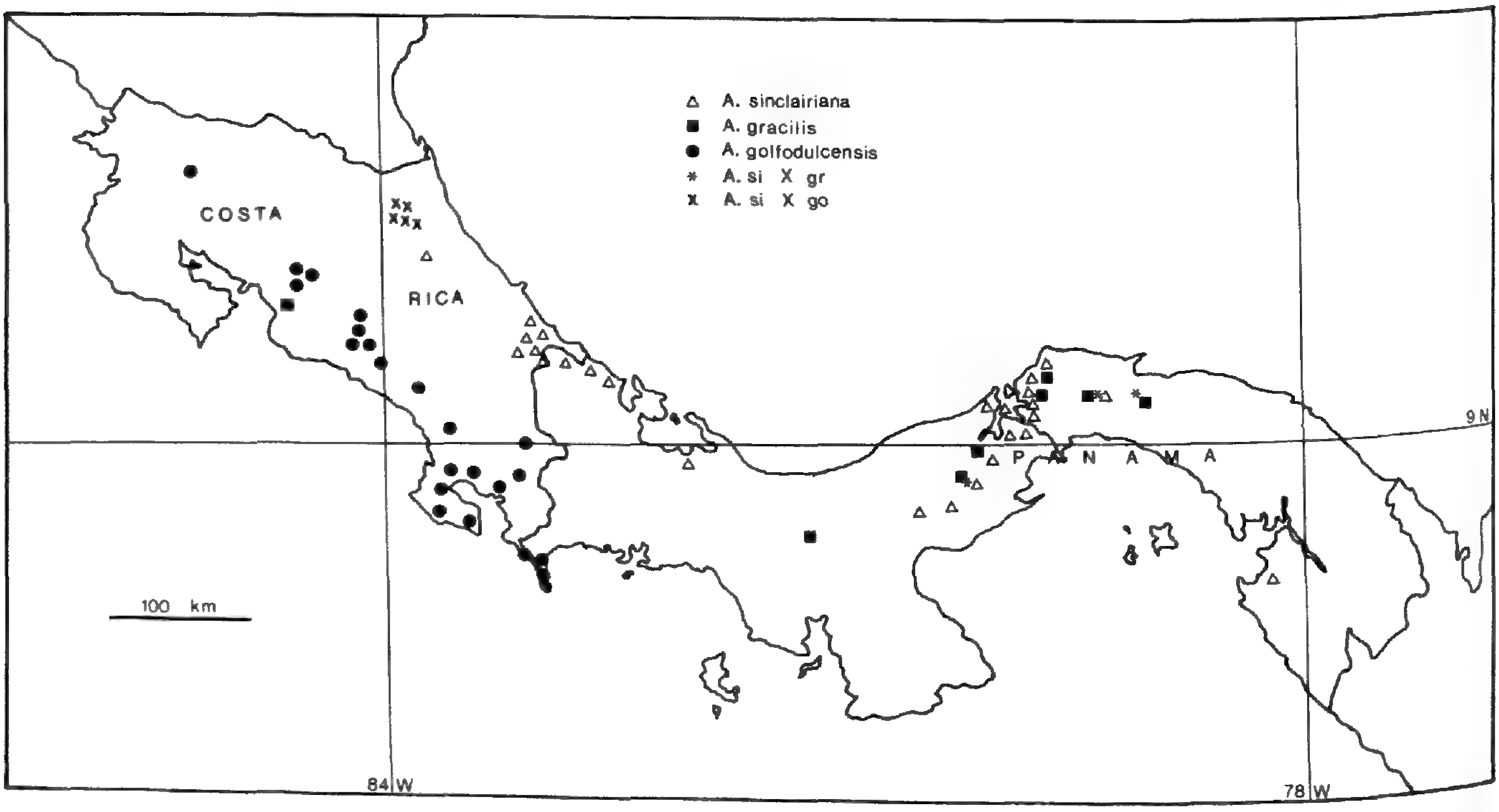


FIGURE 56. Distribution of *Aphelandra sinclairiana, A. gracilis, A. golfodulcensis,* and the hybrids between each of the latter two species, and *A. sinclairiana* in Costa Rica and Panama.

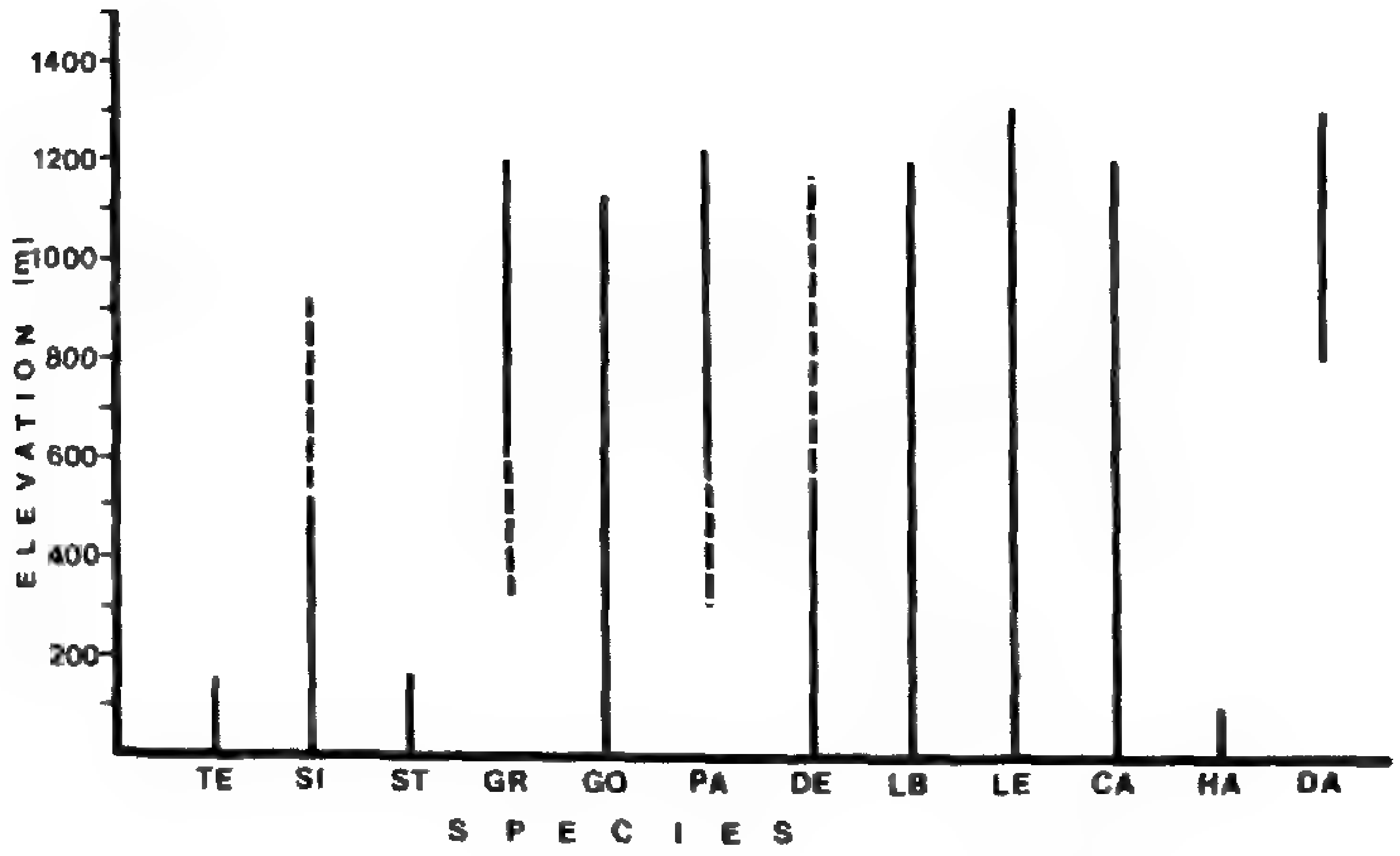


FIGURE 57. Elevational range of the Central American species of the *Aphelandra pulcherrima* complex. Dashed bars indicate elevations at which species are found only when local climatic conditions result in habitat atypical of that elevation in this region.

cause hybrids are rare in nature, further examination of barriers preventing hybridizations between such species is appropriate. Four interrelated factors merit attention: isolation by elevational range, habitat differences, flowering seasonality, and pollinator specificity.

Isolation by elevation, especially if reinforced by similarly restricted pollinator ranges and habitats, may effectively prevent hybridization between species. Several species of *Aphelandra* are restricted to either lowland or mid-elevation localities (Fig. 57). Thus, although the ranges of several lowland species (e.g., *A. deppeana, A. sinclairiana, A. terryae*) are adjacent to those of mid-elevation species (e.g., *A. panamensis, A. gracilis*) (Fig. 56), hybridization events are rare.

Habitat differences may separate species that have adjacent ranges, or can reinforce elevational isolation. The species of *Aphelandra* treated here are found in seasonally drought deciduous lowland forest, lowland wet forest, and cloud forest. *Aphelandra deppeana,* for example, occurs in habitats with a more severe dry season than can be tolerated by other species. This habitat difference, along with pollinator specificities, apparently reduces the possibility of hybridization involving *A. deppeana.* Thus, although hybrids of *A. deppeana* and its close relative, the cloud forest species *A. panamensis,* are easily synthesized (Table 11), naturally occurring hybrids are not found.

Because the wet and dry seasons are quite discrete in many parts of Central America, temporal differences in flowering can be effective as a barrier to hybridization even between fully sympatric species. Four species of *Aphelandra* treated here flower during the dry season, and the remaining nine flower during the wet season (Table 8). For example, *A. panamensis* and *A. gracilis* coexist and share the same pollinators at several localities in Panama. Lack of overlapping flowering seasons effectively prohibits hybridization.

As documented by field observations of flower visitors to the species of *Aphelandra* treated here, all but *A. deppeana* are pollinated by large hermit or hermit-like hummingbirds (Table 9). Pollinator differences thus reinforce reproductive isolation of *A. deppeana* and species with adjacent ranges (e.g., *A. sinclairiana*). The two main pollinators of the remaining species occupy different elevational ranges, perhaps reinforcing eleva-

TABLE 12. Isolating mechanisms operative between Central American species of the *Aphelandra pulcherrima* complex. Pairs not fully allopatric (A) and/or intersterile (I) may be isolated by elevation (E), habitat (H), flowering seasonality (FS), or pollinator specificity (P). Species numbers and abbreviations as in Table 2.

Species	1. TE	2. SI	3. ST	4. GR	5. GO	6. PA	7. DE	8. LB	9. LE	11. CA	12. HA
2. SI	A										
3. ST	A										
4. GR	A	E,H[a]	A								
5. GO	A	A	A	A							
6. PA	E,FS	E,H,FS	A	FS	A						
7. DE	H,FS,P	H,FS,P	A	E,H,FS,P	H,FS,P	E,H,P					
8. LB	E,FS	H,FS	A,I	A	FS	I	A				
9. LE	A	A	A	E,FS	A	E	A	E			
11. CA	A[a]	E,H,FS[a]	A,I	I	A,I	I	A	A,I	A		
12. HA	FS[a]	A[a]	A	A[a]	A,I	I	A,I	I	E	A	
13. DA	A	A	A	A[a]	A	I	A,I	I	E	A[a]	E,H[a]

[a] Species pairs for which data from artificial hybridizations are not available.

tional isolation of geographically proximate species. Long-tailed (lowlands) and green hermits (mid-elevations) are, however, apparently equally effective pollinators of these species. *Aphelandra sinclairiana,* which is usually a lowland species pollinated by long-tailed hermits, is cultivated at 1,200 m at the Las Cruces Botanical Garden in Costa Rica. Visits to flowers by green hermits were apparently effective since these plants set numerous seeds. Similarly, in those parts of its range where disturbance has resulted in the spread of *A. sinclairiana* to mid-elevations, pollinator specificities are lost. Hybridization between *A. sinclairiana* and *A. gracilis,* a species restricted to mid-elevations, results because green hermits pollinate flowers of both species.

The paucity of naturally occurring hybrids is at first striking given the geographic proximity and lack of full sterility between many of these species. However, in the topographically complex terrain of Central America, high mountain ranges and prevailing weather patterns result in small scale environmental partitioning. Under these conditions, isolating factors that fall short of complete intersterility and strict allopatry can effectively prohibit hybridization. Such factors are clearly important among the species of *Aphelandra* treated here.

PHYLOGENETIC ANALYSIS

INTRODUCTION AND METHODS

The goal of phylogenetic systematics (sensu Hennig, 1966) is to classify organisms according to their genealogical relationships. Because a common genealogy is shared by all organisms, phylogeny provides the conceptually unifying basis for biological classification. Provided that only strictly monophyletic taxa are recognized, hierarchical Linnaean classification allows exact retrieval of phylogenetic relationships. Monophyletic groups can be delimited only by recognition of shared derived (advanced) character states (Hennig, 1966; Lundberg, 1972; Wiley, 1981). Character analysis is thus basic to phylogeny reconstruction and involves at least two steps: recognition of strictly homologous characters and formulation of polarity hypotheses. The phylogeny supported by the largest suite of congruent derived character states is the best hypothesis. Homoplasies of several sorts may occur and indicate reversals, parallelisms, and errors in character analysis. Such unreliable characters may be more numerous than reliable ones in the data set, but presumably will not be mutually congruent. An incorrect phylogeny will be accepted as the best hypothesis only if a set of unrecognized and hierarchically correlated homoplasies exists that is larger than the set of cladistically reliable characters.

As recently reviewed by Stevens (1980), several criteria may be used to infer evolutionary polarities of character states, including evidence from the fossil record, ontogeny, and comparison with out-groups. In this study, primary emphasis was on the last criterion because *Aphelandra* has no known fossil record and the ontogeny of most characters used in the analysis has not been studied. Based upon shared possession of a suite of derived character states that result in the distinctive corolla morphology peculiar to this group, the species of the *A. pulcherrima* complex are hypothesized to be monophyletic. These species, along with *A. hylaea* Leonard, *A. impressa* Lindau, and *A. lamprantha* Leonard, are also unique within *Aphelandra* in having nectaries on the floral bracts. Shared possession of the extra-floral nectaries is evidence that these three species and the *A. pulcherrima* complex are together a monophyletic group, and that one or more of the three is the sister group of the *A. pulcherrima* group. Further resolution of the sister group will require further study; all three species were therefore used as the out-group in character comparisons and polarity decisions. Following study of the distribution of states of 42 characters (Table 13) among these species, polarity hypotheses were made following the out-group method (Watrous & Wheeler, 1981). Consideration of the three species out-group resulted in unambiguous hypotheses for 35 of the 43 characters (2–10, 12–29, 33, 34, 36, 39–43). Character states in the out-group were unknown or offered conflicting evidence for determining evolutionary polarities of the remaining eight characters and the analysis was expanded to consider more distantly related groups. Relationships within the genus are not sufficiently resolved to permit identification of the sister group of the species sharing bracteal nectaries and the entire genus was thus used as the next level of comparison. Two additional, more distantly related out-groups are provided by the relationships of *Aphelandra* within Acanthoideae: other genera in Aphelandreae and the Old World Acantheae. The results of character analysis are presented in Table 13 and as a character by taxon matrix in Appendix E. The value of the phylogenetic hypothesis presented for the species of *Aphelandra* treated here rests on the validity of this character analysis. Detailed information on character state distributions among out-group taxa and polarity decisions for each character is available from the author. A phylogenetic hypothesis was constructed from these data using the Wagner method (Wagner, 1969; Kluge & Farris, 1969; Lundberg, 1972).

RESULTS

The 13 species fall into two lineages (Fig. 58) herein referred to as Group I (species 1–7) and Group II (8–13) (Table 3). The species of Group I share several uniquely derived character states: trichomes of distal stems longer than 0.5 mm (character 4); bracteal nectaries of individual, large glands (12, 13); terete fruits (30); sub-globose seeds (35); and semi-hypogeal germination (37) (Fig. 58). Shared possession of these advanced states provides strong evidence of a monophyletic origin of these species. *Aphelandra sinclairiana* (species 2) and *A. storkii* (3) are sister species, sharing long and erect trichomes on distal stems (character 3). *Aphelandra terryae* (1) is hypothesized to be the sister group of these two species. Characters providing evidence for this relationship are, however, homoplasious (reversed or paralleled elsewhere in the cladogram) (Appendix F). *Aphelandra deppeana* (7) and *A. panamensis* (6) are sister species, sharing three uniquely derived character states: dense pubescence of distal stems (2), villous pubescence of lower corolla lip (26), and oblique stigmas (29). The relationships of *A. golfodulcensis* (5) and *A. gracilis* (4) within Group I are tentative. Shared possession of green floral bracts (9), along with six homoplasious characters (Appendix F), suggests that these two species share a monophyletic origin with *A. deppeana* and *A. panamensis*. In conflict with this evidence, *A. deppeana* and *A. panamensis* share derived states of characters 25 (pubescence of the corolla tube) and 26 (long trichomes on the lower lip of the corolla) with *A. terryae* (1), *A. sinclairiana* (2), and *A. storkii* (3).

Evidence in support of a monophyletic origin of species 8–13 (Group II) is provided by shared possession of extremely leathery floral bracts (character 7) and glabrous corollas (25, 26) (Fig. 58). The bracteal nectaries composed of many, minute glands facilitates recognition of these species. This feature, however, is shared by the three species out-group (*A. hylaea, A. impressa, A. lamprantha*) and is thus hypothesized to be primitive for the *A. pulcherrima* complex. The placement of *A. lingua-bovis* (species 8) is tentative. All of the derived character states it possesses are homoplasious (Appendix F). Derived states of characters 23 (narrow upper corolla lip), 28 (anther length) and 39 (syntricolpate pollen) suggest a relationship between this species and the sister species *A. deppeana* (7) and *A. panamensis* (6). This relationship, however, is contradicted by many other characters. Study of South American relatives of *A. lingua-bovis* may provide data for a more satisfactory resolution of the phylogenetic relationships of this species. Strong evidence for a monophyletic origin of species 9–13 (*A. leonardii–A. darienensis*) is provided by shared uniquely derived states of characters 40 (pollen with unsculptured longitudinal bands) and 41 (corolla opening immediate). *Aphelandra laxa* (10) shares leathery and papillate corollas (21, 41) with species 11–13. Shared possession of falcate bracteoles (16) and large seeds (36) provides evidence that *A. campanensis* (11), *A. hartwegiana* (12), and *A. darienensis* (13) are monophyletic. *Aphelandra hartwegiana* and *A. darienensis* share anthers longer than 9 mm (28), as well as three homoplasious derived character states (Appendix F). In conflict with this evidence are characters 19 (calyx lobes obtuse and apiculate) and 5 (parallel evolution of pedunculate inflorescences), which suggest that *A. hartwegiana* and *A. campanensis* are sister species. Additional data will be required to satisfactorily resolve these relationships.

The *A. pulcherrima* complex includes about 25 species that occur only in South America (Appendix A). These species received only cursory attention in the course of this research and have not been incorporated into the phylogeny. It is apparent that the species treated here do not comprise a single, monophyletic sister group of all South American species. Rather, each of the Central American groups described here has South American members. The Central American species thus represent more than one evolutionary line from the older continent. As detailed in the taxonomic treatment, several species apparently have closer relatives among South American members of the complex than among species treated here. Further study of South American species of this complex will permit expansion of the phylogeny to include all species of the monophyletic group. The complete cladogram will facilitate formulation of biogeographic

TABLE 13. Characters and character states used in phylogenetic analysis. Asterisks denote hypothesized primitive states. For multistate characters with an intermediate state primitive, two-directional evolution is hypothesized.

1. Habit
   - *0 Monocaulous
   - 1 Shrub/small tree
2. Pubescence of distal stem, density
   - *0 Sparse
   - 1 Moderate
   - 2 Dense
3. Pubescence of distal stem, orientation
   - 0 Erect
   - *1 Upwardly appressed
   - 2 Downwardly appressed
4. Pubescence of distal stem, length
   - *0 to 0.5 mm
   - 1 0.6–1 mm
   - 2 >1 mm
5. Inflorescence
   - *0 Sessile
   - 1 Pedunculate
6. Floral bracts, margin
   - *0 Toothed
   - 1 Occasional minute teeth
   - 2 Entire
7. Floral bracts, texture
   - *0 Membranous
   - 1 Coriaceous
   - 2 Leathery
8. Floral bracts
   - *0 Imbricate
   - 1 Lax
9. Floral bracts, color
   - *0 Green
   - 1 Brightly colored
10. Floral bracts, length
    - 0 <8 mm
    - *1 8.5–14 mm
    - 2 14.5–22 mm
    - 3 22.5–30 mm
    - 4 >30 mm
11. Floral bracts, apex
    - *0 Acute
    - 1 Obtuse
12. Bracteal nectaries
    - *0 Many minute
    - 1 Few large
13. Bracteal nectaries, diameter
    - *0 <0.25 mm
    - 1 0.25–0.75 mm
    - 2 0.76–1 mm
    - 3 >1 mm

TABLE 13. Continued.

14. Bracteal nectaries, position
    - 0 Sub-medial
    - *1 Medial
    - 2 Supra-medial
15. Floral bracts, orientation
    - *0 Plane
    - 1 Recurved
16. Bracteoles, shape
    - *0 Lance-ovate
    - 1 Slightly falcate
    - 2 Falcate
17. Bracteoles, color
    - *0 Green
    - 1 Brightly colored
18. Calyx, length
    - *0 6–10 mm
    - 1 11–15 mm
    - 2 16–20 mm
19. Sepals, apical shape
    - *0 Acute
    - 1 Obtuse and apiculate
20. Sepals, color
    - *0 Green
    - 1 Brightly colored
21. Corolla, texture
    - *0 Membranous
    - 1 Coriaceous
    - 2 Leathery
22. Corolla, length
    - 0 <5 cm
    - *1 5.1–6 cm
    - 2 6.1–7 cm
    - 3 >7 cm
23. Corolla, width upper lip
    - 0 ≤6 mm
    - 1 6.5–9 mm
    - 2 9.5–11.5 mm
    - 3 ≥12 mm
24. Corolla, apical shape upper lip lobes
    - *0 Acute to acuminate
    - 1 Emarginate and apiculate
25. Corolla tube, pubescence
    - 0 Glabrous
    - *1 <0.25 mm
    - 2 >0.25 mm
26. Corolla, pubescence of lower lip
    - 0 Glabrous
    - *1 <0.25 mm
    - 2 0.26–0.75 mm
    - 3 >0.75 mm
27. Corolla, color
    - *0 Red, pink, orange
    - 1 Yellow

TABLE 13. Continued.

28. Anther, length
    0 1–3 mm
    *1 3.5–6 mm
    2 6.5–9 mm
    3 >9 mm
29. Stigma, morphology
    *0 Bilobed
    1 Oblique
30. Fruit, shape
    *0 Flattened
    1 Terete
31. Fruit, color (immature)
    *0 Other
    1 Orange-brown
32. Fruit, color (immature)
    *0 Other
    1 Black
33. Fruit, length
    *0 <20 mm
    1 21–25 mm
    2 26–30 mm
    3 >30 mm
34. Fruit, vestiture
    *0 Glabrous
    1 Puberulous
35. Seed, shape
    *0 Flattened
    1 Sub-globose
36. Seed, diameter
    0 <4 mm
    *1 4.5–6 mm
    2 >6.5 mm
37. Germination pattern
    *0 Epigeal
    1 Semi-hypogeal
38. Pollen, shape (L/W)
    *0 L/W < 2.1
    1 L/W > 2.1
39. Pollen, colpi
    *0 Tricolpate
    1 Syntricolpate
40. Pollen, sculpturing
    *0 Continuous
    1 Unsculptured bands
41. Corolla opening
    *0 Delayed
    1 Immediate
42. Corolla, vestiture
    *0 Pubescent, glabrous
    1 Papillate
43. Fruit, shape
    *0 Stipitate
    1 Sessile

hypotheses based on phylogenetic relationships and distributional patterns.

COMPARISON OF RESULTS FROM ARTIFICIAL HYBRIDIZATIONS AND PHYLOGENETIC ANALYSIS

The results of artificial hybridizations can be compared with two measures of relationship derived from phylogenetic analysis: number of hypothesized speciation events (cladistic distance) and number of inferred evolutionary changes (patristic distance) between species. Both distances are significantly correlated with crossability indices for each pair of species ($r = 0.442$, cladistic distance; $r = 0.560$, patristic distance; 57 df, $P < 0.001$ for both coefficients). More specific comparisons of the results of the two analyses are made using Figures 55 and 58. Phylogenetic analysis separates the species into two lineages (Fig. 58). Crossability indices generally support this division but suggest an intermediate position for *A. leonardii* (species 9) between the two groups (Fig. 55). Both analyses closely link *A. terryae, A. sinclairiana, A. storkii, A. golfodulcensis, A. gracilis,* and *A. panamensis* (species 1–6). The phylogenetic hypothesis that *A. deppeana* and *A. panamensis* are sister species is supported by high crossability between the two (Table 11). *Aphelandra deppeana* has several uniquely derived character states that distinguish it from other species of Group I (Fig. 58). Low crossability of *A. deppeana* with other species of Group I corroborates its distinctiveness (Table 11, Fig. 55).

The most apparent difference in the results of the two analyses is in respect to interrelationships of Group II (species 8–13). Phylogenetic analysis suggests that species of Group II are as closely interrelated as those of Group I. The available results of artificial hybridizations, however, indicate that these species do not cross readily (Table 11, Fig. 55). This conflict illustrates the difficulty encountered in using artificial crossability to estimate relationships. The rigidity of genetic incompatibility barriers to hybridization between species is apparently not reliably correlated with phylogenetic relationships. The efficacy of other isolating mechanisms may be important: distant relatives separated by effective barriers (e.g., habitat, different pollinators) may remain cross-compatible while sister species lacking additional isolating mechanisms may be highly intersterile. Thus, if genetic incompatibility is relatively unimportant as a barrier to interbreeding

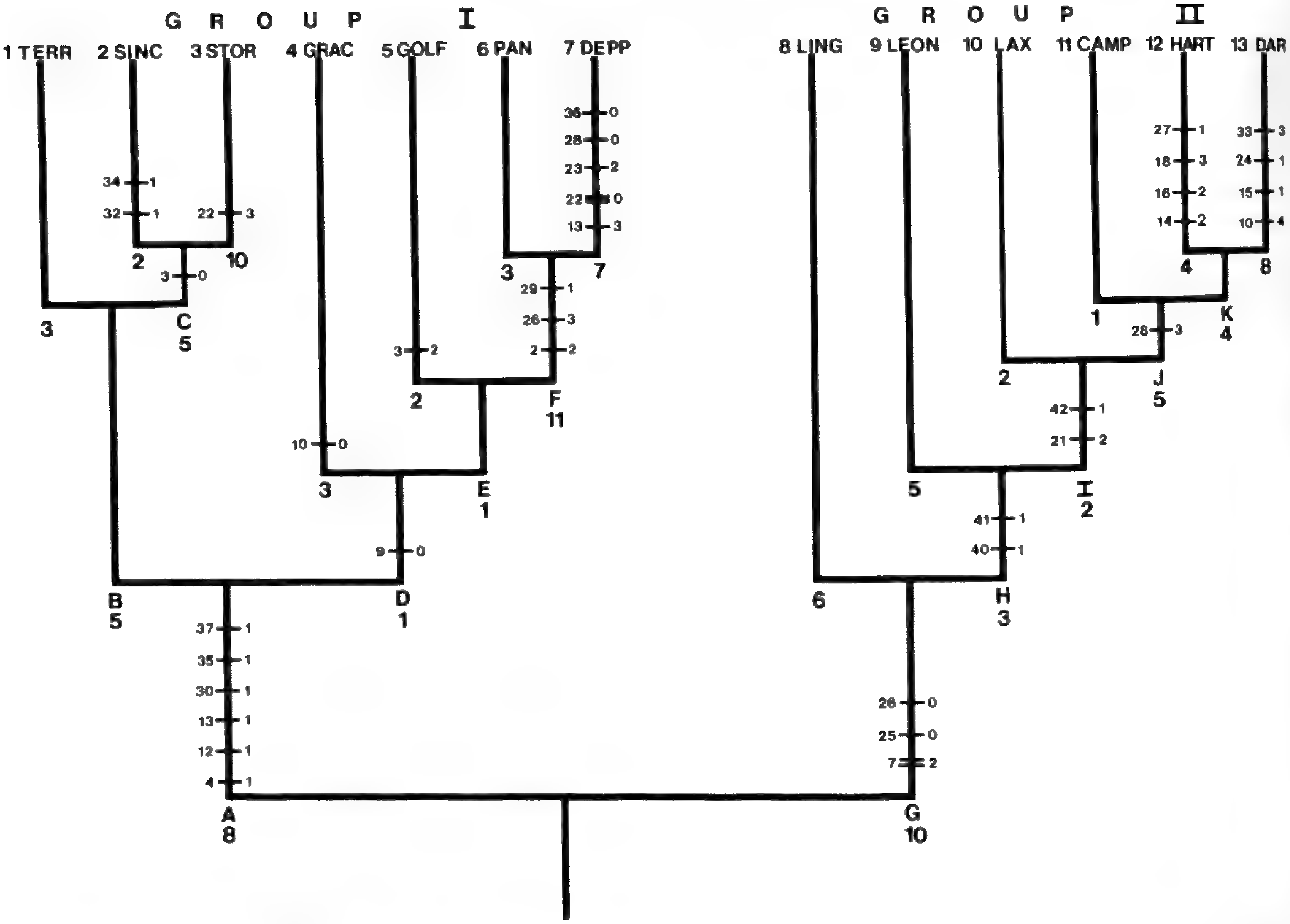


FIGURE 58. Phylogenetic hypothesis of relationships among the Central American species of the *Aphelandra pulcherrima* complex. Each species is located along the upper horizontal of the diagram. Evolution of uniquely derived and unreversed character states is indicated by horizontal slashes, with numerals to the left indicating the changing character and those to the right indicating the state evolved. Non-terminal intervals are identified by letter. Total length (including homoplasies) is given for each interval. Appendix F provides a complete listing of character changes by interval.

among species of Group I, then the results of artificial hybridizations may provide reliable estimates of degree of phylogenetic relationships among these species. In Group II, genetic incompatibility may be more important, resulting in strong intersterility barriers between species.

TAXONOMIC TREATMENT

Aphelandra R. Br., Prodr. 475. 1810. LECTOTYPE: *A. cristata* Jacq.

Synandra Schrader, Gött. Gel. Anz. 1: 715. 1821, non Nuttall 1818.
Amathea Raf., Fl. tellur. 10: 65. 1838.
Strobilorhachis Klotzsch in Otto & Dietrich, Allg. Gartenzeitung 7: 307. 1839.
Hydromestus Scheidw. in Otto & Dietr., Allg. Gartenzeitung 10: 285. 1842.
Hemisandra Scheidw., Bull. Acad. Roy. Sci. Bruxelles 9: 22. 1842.
Lagochilium Nees in Martius, Fl. bras. 9: 85. pl. 10. 1847.

Perennial suffructescent herbs to diffusely branched shrubs, rarely sub-rosettes or small trees; stems terete to quadrangular, soft-wooded, rarely thick and succulent, glabrous to pubescent, nodes frequently swollen. Leaves opposite, rarely verticillate or alternate, petiolate; the blades membranous to coriaceous, marginally toothed, lobed, crenate, undulate or entire; stipules lacking or present as interpetiolar spines. Inflorescences of terminal spikes, solitary to few, or numerous and arranged in a freely branching paniculate inflorescence; each flower subtended by a bract, these small, green and loosely arranged, to large, imbricate, and highly colored, marginally toothed or entire, occasionally bearing lateral glandular areas ("ocelli"); bracteoles two, laterally subtending calyx, usually lanceolate, similar to sepals in shape and texture, rarely rudimentary. Calyx of 5 subequal, usually lanceolate sepals, the adaxial sepal, and the abaxial and lateral pairs of unequal width; corolla straight or curved, limb 5-parted, nearly regular to strongly bilabiate with a basically bilobed upper lip (the lobes sometimes partially or completely united) and a reflexed 3-lobed lower lip, the lobes of the lower lip subequal to strongly dimorphic with lateral lobes reduced or essentially lacking; stamens four, epipetalous, rarely included within corolla tube, usually exserted beyond throat but not extending beyond tip of upper lip, anthers usually borne erectly, within or closely paralleling upper lip, narrow, one-celled; stigma infundibular, entire or shallowly bilobed, style filiform, frequently extending through and slightly beyond the adaxial pair of anthers, ovary bilocular with two ovules per locule. Fruits capsular, clavate to sub-globose, terete to strongly flattened, 4-seeded, explosively dehiscent on drying, seeds borne on hook-like retinacula, brown, rounded to somewhat angled and strongly flattened to sub-globose. Seed germination epigeal or semi-hypogeal.

KEY TO THE CENTRAL AMERICAN SPECIES OF THE *APHELANDRA PULCHERRIMA* COMPLEX

1. Bracteal nectaries composed of a few (1–10) well-defined glands each 0.5–1.25 mm in diameter; capsules terete in cross-section or nearly so; seeds sub-globose (diameter/width < 2/1).
    2. Corolla less than 4.5 cm long; S Mexico to N South America .... 7. *A. deppeana*
    2′. Corolla exceeding 5 cm long.
        3. Bracts consistently bearing 2–3 pairs of marginal teeth, each 1–2 mm long; capsules sessile; leaves epetiolate; central and eastern Panama .... 6. *A. panamensis*
        3′. Bracts marginally entire or occasionally bearing 1–2 pairs of minute teeth (< 1 mm long); capsules stipitate; leaves with distinct petiole.
            4. Plants profusely branched shrubs to small trees with many short (to 20 cm) spikes in a terminal paniculate inflorescence; bracts narrowly to broadly ovate, to 20 mm long.
                5. Bracts green to occasionally dull brown-orange, narrowly ovate to ovate, to 7 mm wide.
                    6. Bracts 5–8 mm long, non-imbricate, internodes 7–10 mm long; leaves glabrous, slightly coriaceous and shiny; central Panama .... 4. *A. gracilis*
                    6′. Bracts >8 mm long, slightly to closely imbricate; leaves pubescent, membranous, and dull.
                        7. Bracts slightly imbricate, apically obtuse, sparsely pubescent; pubescence of distal stems erect; corolla pubescent; central Panama .... *A. gracilis* × *sinclairiana*
                        7′. Bracts imbricate, apically acute, minutely puberulent; pubescence of distal stems downwardly appressed; corolla minutely puberulent; SW Costa Rica and adjacent Panama .... 5. *A. golfodulcensis*
                5′. Bracts bright orange, broadly ovate, 8–20 mm wide.
                    8. Corollas 5.7–6.2 cm long; distal stems, leaves and bracts sparsely pubescent; E Panama and Colombia .... 1. *A. terryae*
                    8′. Corollas 6.4–7.1 cm long; distal stems, leaves and bracts moderately pubescent to pilose.
                        9. Bracts 16–21 mm long, 14–20 mm wide, densely pubescent; distal stems pilose, trichomes erect; anthers 7–8 mm long, fertile; immature capsules dark, pubescent; S Costa Rica to E Panama .... 2. *A. sinclairiana*
                        9′. Bracts 9–13.5 mm long, 5–9 mm wide, sparsely pubescent; distal stems moderately pubescent, trichomes downwardly appressed; anthers 6–6.5 mm long, shriveled and producing little pollen; plants sterile; NE Costa Rica .... *A. golfodulcensis* × *sinclairiana*
            4′. Plants sparsely branched or monocaulous sub-shrubs with one or few long (to 45 cm) terminal spikes; bracts rhombic oblong-ovate, ≥25 mm long; Costa Rica (Limón and Heredia) .... 3. *A. storkii*

1′. Bracteal nectaries of many (>50) minute glands forming oblong patches 2–5 mm in diameter; capsules strongly flattened; seeds strongly flattened (diameter/width > 3/1).
    10. Corolla 5.5–6 cm long; plants rarely taller than 1.5 m; immature capsules orange-brown; SW Costa Rica, Panama, and Colombia .... 8. *A. lingua-bovis*
    10′. Corolla longer than 6 cm; plants taller than 1.5 m when reproductive; immature capsules green or yellow-green.
        11. Bracts non-imbricate, separated by internodes 1.5–2 cm long; Panama (San Blas) .... 10. *A. laxa*
        11′. Bracts imbricate, internodes not visible at anthesis.
            12. Bracts rhombic-ovate, 7–10 mm long, 5–7 mm wide; bracteoles lanceolate; Costa Rica and Panama .... 9. *A. leonardii*
            12′. Bracts broadly ovate, 11–40 mm long, 9–26 mm wide; bracteoles slightly to markedly falcate.
                13. Bracts to 14 mm long, planar; sepals longer than bracts; capsules to 31 mm long.
                    14. Bracts 9–11 mm wide; bracteoles slightly falcate, 11–13 mm long; sepals 15–

18 mm long; corolla orange; capsules 20–24 mm long; S Costa Rica (Limón) to central Panama .... 11. *A. campanensis*

14′. Bracts 11–14 mm wide; bracteoles strongly falcate, 7–10 mm long; sepals 17–22 mm long; corolla yellow (rarely orange) and extremely coriaceous; capsules 28–31 mm long; E Panama and Colombia .... 12. *A. hartwegiana*

13′. Bracts 30–40 mm long, apically recurved; sepals shorter than bracts, not visible at anthesis; capsules about 35 mm long; Panama (Darién) .... 13. *A. darienensis*

1. **Aphelandra terryae** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 381. 1940. TYPE: Panama. Darién: Chepigana District, Tucutí, ca. sea level, *Terry & Terry 1377* (holotype, F; isotype, GH).

Aphelandra incarnata Leonard, Contr. U.S. Natl. Herb. 31: 242. 1953. TYPE: Colombia. Santander: vicinity of Barranca Bermeja, Magdalena Valley, 100–500 m, *Haught 1315* (holotype, US).

Shrubs 1–4 m high, profusely branching; younger stems subquadrangular, moderately pubescent, the trichomes downwardly appressed, white, about 0.25 mm long, older stems terete, glabrate. Leaves opposite (very rarely alternate), oblanceolate, 20–30 cm long, 6–10 cm wide, apically acuminate (the tip acute or blunt), basally attenuate and decurrent on the petiole, marginally entire to slightly undulate; glabrous above and below except veins moderately to sparsely pubescent, the trichomes appressed, white, about 0.25 mm long; petioles 1–2 cm long, sparsely pubescent, the trichomes appressed, white, about 0.25 mm long; leaves subtending inflorescences much reduced, 7–11 cm long, 2.5–4 cm wide, essentially glabrous. Inflorescences terminal, spikes numerous, terete, 3–8 cm long, 1–2 cm wide, arranged in a freely branching paniculate inflorescence; the peduncles 2.5–4 cm long, moderately pubescent, the trichomes erect, white, about 0.25 mm long; rachis minutely puberulous; lowermost 1–2 pairs of bracts leaf-like, 1–2 cm long, 0.5–1 cm wide; floral bracts imbricate, broadly ovate, apically obtuse, marginally entire, 10–12 mm long, 8–10 mm wide, orange, frequently fading to green at base, glabrous within, moderately pubescent without, the trichomes appressed, white, 0.5–0.75 mm long, margins minutely ciliolate, the nectaries medial, composed of several (5–12) individual glands, each 0.5–0.75 mm in diameter; bracteoles narrowly ovate, apically acute, 4.5–6 mm long, 2–2.5 mm wide, orange fading to green toward base, glabrous or with moderately pubescent keel, the trichomes appressed, white, about 0.5 mm long. Sepals 6–7 mm long, apically acute, greenish orange, essentially glabrous, the adaxial segment narrowly ovate, 3–4 mm wide, the abaxial pair lanceolate, 2–2.5 mm wide, the lateral pair narrowly lanceolate, 1.25–1.5 mm wide; corolla pink or orange, 5.7–6.2 cm long, sparsely pubescent except lower lip moderately pubescent, the trichomes erect, white, 0.5–0.75 mm long, the tube 42–45 mm long, about 3 mm in diameter at base, constricted to about 1.5 mm above ovary (7 mm above base), expanding to 6–7 mm deep at throat, the upper lip erect, ovate, 16–18 mm long, 7.5–11.5 mm wide, bilobed, the lobes triangular, 8–9 mm long, anther pocket well-developed, the middle lobe of lower lip broadly lanceolate, 23–26 mm long, 7–8 mm wide, minutely apiculate at apex, the lateral lobes about 1 mm long and 6–7 mm wide; filaments inserted 11 mm from base of corolla tube, free portion of each about 4 cm long, the anthers 5–6 mm long, extending 4–5 mm from tip of upper lip, pollen pale orange; stigma pink, minutely bilobed, the style filiform, extending 3–5 mm beyond the anthers, the ovary apically red, glabrous. Capsules clavate, terete, glabrous, green with red-tinged apex when immature, becoming dark brown to black at dehiscence, 17–19 mm long, 4.5–6 mm wide, 5–6 mm thick, strongly constricted 4–5 mm above base to form narrow stipe; seeds dark brown, 3–4.5 mm in diameter, 1.5–2 mm thick. Seed germination semi-hypogeal.

Habitat and distribution. This species occurs in eastern Panama in the provinces of Darién and San Blas, and in adjacent Colombia. *Aphelandra terryae* is found primarily in lowland forests (occasionally to 500 m elevation) where seasonality of rainfall is not pronounced [tropical moist and wet forests (Holdridge, 1967)]. Individuals of this species are found in gaps in primary forest and along forest edges (streams, trails).

Flowering and fruiting. Peak flowering is during the driest months of the year (Dec. through March). Fruits mature during the late dry season and early wet season.

Leonard (1953) described *A. incarnata*, based on Colombian plants, as distinct from *A. sinclairiana*, and apparently overlooked the earlier description of essentially identical Panamanian plants as *A. terryae* by Standley (in Standley & Steyermark, 1940). Although I have been unable to study Colombian plants in the field, herbarium specimens are not distinguishable from collections of *A. terryae.* I therefore concur with Wasshausen's (1975) decision to synonymize *A. incarnata* Leonard under *A. terryae* Standley.

Plants of *A. terryae* are distinguished from close relatives by their overall sparse vestiture, size and color of the bracts, short inflorescences and corollas, and green, glabrous capsules.

Relationships. *Aphelandra terryae* is a member of Group I, which includes species with bracteal nectaries of individual, large glands. Phylogenetic analysis indicates that it is most closely related to *A. sinclairiana* and *A. storkii* (Fig. 58). These three species share bright orange floral bracts, bracteoles and sepals, and long trichomes on the corollas.

Additional specimens examined. PANAMA. DARIÉN: W slopes of Cerro Pirre, *Mori & Kallunki 5516* (MO); Río Pirre near town of Pirre, *Gentry & Clewell 6937* (F, MO); Río Pirre near crossing of trail from El Real to Tucutí, 20 mi. W of Tucutí, *Duke 5187* (MO); trail between Pinogana and Yaviza, *Allen 256* (A, MO, US); Cerro Piriaque, *Tyson et al. 3815* (DUKE, FSU, MO); trail from Pucuro to Cerro Mali, ridge between Pucuro and Tapalisa Rivers, *Gentry & Mori 13550* (MO); near helipad at hydrocamp on Río Mortí, *Duke 15421* (US). SAN BLAS: mainland opposite Achituppu, *Lewis et al. 126* (GH, MO, US).

COLOMBIA. ANTIOQUIA: along Río Anorí, Zaragoza, 500 m, *Soejarto & Villa 2734* (GH); Malena, 140–160 m, *Pennell 3782* (US); between Río Guapá and León, 100 m, *Yepes et al. 18300* (US); La Llorona near Dabeiba, highway to Mutatá, *Barkley & Guttierez 35442* (US). BOLÍVAR: Boca Verde, on Río Sinú, *Pennell 4581* (NY). CHOCÓ: near Ciudad Mutis, Bahía Solano, sea level–75 m, *Killip & Garcia 33576* (US); hydrocamp 15, on Río Curiche, 100 m, *Duke 15380* (US). CUNDINAMARCA: San Antonio, 200 m, *Haught 6243* (NY, US). SANTANDER: Magdalena Valley between Sogamoso and Colorado Rivers, 100–500 m, *Haught 2098* (F, NY, US).

2. **Aphelandra sinclairiana** Nees in Benth., Bot. Voy. Sulphur 146. pl. 47. 1844. TYPE: Panama. Province not given, *Sinclair s.n.* (holotype, K, not seen).

Shrubs 2–6 m high, profusely branched; stems terete, younger surfaces moderately pilose, trichomes erect, white, 1–1.5 mm long, older surfaces sparsely pilose to glabrate. Leaves opposite, elliptic to oblanceolate, 20–30(–40) cm long, 6–10(–15) cm wide, apically acuminate to attenuate, basally attenuate and decurrent on petiole, marginally entire to slightly undulate, upper surface sparsely strigose, the trichomes appressed, white, about 1 mm long, sparingly pilose below (moderate on veins), the trichomes appressed (erect on veins), white, about 1 mm long; petioles 1–2 cm long, sparingly pilose, the trichomes erect, white, 1–1.25 mm long. Inflorescences terminal, spikes numerous, terete, 8–15(–20) cm long, 2 cm wide, arranged in a freely branching paniculate inflorescence; peduncles lacking or to 6 cm long, moderately pilose, the trichomes erect, white, 1–1.25 mm long; rachis densely pubescent, the trichomes erect, white, about 0.5 mm long; lowermost 2–3 pairs of bracts sterile and leaf-like; floral bracts densely imbricate, broadly obovate, apically obtuse, marginally entire or with 2–3 pairs of minute teeth, 16–20 mm long, 14–20 mm wide, orange, densely minutely puberulous within, densely pubescent without, the trichomes appressed, white, about 0.25 mm long, margins ciliate, the trichomes white, 0.5–0.75 mm long, the nectaries medial, composed of several (4–10) individual glands, each about 0.5 mm in diameter; bracteoles narrowly ovate, apically acute, 7–9 mm long, 2–3 mm wide, orange, moderately pubescent, the trichomes appressed, white, about 0.25 mm long. Sepals 7–9 mm long, apically acute, orange, striate, very minutely puberulous, the adaxial segment oblong, 2–3 mm wide, the abaxial pair lanceolate, 2 mm wide, the lateral pair lanceolate, 1.5 mm wide; corolla pink or orange-red (rarely white), 6.5–7 cm long, moderately pubescent, the trichomes erect, white, 0.5–0.75 mm long, the tube 48–50 mm long, 3 mm in diameter at base, constricted slightly to 1.5–2.5 mm above ovary (8–11 mm above base), expanding to 8–10 mm deep at throat, the upper lip ovate, 16–20 mm long, 9–10 mm wide, bilobed, the lobes triangular, 7–9 mm long, anther pocket well-developed, the middle lobe of lower lip elliptic, 25–29 mm long, 8–10 mm wide, recurled slightly at tip, the lateral lobes 1–2 mm long, 8–9 mm wide; filaments inserted about 11 mm above base of corolla tube, free portion of each about 5 cm long, the anthers 7–8 mm long, extending to within 2–6 mm from tip of upper lip, pollen orange; stigma pink, minutely bilobed, the style filiform, extending 2–5 mm beyond anthers, the ovary glabrous. Capsules clavate, terete, dark brown to black when immature and at dehiscence, very minutely puberulous, 23–25 mm long, 6–7 mm wide, 5–6 mm thick; seeds dark brown, orbicular, slightly flattened, 5–6 mm in diameter, 2–3 mm wide. Seed germination semi-hypogeal.

Habitat and distribution. *Aphelandra sinclairiana* ranges from southern Costa Rica to eastern Panama (Fig. 56). In Costa Rica, numerous collections of this species have come from the wet Caribbean lowlands of southern Limón province. A collection from Atirro, Cartago by Donnell Smith in 1896 is apparently *A. sinclairiana,* but lack of collections between this locality and southern Limón make it difficult to determine the northern limit of this species. This is true as well of the eastern distributional limit: in addition to numerous collections from central Panama (east to Cerro Brewster), one specimen from the Pacific coast of the Darién is apparently of this species. Additional collections from intervening areas, particularly the Caribbean lowlands of San Blas and Bocas del Toro will help to resolve the distributional limits of this species.

Aphelandra sinclairiana is primarily a species of the seasonally dry lowlands [Holdridge's (1967) tropical moist forest]. Although it is not found in areas with severe dry seasons of long duration, it does occur in seasonally partially deciduous forests that experience a 2–4 month period with markedly reduced precipitation. *Aphelandra sinclairiana* occurs in small to large gaps in primary forest, but also colonizes disturbed edge habitats. Although primarily a lowland species, it occurs occasionally at mid-elevations (to 1,200 m), especially where disturbed cloud forests [premontane wet forests (Holdridge, 1967)] are located at the crest of the central mountain range adjacent to extensive lowland, seasonally dry areas.

Flowering and fruiting. Individuals flower during the driest months of the year (Dec. through March) with apparently very little variation. Most plants have completed fruiting by the onset of the wet season.

Aphelandra sinclairiana may be readily distinguished from other species by its pilose stems, leaves and corollas; large, bright orange bracts; citrus-like odor of the inflorescences and distinctively colored, puberulous capsules. There is some variability in bract size and, most notably, corolla color in this species. I have found plants with pink, red-orange, and white corollas at the same locality. These differences are apparently not of systematic importance.

Relationships. Phylogenetic analysis indicates that *A. sinclairiana* is most closely related to *A. storkii.* These two species share erect, pilose pubescence of stems and floral structures. *Aphelandra sinclairiana* crosses readily with *A. teryae, A. golfodulcensis,* and *A. gracilis* (Table 11). Where geographic and elevational isolation break down, it hybridizes readily with the latter two species.

Additional specimens examined. Costa Rica. cartago: Atirro, 600 m, *Donnell Smith 6694* (GH, US). Limón: Río Valle Estrella drainage, *Shank & Molina 4545* (F); Río Lari, *Jimenez-M. 1916* (F, NY); along Río Sixaola, between Bribri and Bratsi, 10–50 m, *Burger et al. 10420* (DUKE, F); Talamanca Valley, *Carleton 124* (US).

Panama. bocas del toro: vincinity of Chiriquí Lagoon, *von Wedel 1083* (GH, MO, US); Changuinola, 30–60 m, *Lewis et al. 803* (GH, MO, US); hillside above Almirante, *Gentry 2684* (DUKE, F, MO). coclé: vicinity of El Valle, 800–1,000 m, *Allen 125* (A, F, MO); Bismark above Penonomé, *Williams 370* (NY, US); El Copé, 250 m, *McDaniel & Cooke 14831* (FSU, MO). colón: edge of forest along Pipeline Road ca. 10 km NW of Gamboa, *Wilbur & Teeri 13365* (DUKE, F), *McDade 389* (DUKE); 8.7 mi. N of Río Chagres, along Boyd-Roosevelt Hwy., *McDade 384* (DUKE); along Río Buenaventura near Portobelo, *Kennedy & Gra 2239* (F, MO), *McDade 289* (DUKE); W end of Gatún Lake Dam, *Blum & Tyson 1975* (FSU, MO); between Fort Sherman and Gatún, 0–175 m, *Burch et al. 1016* (F, MO, NY); Road S-10, N of Escobal, *Croat 12443* (DUKE, F, MO). darién: Boca de Pauarando, on Sambú River, *Pittier 5572* (NY). panamá: SE side of Madden Lake near Puente Natural, 90 m, *Nee & Hansen 14047* (DUKE, MO, WIS); 5 mi. SW of Cerro Brewster, 1,000 ft., *Lewis et al. 3316* (DUKE, F, MO, NY, US); Capira, along trail between Lídice and Aguacate, 300 m, *Foster 2140* (DUKE); Nuevo Emperador, *Barrasco 28* (MO, PMA); slopes of Cerro Campana, 2,500–2,900 ft., *Wilbur 24367* (DUKE).

3. **Aphelandra storkii** Leonard, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1197. 1938. type: Costa Rica. Limon: Livingston, Río Reventazón, *Rowles & Stork 690* (holotype, US).

Shrubs 1–3 m high, sparsely branched; stems terete, younger surfaces moderately pilose, the trichomes erect, white, about 1 mm long, older surfaces glabrate. Leaves opposite, obovate to broadly oblanceolate, 30–45 cm long, 15–20 cm wide, apically acuminate (the tip acute or blunt), basally long attenuate and decurrent on petiole, marginally entire to crenulate, sparsely strigose above, the trichomes appressed, white, about 0.75 mm long, moderately tomentose below, the trichome appressed, white, about 0.75 mm long, somewhat twisted, veins pilose, the trichomes erect, white, about 1 mm long; petioles 1–3 cm long, densely pilose, the trichomes erect, white, about 1 mm long. Inflorescence terminal, spikes usually single (rarely 2–5), terete to subquadrangular, 15–25(–45) cm long, about 2 cm wide; peduncles 1–3 cm long (to 5 cm below lateral inflorescences), densely pilose, the trichomes erect, white, about 1 mm long; rachis densely pubescent, the trichomes erect, white, about 0.5 mm long; bracts imbricate, rhombic oblong-ovate, apically acute, marginally entire or bearing 2–3 minute teeth along each edge (each about 1 mm long and 0.25 mm wide), orange, 25–30 mm long, 13–18 mm wide, minutely puberulous within, moderately pubescent without, the trichomes appressed, white, about 0.5 mm long, margins ciliate, the trichomes white, about 1 mm long, the nectaries medial, composed of 10–15 individual glands, each about 0.5 mm long and 0.25 mm wide; bracteoles lanceolate, apically acute, 9–14 mm long, 2–4 mm wide, pale orange, moderately pubescent, the trichomes ascending, white, about 0.25 mm long. Sepals 13–17 mm long, apically acute, pale orange, striately nerved, moderately pubescent, the trichomes erect, white, about 0.25 mm long, the adaxial segment broadly lanceolate, 3.5–7 mm wide, the abaxial pair lanceolate, 2–4 mm wide, the lateral pair narrowly lanceolate, 1–2 mm wide; corolla orange, 6.5–7.5 cm long, moderately tomentose, the trichomes erect, white, about 0.5 mm long, frequently twisted, the tube 48–56 mm long, 4–5 mm in diameter at base, constricted to 2.5–3 mm above ovary (8 mm above base), expanding to 6–8 mm deep at throat, the upper lip erect, elliptic, 17–20 mm long, 10–15 mm wide, bilobed, the lobes triangular, acuminate, 8–11 mm long, anther pocket well-developed, the middle lobe of lower lip elliptic, 27–30 mm long, 9–12 mm wide, acute, the lateral lobes about 2 mm long and 5–6 mm wide; filaments inserted 9–10 mm from base of corolla tube, free portions about 5 cm long, the anthers 7–9 mm long, extending to within 5–6 mm of tip of upper lip, pollen orange; stigma very pale orange or uncolored, minutely bilobed, the style filiform, extending 1–7 mm beyond anthers, the ovary glabrous. Fruits clavate, terete, glabrous, green when immature, becoming black-brown at dehiscence, 28–32 mm long, about 7 mm wide, 5–6 mm thick; seeds brown, angularly orbicular, slightly flattened, 5–7 mm in diameter, 3–4 mm thick. Seed germination semi-hypogeal.

Habitat and distribution. This species is endemic to the Caribbean lowlands of northeastern Costa Rica, occurring in forests with slight seasonal differences in rainfall [tropical wet to premontane wet forests (Holdridge, 1967)]. *Aphelandra storkii* is found in the understory of primary forest and in gaps of varying sizes, but rarely in extensively disturbed areas.

Flowering and fruiting. *Aphelandra storkii* flowers during the wettest months of the year (July through Nov.). Fruits are matured during the driest months of the year (Jan. to March).

This species may be readily distinguished from all other Aphelandras by the combination of monocaulous growth form and pilose pubescence of leaves and stems, distinctively colored floral bracts and corollas and large size of the bracts, calyx, and corolla. The few collections known of *A. storkii* show little morphological variability over its limited range.

Relationships. Among Central American species of Group I, *A. storkii* is most closely related to *A. sinclairiana.* It is a distinctive species with many uniquely derived character states. Closer relatives of this species may be found in South America. Among South American species, *A. grandis* Leonard, *A. aristei* Leonard, and *A. trianae* Leonard bear at least a superficial resemblance to *A. storkii* (Leonard, 1953).

Additional specimens examined. COSTA RICA. HEREDIA: past town of Pto. Viejo on road to Río Frío, 100 m, *McDade 232* (DUKE); Finca La Selva, along Río Pto. Viejo near town of Pto. Viejo, 100 m, *Grayum 2361* (DUKE), *McDade 350* (DUKE), *Opler 988* (F, MO), *Sperry 650* (DUKE), *Sperry 765* (DUKE), *Sperry 831* (DUKE), *Wilbur 33599* (DUKE); Río Bijagual, 2 km E of Tirimbina, *Maas 1324* (US).

4. **Aphelandra gracilis** Leonard, Proc. Biol. Soc. Wash. 56: 54. 1943. TYPE: Panama. Coclé: N of El Valle de Antón, 1,000 m, *Allen 2908* (holotype, US; isotypes, AAH, MO).

Shrubs or small trees, 2–7 m high, profusely branched; younger stems quadrangular, moderately pubescent, the trichomes upwardly appressed, white, 0.25–0.5 mm long, older stems terete, glabrate. Leaves opposite, elliptic to ovate, 10–20 cm long, 5–8 cm wide, apically acuminate (tip acute or blunt), basally acute or attenuate and decurrent on petiole, marginally entire, somewhat coriaceous and shiny, essentially glabrous above (few trichomes on veins), essentially glabrous below although sparsely pubescent on veins, the trichomes appressed, white, about 0.25 mm long; petioles 1–2 cm long, moderately pubescent, the trichomes appressed, white, about 0.25 mm long. Inflorescences terminal, spikes solitary or 2–5, terete, 8–12(–15) cm long, about 1 cm wide, sessile; the rachis sparsely pubescent, the trichomes erect, white, about 0.25 mm long; bracts non-overlapping, internodes 7–10 mm long, bracts ovate, apically acute, marginally entire, 5–8 mm long, 3–4.5 mm wide, green, glabrous within, sparsely pubescent towards tip of midvein without, the trichomes appressed, white, about 0.25 mm long, margin sparsely and minutely ciliolate, the nectaries medial, composed of few (3–7) individual glands, each 0.5 mm in diameter; bracteoles narrowly ovate, apically acute, 4–6 mm long, 1.5–3 mm wide, green, essentially glabrous or with a few trichomes toward apex, these appressed, white, about 0.25 mm long. Sepals 7–9 mm long, apically acute, green, striate with narrow hyaline margins, essentially glabrous, the adaxial segment narrowly ovate, 2.5–4 mm wide, the abaxial pair lanceolate, 2–3 mm wide, the lateral pair narrowly lanceolate, 1–1.5 mm wide; corolla pink or orange-red, 6.5–7 cm long, minutely puberulous with erect trichomes, the tube 48–50 mm long, 3 mm in diameter at base, constricted to about 1.5 mm above ovary (5–7 mm above base), expanding to 8–10 mm deep at throat, the upper lip erect, ovate, 16–17 mm long, 9–12 mm wide, bilobed, the lobes triangular, apiculate, 6–9 mm long, anther pocket well-developed, the middle lobe of lower lip elliptic, 23–26 mm long, 8–10 mm wide, acute, the lateral lobes about 1 mm long, 5–6 mm wide; filaments inserted about 12 mm above base of corolla tube, free portion of each 4.3–4.6 cm long, the anthers 5–6 mm long, extending to within 4–6 mm from tip of upper lip, pollen cream-colored; stigma not distinctively colored, very minutely bilobed, the style filiform, extending 1–3 mm beyond anthers, the ovary glabrous. Capsules clavate, terete, green when immature, black at dehiscence, 20–22 mm long, about 6.5 mm wide and 4.5 mm thick; seeds brown, orbicular, slightly flattened, 3.5–5 mm in diameter, about 3 mm wide. Seed germination semi-hypogeal.

Habitat and distribution. *Aphelandra gracilis* is restricted to the provinces of Veraguas, Coclé, Colón and Panamá in central Panama (Fig. 56). It occurs from 700 to 1,200 m elevation in wet cloud forest habitat, and at lower elevations where local conditions combine to produce a wet, frequently fog-bound climate [Holdridge's (1976) premontane wet to premontane rain forests]. The species is apparently limited to primary forest and is unable to survive in open areas.

Flowering and fruiting. Flowering occurs during the driest months of the year (late Dec. through early March), and fruits are matured during the late dry and early wet seasons.

Aphelandra gracilis is readily distinguished from all other Aphelandras treated here by its small green bracts that are distantly spaced along the rachis and its glabrous, slightly coriaceous and somewhat shiny leaves. Both field and herbarium studies suggest that hybridization between *A. gracilis* and *A. sinclairiana* occurs in areas where disturbed cloud forest habitats occur adjacent to seasonally dry low and premontane habitats on the Pacific slope of the central mountain range of Panama. Hybrids between these two species are quite vigorous and are intermediate in bract size, color, and spacing; leaf texture and pubescence; and overall plant pubescence. Collections of these hybrid plants have previously been identified as *A. gracilis, A. sinclairiana,* or the South American species *A. pilosa.* The misidentification of hybrid plants from El Llano (Panamá) as *A. pilosa* (Durkee, 1978) is readily understandable. These hybrids have the pubescence of *A. sinclairiana* (e.g., pilose stems), but much smaller bracts than are typical of this species, resulting in a superficial resemblance of these plants to *A. pilosa.*

Relationships. The bracteal nectaries, fruit and seed shape, and germination pattern of *A. gracilis* place it in Group I. Within Group I, its green bracts ally it with *A. golfodulcensis, A. panamensis,* and *A. deppeana.*

Additional specimens examined. PANAMA. COCLÉ: vicinity of El Valle de Antón, 700–1,200 m, *Hunter & Allen 311* (US), *Allen 1671* (F, GH, NY), *Gentry & Dwyer 3587* (F, MO). COLÓN: Santa Rita Ridge, 200 m, *Lewis et al. 5392* (MO), *Mori & Kallunki 3025* (MO). PANAMÁ: 10 km above InterAm. Hwy. on road from El Llano to Cartí-Tupile, 150–350 m, *Kennedy & Dressler 2954* (MO), *Mori & Kallunki 2260* (MO); Cerro Jefe, about 10 km past Goofy Lake, 600 m, *McDade 386* (DUKE), *Nee 9291* (MO), *Gentry et al. 3490* (MO), *Gentry & Mori 13432* (F, MO), *Wilbur et al. 11326* (DUKE); Gorgas Memorial Labs research camp, 5–10 km NE of Altos de Pacora, 600 m, *Mori & Kallunki 3343* (MO); slopes of Cerro Campana, 800 m, *Smith & Smith 3356* (F, US), *Croat 22793* (F, MO, NY), *Maas & Dressler 726* (MO). VERAGUAS: past Santa Fé, along road past Escuela Agrícola, slopes of Cerro Tute, 800–1,200 m, *Croat 23038, 34200* (MO), *Gentry 6247* (MO).

Putative hybrids between A. gracilis *and* A. sinclairiana. PANAMA. COCLÉ: vicinity of El Valle, 500–700 m, *Allen 1671, 2300* (US), *Dwyer 11845* (MO), *Lewis et al. 2614* (MO). PANAMÁ: road from El Llano to Cartí-Tupile, 10–12 km above InterAm. Hwy., 200–500 m, *Nee et al. 8873* (MO), *Croat 22891* (MO).

5. **Aphelandra golfodulcensis** McDade, Ann. Missouri Bot. Gard. 69: 405. 1982 [1983]. TYPE: Costa Rica. San José: vicinity of El General, beside Río Chirripó, *Skutch 2573* (holotype, MO; isotypes, A, GH, NY, US).

Shrubs or small trees 1–6 m high, profusely branching; stems terete, younger stems densely pubescent, becoming moderate to sparse on older surfaces, the trichomes downwardly appressed, white, about 0.75 mm long. Leaves opposite (very rarely alternate), elliptic to oblanceolate, 25–30(–45) cm long, 12–15 cm wide, apically acute to acuminate (the tip acute or blunt), basally attenuate and decurrent on petiole, marginally entire or slightly undulate, upper surface essentially glabrous, sparsely pubescent on veins, the trichomes appressed, white, about 0.5 mm long, moderately pubescent below, the trichomes appressed (erect on veins), white, about 0.75 mm long; petioles to 1 cm long, moderately pubescent, the trichomes erect, white, about 0.5 mm long; leaves subtending inflorescences much reduced, 3–6 cm long, 1–2.5 cm wide, pubescence as of cauline leaves. Inflorescences terminal, spikes numerous, terete, 3–15 cm long, 0.75–1 cm wide, arranged in a freely branching paniculate inflorescence; the peduncles 0.5–10 cm long, moderately pubescent, the trichomes erect to downwardly appressed, white, about 0.75 mm long; the rachis minutely puberulous, the trichomes erect, white; bracts imbricate, rhombic-ovate, apically acute, entire, 8–13 mm long, 4–7 mm wide, green to dull brown-orange, glabrous to sparsely papillate within, minute puberulous without, the trichomes appressed, white, margin ciliolate, the trichomes white, about 0.25 mm long, the nectaries medial, composed of several (1–7) individual glands, each about 0.75 mm long and 0.5 mm wide; bracteoles narrowly ovate, apically attenuate, 4–6.5 mm long, 2–4 mm wide, green, moderately puberulous, the trichomes appressed, white. Sepals 6–9 mm long, apically acute, green, finely striate, minutely puberulous, the trichomes appressed, white, the adaxial segment narrowly ovate, 3–4 mm wide, the abaxial pair broadly lanceolate, 2–2.5 mm wide, the lateral pair narrowly lanceolate, about 1.5 mm wide; corolla orange to red, 6.3–7.3 cm long, minutely puberulous, the trichomes erect, white, the tube about 4.7 cm long, 2–3 mm in diameter at base, slightly constricted above ovary (6 mm above base), expanding to 6–8 mm deep at throat, the upper lip erect, elliptic, 17–19 mm long, 7–11 mm wide, bilobed, the lobes triangular, acuminate, 6–10 mm long, anther pocket well-developed, the middle lobe of lower lip broadly lanceolate, 22–26 mm long, 6–9 mm wide, acuminate, the lateral lobes 1–3 mm long, 5–7 mm wide; filaments inserted about 15 mm above base of corolla tube, free portion of each about 4 cm long, the anthers 6–8 mm long, extending to within 5 mm from tip of upper lip, pollen very pale orange; stigma red, slightly bilobed, the lobes about 0.5 mm long, the style filiform, extending 3–5 mm beyond anthers, the ovary glabrous. Fruits clavate, terete, glabrous, green when immature, turning black-brown at dehiscence, 19–23 mm long, 5–8 mm wide, 5.5–7 mm thick. Seeds dark-brown, orbicular, slightly flattened, 4–6 mm in diameter, 2.5–3 mm wide. Seed germination semi-hypogeal.

Habitat and distribution. *Aphelandra golfodulcensis* is found primarily in the tropical wet forests (Holdridge, 1967) of the Golfo Dulce region of Puntarenas province, Costa Rica (Fig. 56). Its range extends into the adjacent Burica Peninsula of Panama (Chiriquí province), to mid-elevations above the Golfo Dulce region [premontane rain forests (Holdridge, 1967)], and to the north into Alajuela and Guanacaste provinces where local conditions result in a climate substantially wetter and less seasonal than is typical of these areas. The plants occur as understory shrubs in primary forests and also colonize successional and edge habitats.

Flowering and fruiting. Peak flowering occurs during the dry season (late Dec. through March). Fruits mature rapidly and few individuals still bear fruits when the wet season begins in this area.

Plants of *A. golfodulcensis* have previously been referred to *A. sinclairiana*. Morphological features distinguishing these two species include bract size, color, and pubescence; corolla tube vestiture; fruit color and pubescence; and overall vestiture of the plants. Data from artificial hybridizations support recognition of the two as distinct but closely related (Table 11). Several collections of putative hybrids between *A. golfodulcensis* and *A. sinclairiana* are known from northeastern Costa Rica. These plants are sterile and are morphologically intermediate between the two parental species, most notably in vestiture of leaves, stems and corollas, and bract size and color.

Relationships. *Aphelandra golfodulcensis* is a member of Group I and is phylogenetically most closely related to *A. gracilis, A. panamensis,* and *A. deppeana* (Fig. 58).

Additional specimens examined. Costa Rica. ALAJUELA: vicinity of Capulín on Río Grande de Tárcoles, 80 m, *Standley 40160* (US); Santiago de San Ramón, *Brenes 6625* (A, F, NY). GUANACASTE: El Arenal, *Standley & Valerio 45105* (US). PUNTARENAS: ca. 10 km SE (toward Panama) of Palmar N. along InterAm. Hwy., *Burger & Matta-U. 4646* (F, MO, NY), *McDade 378* (DUKE); Esquinas forest, between Río Esquinas and Palmar S., *Allen 5775* (F, GH, US); Golfo Dulce and Río Térraba, *Skutch 5406* (F, US); forests of Santo Domingo de Golfo Dulce, *Tonduz 9969* (NY, US); Rincón de Osa, *Burger & Gentry 8851* (F); Sirena, Corcovado National Park, sea level, *McDade 401* (DUKE); Cañas Gordas, *Pittier 11193* (US); ca. 5 mi. from San Vito de Java, Las Cruces Botanical Garden, *McDade 395* (DUKE). SAN JOSÉ: Río Pacuar, vicinity of El General, *Skutch 3941* (MO, NY, US); Río Chirripó del Pacífico between Canaán and Chimiról, *Burger & Liesner 7117* (F, MO).

Panama. CHIRIQUÍ: Pto. Armuelles, 1 mi. W of airport, *Croat 21884* (F, MO, NY); ca. 2 mi. S of Pto. Armuelles, *Wilbur et al. 13583* (DUKE, F); San Bartolo Limite near Costa Rican border, 12 mi. W of Pto. Armuelles, 400–500 m, *Croat 22194* (DUKE, MO).

Putative hybrids between A. golfodulcensis *and* A. sinclairiana. Costa Rica. HEREDIA: Finca La Selva, on Río Pto. Viejo near town of Pto. Viejo, 100 m, *McDade 367, 372* (DUKE). LIMÓN: Los Diamantes, Guapiles, 280 m, *Carpenter 373* (US), *Schubert 1109* (US), *Carlson 3457* (F, US); Llanos de Santa Clara, 650 ft., *Donnell Smith 4917* (GH, US); Santa Clara, Las Delicias, 500 m, *Biolley 10669* (US); Río Chirripó, hwy. from Río Frío to Guapiles, *Poveda 991* (F).

6. **Aphelandra panamensis** McDade, Ann. Missouri Bot. Gard. 69: 402. 1982 [1983]. TYPE: Panama. Panamá: slopes of Cerro Jefe, past Goofy Lake and large coffee finca, 800 m, *McDade 411* (holotype, DUKE; isotypes, F, MO).

Shrubs or small trees 1–6 m high, sparsely branched; stems terete, younger stems densely pubescent, the trichomes upwardly appressed, white, 0.5–0.75 mm long, older surfaces glabrate. Leaves opposite, narrowly elliptic, 15–18(–22) cm long, 3–6.5 cm wide, apically acuminate to acute, basally attenuate and decurrent on the petiole, marginally entire or undulate, the upper surface of youngest leaves sparsely pubescent, glabrate with age, lower surface moderately pubescent, the trichomes appressed, white, about 0.5 mm long; petioles lacking or to 5 mm long, densely pubescent, the trichomes erect, white, about 0.5 mm long; uppermost leaves subtending inflorescences frequently reduced. Inflorescences terminal, spikes usually solitary (rarely to 5), terete, 4–12 cm long, 0.8–1.2 cm wide, sessile; the rachis densely pubescent, the trichomes erect, white, about 1 mm long; bracts slightly imbricate, narrowly rhombic-ovate, apically attenuate, marginally with 2–3 pairs of teeth (each 1–2 mm long), 11–15 mm long, 6–8 mm wide, green to pale dull orange, sparsely pubescent within, moderately pubescent without, the trichomes appressed, white, about 0.5 mm long, margins ciliate, the trichomes white, 0.25–0.5 mm long, the nectaries medial, composed of several (5–10) individual glands, each about 0.5 mm long and 0.3 mm wide; bracteoles lanceolate, apically acute, 6–10 mm long, 1.5–2.5 mm wide, straw-colored or green, glabrous except keel and apically sparsely pubescent, the trichomes erect, white, about 0.75 mm long. Sepals 8–12 mm long, apically acute, green or straw-colored, glabrous except for the sparsely pubescent tip, the trichomes erect, white, about 0.75 mm long, the adaxial segment narrowly ovate, 3–5 mm wide, the abaxial pair lanceolate, 2–3 mm wide, the lateral pair narrowly lanceolate, 1.5–2 mm wide; corolla bright red, 5.5–7 cm long, minutely puberulous except tip of lower lip sparsely pubescent, the tube about 5 cm long, 2.5–3 mm in diameter at base, constricted to 1.5 mm above ovary (about 8 mm above base), expanding to 5–7 mm deep at throat, the upper lip erect, elliptic, 14–20 mm long, 6–8 mm wide, bilobed, the lobes triangular, acute, 5–7 mm long, anther pocket poorly developed, the middle lobe of lower lip narrowly elliptic, 18–23 mm long, 4–7 mm wide, acute, tip strongly curled back toward tube, the lateral lobes about 0.5 mm long and 3 mm wide; filaments inserted about 5 mm above base of tube, free portion of each about 5 cm long, the anthers 4–5 mm long, extending to within 2–3 mm of tip of upper lip, pollen very pale yellow; stigma not distinctively colored, oblique and appearing hollow, the style filiform, extends 1–2 mm beyond anthers, the ovary glabrous. Fruits globose, terete, glabrous, green tinged with orange when immature, becoming yellow-brown at dehiscence, 16–19 mm long, 4.5–6.5 mm wide, 5.5–7 mm thick; seeds dark brown, irregularly orbicular, slightly flattened, 4–6 mm in diameter, 2–3 mm thick. Seed germination semi-hypogeal.

Habitat and distribution. *Aphelandra panamensis* is known only from central and eastern Panama in the provinces of Coclé, Colón, Panamá, San Blas, and Darién. It occurs in wet cloud forest habitats, predominantly above 600 m elevation, but occasionally lower where local climatic conditions result in high rainfall and frequent fog cover [Holdridge's (1967) premontane wet and premontane rain forests]. Individuals of this species are primarily understory shrubs of primary forest, but are found in advanced secondary forest as well.

Flowering and fruiting. Peak flowering occurs in the wet season (Sept. to Dec.) and fruits mature during the driest months of the year (late Dec. to early March). There is, however, considerable asynchrony among individuals at some sites. Notably, at Santa Rita Ridge, in the province of Colón, flowering individuals can be collected during most months.

The combination of toothed bracts with extrafloral nectaries and the 5.5–7 cm long corolla serve to distinguish *A. panamensis* from other species. Specimens of *A. panamensis* have previously been referred to *A. deppeana* from which it may be readily distinguished. The two species differ in habit, leaf vestiture, corolla length, and fruit size and color. They are found in different habitats and are pollinated by two distinct groups of hummingbirds.

Relationships. Within Group I, *A. panamensis* and *A. deppeana* are sister species, sharing toothed bracts, oblique stigmas, sub-globose fruits, and villous pubescence of the lower corolla lip. Artificial hybridizations indicate that *A. panamensis* crosses readily with all other species of Group I.

Additional specimens examined. PANAMA. COCLÉ: 8 km N of El Copé, near sawmill, 600–750 m, *Berg & Dressler 2770* (US). COLÓN: ca. 7 mi. from Transisthm. Hwy., Santa Rita Ridge, *Wilbur et al. 15078* (DUKE), *McDade 283, 388* (DUKE), *Smith & Smith 3433* (US). DARIÉN: S of El Real on slopes of Cerro Pirre, 500–1,000 m, *Foster & Kennedy 1263* (DUKE), *McDade 428* (DUKE). PANAMÁ: Cerro Jefe, about 8 km above Goofy Lake, 800 m, *Blum et al. 1834* (FSU), *Foster & Kennedy 1872* (DUKE, US), *Wilbur et al. 11316* (DUKE), *Lewis et al. 282* (DUKE, MO, US). SAN BLAS: between Río Diablo and Río Acuatí near Narganá, *Duke 14887* (US).

7. **Aphelandra deppeana** Schldl. & Cham., Linnaea 5: 96. 1830. TYPE: Mexico. State not given, Hacienda de la Laguna, *Schiede & Deppe s.n.* (holotype, B, destroyed, not seen; F photo 8704 in US).

Aphelandra pectinata Nees in DC., Prodr. 11: 297. 1847. TYPE: Colombia. Department not given, Río Sinú, *Cuming 1099* (lectotype, K, photo in US).

Aphelandra haenkeana Nees in DC., Prodr. 11: 298. 1847. TYPE: Mexico. Veracruz: Cordillera de Veracruz, *Galeotti 909* (lectotype, US; isolectotypes, K, P, W).

Aphelandra dukei Wassh., Phytologia 25: 475. 1973. TYPE: Panama. Panamá: Río Bayano, 1–4 mi. above Piria, 100 m, *Duke 14397* (holotype, US; isotype, MO).

Shrubs 1–4 m high, profusely branched; youngest stems subquadrangular, moderately tomentose, the trichomes appressed, white, 0.75–1 mm long, twisted and somewhat matted, older stems terete, glabrate. Leaves opposite, elliptic, 15–22 cm long, (1.5–2–)5–8 cm wide, apically acute to short attenuate, basally attenuate and decurrent on petiole, marginally entire to undulate, both surfaces moderately tomentose (dense on veins below), the trichomes erect, white, 0.75–1 mm long, curling; petioles lacking or to 1 cm long, densely pubescent, the trichomes appressed, white, 0.5–0.75 mm long. Inflorescences terminal, spikes solitary or more frequently several (3–7), terete to sub-quadrangular, 8–12(–19) cm long, about 1 cm wide, sessile; the rachis moderately pubescent, the trichomes erect, white, about 0.5 mm long; bracts densely imbricate, broadly elliptic, apically long attenuate, marginally with 2–4 pairs of short teeth (1–2 mm long, 0.5 mm wide) on each side, 13–16 mm long, 6–8 mm wide, green to dull orange, glabrous within, moderately pubescent without, the trichomes appressed, white, about 0.5 mm long, margins ciliate, the trichomes 0.75–1 mm long; the nectaries medial, composed of several (2–5) individual glands, each about 1.25 mm long and 0.75 mm wide; bracteoles lanceolate, apically long attenuate and acute, 6–8.5 mm long, about 1.5 mm wide, green to pale orange, sparsely pubescent, the trichomes appressed, white, about 0.25 mm long. Sepals 8–9.5 mm long, apically acute, green to dull orange, glabrous except ciliate near apex, the trichomes white, about 1 mm long, the adaxial segment narrowly ovate, about 3 mm wide, the abaxial pair lanceolate, about 1.5 mm wide, the lateral pair narrowly lanceolate, about 1 mm wide; corolla pink, orange, or red, 36–41 mm long, moderately pubescent, the trichomes erect, white, 0.25–0.5 mm long (except trichomes of lower lip 1 mm long), the tube 27–29 mm long, 2 mm in diameter at base, constricted to 1–1.5 mm wide above ovary (5 mm above base), expanding to 4–5 mm deep at throat, the upper lip erect, elliptic, 11–13 mm long, 5–6 mm wide, bilobed, the lobes triangular, 3–4 mm long, acute, anther pocket poorly developed, the middle lobe of lower lip narrowly oblong, strongly recurved at anthesis, 14–15 mm long, 3–4.5 mm wide; filaments inserted about 5 mm above base of corolla, free portion of each 2.5–2.7 cm long, the anthers 3–4 mm long, extending to within 2–4 mm from tip of upper lip, pollen cream or yellow; stigma not conspicuously colored, appears hollow, oblique at tip, the style filiform, extends 0.5–1.5 mm beyond anthers, the ovary glabrous. Capsules globose, terete, green when immature, turning brown-black at dehiscence, 13–17 mm long, 5–6 mm wide, 5–6.5 mm thick; seeds brown, orbicular, slightly flattened, 3.5–4.5 mm in diameter, 2–3 mm wide. Seed germination semihypogeal.

Habitat and distribution. Ranging from southern Mexico through Central America south to Bolivia and east to Surinam, *Aphelandra deppeana* is one of the most widely distributed species in the genus. It is the most xerophytic of the species treated here and is found primarily in seasonally dry lowland habitats [tropical dry to moist forests (Holdridge, 1967)], occasionally ranging to mid-elevations on leeward slopes. In Costa Rica and Panama, it is a common understory shrub in the seasonally deciduous forest and shrub communities of the Pacific lowlands and colonizes the disturbed secondary and edge habitats now common in these regions.

Flowering and fruiting. Flowering occurs primarily during the wet season (July through Dec.), with fruits maturing during the early dry season (Jan. through March). There is some variability among individuals at some sites and unusual individuals can be found in flower at most times of year.

This species is readily distinguished from all other Central American Aphelandras by the combination of short corollas (36–41 mm) and toothed bracts with extrafloral nectaries. Although there is some variability among collections from different areas of the range, especially in leaf morphology, this species is remarkably uniform and is easily recognized.

Wasshausen (1973a) described *A. dukei* as a distinct species on the basis of its very narrow (1.5–2 cm) leaves. I consider *A. dukei* to be a morphological variant of *A. deppeana* unworthy of formal recognition for several reasons. No other morphological characters consistently separate the two; inflorescence characters are essentially uniform. Pollen grains of *A. dukei* are identical in size and ultrasculpturing to those of *A. deppeana*. The habitats of the two are identical and narrow-leaved plants are known only from within the range of *A. deppeana*. Narrow-leaved individuals have been collected from three locations in eastern Panama.

Relationships. Phylogenetic analysis indicates that *A. deppeana* and *A. panamensis* share several derived character states and are sister species. *Aphelandra deppeana* possess uniquely derived states of many characters, suggesting that it is a very divergent member of Group I. Crossing relationships corroborate this hypothesis: *A. deppeana* crossed readily only with its sister species, *A. panamensis* (Table 11).

The unique features of *Aphelandra deppeana* are perhaps related to its xerophytic habitat and weedy nature. Especially noteworthy are the short corollas that are apparently reduced from the 6–7 cm length considered primitive for this group. This change may have functional significance: long-billed hummingbirds do not generally occur in areas with harsh dry seasons. The only available hummingbird pollinators in such areas are species with relatively short bills.

Among South American species, comparative morphology suggests that *A. lasia* Leonard is the only close relative of *A. deppeana* (Leonard, 1953). Plants of this Colombian species are distinguished from *A. deppeana* by their longer corollas and larger and more densely pilose bracts with few, if any, minute teeth.

Additional specimens examined. MEXICO. CAMPECHE: beyond Hopalchen on Campeche-Mérida road, *Moore 8078* (US). CHIAPAS: along road to El Sumidero, 9 km N of Tuxtla Gutierrez, 2,500 ft., *Breedlove 13879* (US); 5.6 mi. SE of Chiapa de Corzo, along Hwy. 190, *Shilom Ton 2950* (DUKE, US); 13 km N of Arriaga along Hwy. 195, 830 m, *Breedlove 28299* (DUKE); along road from El Bosque to Simojovel, 3,000 ft., *Shilom Ton 3076* (DUKE). GUERRERO: Hwy. 95, 5–6 mi. E of Acapulco, 400 ft., *Carlson 3066* (DUKE, US); Vallecitos, Montes de Oca, 520 m, *Hinton 9903* (US); vicinity of Acahuizotla between Chipalcingo and Acapulco, *Moore 8124* (US); between Copala and Juchitango, 200–600 ft., *Nelson 2297* (US). OAXACA: Tehuantepec, Tapesco, S of Tres Cruces, 3,000 ft., *MacDougall H56* (US); E of La Soledad, near Mitla, *Ernst 2555* (US); Cerro de Cosolapa, Cosolapa, *Vera-Santos 2617* (US); Tuxtepec, Chiltepec, and vicinity, 20 m, *Martinez-Calderón 254* (US); Cerro Santo Domingo, district of Juchitan, 240 m, *Conzatti 3735* (US). QUINTANA ROO: 36 km S of Dzuiche on Hwy. 164, 30 m, *Roe et al. 1349* (US). VERACRUZ: Ciudad Alemán, Cosamaloapan, 10 m, *Martinez-Calderón s.n.* (US); along river draining Laguna de Catemaco, region of San Andres Tuxtla, *Dressler & Jones 230* (US); Zacaupan and vicinity, *Purpus 1938* (US). YUCATAN: Chichen Itza, *Rudd 2033* (US); Uxmal, *Degener & Degener 26785* (US); Coba, *Crockett 150* (US); Progreso, *Steere 3012* (US); vicinity of Chiceh, *Gaumer 23798* (US).

Guatemala. ALTA VERAPAZ: near Pancajche, 900 m, *Standley 91831* (US); Sacolal, 3,000 ft., *Turckheim 825* (US); 1 km past Tucuru on road from Tactic to El Estos, 1,400 ft., *McDade 211* (DUKE). CHIQUIMULA: between Esquipulas and Ataluapa, 800 m, *Molina & Molina 25346* (US); 3 mi. SE of Quetzaltepeque, 1,200–1,500 m, *Steyermark 31291* (US). ESCUINTLA: SE of Escuintla along Río Michatoya, 250–300 m, *Standley 89138* (US); San Antonio Jute, 780 m, *Standley 64901* (US); near San José, sea level, *Standley 64076* (US). GUATEMALA: Sanarate, 810 m, *Kellerman 6653* (US). HUEHUETENANGO: El Reposo, 900–1,000 m, *Williams et al. 41247* (US); slopes above Río Selegua, 6,100 ft., *Harmon 4801* (US). IZABAL: between Ceja and Cienaga, *Ortiz 2299* (US); vicinity of Quirigua, 75–225 m, *Standley 23910* (US). JALAPA: between Jalapa and San Pedro Pinula, 1,400–1,800 m, *Standley 77087* (US). JUTIAPA: Jutiapa, 850 m, *Standley 75121* (US). PETÉN: Parque Nacional de Tikal, *Tun Ortiz s.n.* (DUKE, US); Ceibal, 150 m, *Molina 15861* (US); San Clemente de Dos Arroyos, *Bartlett 12827* (US). QUETZALTENANGO: Colomba, 1,900 ft., *Skutch 1370* (US). RETALHULEU: between Nueva Linda and Champerico, 120 m, *Standley 87650* (US); Retalhuleu, *Kellerman 6584* (US). SANTA ROSA: Llano Entero, SE of Chiquimulilla, 150 m, *Standley 78737* (US); Guazacapán, 220 m, *Standley 78702* (US); Jumaytepeque, 6,000 ft., *Donnell Smith 4379* (US). SOLOLÁ: Patalul, 1,370 ft., *Donnell Smith 154* (US). SUCHITEPEQUEZ: Patulul, 330–600 m, *Standley 62184* (US). ZACAPA: above Teculutan, 250–275 m, *Steyermark 42150* (US); road between Zacapa and Chiquimula, 500–660 m, *Standley 73849* (US).

Belize. BELIZE: Gracie Rock on Western Hwy., *Croat 23905* (DUKE, US); Mt. Polo group, *Bartlett 11349* (US). CAYO: 2–4 mi. SE of Georgeville along road to Augustine, *Sorensen 7121* (US); N of Cayo, *Bartlett 11947* (US); Mountain Pine Ridge, *Hunt 42* (US); 47.2 mi. SW of Belize City on Western Hwy., *Ugent 83* (WIS). COROZAL: San Antonio, *Lundell 4969* (US). TOLEDO: Monkey River, Pine Ridge, *Gentle 3774* (US).

El Salvador. AHUACHAPÁN: Ahuachapán, 800–1,000 m, *Standley 19893* (US). LA UNION: La Union, 150 m, *Standley 20672* (US). MORAZÁN: N of Montecristo (NE of San Miguel), 200 m, *Tucker 450* (US). SAN SALVADOR: Tonacatepeque, *Standley 19440* (US). SAN VICENTE: San Vicente, 350–500 m, *Standley 21220* (US). SONOSANTE: San Antonio del Monte, 250 m, *Standley 22166* (US).

Honduras. COMAYAGUA: Siguatepeque, 1,100 m, *Williams & Williams 18475* (US). CORTÉS: San Pedro Sula, 1,000 ft., *Thieme 5403* (US). EL PARAISO: road to Yuscarán, *Swallen 11335* (US). MORAZÁN: Cerro de Uyuca, 900 m, *Morton 7031* (US). SANTA BARBARA: Santa Barbara, 300 m, *Molina 3669* (US).

Nicaragua. CHINANDEGA: Chinandega, *Baker 2057* (US). CHONTALES: Cuapa, *Marshall & Neill 6675* (DUKE). ESTELÍ: Pueblo Nuevo, 600–700 m, *Williams & Molina 42405* (US). MANAGUA: Rt. 1 km 17, Tipitapa, *Atwood 2825* (WIS). MATAGALPA: 5–10 km W of Matagalpa, 600–700 m, *Williams et al. 23801* (US). NUEVA SEGOVIA: Ocotal, *Hamblett 802* (WIS). RIVAS: Ometepe Island, Lake Nicaragua, *Shimek & Smith 146* (US); near Tola and Rivas, *White 5354* (US).

Costa Rica. ALAJUELA: Grecia, *Jimenez 1142* (US); Turrubres near San Mateo, *Biolley 7075* (US); Atenas, *Schubert & Madriz 1036* (US). GUANACASTE: 5 mi. N of Cañas along InterAm. Hwy., 50 m, *McDade 221, 377* (DUKE); Santa Rosa National Park, 30 km NW of Liberia, *Wilbur 25092* (DUKE); Bahía el Coco and Sardinal, 0–150 m, *Burger & Baker 9923* (DUKE); between Guayabo and Salitral, *Utley & Utley 4009* (DUKE); Cabo Blanco Nature Preserve, southern tip of Nicoya Peninsula, 0–200 m, *Burger & Liesner 6591* (US); 12 km E of Esparta on InterAm. Hwy., *Utley & Utley 3644* (DUKE). PUNTARENAS: near Quepos and Río Naranjo, 20–150 m, *Burger et al. 10543* (DUKE); ca. 10 mi. before Palmar N. on InterAm. Hwy. between Paso Real and Palmar N., *McDade 290* (DUKE); 8 km NE of Buenos Aires, 600 m, *Wilbur 25266* (DUKE); Las Cruces Botanical Garden, ca. 8 km from San Vito de Java, 1,200 m, *McDade 396* (DUKE).

Panama. CHIRIQUÍ: 17 km NE of San Felix, new road to Cerro Colorado Copper Mines, 1,000 m, *Nee 10680* (US); 12.4 mi. N of David, *Lewis et al. 718* (US). COCLÉ: Ola, 100–350 m, *Pittier 5036* (US); El Valle de Antón, 600 m, *Lewis et al. 2595* (DUKE). DARIÉN: Punta Garachiné, *Duke 10475* (US); Púcuro, 70 m, *Mori & Gentry 4245* (MO). HERRERA: between Las Minas and Pesé, *Oliver 1349* (US); Ocú, *Stern et al. 1738* (US). LOS SANTOS: vicinity of Tonosí, 117 ft., *Stern et al. 1854* (US). PANAMÁ: Balboa, *Standley 26047* (US); Paraiso, *Dwyer 7143* (US); Fort Clayton, *Tyson & Blum 3891* (FSU); 1 mi. SW of Cocoli, Rodman Naval Ammunition Depot, *Wilbur et al. 12893* (DUKE, US); near Miraflores locks, *Croat 12729* (DUKE); between Las Sabanas and Matias Hernandez, *Standley 31911* (US); Taboguilla Island, *Miller 1999* (US); Taboga Island, *Standley 27864* (US); Río Bayano, 1–4 mi. above Piria, *Duke 14397* (MO, US); road to El Valle de Antón, ca. km 18 from InterAm. Hwy., *Wilbur et al. 1558* (DUKE); along InterAm. Hwy. near Jenine, Río Cañita, *Duke 3840* (US). VERAGUAS: 11 km S of Santa Fé, 220 m, *Nee 8153* (US); Soná, 500 m, *Allen 1042* (US); 2 km NW of Atalaya, 100 m, *Nee 8253* (US).

Colombia. BOLÍVAR: San Martín de Loba, *Curran 99* (US); Sincelejo, *Pennell 4057* (US); vicinity of Cartagena, *Heriberto 357* (US). BOYACÁ: San Antonio on Río Cusiari, 10 km above Maní, 250 m, *Haught 2613* (US). META: San Juan de Arama, Río Guejar, 500 m, *Idrobo & Schultes 1223* (US); 65 km E of Villavicencio, *Haught 2501* (US); Los Llanos, La Venturoso on Rio Meta, *Cuatrecasas 4195* (US); Los Llanos, Río Casanare, Esmeralda, 130 m, *Cuatrecasas 3816* (US). VAUPÉS: Cerro de Mitú, 380 m, *Cuatrecasas 6878* (US). VICHADA: 10 km W of Las Gaviotas along road to Pto.

Gaitan, 180 m, *Davidse 5344* (US); 7 km NE of San José de Ocuné, 100 m, *Hermann 10973* (US).

Venezuela. amazonas: Alto Orinoco, Salto Salas, *Croizat 513* (US); Alto Río Orinoco, 30 km above Santa Barbara, 125 m, *Maguire et al.* (US); 12.5 km S of Pto. Ayacucho, 230 m, *Davidse 2795* (US). anzoátegui: on Caracas-Barcelona Hwy., 16 km E of Boca de Uchiré, *Gentry & Berry 14824* (US). apure: bank of Río Meta, 19 km WSW of Paraquito, 75 m, *Davidse & Gonzalez 13973* (US). bolívar: 14 km SE of Caicara along Hwy. 19 to Cd Bolívar, 160 m, *Davidse 4338* (US). guarico: 14 km NWN of Altagracia de Orituco, road to Caucagera, 420 m, *Davidse 4160* (US). sucre: 7 km E of Mochima Hwy. between Cumaná and Pto. La Cruz, 250 m, *Davidse 5032* (US).

Guyana. Maniparu Falls, *Atkinson 59* (US); junction of Mazaruni and Cuyuni Rivers, *Graham 336* (US); Ahyma, Demerara River above Wismar, *Hitchcock 17419* (US); SE of Georgetown, along coast, *Hitchcock 16916* (US).

Surinam. Lower Saramacca River, Betti Creek, *Jonker-Verhoef & John 539* (US).

8. **Aphelandra lingua-bovis** Leonard, Contr. U.S. Natl. Herb. 31: 268. 1953. type: Colombia. Chocó: La Concepción, 15 km E of Quibdó, 75 m, *Archer 2012* (holotype, US).

Shrubs 1–2 m high, very sparsely branched or more frequently unbranched; younger stems subquadrangular, moderately pubescent, the trichomes upwardly appressed, white, about 0.5 mm long, older stems terete and glabrate. Leaves opposite, elliptic to obovate, 20–35(–45) cm long, 11–17 cm wide, apically acuminate, basally acute to slightly attenuate, marginally entire to crenate, blades coriaceous, glabrous above, with few trichomes on veins, sparsely pubescent below (moderately on veins), the trichomes appressed, white, about 0.5 mm long; petioles 0.5–6 cm long, moderately pubescent, the trichomes appressed, white, about 0.5 mm long. Inflorescence terminal, spikes solitary (rarely 2–3), quadrangular, 20–35(–70) cm long, 1.2–1.5 cm wide; peduncle lacking or very rarely to 1 cm long, densely pubescent, the trichomes appressed, white, about 0.5 mm long; rachis sparsely pubescent, the trichomes erect, white, about 0.5 mm long; bracts closely fitting but not imbricate, 2–4 pairs of sterile bracts subtending spikes, floral bracts narrowly rhombic-ovate, apically attenuate and acute, entire, red-orange, 12–17 mm long, 7–11 mm wide, glabrous within, sparsely and minutely pubescent without, keel sometimes with a narrow band of trichomes, margin sub-hyaline, very finely ciliolate, the nectaries medial, about 2.5 mm long and 1–1.5 mm wide, composed of many minute glands; bracteoles linear-lanceolate, apically acute, 11–17 mm long, 2–3.5 mm wide, pale orange, glabrous except keel densely pubescent, the trichomes erect, white, 0.5–0.75 mm long. Sepals 12–18 mm long, apically acute, pale orange, minutely puberulous except few longer trichomes near tips, these appressed, white, about 0.5 mm long, the adaxial segment narrowly ovate, 3.5–8 mm wide, the abaxial pair lanceolate, 2–3.5 mm wide, the lateral pair narrowly lanceolate, 1.5–2.5 mm wide; corolla red-orange or pink-orange, 5.5–6 cm long, minutely papillate, with few scattered trichomes, coriaceous, the tube 4–4.4 cm long, 3.5–5 mm wide at base, scarcely narrowed above ovary, expanding to about 6 mm deep at throat, the upper lip erect, broadly ovate, 10–12 mm long, 7–9 mm wide, bilobed, the lobes triangular, 2.5–3.5 mm long, minutely apiculate, anther pocket well-developed, the middle lobe of lower lip scarcely reflexed at anthesis, narrowly ovate, 15–17 mm long, 6–7 mm wide, minutely apiculate, the lateral lobes about 1 mm long, 4–5 mm wide; filaments inserted about 5 mm above base of tube, free portion of each about 40 mm long, the anthers 5–6.5 mm long, extending to within 2–5 mm of tip of upper lip, pollen light yellow; stigma not distinctively colored, minutely bilobed, the style filiform, extending 1–2 mm beyond anthers, the ovary glabrous. Fruits oblong, flattened, oval in cross-section, glabrous, orange-brown when immature, dark brown at dehiscence, 17.5–22 mm long, 5–6 mm wide, 3.5–5 mm thick; seeds brown, orbicular to somewhat angular in outline, flattened, 4–6.5 mm in diameter, 1.5–2 mm wide. Seed germination epigeal.

Habitat and distribution. *Aphelandra lingua-bovis* is a species of lowland, premontane and, more rarely, middle elevation forests (to 1,200 m) [tropical wet through lower montane rain forest (Holdridge, 1967)] from southern Costa Rica, through Panama to northern Colombia. The Panamanian distribution of this species is difficult to establish with certainty since collections from the entire Caribbean slope of that country are as yet very incomplete. The plants are understory sub-shrubs of wet forests that experience only a very short dry season, and are limited to minimally disturbed sites.

Flowering and fruiting. *Aphelandra lingua-bovis* flowers during the wettest months of the year (July through Nov.) and matures fruits during those months with least rainfall.

Individuals of this species may be identified by their diminutive size, narrowly rhombic-ovate floral bracts that are 12–17 mm long and apically attenuate, linear-lanceolate bracteoles, and relatively short corollas. There is considerable variation among specimens, especially with respect to leaf texture and bract size. Collections are as yet too few, however, to discern any geographic patterns of variability.

Costa Rican plants referred by Leonard (1938) to the Venezuelan species *A. micans* are properly placed in *A. lingua-bovis*. Leonard also reported collections of *A. micans* from Guatemala, but I have found no indication that *A. micans* occurs in Central America or that *A. lingua-bovis* ranges north of southwestern Costa Rica.

Relationships. The phylogenetic relationships of *A. lingua-bovis* remain incompletely resolved. Phylogenetic analysis placed it as the basal species of the Central American lineage sharing minute bracteal nectaries (Group II, Fig. 58). Artificial hybridizations and distribution patterns of the states of many characters, however, indicate that its relationships with this group are more distant than the interrelationships of the remaining five species. More closely related species probably occur in South America, including *A. garciae* Leonard, *A. longispica* Leonard, and *A. straminea* Leonard (Leonard, 1953).

Additional specimens examined. COSTA RICA. LIMÓN: Río Valle Estrella drainage, *Shank & Molina-R. 4509* (F). PUNTARENAS: near Quepos and Río Naranjo, 20–150 m, *Burger et al. 10627* (F); between Golfo Dulce and Río Térraba, 30 m, *Skutch 5284* (F, US); ca. 10 km SE of Palmar N. along InterAm. Hwy., ca. 20 m, *Burger & Matta-U. 4650* (DUKE, US); ca. 10 km E of Golfito, 50 m, *Lent 424* (F, MO); Rincón de Osa, 20–300 m, *Liesner 1883* (MO); vicinity of Tinoco station, between Río Esquinas and Palmar, 30 m, *Allen 5477* (F, US); between Palmar N. and Pto. Cortez, 50 m, *Jimenez-M. 2245* (F); Rincón de Osa, SW of airstrip, 20–60 m, *Utley & Utley 1060* (DUKE); 5 km W of Rincón de Osa, 50–200 m, *Burger & Liesner 7235* (F, MO, NY); near mi. 4 on camino al Pacífico W of Rincón de Osa, 30 m, *Raven 21477* (F); Parque Nacional de Corcovado, sea level, *McDade 402* (DUKE); between Agua Buena and San Vito de Java, 1,200 m, *Jimenez M. 2452* (F); San Vito de Java, vicinity of Las Cruces Botanical Garden, 1,200 m, *Raven 22017* (F, NY), *McDade 442* (DUKE). SAN JOSÉ: low hills above Río Paquita, 5–50 m, *Dodge & Goerger 9883* (F, MO).

PANAMA. COLÓN: Río Guanche, 1–4 km upstream from Portobelo road, 1–100 m, *Gentry 8783* (MO), *Mori & Kallunki 3009* (MO), *McDade 287, 380* (DUKE); near bridge over Río Buenaventura, near Portobelo, sea level, *Foster & Kennedy 1794* (DUKE), *McDade 383* (DUKE). DARIÉN: ascent of Cerro Pirre from Río Pirre S of El Real, 750–1,030 m, *Duke 5329* (MO), *McDade 429* (DUKE).

COLOMBIA. ANTIOQUIA: near Villa Arteaga, hwy. to sea, *Hodge 7012* (F, US). BOYACÁ: Mt. Chapon, NW of Bogotá, extreme W part of Boyacá, *Lawrance 18* (GH). CHOCÓ: Río Atrato, Tanando, 60 m, *Cuatrecasas & Llano 24118* (US); Río Taparal off San Juan, 30 m, *Robinson 229* (US); between La Oveja and Quibdó, *Archer 1731* (US).

9. **Aphelandra leonardii** McDade, Ann. Missouri Bot. Gard. 69: 408. 1982 [1983]. TYPE: Panama. Panamá: Majé, about 5 mi. up Río Nuevo, a branch of Río Majé, *Foster & Kennedy 1993* (holotype, DUKE; isotypes, F, MO).

Shrubs 1–5 m high, profusely branching; younger stems quadrangular, sparsely pubescent, the trichomes upwardly appressed, white, about 0.5 mm long, older stems terete, glabrate. Leaves opposite, obovate to elliptic, 10–20(–30) cm long, 4–10 cm wide, apically acuminate, basally acute to attenuate, marginally entire to slightly undulate, upper surface glabrous, lower surface glabrous to sparsely pubescent except veins sparsely to densely pubescent, the trichomes appressed, white, 0.5–0.75 mm long; petioles 0.3–1.5 cm long (rarely to 3 cm), sparsely pubescent, the trichomes appressed, white, about 0.5 mm long. Inflorescence terminal, spikes solitary to numerous, quadrangular, 3.5–14 cm long, 0.8–1 cm wide, sessile or rarely very short pedunculate; rachis sparsely pubescent, except frequently densely pubescent just below insertion point of each bract, the trichomes erect, white, about 0.5 mm long; 2–3 pairs of imbricate, densely pubescent sterile bracts borne below fertile bracts, the trichomes appressed, white, about 0.75 mm long; floral bracts barely imbricate, rhombic-ovate, apically acute, marginally entire, 7–10 mm long, 5–7 mm wide, green to bright orange, glabrous within, sparsely and minutely puberulous without, margin minutely ciliolate, the trichomes white, the nectaries medial, 2–3 mm long and 1–2 mm wide, composed of many minute glands (each ca. 0.1 mm in diameter); bracteoles lanceolate, apically attenuate, 6–9 mm long, 2–3 mm wide, green, finely striate, glabrous except densely pubescent on keel, the trichomes erect, white, about 0.5 mm long. Sepals 10–12 mm long, apically acute, yellow-green, finely striate, margins hyaline, essentially glabrous, the adaxial segment narrowly ovate, 3–5 mm wide, the abaxial pair lanceolate, about 3 mm wide, the lateral pair narrowly lanceolate, 1.5–2 mm wide; corolla bright red, 6–7.3 cm long, essentially glabrous, the tube about 5 cm long, 4–5 mm in diameter at base, constricted to 1.5–2 mm above ovary (about 7 mm above base), expanding to 7–9 mm deep at throat, the upper lip erect, elliptic, 17–21 mm long, 8–10 mm wide, bilobed, the lobes triangular, acute, apiculate, 9–10 mm long, anther pocket well-developed, the middle lobe of lower lip narrowly ovate, strongly reflexed to lie along tube at anthesis, 21–28 mm long, 8–10 mm wide, acute, apiculate, the lateral lobes about 1 mm long and 6 mm wide; filaments inserted 8–11 mm from base of tube, free portion of each 4.5–5.3 cm long, the anthers 7–8 mm long, extending to within 4–6 mm from tip of upper lip, pollen yellow; stigma not distinctively colored, slightly bilobed, the lobes about 0.2 mm long, the style filiform, extends 1–6 mm beyond anthers, the ovary glabrous. Fruits oblong, flattened, oval in cross-section, glabrous, yellow-green when immature, yellow-brown at dehiscence, 17.5–19 mm long, about 5 mm wide, 3.5–4 mm thick; seeds brown, irregularly orbicular, strongly flattened, 3.5–6.5 mm in diameter, 1.5–2 mm thick. Seed germination epigeal.

Habitat and distribution. This species is known from lowland and premontane wet forests (Holdridge, 1967) in eastern Panama (Colón, Panamá, Darién, and San Blas), and from two localities in Costa Rica. Extensive collecting on the Caribbean slope of Panama will be required to firmly establish the range of this species. *Aphelandra leonardii* is a shrub of the forest understory and margins. The plants are found mostly in areas with little annual variation in rainfall, but a few collections have been made in seasonally dry areas.

Flowering and fruiting. Individuals of *A. leonardii* flower during the late wet season (Sept. to Dec.) and fruits mature during the driest months of the year (Jan. to April).

Individuals of this species may be distinguished from other Central American members of the *A. pulcherrima* complex by their shrubby habit, sessile, terminal clusters of inflorescences and small, rhombic-ovate and entire bracts. Specimens of this species were formerly referred to *A. pulcherrima* H.B.K. from which they differ most notably in the morphology of the bracteal nectaries. In *A. pulcherrima* the glands are few and large, whereas in *A. leonardii,* they are numerous, minute, and form a well-defined, oblong patch on each side of the bract. The two species differ also in fruit and seed morphology, with terete capsules and sub-globose seeds present in *A. pulcherrima,* and strongly flattened capsules and seeds in *A. leonardii. Aphelandra pulcherrima* is wholly South American and appears to include at least three closely related species (contrast, for instance, the treatments of Leonard, 1953 and Wasshausen, 1975).

Although there is little morphological variability among the eastern Panama populations of this species, plants from Costa Rica are rather distinct in several features of vegetative morphology. Costa Rican plants are larger and more diffusely branched, and have leaves that are membranous, narrower (3–5 cm), and sparsely tomentose. With respect to inflorescence and floral characters, however, plants from the two regions are almost identical. The systematic significance of these differences is as yet unclear and will perhaps be clarified by further collections from intervening areas where the species is currently unknown. Although it is possible that collections from the two countries represent distinct species, data from interpopulation crosses (Table 10) support recognition of a single taxon.

Relationships. Aphelandra leonardii is a member of the lineage sharing bracteal nectaries of many minute glands (Group II). This group includes *A. laxa, A. campanensis, A. hartwegiana, A. darienensis,* and, provisionally, *A. lingua-bovis.* Excepting the last, problematic species, these share several derived character states including immediate opening of the corollas and pollen grains with unsculptured bands (Type II). Phylogenetic analysis indicates that *A. leonardii* is the sister group of the remaining four Central American members of this lineage (*A. laxa, A. campanensis, A. hartwegiana,* and *A. darienensis*).

Additional specimens examined. COSTA RICA. SAN JOSÉ: along Río Tarrazú between Frailes and San Andrés, 1,300 m, *Burger 4041* (DUKE, F, MO, NY). PROVINCE UNKNOWN: near Boca Culebra, Pacific coast (Puntarenas?), *Pittier 11988* (US).

PANAMA. COLÓN: forest along Río Indio de Gatún, sea level, *Maxon 4807* (NY, US); Río Providencia, 3 km SE of Achiote, 5–100 m, *Gentry & Nee 8652* (MO). Río Guanche, *D'Arcy 9696* (MO). DARIÉN: slopes of Cerro Pirre, 500–2,500 ft., *Duke & Elias E13889* (MO); summit camp between Sasardí and Mortí, 400 m, *Duke 10033* (MO); summit camp adjacent Darién-San Blas border along sea level canal route 17, 1,000–1,200 ft., *Oliver et al. 3676* (MO, US); between upper Río Membrillo and Camp 7 on the construction road to San

Blas, *Duke 10865* (NY); Río Tucutí between Tucutí and Río Uroganti, *Duke 5287* (MO); Río Aruza, *Bristan 1248* (MO). PANAMÁ: along Río Chavaré above Chepo, 50–200 m, *Pittier 4723* (US); along InterAm. Hwy. between El Llano and Río Mamoní, *Duke 5631* (MO). SAN BLAS: along beach east of Pto. Obaldia, *Croat 16890* (US); forest around Pto. Obaldia, *Pittier 4280* (GH, NY, US); mainland opposite Ailigandí from mouth of Ailigandí River, *Lewis et al. 172* (DUKE, MO, NY, US).

10. Aphelandra laxa Durkee, Ann. Missouri Bot. Gard. 65: 161. 1978. TYPE: Panama. San Blas: 15–20 km WSW of Pto. Obaldia on trail to Darién, Caribbean slope of cordillera, *Mori et al. 6854* (holotype, MO).

Shrubs to 1.5 m high, sparsely branching; younger stems quadrangular, glabrous. Leaves opposite, ovate-elliptic, to about 35 cm long and 8.5 cm wide, apically acuminate, basally attenuate, marginally entire to undulate, glabrous above and below; petioles to about 4 cm long, glabrous. Inflorescences terminal, spikes solitary or few, sessile, to about 18 cm long and 0.5–1 cm wide; rachis glabrous; floral bracts non-overlapping, internodes 1.5–2 cm long, rhombic-ovate, apically acute, marginally entire, 7–10 mm long, 5–6 mm wide, glabrous within and without, margin minutely ciliolate, the nectaries sub-medial, about 2 mm long and 0.75 mm wide, composed of many minute glands; bracteoles narrowly ovate, keeled, apically acute, 7–8 mm long, 2–2.5 mm wide, glabrous. Sepals 11–12 mm long, apically acute and apiculate, striately nerved, glabrous, the adaxial segment narrowly ovate, about 3.5 mm wide, the abaxial pair lanceolate, about 3 mm wide, the lateral pair lanceolate, 2–2.5 mm wide; corolla to about 7 cm long, red, minutely puberulous, the tube 42–46 mm long, about 4 mm in diameter at base, narrowed to 2 mm in diameter above ovary (3–4 mm above base), expanding to about 9 mm at throat, the upper lip erect, ovate, about 25 mm long and 8–10 mm wide, bilobed, the lobes triangular, about 11 mm long, acuminate, the middle lobe of lower lip narrowly ovate, 28–30 mm long, 9–11 mm wide, apically acute, the lateral lobes about 1 mm long and 6–7 mm wide; anthers 7–8 mm long, extending to tip of upper lip; stigma minutely bilobed, the style filiform, extending beyond anthers, the ovary glabrous. Fruits clavate, flattened, glabrous, about 16 mm long and 9 mm wide; seeds orbicular, strongly flattened, about 5 mm in diameter, 2.5 mm thick.

Habitat and distribution. This species is known only from the type specimen which is from eastern Panama in the province of San Blas. It is apparently found in wet forests of the Caribbean lowlands, but its range and habitat requirements cannot yet be delimited.

Flowering and fruiting. *Aphelandra laxa* apparently flowers and fruits during the wet season because the type specimen (collected in June) bore both flowers and capsules.

This species is distinguished from other Central American species of *Aphelandra* by its very large leaves, small bracts with minute glands, and elongated internodes between pairs of floral bracts.

Relationships. *Aphelandra laxa* is a member of Group II (species 8–13). Its leathery bracts and papillate corollas indicate that, among Central American species, it is the sister group of *A. campanensis, A. hartwegiana,* and *A. darienensis.*

Aphelandra laxa is known only from the type specimen.

11. Aphelandra campanensis Durkee, Ann. Missouri Bot. Gard. 65: 162. 1978. TYPE: Panama. Panamá: Cerro Campana, 1,000 m, *Croat 12215* (holotype, MO; isotypes, DUKE, NY).

Shrubs 2–4 m high, sparsely branched; youngest stems quadrangular, moderately pubescent, the trichomes upwardly appressed, white, about 0.25 mm long, older stems terete, glabrate. Leaves opposite, elliptic to ovate, 20–30 cm long, 8–18 cm wide, apically acute to acuminate, basally acute to slightly attenuate, marginally entire to crenulate, glabrous above, sparsely pubescent below (denser on veins), the trichomes appressed, white, about 0.25 mm long; petioles 3–12 cm long, very narrow, moderately pubescent, the trichomes appressed and curling, white, about 0.25 mm long; leaves subtending inflorescence usually much reduced, 4–7 cm long, 2–4 cm wide, pubescence as of cauline leaves. Inflorescences terminal, spikes usually 1–3 (rarely 5 or more), quadrangular, 10–25 cm long, about 1.5 cm wide; peduncle lacking or to 1 cm long (longer below lateral inflorescences), essentially glabrous; rachis essentially glabrous; bracts barely imbricate, broadly rhombic-ovate, apically acute to slightly obtuse and apiculate, marginally entire, 11–14 mm long, 9–11 mm wide, deep red-orange, minutely puberulous within and without, keel moderately pubescent, the trichomes appressed, white, about 0.25 mm long, margin sub-hyaline, glabrous, the nectaries medial, 2–2.5 mm long and 1–1.5 mm wide, composed of many minute glands; bracteoles keeled and slightly falcate, apically acute, 11–13 mm long, 2–3 mm wide, pale orange, glabrous except densely pubescent on keel, the trichomes erect, white, 0.5–0.75 mm long. Sepals 15–18 mm long, apically obtuse and frequently minutely apiculate, pale orange, striate, glabrous, the adaxial segment narrowly oblong, 4–6.5 mm wide, the abaxial pair narrowly oblong, 3–4 mm wide, the lateral pair linear, 2–3 mm wide; corolla deep red-orange, 6–7 cm long, coriaceous, minutely puberulous and papillate; the tube 43–48 mm long, about 3 mm in diameter at base, slightly constricted above ovary (4–5 mm above base), expanding to 7–9 mm deep at throat, the upper lip erect, ovate, 17–20 mm long, 10–12 mm wide, bilobed, the lobes triangular, apiculate, 6–7 mm long, anther pocket well-developed, the middle lobe of lower lip elliptic, 22–25 mm long, 8–11 mm wide, acuminate and apiculate, strongly reflexed at anthesis to lie parallel to tube; filaments inserted about 7 mm above base of corolla, free portion of each 4.6–4.8 cm long, the anthers 8–9 mm long, extending to within 3–5 mm from tip of upper lip, pollen yellow; stigma minutely bilobed, pink, the style filiform, extends 2–4 mm beyond anthers, the ovary glabrous. Fruits oblong, flattened, oval in cross-section, green when immature, brown-black at dehiscence, 20–24 mm long, 6–8 mm wide, 5–6 mm thick; seeds brown, orbicular, strongly flattened, 4–6 mm in diameter, about 2 mm thick. Seed germination epigeal.

Habitat and distribution. *Aphelandra campanensis* is found predominantly at mid-elevations in central Panama in the provinces of Coclé, Panamá, Veraguas, and Colón, and in the Caribbean lowlands of western Panama (Bocas del Toro) and extreme southern Costa Rica (Limón). The distribution of *A. campanensis* is imperfectly known because only a few collections from the Caribbean lowlands of Panama have been made. Plants of this species occur in cloud forest habitat at mid-elevations and in wet lowland forests (Holdridge's premontane wet and premontane rain forests). The species grows in the forest understory, gaps, and disturbed, second-growth areas.

Flowering and fruiting. Peak flowering occurs during the mid wet season (Aug. through Nov.) and fruits mature late in the wet season and into the drier months of the year (Jan. and Feb.).

Aphelandra campanensis may be distinguished from most Central American species by its large, glabrous leaves, broadly rhombic-ovate bracts, bracteoles that are keeled and slightly falcate and calyx lobes that exceed the bracts. *Aphelandra hartwegiana* is similar in many respects but has strongly falcate bracteoles, larger and more ovate bracts that diverge from the rachis, longer calyx segments, and extremely coriaceous corollas.

There is some confusion about the identity of plants from the lowlands of western Bocas del Toro province. Collections from this region have been identified as *A. campanensis*, *A. crenata*, and *A. hartwegiana*. Part of the difficulty is due to the incomplete condition of some of the specimens in question. There is certainly variability among plants from this area, but I found that none of these specimens was outside of the range of variability encountered in *A. campanensis*. Until more collections are made and field and experimental studies carried out, these collections are best referred to *A. campanensis*.

Relationships. Phylogenetic analysis indicates that *A. campanensis*, *A. hartwegiana*, and *A. darienensis* are members of a monophyletic subgroup within Group II. The relationships of these species with other Central American members of the *A. pulcherrima* complex, and with South American species are discussed under *A. hartwegiana*.

Additional specimens examined. COSTA RICA. LIMÓN: between Cahuita and Bribri, 100 m, *McDade 242* (DUKE); Toro Amarillo, Cantón de Pococí, *Solis R. 443* (F).

PANAMA. BOCAS DEL TORO: hillside above Almirante, *Gentry 2748* (MO, US); Water Valley, vicinity of Chiriquí Lagoon, *von Wedel 1428* (GH, MO); Pumpkin River, vicinity of Chiriquí Lagoon, *von Wedel 2589* (GH, US). COCLÉ: El Copé, 250 m, *McDade 531* (DUKE); vicinity of El Valle and Cerro Pilón, 700–900 m, *Gentry & Dwyer 3665* (MO, NY), *Luteyn & Kennedy 1683* (DUKE, F, MO), *McDade 273, 441* (DUKE). COLÓN: around Dos Bocas, Río Fato valley, 40–80 m, *Pittier 4195* (NY, US). PANAMÁ: Cerro Campana, ca. 900 m, *Porter et al. 4966* (MO, US), *McDade 279* (DUKE), *Lewis et al. 3059* (US); 25 km NE of Cerro Azul on Río Piedras, 550 m, *Mori & Kallunki 3284* (MO). VERAGUAS: valley of Río Dos Bocas on road between Alto Piedra and Calovébora, 350–400 m, *Croat 27356* (MO); ca. 5 mi. past Santa Fé on road past Agricultural School, 700 m, *McDade 268* (DUKE).

12. **Aphelandra hartwegiana** Nees ex Benth., Pl. Hartw. 236. 1846. TYPE: Colombia. Cundinamarca: Hacienda de Palmar, near Guaduas, *Hartweg 1270* (holotype, K, not seen).

Shrubs 1–4 m high, sparsely branched; younger stems subquadrangular, sparsely pubescent, the trichomes upwardly appressed, white, about 0.5 mm long, older stems terete, glabrate. Leaves opposite, broadly elliptic, 25–40 cm long, 10–15 cm wide, apically acute to slightly acuminate, basally acute or attenuate, marginally entire, undulate or crenate, essentially glabrous above, sparsely pubescent below (moderate on veins), the trichomes appressed, white, 0.25–0.5 mm long; petioles 1–4 cm long, moderately pubescent, the trichomes appressed, white, 0.25–0.5 mm long; leaves reduced in size towards inflorescence. Inflorescences terminal, spikes solitary (rarely 2–5), subquadrangular, 15–30(–40) cm long, 1.5–2 cm wide; peduncles 0.5–1.5 cm long (longer below lateral inflorescences), sparsely pubescent, the trichomes appressed, white, about 0.25 mm long; rachis glabrous; 3–5 pairs of sterile bracts subtend spikes; floral bracts imbricate, broadly ovate, apically obtuse, entire, 13–16 mm long, 11–14 mm wide, deep orange, striate, essentially glabrous within and without, the nectaries supra-medial, 3.5–4.5 mm long and 2–2.5 mm wide, composed of many minute glands; bracteoles falcate, keeled, apically acute, 7–10 mm long, 3–5 mm wide, orange, glabrous or sparsely pubescent on keel, the trichomes appressed, white, about 0.5 mm long. Sepals 17–22 mm long, orange, frequently fading to white toward base, striate, glabrous or with a few trichomes toward apex, the adaxial segment oblong, apically obtuse, 6–9 mm wide, the abaxial pair narrowly oblong, apically acute, 4–5.5 mm wide, the lateral pair narrowly oblong, apically acute, 3–4 mm wide; corolla 6.5–7 cm long, yellow (infrequently orange), glabrous, very coriaceous, the tube 44–48 mm long, about 4 mm in diameter at base, narrowed to about 3 mm above ovary (about 7 mm above base), expanding to 8–9 mm deep at throat, the upper lip erect, ovate, 20–22 mm long, 11–13 mm wide, bilobed, the lobes triangular, 9–12 mm long, anther pocket very well-developed, the middle lobe of lower lip elliptic, about 25 mm long and 12 mm wide, apically acute, the lateral lobes about 1 mm long and 5 mm wide; filaments inserted about 7 mm above base of corolla tube, free portion of each 4.2–4.6 cm long, the anthers 9–10 mm long, extending to within 3–5 mm from tip of upper lip, pollen yellow; stigma not distinctively colored, minutely bilobed, the style filiform, extending 3–5 mm beyond anthers, the ovary glabrous. Fruits clavate, flattened, oval in cross-section, green when immature, turning brown-black at dehiscence, 28–31 mm long, 7–8.5 mm wide, 5–7 mm thick; seeds brown, orbicular, strongly flattened, 5–7 mm in diameter, about 2 mm thick. Seed germination epigeal.

Habitat and distribution. *Aphelandra hartwegiana* is found in the lowlands of eastern Panama and northern Colombia. It is a species of wet forests with mild dry seasons (or essentially aseasonal precipitation) [Holdridge's (1967) tropical wet forest]. The plants grow in gaps in the forest, very frequently along streams, trails and clearings, and in extensive secondary areas.

Flowering and fruiting. Peak flowering occurs during the wettest months of the year (Aug. through Nov.), with fruits maturing during the drier months of Jan. through March.

The large, broadly ovate bracts, strongly falcate bracteoles, 2 cm long calyx lobes, and extremely coriaceous, yellow corolla readily distinguish this species from all other Central American Aphelandras. Specimens of *A. hartwegiana* show a definite decrease in bract size from west to east. The systematic significance of this apparently very gradual, clinal variation is as yet unclear. Collections are quite few and I have not been able to study Colombian plants in the field.

A single collection from the Darién (*Allen 5094*) of Panama was identified as the South American species *A. crenata* by Durkee (1978). I found this specimen to be within the range of variability encountered in collections of *A. hartwegiana* from this region, but recognize the need for further study of these two species, especially in light of the clinal decrease in bract size of *A. hartwegiana* that results in Panamanian specimens at least superficially similar to *A. crenata.*

Relationships. Among the species treated here, *A. hartwegiana* is a member of Group II and is most closely related to *A. campanensis* and *A. darienensis. Aphelandra hartwegiana* and *A. campanensis* are also similar to the South American species *A. crenata* Leonard and *A.*

chaponensis Leonard (Leonard, 1953; Durkee, 1978). These four species are similar in a number of morphological features including habit; large, essentially glabrous leaves that are frequently marginally crenate; broadly ovate floral bracts; sepals markedly longer than the bracts; and falcate bracteoles. Elucidation of the phylogenetic relationships among these species will require further study of the South American species.

Additional specimens examined. PANAMA. DARIÉN: Cocalito, Pacific coast near Darién-Colombia border, *Dwyer 4339* (MO); along Sambú River, southern Darién, sea level, *Pittier 5557* (US); vicinity of Pinogana, 20 m, *Allen 921* (NY, US); trail between Pinogana and Yaviza, 15 m, *Allen 257* (A, GH); Río Chico, vicinity of Yaviza, 10 m. *Allen 5094* (MO); vicinity of Paya, Río Paya trail between Paya and Payita, *Stern et al. 177* (US); S of El Real, headwaters of Río Pirre, ca. 100 m, *Foster & Kennedy 1247* (DUKE), *McDade 425* (DUKE); Río Tacarcuna, vicinity of old Tacarcuna village, 580 m, *Gentry & Mori 13583* (MO). SAN BLAS: mainland opposite Ailigandí, *Lewis et al. 191* (US).

COLOMBIA. ANTIOQUIA: near Villa Arteaga on hwy. to sea, 150 m, *Hodge 7053* (US); near Chigorodó, 40 km S of Turbo, 50 m, *Haught 4699* (US); Uraba, Mutatá, 100 m, *Uribe 1505* (US); between Villa Arteaga and Chigorodó at Lomitas, *Cuatrecasas & Willard 26108* (US). BOLÍVAR: Boca Verde on Río Sinú, *Pennell 4580* (NY). CHOCÓ: Río Atrato, Quibdó, 40 m, *Forero et al. 1451* (MO); mouth of Río Truando, *Castaneda 4669* (NY); Pacific coast, Cupica, *Fernandez 354* (US); Bahía Solano, along Quebrada Jellita, 50–100 m, *Killip & Garcia 35639* (US); Río Chintado, above La Nueva, *Duke 9863* (US).

13. **Aphelandra darienensis** Wassh., Phytologia 25: 480. 1973. TYPE: Panama. Darién: Cerro Pirre, 750–1,350 m, *Duke & Elias 13756* (holotype, US; isotype, MO).

Shrubs 1–4 m high, sparsely branching; younger stems subquadrangular, sparsely pubescent, the trichomes upwardly appressed, white, about 0.5 mm long, older stems terete, glabrate, stems very thick and almost succulent. Leaves opposite, broadly elliptic, 25–35(–45) cm long, 10–17(–20) cm wide, apically acute, basally acute, marginally entire to crenulate, essentially glabrous to very sparsely pubescent above, the trichomes appressed, white, 0.75–1 mm long, sparsely pubescent below (except moderate on veins), the trichomes appressed, white, 0.5–0.75 mm long; petioles 3–9 cm long, moderately pubescent, the trichomes appressed, white, 0.75–1 mm long. Inflorescences terminal, spikes solitary (rarely 2–3), 10–18 cm long, 2.5–3 cm wide, sessile; rachis essentially glabrous; lower 1–3 pairs of bracts leaf-like and sterile; floral bracts densely imbricate, ovate, apically obtuse and arching away from rachis, entire, frequently notched at apex, 30–40 mm long, 18–26 mm wide, deep orange, very leathery-coriaceous, sparsely puberulous within and without, with few scattered longer (about 1 mm) trichomes, the nectaries medial, 3–4.5 mm long and 1–2 mm wide, composed of many minute glands; bracteoles slightly falcate, apically acute, 9.5–13 mm long, 4–6 mm wide, pale orange, essentially glabrous. Sepals 15–18 mm long, apically acute, dull orange, essentially glabrous or with few scattered trichomes, the adaxial segment broadly elliptic, 8.5–9 mm wide, the abaxial pair elliptic, about 5 mm wide, the lateral pair lanceolate, 3.5–4 mm wide; corolla orange, minutely papillate, 6.8–7.2 cm long, coriaceous, the tube 48–49 mm long, about 5 mm in diameter at base, narrowed to about 3 mm above ovary (about 6 mm above base), expanding to about 7 mm deep at throat, the upper lip erect, oblong, 18–20 mm long, 11–13 mm wide, bilobed, the lobes triangular, about 8 mm long, 11–13 mm wide, apically emarginate and apiculate, anther pocket well-developed, the middle lobe of lower lip ovate, 27–29 mm long, 10–12 mm wide, apically obtuse, the lateral lobes 2–2.5 mm long and 7 mm wide; filaments inserted about 8 mm above base of corolla tube, free portion of each 4.7–4.8 cm long, the anthers 8–9 mm long, extending to within 5–6 mm from tip of upper lip, pollen yellow; stigma orange, bilobed, the lobes about 0.2 mm long, style filiform, extending about 5 mm beyond anthers, the ovary glabrous. Fruits elliptic, flattened, oval in cross-section, green when immature, black at dehiscence, about 35 mm long, 8.5–9.5 mm wide, about 5 mm thick; seeds dark brown, strongly flattened, about 9 mm in diameter and 2–2.5 mm wide. Seed germination epigeal.

Habitat and distribution. Aphelandra darienensis is apparently endemic to the mountains of the Darién in eastern Panama. It is restricted to mid-elevation cloud forest habitats and occurs only in primary forest [lower montane rain forest (Holdridge, 1967)].

Flowering and fruiting. Flowering occurs during the early wet season (July through Sept.) and fruits mature during the remainder of the wet season (through Dec.). Data on seasonality of reproduction are rather tentative because collections of this species are still quite few.

Aphelandra darienensis is extremely distinctive and is readily identified from flowering or fruiting material. Most characteristic are the large (to 40 mm), leathery and strongly recurved floral bracts. The extremely large leaves and thick, almost succulent stems, as well as the unique apical shape of the upper corolla lip lobes (emarginate and apiculate), and very long capsules also distinguish the species.

Relationships. The results of phylogenetic analysis indicate that this species is a member of the lineage including the other Central American species with minute glands (Group II). Within this group, closest relatives are *A. hartwegiana* and *A. campanensis*. Wasshausen (1973a) suggests a relationship based on morphological similarity with *A. fernandezii* Leonard, a Colombian species that bears at least a superficial resemblance to *A. darienensis*. Further study of South American members of the *A. pulcherrima* complex will be necessary to satisfactorily resolve the phylogenetic relationships of this unusual species.

Additional specimens examined. PANAMA. DARIÉN: W slope of Cerro Pirre, 2,500–4,500 ft., *Duke 6101* (MO), *McDade 430* (DUKE); between Tres Bocas and Cerro Campamiento on Cuasí-Caña trail, *Kirkbride & Duke 1350* (MO); Cerro Campamiento, S of Cerro Pirre, *Duke 15620* (US).

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APPENDIX A. Members of the *Aphelandra pulcherrima* complex.

A. albert-smithii Leonard
A. aristei Leonard
A. attenuata Wassh.
A. barkleyi Leonard
A. blandii Lindau
A. campanensis Durkee
A. chaponensis Leonard
A. crenata Leonard
A. darienensis Wassh.
A. deppeana Schldl. & Cham.
A. dielsii Mildbr.
A. fasciculata Wassh.
A. fernandezii Leonard
A. garciae Leonard
A. golfodulcensis McDade
A. gracilis Leonard
A. grandis Leonard
A. hartwegiana Nees ex Benth.
A. haughtii Leonard
A. lasia Leonard
A. laxa Durkee
A. leonardii McDade
A. lingua-bovis Leonard
A. macrophylla Leonard
A. macrostachya Nees
A. micans Moritz ex Vatke
A. mildbraediana Leonard
A. panamensis McDade
A. parvispica Leonard
A. pharangophila Leonard
A. pilosa Leonard
A. pulcherrima (Jacq.) H.B.K.
A. schieferae Leonard
A. scolnikae Leonard
A. sericantha Leonard
A. sinclairiana Nees
A. storkii Leonard
A. straminea Leonard
A. taborensis Leonard
A. terryae Standley
A. tetragona (Vahl) Nees
A. trianae Leonard
A. xanthantha Leonard

APPENDIX B. Sources of pollen for size analysis (LW) and scanning electron microscopy study (SEM).

Collector and Number	Location	Used for
1. *A. terryae*		
Lewis et al. 126 (US)	Achituppu, San Blas, Pan.	LW
Tyson et al. 3815 (DUKE)	Cerro Piriaque, Darién, Pan.	LW
Haught 2098 (US)	Santander, Col.	LW
Duke 5187 (MO)	Río Pirre, Darién, Pan.	LW
McDade 431 (DUKE)	Río Pirre, Darién, Pan.	SEM/LW
Gentry & Mori 13550 (MO)	Pucuro, Darién, Pan.	LW
2. *A. sinclairiana*		
Donnell-Smith 6694 (US)	Atirro, Cartago, C.R.	LW
Wilbur et al. 13365 (DUKE)	Colón, Pan.	LW
McDade 280 (DUKE)	Colón, Pan.	SEM/LW
McDade 384 (DUKE)	Portobelo, Colón, Pan.	SEM/LW
Burger et al. 1977 (F)	Bribri, Limón, C.R.	LW
McDaniel & Cooke 14831 (FSU)	El Copé, Coclé, Pan.	LW
McDade 532 (DUKE)	El Copé, Coclé, Pan.	SEM/LW
Hunter & Allen 358 (MO)	El Valle, Coclé, Pan.	LW
McDade 528 (DUKE)	El Valle, Coclé, Pan.	SEM/LW
Pittier 5572 (NY)	Sambú River, Darién, Pan.	LW
Von Wedel 973 (MO)	Bocas del Toro, Pan.	LW
3. *A. storkii*		
McDade 350 (DUKE)	Pto. Viejo, Heredia, C.R.	SEM/LW

APPENDIX B. Continued.

Collector and Number	Location	Used for
4. *A. gracilis*		
Nee 9291 (MO)	Cerro Jefe, Panamá, Pan.	LW
McDade 421 (DUKE)	Cerro Jefe, Panamá, Pan.	SEM/LW
Lewis et al. 5392 (MO)	Sta. Rita Ridge, Colón, Pan.	LW
Mori & Kallunki 1801 (MO)	Sta. Rita Ridge, Colón, Pan.	LW
Allen 1671 (US)	El Valle, Coclé, Pan.	LW
McDade 529 (DUKE)	El Valle, Coclé, Pan.	SEM/LW
Kennedy & Dressler 2954 (MO)	El Llano, Panamá, Pan.	LW
Croat 22793 (F)	Cerro Campana, Panamá, Pan.	LW
5. *A. golfodulcensis*		
Skutch 3941 (US)	El General, San José, C.R.	LW
McDade 378 (DUKE)	Palmar, Puntarenas, C.R.	SEM/LW
McDade 401 (DUKE)	Corcovado, Puntarenas, C.R.	SEM/LW
Croat 21884 (F)	Pto. Armuelles, Chiriquí, Pan.	LW
Pittier & Biolley 7072 (US)	San Mateo, San José, C.R.	LW
Allen 5775 (US)	Esquinas, Puntarenas, C.R.	LW
Liesner 389 (MO)	Burica, Chiriquí, Pan.	LW
McDade 251 (DUKE)	San Vito, Puntarenas, C.R.	SEM/LW
6. *A. panamensis*		
Foster & Kennedy 1872 (DUKE)	Cerro Jefe, Panamá, Pan.	LW
McDade 411 (DUKE)	Cerro Jefe, Panamá, Pan.	SEM/LW
Foster & Kennedy 1263 (DUKE)	Cerro Pirre, Panamá, Pan.	LW
McDade 428 (DUKE)	Cerro Pirre, Panamá, Pan.	SEM/LW
McDade 284 (DUKE)	Sta. Rita Ridge, Colón, Pan.	SEM/LW
7. *A. deppeana*		
Ton 3076 (DUKE)	Chiapo de Corzo, Chiapas, Mex.	LW
McDade 377 (DUKE)	Cañas, Guanacaste, C.R.	SEM/LW
McDade 252 (DUKE)	San Vito, Puntarenas, C.R.	SEM/LW
McDade 290 (DUKE)	Palmar, Puntarenas, C.R.	SEM/LW
Ortiz s.n. (DUKE)	Tikal, El Petén, Guat.	LW
McDade 533 (DUKE)	El Copé, Coclé, Pan.	SEM/LW
McDade 530 (DUKE)	El Valle, Coclé, Pan.	SEM/LW
A. dukei (= *A. deppeana*)		
Duke 14397 (US)	Piria, Panamá, Pan.	LW
Mori & Gentry 4245 (MO)	Pucuro, Darién, Pan.	SEM/LW
8. *A. lingua-bovis*		
Archer 2012 (US)	Chocó, Col.	SEM/LW
Skutch 5284 (US)	Golfo Dulce, Puntarenas, C.R.	LW
McDade 399 (DUKE)	Corcovado, Puntarenas, C.R.	SEM/LW
Allen 924 (GH)	Pinogana, Darién, Pan.	LW
McDade 429 (DUKE)	Río Pirre, Darién, Pan.	SEM/LW
McDade 442 (DUKE)	San Vito, Puntarenas, C.R.	SEM/LW
9. *A. leonardii*		
Duke et al. 3611 (US)	Cerro Diablo, San Blas, Pan.	LW
Foster 1996 (F)	Majé, Panamá, Pan.	LW
Lewis et al. 172 (DUKE)	Ailigandí, San Blas, Pan.	LW
D'Arcy 9696 (MO)	Portobelo, Colón, Pan.	LW
McDade 310 (DUKE)	Frailes, San José, C.R.	SEM/LW
Pittier 11988 (US)	Boca Culebra, San José, C.R.	LW
McDade 432 (DUKE)	Cerro Pirre, Darién, Pan.	SEM/LW

APPENDIX B. Continued.

Collector and Number	Location	Used for
10. *A. laxa*		
Mori et al. 6854 (MO)	Pto. Obaldia, San Blas, Pan.	SEM/LW
11. *A. campanensis*		
Weaver 1648 (DUKE)	El Valle, Coclé, Pan.	LW
McDade 271 (DUKE)	El Valle, Coclé, Pan.	SEM/LW
Von Wedel 1428 (GH)	Chiriquí Lagoon, Bocas del Toro, Pan.	LW
McDade 242 (DUKE)	Bribri, Limón, C.R.	SEM/LW
McDade 531 (DUKE)	El Copé, Panamá, Pan.	SEM/LW
12. *A. hartwegiana*		
Allen 921 (US)	Pinogana, Darién, Pan.	LW
McDade 425 (DUKE)	Rio Pirre, Darién, Pan.	SEM/LW
Cuatrecasas 26108 (US)	Antioquia, Col.	LW
Lewis et al. 191 (US)	Ailigandí, San Blas, Pan.	LW
13. *A. darienensis*		
Duke & Elias 13756 (US)	Cerro Pirre, Darién, Pan.	LW
McDade 430 (DUKE)	Cerro Pirre, Darién, Pan.	SEM/LW
A. pulcherrima		
Blum 3523 (US)	La Popé, Bolívar, Col.	SEM
Killip & Smith 14516 (US)	Arjona, Bolívar, Col.	SEM

APPENDIX C. Locations of populations of *Aphelandra* species used in field and greenhouse studies: (O) = sites of field observations for flower visitors, (IC) = sources of greenhouse grown plants used in interpopulation crosses.

2. *A. sinclairiana*
   - Colón (O)—Panama, Colón: Pipeline Rd., 5 km from Gamboa, 50 m. (Now part of Parque Nacional Soberanía.)
3. *A. storkii*
   - Pto. Viejo (O)—Costa Rica, Heredia: Finca La Selva, ca. 6 km from Pto. Viejo, along Río Pto. Viejo, 100 m.
4. *A. gracilis*
   - El Valle (O)—Panama, Coclé: 10 km beyond El Valle de Antón, 800 m.
5. *A. golfodulcensis*
   - Corcovado (O, IC)—Costa Rica, Puntarenas: Corcovado National Park, Osa Peninsula, sea level.
   - San Vito (O, IC)—Costa Rica, Puntarenas: 6 km from San Vito de Java, forest below Las Cruces Botanical Garden, 1,200 m.
6. *A. panamensis*
   - Santa Rita (IC)—Panama, Colón: 25 km from Transisthmian Hwy., Santa Rita Ridge, 300 m.
   - Cerro Jefe (IC)—Panama, Panamá: 30 km above InterAmerican Hwy. on road to Cerro Jefe, 800 m.
   - Cerro Pirre (O, IC)—Panama, Darién: upper slopes of Cerro Pirre, about 12 km S of El Real, 600–800 m.
7. *A. deppeana*
   - Cañas (O, IC)—Costa Rica, Guanacaste: 8 km N of Cañas along InterAmerican Hwy., 50 m.
   - San Vito (IC)—Costa Rica, Puntarenas: 6 km from San Vito de Java, Las Cruces Botanical Garden, 1,200 m.
   - Palmar (IC)—Costa Rica, Puntarenas: 10 km SE (toward Panama) of Palmar N., along InterAmerican Hwy., 100 m.
8. *A. lingua-bovis*
   - Corcovado (O, IC)—Costa Rica, Puntarenas: Corcovado National Park, Osa Peninsula, sea level.
   - San Vito (O, IC)—Costa Rica, Puntarenas: 6 km from San Vito de Java, forest before Las Cruces Botanical Garden, 1,200 m.
   - Portobelo (IC)—Panama, Colón: near bridge over Río Buenaventura near town of Portobelo, sea level.
9. *A. leonardii*
   - Frailes (O, IC)—Costa Rica, San José, Río Tarrazú near Frailes, 1,300 m.
   - Cerro Pirre (IC)—Panama, Darién: lower slopes of Cerro Pirre, about 12 km S of El Real, 500 m.
11. *A. campanensis*
   - El Valle (O)—Panama, Coclé: 10 km beyond El Valle de Antón, 800 m.
   - El Copé (O)—Panama, Coclé: about 10 km past El Copé, 250 m.
12. *A. hartwegiana*
   - Río Pirre (O)—Panama, Darién: along Río Pirre about 12 km S of El Real, 400 m.
13. *A. darienensis*
   - Cerro Pirre (O)—Panama, Darién: upper slopes and summit of Cerro Pirre, about 12 km S of El Real, 800–1,300 m.

APPENDIX D. Crossability indices between Central American species of the *Aphelandra pulcherrima* complex. NA indicates data not available. Species numbers and abbreviations as in Table 2.

		Pollen Parent											
	Species	1. TE	2. SI	3. ST	4. GR	5. GO	6. PA	7. DE	8. LB	9. LE	11. CA	12. HA	13. DA
O	1. TE	—	0.66	0.59	0.59	0.55	0.24	0	0.03	0.08	NA	NA	0.07
v	2. SI	0.26	—	0.39	NA	0.56	0.04	0.13	0.07	0.16	NA	NA	0.01
u	3. ST	0.29	0	—	0.62	0	0.29	0.29	0	0.10	0	0	0
l	4. GR	0	NA	0	—	NA	0	NA	NA	0	NA	NA	NA
e	5. GO	0.86	0.98	0.51	0.51	—	0.26	0.17	0.04	0.27	0	0	0.03
	6. PA	0.80	0.99	0.58	0.37	0.64	—	0.89	0	0.10	0	0	0
P	7. DE	0.11	0.11	0.14	0.05	0.04	0.50	—	0.01	0.15	0.07	0	0
a	8. LB	0	0	0	0.45	0	0	0.08	—	0	0	0	0
r	9. LE	0.11	0.11	0.12	0.49	0.13	0.90	0.03	0.12	—	0.17	0.26	0.39
e	11. CA	NA	NA	0	0	0	0	0	0	0	—	0	NA
n	12. HA	NA	NA	0.03	NA	0	0	0	0	0	0.04	—	NA
t	13. DA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	—

APPENDIX E. Character by taxon matrix. Species numbers and abbreviations as in Table 2, characters as in Table 13.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. TE	1	0	1	1	1	2	0	0	1	1	1	1	1	1	0	0	1	0	0	1	0
2. SI	1	1	0	2	1	1	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0
3. ST	0	1	0	2	1	1	1	0	1	3	0	1	1	1	0	0	1	2	0	1	1
4. GR	1	1	1	1	1	2	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0
5. GO	1	1	2	1	1	2	0	0	0	1	0	1	2	1	0	0	0	0	0	0	0
6. PA	1	2	1	2	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0
7. DE	1	2	1	1	0	0	0	0	0	1	0	1	3	1	0	0	0	0	0	0	0
8. LB	0	0	1	0	0	2	2	0	1	2	0	0	0	1	0	0	1	2	0	1	1
9. LE	1	1	1	0	0	2	2	0	1	1	0	0	0	1	0	0	0	1	0	0	1
10. LA	0	0	1	0	0	2	2	1	1	1	0	0	0	0	0	0	1	1	0	1	1
11. CA	0	0	1	0	1	2	2	0	1	1	0	0	0	1	0	1	1	2	1	1	2
12. HA	0	0	1	0	1	2	2	0	1	2	1	0	0	2	0	2	1	3	1	1	2
13. DA	0	0	1	0	0	2	2	0	1	4	1	0	0	1	1	1	1	2	0	1	2
Ancestor	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0

APPENDIX E. **Extended.**

22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
1	2	0	2	2	0	1	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0
2	2	0	2	2	0	2	0	1	0	1	1	1	1	1	1	1	0	0	0	0	0
3	3	0	2	2	0	2	0	1	0	0	2	0	1	1	1	1	0	0	0	0	0
2	2	0	1	1	0	1	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0
2	2	0	1	1	0	2	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0
2	1	0	1	3	0	1	1	1	1	0	0	0	1	1	1	0	1	0	0	0	1
0	0	0	2	3	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	0	1
1	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0
2	2	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0
2	2	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0
2	2	0	0	0	0	2	0	0	0	0	1	0	0	2	0	1	0	1	1	1	0
2	3	0	0	0	1	3	0	0	0	0	2	0	0	2	0	1	0	1	1	1	0
2	3	1	0	0	0	3	0	0	0	0	3	0	0	2	0	1	0	1	1	1	0
1	2	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

APPENDIX F. Character state changes for phylogenetic hypothesis presented in Figure 58, by character and stem in which change occurs; characters and character states as in Table 13; and stem abbreviations as in Figure 58. Letters denote apparent type of evolutionary change: P = parallelism, R = reversal, A = derived character state unique to species, S = derived state shared by all distal taxa.

1.	ST:	0	(R)
	LE:	1	(P)
	A:	1	(P)
2.	TE:	0	(R)
	LB:	1	(P)
	DA:	1	(P)
	F:	2	(S)
	H:	0	(R)
3.	GO:	2	(A)
	C:	0	(S)
4.	PA:	2	(P)
	A:	1	(S)
	C:	2	(P)
5.	DA:	0	(R)
	A:	1	(P)
	F:	0	(R)
	J:	1	(P)
6.	AN:	2	(S)
	C:	1	(R)
	F:	0	(R)
7.	ST:	1	(P)
	G:	2	(S)
8.	GR:	1	(P)
	LA:	1	(P)
9.	AN:	1	(S)
	D:	0	(R)
10.	ST:	3	(P)
	GR:	0	(A)
	LB:	2	(P)
	DA:	4	(A)
	C:	2	(P)
	K:	2	(P)
11.	ST:	0	(R)
	B:	1	(P)
	K:	1	(P)
12.	A:	1	(S)
13.	GO:	2	(P)
	DE:	3	(A)
	A:	1	(S)
14.	GR:	0	(P)
	LA:	0	(P)
	HA:	2	(A)
15.	DA:	1	(A)
16.	HA:	2	(A)
	J:	1	(S)
17.	LB:	1	(P)
	B:	1	(P)
	I:	1	(P)
18.	ST:	2	(P)
	LB:	2	(P)
	HA:	3	(A)
	G:	1	(P)
	J:	2	(P)
19.	DA:	0	(R)
	J:	1	(S)
20.	LE:	0	(R)
	B:	1	(P)
	G:	1	(P)
21.	ST:	1	(P)
	G:	1	(P)
	J:	2	(S)
22.	TE:	1	(R)
	ST:	3	(A)
	DE:	0	(A)
	A:	2	(P)
	H:	2	(P)
23.	ST:	3	(P)
	DE:	0	(A)
	LB:	1	(P)
	F:	1	(P)
	K:	3	(P)
24.	DA:	1	(A)
25.	DE:	2	(P)
	B:	2	(P)
	G:	0	(S)
26.	B:	2	(P)
	F:	3	(S)
	G:	0	(S)
27.	HA:	1	(A)
28.	GO:	2	(P)
	DE:	0	(A)
	LB:	1	(P)
	C:	2	(P)
	G:	2	(P)
	K:	3	(S)
29.	F:	1	(S)
30.	A:	1	(S)
31.	PA:	1	(P)
	LB:	1	(P)
32.	SI:	1	(A)
33.	TE:	0	(R)
	ST:	2	(P)
	DA:	3	(A)
	A:	1	(P)
	F:	0	(R)
	J:	1	(P)
	K:	2	(P)

Appendix F. Continued.

34. SI: 1 (A)
35. A: 1 (S)
36. DE: 0 (A)
J: 2 (S)
37. A: 1 (S)
38. LB: 0 (R)
AN: 1 (S)
F: 0 (R)
39. LB: 1 (P)
F: 1 (P)
40. H: 1 (S)
41. H: 1 (S)
42. I: 1 (S)
43. F: 1 (S)

KLAINEDOXA (IRVINGIACEAE) AT MAKOKOU, GABON: THREE SYMPATRIC SPECIES IN A PUTATIVELY MONOTYPIC GENUS[1]

ALWYN H. GENTRY[2]

ABSTRACT

This paper, in effect constituting a revision of the genus *Klainedoxa,* is a byproduct of ecological studies of tropical forest diversity carried out at the CENAREST laboratory near Makokou, Gabon in 1981. Collections from the rain forest canopy included at least 69 taxa new to the field station, a number new to Gabon, and several apparently undescribed species. In the case of *Klainedoxa,* as well-known but taxonomically difficult genus of large trees, these collections indicate a clear resolution of the heretofore problematical taxonomic relationships.

Canopy trees and lianas of the tropical rain forest are notoriously poorly understood taxonomically, in large part because the difficulty of collecting them has led to a dearth of herbarium material. New techniques for collecting canopy plants, which have recently been developed in Amazonia but little used elsewhere, were critical to the study reported here. Collections of canopy trees and lianas at Makokou were made by using a tree-climbing bicycle (Forestry Suppliers cat. no. 27170) to reach the canopy and a lightweight set of aluminum tree trimming poles (available from the Missouri Botanical Garden) to reach flowering or fruiting outer branches. A similar technique using a movable platform to climb into the canopy has previously been used successfully to collect specimens of large trees at Makokou (Hladik & Hallé, 1973, pl. 3). However, the system employing a tree bicycle (which can climb trees up to 65 cm in diameter) and telescoping tree-trimming pole (potentially 12 m long) is both much more flexible and less physically demanding. Another relevant problem arises when taxonomic work, as has often been the case for tropical plants, is restricted to the herbarium with little communication between systematists and the foresters, ecologists, or native peoples who may know plants in the field and be well aware of obvious differences in characters such as those of large fruits that are rarely preserved in the herbarium. As a rule, and within a single geographic area, one who knows plant populations intimately in the field, no matter what his training, is likely to be able to evaluate what constitutes a species better than the most eminent herbarium taxonomist. The work reported here draws heavily on the field experience of the team of vertebrate ecologists working at the Makokou laboratory.

Klainedoxa, a small genus of tropical African canopy and emergent trees with large elephant-dispersed fruits, epitomizes these problems. Recent treatments (Aubréville, 1962; Gilbert, 1958) of the genus, variously treated as belonging to Irvingiaceae or to Simaroubaceae, have recognized two species, *K. gabonensis* Pierre ex Engl. and *K. busgenii* Engl., the latter differentiated by its generally larger, more cordate leaves. The "Flora of West Tropical Africa" (Hutchinson & Dalziel, 1958) recognized, in addition to the widespread *K. gabonensis,* an unnamed *Klainedoxa* designated as "imperfectly known." Since *K. busgenii* proves to be no more than an extreme form of variable *K. gabonensis* (Letouzey, pers. comm.), *Klainedoxa,* as currently understood, would seem to contain only a single highly variable species.

The forest surrounding the field station at Makokou, Gabon is one of the best known areas of tropical Africa floristically (Hallé, 1964, 1965; Hallé & Le Thomas, 1967, 1970; Hladik & Hallé, 1973; Florence & Hladik, 1980). Nevertheless, only a single species of *Klainedoxa* has been reported to occur at the field station (Hallé & Le

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[1] I thank Drs. A. Hladik, R. Letouzey, P. Raven, and L. Emmons for reviewing the manuscript; Dr. Emmons for originally pointing out to me the three different *Klainedoxa* fruit types; and Paul Posso and the Institut de Recherche sur L'Écologie Tropicale (CENAREST) for making possible my field work in Gabon. This research was supported by grants from the Explorers Club and National Geographic Society.

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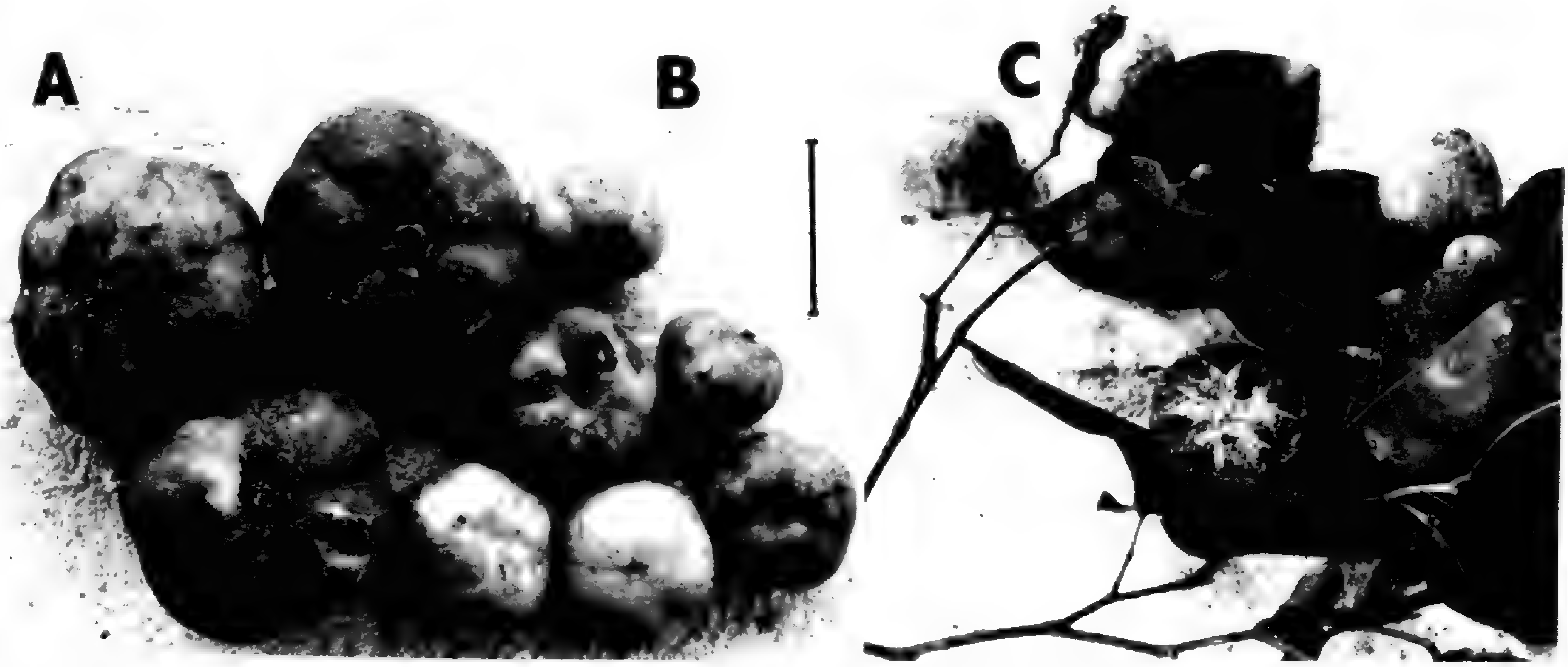

FIGURE 1. Fruits of *Klainedoxa* at Makokou, Gabon.—A. *K. gabonensis* (large fruits).—B. *K. trillesii* (small fruits).—C. *K. microphylla.* Line is 4 cm.

Thomas, 1967), although Florence and Hladik (1980: 237) mention two sympatric "forms" of *Klainedoxa* of unspecified taxonomic rank, and ecologists working there discriminate three different types of *Klainedoxa* fruit on their study grid (Emmons, pers. comm.; Fig. 1). The common species at Makokou is *K. gabonensis* [*Gentry 33303A, 33779* (MO)], which has large, 5-lobed, depressed-globose fruits 4–4.5 cm long and 5–7 cm wide that remain green at maturity, and ovate acute-tipped leaves that are 7–20(–30 in juveniles) cm long. This emergent tree is one of the best known and most distinctive plants of tropical Africa.

A second species [*Gentry 33183, 33508* (MO)], also an emergent giant, has distinctly smaller fruits that are only 2–3 cm long and 3–4 cm wide though of a similar depressed-globose, 5-angled shape. The smaller seeds, though still hard-shelled, are possible to cut with a plant clipper, unlike those of *K. gabonensis.* This species has leaves similar in shape to those of *K. gabonensis* but smaller [(5–)7–9(–11) cm long]; although there is some overlap between the two species, most leaves of all collections of *K. gabonensis* are more than 9 cm long. The fruits of this small-leaved small-fruited plant often turn yellow at maturity unlike those of *K. gabonensis* (Emmons, pers. comm.).

The third type of fruit [*Gentry 33178, 33182* (MO)] is even more distinctive. It is globose, unlobed, glaucous gray-green in color, and 3.5–4.5 cm in diameter. The leaves of this species are also distinctive in being obtuse apically, elliptic to obovate in shape, and small (8–10.5 cm by 4.5–6 cm). All three of these plants occur along trails in the main ecological study grid at Makokou and no intermediates between them have been observed. All key out to *K. gabonensis* in the "Flore du Gabon" (Aubréville, 1962).

A survey of the literature reveals that 20 names have been proposed for different collections of what is now generally treated as *K. gabonensis* sensu lato. Van Tieghem (1905) proposed 14 specific epithets for *Klainedoxa,* basing them largely on vegetative characters, and several additional species were proposed subsequently by Engler (1907, 1911) and others. Pellegrin (1924) reviewed the species and accepted nine of them, still based almost entirely on vegetative characters. Letouzey (1975 and pers. comm.) has recognized two taxa in Cameroun, the second treated as *K. gabonensis* var. *microphylla* but now considered by him to constitute a distinct species.

Two of the extant synonyms clearly are applicable to the two nameless Makokou species. *Klainedoxa trillesii* was characterized by exactly the same combination of smaller leaves and much smaller fruits than *K. gabonensis* that marks the small-fruited Makokou taxon. *Klainedoxa gabonensis* var. *microphylla* is characterized by the small, blunt-tipped leaves that mark the glaucous-fruited Makokou plant. Since there is no doubt that this represents a distinct species and none of the published specific epithets seems applicable to a blunt-leaved entity, elevation of var. *microphylla* to species rank is unavoidable.

Klainedoxa microphylla (Pellegrin) A. Gentry, comb. et stat. nov., *K. gabonensis* var. *microphylla* Pellegrin, Bull. Soc. Bot. France 71: 54. 1924. TYPE: Gabon. Maboumi *LeTestu 1823* (P, not seen).

This is apparently the same taxon as the "imperfectly known" *Klainedoxa* species from Ghana mentioned in the "Flora of West Tropical Africa." It is possible that the earlier name *K. sphaerocarpa* Tieghem (1905: 303) applies to this taxon. However, that species was based entirely on fallen fruits, described as spherical and 3–4 cm in diameter. Since the fruits that constitute the type of *K. sphaerocarpa* are apparently no longer extant (Letouzey, pers. comm.), and since aberrant or immature fruits of either *K. trillesii* or *K. gabonensis* could also fit the inadequate description, it seems preferable to raise the well-known and well-typified var. *microphylla* to specific rank rather than resurrect the undocumented epithet *sphaerocarpa*.

The three species of *Klainedoxa* at Makokou (and in the world) may be separated by the following key. Note that the leaf dimensions refer only to mature leaves. The juvenile leaves of *K. microphylla* and *K. trillesii* are unknown. However, since juvenile leaves of *K. gabonensis* are often much larger than mature leaves, it is likely that the same will prove true for the other two species. If so, their juvenile leaf dimensions may overlap with those of *K. gabonensis*.

KEY TO SPECIES

1. Leaves obtuse at apex, elliptic to obovate; fruits globose, 3.5–4.5 cm in diameter, glaucous gray-green .... *K. microphylla*
1'. Leaves acute at apex, ovate to ovate-lanceolate; fruits depressed-globose, distinctly broader than long, 5-angled, not glaucous.
    2. Mature leaves mostly less than 9 cm long (a few rarely to 11 cm long) and 5(–6) cm wide; fruits less than 3 cm long and 4 cm wide, turning yellow at maturity .... *K. trillesii*
    2'. Leaves mostly more than 9 cm long and (4–)5 cm wide; fruits 4–4.5 cm long and 5–7 cm wide, green at maturity .... *K. gabonensis*

Since no attempt has been made to study all extant material of *Klainedoxa*, it may seem premature to apply the Makokou results to the entire genus throughout its geographic range. However, all available evidence suggests that there is no breakdown of the key differentiating characters elsewhere in Africa, despite the notorious intraspecific variability of *K. gabonensis*. Moreover, the three Makokou taxa clearly "pass the test of sympatry," mandating taxonomic recognition at the species level even were the species limits obscured elsewhere. By definition subspecies are allopatrically distributed variants. Recognition of the three Makokou taxa at varietal level would imply differences in only a few genes, clearly incompatible with the whole suite of consistent differentiating characters in both fruit and leaves reported here.

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NOTE ADDED IN PROOF: After reading this manuscript, John Hart and Terese Hart inform me that they independently recognized the same three sympatric species of *Klainedoxa* while studying ungulate dispersal in the Ituri Forest of Zaire.

PSYCHOTRIA HEBECLADA DC. (RUBIACEAE), AN OVERLOOKED SPECIES FROM CENTRAL AMERICA[1]

CHARLOTTE M. TAYLOR[2]

ABSTRACT

Two species of *Psychotria, P. pubescens* and *P. hebeclada,* occur sympatrically in Central America and have been erroneously combined in several recent floras. Distinctions are drawn between these two species, primarily using characters of the flowers and inflorescences, and a description, range map, and illustration of each species is presented.

The Rubiaceae are one of the largest families of plants, and a very conspicuous component of the flora of Central America. Dwyer (1980) estimated that this is the largest dicotyledonous family in Panama. *Psychotria* is the largest genus in the family, currently estimated to include about 800 (Dwyer, 1980) to 1,000 (Standley & Williams, 1975) species distributed through the moist tropical regions of the world. This genus is well represented in the New World tropics, and many new species are being described as new areas are explored. For instance, Dwyer recently (1980) reported 97 species of *Psychotria* from Panama, 34 of them new.

Psychotria pubescens Sw. is a common species found in lowland Central America, southern Mexico, and the West Indies. *Psychotria hebeclada* DC. is also found in Central America, as well as in northern South America, but it is much less common. These species are quite distinct and can be easily separated from each other, but recently *P. hebeclada* has been treated in several floras as a synonym of *P. pubescens* (Croat, 1978; Dwyer, 1980) or even overlooked altogether (Standley & Williams, 1975).

THE DIFFERENCES BETWEEN *PSYCHOTRIA PUBESCENS* AND *P. HEBECLADA*

Although superficially similar, these two species differ in distinctive features of the inflorescence, calyx, and pubescence, as well as in flower color, bract length, ecology, and distribution. These latter dissimilarities are less consistent, but do support the separateness of the two taxa. These distinctions are discussed below, and summarized in Table 1 and in a key. The descriptions presented here are based on examination of approximately 1,400 herbarium specimens from the collections of A, CAS, DS, DUKE, ENCB, F, GH, MICH, MO, NY, and US.

These species differ most strikingly in the shape of the inflorescence. In both species the inflorescence is composed of a thyrse of similar, rather irregular cymes of both pedicellate and sessile flowers. However, as noted by de Candolle in his original description of *Psychotria hebeclada,* the inflorescence of *P. pubescens* is corymbiform in arrangement. The primary branches at each node are nearly equal in size to the central axis and are ascending to spreading in orientation, and the resulting outline of the top of the inflorescence is a gentle convex curve. In contrast, the inflorescence of *P. hebeclada* has a well-developed central axis from which smaller branches diverge nearly horizontally. This inflorescence is thyrsiform or racemiform, and its overall outline is conical or even somewhat trapezoidal (Fig. 1).

The inflorescence shapes are correlated with a difference in the morphology of the calyx. The lobes of the calyx are characteristically very short in *Psychotria,* and *P. pubescens* is typical with broadly triangular or somewhat ovate lobes which are commonly 0.3–0.8 mm long but may be as much as 1–1.1 mm long. The calyx lobes of *P. hebeclada* are 0.6–2.3 mm long and are lanceolate or ovate. Unlike those of *P. pubescens,* these lobes are usually acuminate and are often apically reflexed as well. Further, the inner surface, thus exposed, often shows two well-developed

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[1] Thanks are due to the curators of the herbaria listed above for their prompt and courteous loan of specimens of these two species. Special thanks also go to Dr. R. L. Wilbur, curator of DUKE, and to Dr. Lucinda McDade and Mr. Melvin Turner for their help and suggestions.

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TABLE 1. Summary of the characters which distinguish *Psychotria hebeclada* and *P. pubescens.*

Character	*P. hebeclada*	*P. pubescens*
Calyx Length	(0.6–)0.8–2(–2.3) mm long, longer than gland.	0.3–1.1 mm long, equal to or shorter than gland.
Calyx Lobe Shape	Lanceolate or ovate, apically acuminate.	Triangular, apically acute.
Inflorescence Shape	Thyrsiform or racemiform, about (0.6–)0.8–1.3 times as long as broad, central axis well-developed, branches horizontal.	Corymbiform, about 0.5–0.7 times as long as broad, central axis poorly developed, branches ascending.
Pubescence	Pilosulous to hirsutulous, hairs (0.1–)0.3–0.7(–0.9) mm long.	Puberulous to pilosulous, hairs (0.1–)0.15–0.4(–0.5) mm long.
Bracts	Linear, those subtending the flowers 1.5–2.5 mm long.	Triangular to lanceolate, those subtending flowers 0.5–1.5 mm long.
Flower Color	White, usually tinged with pink or rose, rarely yellowish.	Yellow-white or yellow, occasionally tinged with pink.
Habitat	Moist to wet forests and edges, often along rivers.	Forests and disturbed areas, moist or seasonally dry areas, often on limestone.
Habit	Erect or scandent.	Erect.
Distribution	Mexico, Central America, northwestern South America.	Mexico, Central America, West Indies.

marginal veins paralleling the midvein. The calyx lobes of *P. pubescens* are almost never acuminate and are only rarely reflexed, and when reflexed the midvein is the only vein apparent on the inner surface.

Plants of both species are usually covered with soft, spreading, pilosulous pubescence, although a few specimens of each species were seen that were only sparsely pubescent or very minutely puberulent. The hairs of *Psychotria pubescens* are usually straight and uniform in length and distribution. The hairs of *P. hebeclada* are usually somewhat uneven in length and distribution, and often wavy. This species is often more sparsely pubescent than *P. pubescens,* and the pubescence is sometimes rather more hirsutulous than pilosulous.

The corollas of *Psychotria pubescens* are usually yellowish white, although they may be white or even tinged with pink. *Psychotria hebeclada* has corollas that are usually white or pink-tinged, and are rarely yellowish. This species also has very narrow floral bracts, which may be as short as 0.5 mm but are generally 1.5–2.5 mm long, nearly as long as the flowers they subtend. These bracts commonly persist on the infructescences and are easily seen. The floral bracts of *P. pubescens* are also narrow, but these tend to be more triangular than linear and are usually about 0.5–1.5 mm long, much shorter than the flowers they subtend. These bracts are also usually persistent, but are much less obvious on the infructescence because of their small size.

Psychotria pubescens is found from sea level to about 1,500 m, and is most common in dry or seasonally dry forests and edges but also occurs in moist or wet forests and along streams and rivers. *Psychotria hebeclada* has a similar elevational range, but it has nearly always been collected in moist forests, and very often on riverbanks. This species is especially well represented by material from the La Selva field station in lowland northeastern Costa Rica, where an intensive program of collecting is presently underway (Hammel & Grayum, 1982). This area has been quite extensively explored, but *P. hebeclada* is known only from river edge forest. Interestingly, no *P. pubescens* has so far been collected at the La Selva station. In Costa Rica, *P. pubescens* is largely found on the western side of the continental divide, in the seasonally dry regions (Fig. 2).

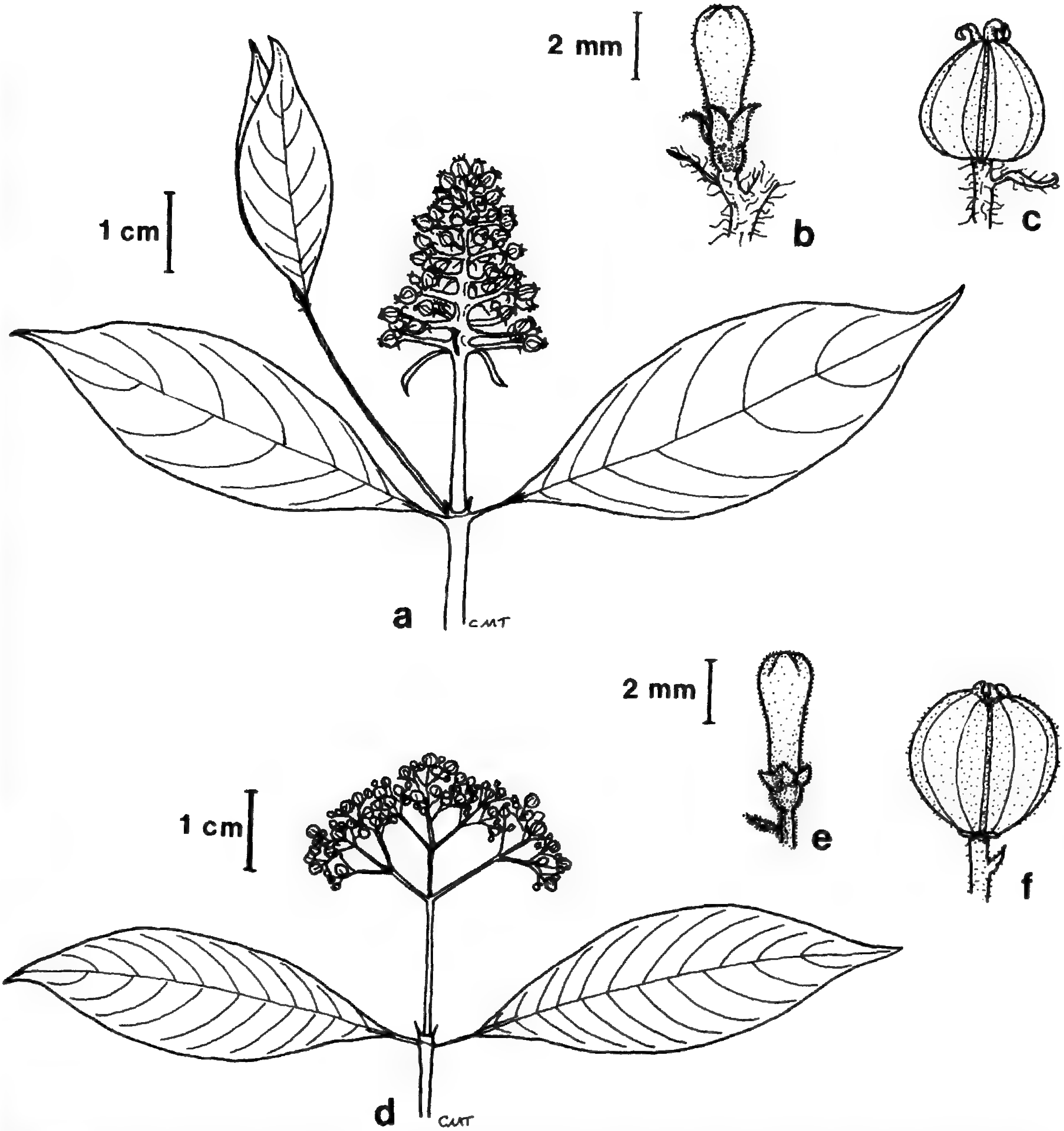

FIGURE 1. *Psychotria hebeclada.* a–c: a, inflorescence; b, flower, showing calyx; c, fruit. *Psychotria pubescens.* d–f: d, inflorescence; e, flower, showing calyx; f, fruit. Composite drawings, based on examination of numerous specimens.

Psychotria pubescens is found from Panama northward through Central America to southern Mexico, and in the West Indies (Fig. 2). It has been most commonly collected in Belize, Guatemala, Cuba, and the Dominican Republic, where it is often noted as a plant of limestone outcrops or hillsides. Numerous collections have been made around the ruins of the limestone Indian buildings in southern Mexico, Belize, and Guatemala. No collections of this species were seen from east of the former Canal Area in Panama. Conversely, *P. hebeclada* increases in abundance southward and is not known to occur in the West Indies. This species is found from Central Mexico south into northern South America. It has been collected only sporadically in the northern part of its range, and most of the specimens in the collections examined are from Costa Rica, Panama, and Colombia. Although some specimens from Colombia have smaller and more

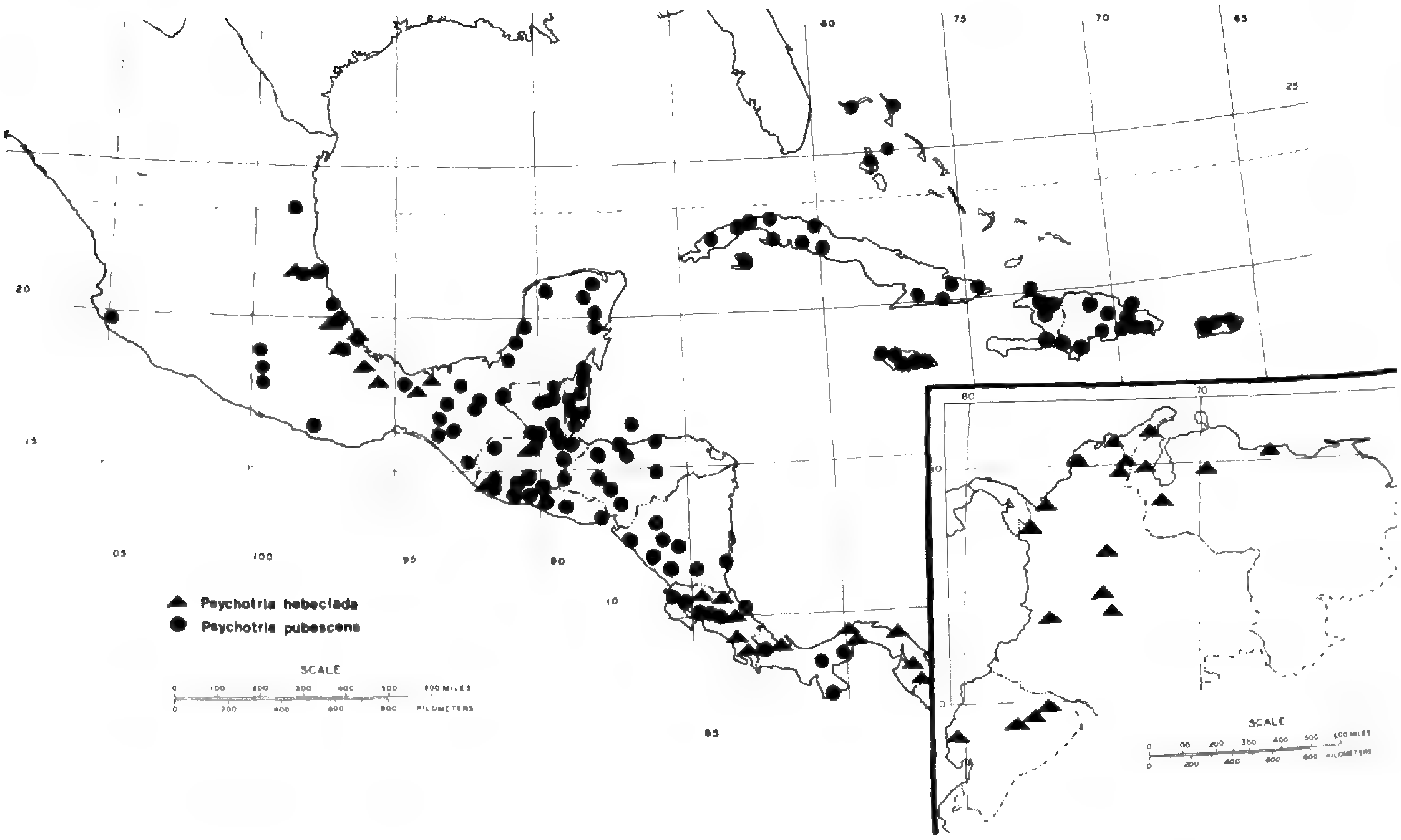

FIGURE 2. Distribution of *Psychotria pubescens* (circles) and *P. hebeclada* (triangles).

attenuated inflorescences, the distinctive conical, racemiform shape of the panicle and the comparatively long calyx lobes are still evident.

At first glance, stipule morphology seems to be a reliable character as well. However, both of these species display an exceptional diversity of stipule shapes that precludes the use of this character. In both of these species the stipules are fused both interpetiolarly and intrapetiolarly to form a sheath. This is truncate and bears two triangular lobes or awns on each side. However, the stipule sheath of *Psychotria pubescens* may be very poorly or very strongly developed, and the lobes may range from rounded, minute projections to aciculate awns 5–6 mm long. Further, stipule shape often changes along a single branch. At young nodes, the lobes are very close together, so that they often resemble one point. Alain (1962) in fact describes the stipules of this species only in this way, and since his key to *Psychotria* uses this feature many specimens of *P. pubescens* from Cuba cannot be keyed here. As the stems increase in girth with age, the stipules may increase in diameter in several ways. Sometimes there is intercalary growth between the lobes, so that these are moved further apart, and the sheath remains in a continuous ring. Often, the sheath expands to a limited extent between the lobes, then tears partially or completely as the stem continues to grow. Occasionally, the sheath may simply tear as the stem expands, leaving two separate stipule lobes with no evidence of interpetiolar fusion. The variation in stipule morphology encountered in this species alone, or even on one branch of one individual of this species, demonstrates the source of some of the confusion which surrounds the identity of many species of *Psychotria*.

KEY TO *PSYCHOTRIA PUBESCENS* AND *P. HEBECLADA*

1. Inflorescence thyrsiform or racemiform, usually (0.6–)0.8–1.3 times as long as wide, with a well-developed central axis and the lateral branches (especially the middle and upper branches) more slender than the axis and held horizontally; calyx lobes lanceolate to ovate, (0.6–)0.8–2(–2.3) mm long, longer than the gland, somewhat foliaceous, usually shortly acuminate and reflexed apically; pubescence of the inflorescence hirsutulous or pilosulous, the hairs often somewhat crinkled or of irregular lengths, 0.1–0.9 mm long, the longest hairs usually about 0.3–0.7 mm long ... 1. *P. hebeclada*

1. Inflorescence corymbiform, usually 0.5–0.7 times as long as broad, with a central axis which is usually little stouter or more emphasized than the branches and the lateral branches spreading or ascending; calyx lobes broadly

triangular or slightly ovate, 0.3–1.1 mm long, as long as or usually shorter than the gland, hardly or usually never acuminate or reflexed apically; pubescence of the inflorescence puberulous or pilosulous, the hairs straight and of uniform lengths, 0.1–0.5 mm long, the longest hairs usually about 0.15–0.4 mm long .... 2. *P. pubescens*

1. **Psychotria hebeclada** DC., Prodr. 4: 513. 1830. TYPE: Mexico, not seen.

Psychotria justicioides Schldl., Linnaea 9: 596. 1834. TYPE: Mexico. Barranca de Tioselo, not seen. *Uragoga justicioides* Kuntze, Rev. Gen. 1: 300. 1891.
Psychotria molliramus Schumann & Krause, Bot. Jahrb. Syst. 40: 331. 1908. TYPE: Colombia. Prope las Juntas ad Rio d'Agua, Cauca, 200–500 m, *Lehmann 4667* (holotype, B, not seen; photograph NY!; isotype, K, not seen; photograph NY!). *Psychotria molliramus* Steyerm., Mem. New York Bot. Gard. 23: 529. 1972.

Herbs or more often shrubs 1–4(–8) m tall, erect or sometimes lax or scandent. *Stems* rounded, sparsely to somewhat densely puberulent or pilosulous with spreading hairs, generally glabrescent with age, with a fleshy section about 0.5–0.8 cm long usually present immediately below each node and generally constricted with drying. *Stipules* persistent, puberulent or pilosulous with spreading hairs, composed of a short sheath bearing two triangular lobes; sheath about 0.3–1 mm long, continuous around the stem or sometimes splitting interpetiolarly instead of expanding; lobes about 1–3.5 mm long, acute to aciculate at the apex. *Leaves* with membranous blades, these narrowly to widely elliptic or somewhat oblong, apically acuminate with an acumen about 0.5 cm long, basally acute to attenuate, (3.5–)7.5–17 cm long, (1–)2.5–8 cm wide, about 2–3.5 times as long as broad, glabrescent above with the costa and margins sparsely pilosulous or puberulent, glabrescent or sparsely puberulent below with the costa and sometimes the lateral veins spreading-pilosulous, with the lateral veins about 8–15 on each side of the midrib and broadly arching, with petioles (0.2–)0.5–1(–2.5) cm long and puberulent or pilosulous with spreading hairs. *Inflorescences* terminal, erect, usually pedunculate but rarely subsessile, the peduncle (0.5–)1–4.5 cm long, the panicle thyrsiform or racemiform, conic or sometimes somewhat trapezoidal, with a well-developed central axis and horizontally spreading lateral branches, 1.7–4.5 cm long, 1.5–5.5 cm wide, (0.6–)0.8–1.3 times as long as broad at the base, the peduncle, axis, branches, bracts, and pedicels green or more often purplish, sparsely or usually rather densely spreading-pilosulous or spreading-hirsutulous, the hairs 0.1–0.9 mm long, the longest usually about 0.3–0.7 mm long; bracts linear, often with ciliolate margins, 1.5–6 mm long, those immediately subtending flowers about 1.5–2.5 mm long. *Flowers* sessile or borne on pedicels to 5 mm long; *calyx* spreading-pilosulous or spreading-hirsutulous, the free portion cut into five lobes, these narrowly lanceolate or ovate or sometimes widely so, somewhat foliaceous, acuminate and usually recurved at the apex, (0.6–)0.8–2(–2.3) mm long, with the costa and two marginal veins prominent on the inner surface and the margin generally somewhat ciliate; *corolla* tubular, puberulous or very shortly pilosulous outside with spreading hairs, glabrous within except for a short-pilose ring at the level of the attachment of the filaments, white or sometimes tinged with green or rose, the tube about 3–4 mm long, the five lobes triangular, (1.2–)1.5–2 mm long and about half as wide as long at the base; *anthers* narrowly oblong, about 1.2–2 mm long, in the long-styled form included in the tube, in the short-styled form partially exserted; *styles* dimorphic, the short form extending to the level of the stamen attachment, the long form conspicuously exserted, both forms with a bilobed stigma and surrounded at the base by a gland or nectary about 0.5 mm long, this gland composed of two cycles, the outer one somewhat lobed and foliaceous, the inner bilobed or rather toroid and smooth and glandular; *fruit* elliptic, compressed-globose, didymous, angled when dry with five smooth, nearly plane faces on each half, about 3–5 mm long and wide, sparsely puberulent, maturing to blue-black; *seed* angled, with about 5 smooth planar faces and a longitudinal invagination on the inner face.

Moist or wet forests and edges, and along rivers; sea level to about 1,500 m, most often collected between 100 and 400 m. Flowering and fruiting throughout the year, and often concurrently on the same plant. Figure 1a–c.

Steyermark (1972) maintained *Psychotria molliramus* (Schumann & Krause) Steyerm. as a species separate from *P. hebeclada* primarily because of a unique, five-lobed foliaceous gland found at the base of the style. He placed this species in a monotypic series, *Mollirami* Steyerm., but suggested that because of this specialized structure *P. molliramus* may deserve recognition as a separate genus. He reported the geographic range of *P. molliramus* as including Costa Rica, Panama, Venezuela, Colombia, and Ecuador. According to Steyermark, *P. hebeclada* is found in Guatemala and southern Mexico, and has a solid, bilobed gland. However, examination of specimens from all of these areas, including specimens cited as *P. molliramus* by Steyermark (1972), suggests that there are difficulties with this distinction. The form of the gland is similar on all specimens examined, and consists of both an outer, rather foliaceous ring, which is usually lobed, and an inner, solid portion, which is often bilobed. Thus, Steyermark's description of the disk of *P. molliramus* as an "elevated, conical form ending in five, [sic] loose, erose or dentate lobules" was accurate, but incomplete, as was his description of the gland of *P. hebeclada* as a "bilobed disk." The other differences between these species that he lists, in inflorescence shape and size, morphology of the inflorescence bracts, and presence or absence of the constricted zone below the nodes, are not distinctive. The differences in inflorescence characters are not consistently correlated with each other or with any geographic distribution and represent the normal variation of these characters within the species. The presence of the constricted zone beneath each node on dried specimens is characteristic of the subgenus *Heteropsychotria* Steyerm.; these zones were seen on all sheets examined. Thus, *P. molliramus* cannot be maintained as a separate species.

Standley (1926) indicated that the descriptions of *Psychotria aureola* Bartling ex DC. and *P. bracteolata* Martius & Galeotti suggest that these species are "closely related" to *P. hebeclada*. Since no material has been seen, it is unclear whether these species are in fact synonymous with either *P. hebeclada* or *P. pubescens*. Judging from the description, *P. aureola* is certainly not synonymous with *P. hebeclada*; however, it may be a form of *P. pubescens*.

Dimorphic heterostyly has been noted often in species of *Psychotria*. Herbarium material suggests that this condition occurs in *P. hebeclada* but examination of living plants will be necessary for confirmation.

2. **Psychotria pubescens** Sw., Prodr. Veg. Ind. Occ. 44. 1788. TYPE: Jamaica. *Brown 161*, not seen. *Uragoga pubescens* Kuntze, Rev. Gen. 2: 962. 1891. *Myrstiphyllum pubescens* A. Hitchc., Annual Rep. Missouri Bot. Gard. 4: 95. 1893.

Psychotria horizontalis Swartz var. *cuspidata* DC., Prodr. 4: 515. 1830. TYPE: Santo Domingo. *Bertero*, not seen.

Psychotria scabriuscula Bartling ex DC., Prodr. 4: 513. 1830. TYPE: Mexico. Acapulco, not seen. *Uragoga scabriuscula* Kuntze, Rev. Gen. 2: 962. 1891.

Psychotria glauca Polak., Linnaea 41: 569. 1877. SYNTYPES: Costa Rica. San José, *Polakowsky 377 & 378*, not seen. *Uragoga glauca* Kuntze, Rev. Gen. 2: 960. 1891.

Shrubs 1.5–2.5(–6) m tall, erect. *Stems* rounded, sparsely or more often moderately to densely spreading-puberulent or spreading-pilosulous, occasionally glabrescent, with a fleshy section about 0.5–1 cm long usually present immediately below each node and generally constricted on dried specimens. *Stipules* persistent, often becoming indurate with age, puberulent or pilosulous with spreading hairs or sometimes glabrescent, variable in shape but usually composed of a short sheath bearing two triangular lobes, sheath to 1.2 mm long, continuous around the stem or sometimes splitting partially or completely to the base instead of expanding, lobes (1.1–)1.5–2.5(–4) mm long, acute or aciculate at the apex, sometimes fused into one entire or partially bifid lobe. *Leaves* with membranous blades, these narrowly to widely elliptic or somewhat oblong, apically acute or more commonly attenuate, (5–)8–13(–17) cm long, (1.2–)3–4.5(–6.5) cm wide, usually about (1.5–)2–3.3 times as long as wide, spreading-puberulous or spreading-pilosulous throughout or sometimes glabrescent, with lateral veins about (7–)8–13(–16) on each side of the midrib and arching, with petioles 0.2–2 cm long, puberulous or short-pilosulous with spreading hairs or sometimes glabrescent. *Inflorescences* terminal, erect, the peduncle (1–)2–3(–4) cm long, the panicle corymbiform, rather open and lax, the main axis not strongly developed and the lateral branches usually spreading to ascending or occasionally widely spreading, 1.5–7 cm long, 3–9.5 cm wide, usually about 0.5–0.7 times as long as wide (1.5–2 times as wide as long) at the base; peduncle, axis, branches, bracts, and pedicels often flushed with purple, spreading-puberulent or spreading pilosulous, usually densely so but rarely glabrescent, the hairs 0.1–0.5 mm long, the longest usually about 0.15–0.4 mm long; bracts triangular to lanceolate, with entire margins, 0.5–5 mm long, those immediately subtending the flowers about 0.5–1.5 mm long. *Flowers* usually sessile to subsessile or sometimes borne on pedicels to 5 mm long; *calyx* glabrescent or usually puberulous or pilosulous with spreading hairs, the free portion cut into five triangular or shortly ovate lobes, these apically acute or rarely shortly acuminate, 0.3–1.1 mm long, with the midvein sometimes visible but usually without apparent nerves; *corolla* tubular, puberulous or sometimes glabrous outside, glabrous within or often bearing a pilose ring at the level of the stamen attachment, white or more often yellowish white or yellow and sometimes tinged with green or rarely with pink, the tube about 3–4 mm long, the lobes 5, triangular, 1.6–2.1 mm long and about half as broad as long at the base; *anthers* narrowly oblong, 1.1–1.6 mm long, in the long-styled form included in the tube, in the short-styled form partially exserted; *styles* dimorphic, the short form extending to the level of the stamen attachment, the long form conspicuously exserted, with the stigma bilobed on both forms and both forms surrounded at the base by a gland or nectary about 0.5–1 mm long and composed of two cycles, the outer one somewhat lobed and foliaceous, the inner bilobed or rather toroid and glandular; *fruit* elliptic, compressed-globose, didymous, angled when dry with 5 smooth, somewhat plane faces on each half, about 3–5 mm long and wide, sparsely puberulent or glabrescent, maturing to blue-black or black; *seed* angled, with about 5 smooth planar faces and a longtudinal invagination on the inner face.

Moist or wet forests and edges, seasonally dry forests and edges, disturbed ground, and often on limestone slopes or pavement; sea level to about 1,500 m. Flowering and fruiting throughout the year, often concurrently on a single plant. Figure 1d–f.

This species also appears to be heterostylous, but again this must be confirmed with living material.

Psychotria pubescens is very common throughout most of its range, and it often grows in very accessible areas. Because of this a very large number of specimens of this species are available in most collections. This species is also rather nondescript, and it is often misidentified. It is commonly mistaken for other species of *Psychotria* and it is often found among unidentified specimens of Rubiaceae.

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ESTIMATION OF GENOME SIZE (C-VALUE) IN IRIDACEAE BY CYTOPHOTOMETRY[1]

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ABSTRACT

Nuclear genome sizes have been calculated for 19 genera and 30 species of Iridaceae using cytospectrophotometry. Mean extinction values for nuclei in squashes of actively growing root tips stained in Schiff's reagent were compared with a standard, maize, of known genome size, treated in the same way. Values range from lows of 1.1 to 4.9 pg DNA per nucleus in diploid species of subfamily Ixioideae to a high of 65.1 pg in *Iris histrio,* subfamily Iridoideae. Genome size in diploid Iridoideae ranges from a low in *Galaxia fugacissima* of 6.4 pg to the ten fold high observed in *I. histrio.* Results are, in general, consistent with what is known about cytology and phylogenetic relationships of the taxa studied. Polyploid species have close to twice the values obtained in closely related diploids, and allied species or genera have very similar genome sizes.

Iridaceae are a plant family of nearly worldwide distribution, comprising some 1,500 species in about 85 genera usually assigned to two or three subfamilies, Iridoideae, from which Sisyrinchioideae may not be separable, and Ixioideae. Species are concentrated in Africa where more than half the genera and species occur, and in South and Central America including Mexico. The systematics of the family is comparatively well known, particularly in the Old World. Chromosome cytology is also well known, and unusually varied for a family of this size. Chromosome size ranges from very small in some Australasian and South American genera to very large in Old World genera such as *Iris, Moraea,* and their allies, while base numbers for genera range from $x = 16$ to 6. Chromosome numbers and karyotypes are known for most genera and for many species in most of these but there have not been until now any satisfactory measurements of absolute size of the genome of various genera and species, i.e., the amount of DNA per cell or C-value. In this paper we present measurements of nuclear genome size for a wide range of species and genera of Iridaceae following a standard cytospectrophotometric method for estimating DNA content. Genome sizes for the 30 species in 19 genera studied here have been calculated by comparison against a standard, *Zea mays,* of known genome size, 6.3 pg (Hake & Walbot, 1980).

MATERIALS AND METHODS

Plants studied were all of wild origin, the collection data and voucher information for which is presented in Table 1. Measurements were made on nuclei in root tip apices fixed in Carnoy's 3:1 absolute ethanol:glacial acetic acid and stained in Schiff's reagent. Root tips of the maize standard were fixed and stained at the same time and in the same way as the species of Iridaceae. Cytophotometric determinations were made using a Zeiss Universal microscope equipped with a Zeiss Type 03 Microphotometer with an automatic scanning stage. A planapochromat oil immersion objective NA 1.32 × 100 was used for all measurements.

Approximately 20 measurements were made for each species. Mean relative values of the amount of DNA per cell were calculated for each species by obtaining the average of the lower readings (2C-values) and half the high readings (4C-values). Low readings represent cells in a post mitotic phase before the onset of duplication of the genome and the high readings represent cells that have completed the duplication of the

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TABLE 1. Voucher information for the species used in this study. All specimens are housed at Missouri Botanical Garden (MO).

Species	Collection Data
Subfamily Iridoideae (Including Sisyrinchioideae)	
Old World Taxa	
Iris histrio L.	Israel, Golan Heights, *Goldblatt s.n.*, no voucher
Dietes grandiflora N. E. Br.	S. Africa, Cape, Riebeek East, *Bayliss 7014*
Galaxia fugacissima (L. f.) Druce	S. Africa, Cape, Middleton, Caledon, *Goldblatt 2631*
Moraea anomala Lewis	S. Africa, Cape, Elim, *Goldblatt 2616*
M. inconspicua Goldbl.	S. Africa, Cape, Botrivier-Hawston, *Goldblatt 3300*
M. ciliata (L. f.) Ker	S. Africa, Cape, Wolseley, *Goldblatt s.n.*, no voucher
M. fugax (de la Roche) Jacq.	
population 1	S. Africa, Cape, Klawer, *Goldblatt 5778*
population 2	S. Africa, Cape, Koeberg, *Goldblatt 4080*
M. atropunctata Goldbl.	S. Africa, Cape, Caledon distr., *Goldblatt 5635*
M. calcicola Goldbl.	S. Africa, Cape, Saldanha hills, *Goldblatt 4118*
M. tulbaghensis L. Bol.	S. Africa, Cape, Gouda, *Goldblatt s.n.*, no voucher
M. villosa (Ker) Ker	S. Africa, Cape, below Gydo Pass, *Goldblatt 2594*
M. unguiculata Ker	S. Africa, Cape, Steinkopf, *Goldblatt 2777*
M. bipartita L. Bol.	S. Africa, Cape, near Hankey, *Goldblatt 2076*
Hexaglottis namaquana Goldbl. ined.	S. Africa, Cape, Spektakelberg, Namaqualand, *Goldblatt 3059*
Homeria bifida L. Bol.	S. Africa, Cape, Rebunie, Calvinia, *Goldblatt 3894*
H. pendula Goldbl.	S. Africa, Cape, Kamiesberg, *Goldblatt 4306*
H. flaccida Sweet	S. Africa, Cape, Twenty Four Rivers, *Goldblatt 3924*
Sessilistigma radians Goldbl. ined.	S. Africa, Cape, near Macgregor, *Goldblatt 5903*
Gynandriris setifolia (L. f.) Foster	S. Africa, Cape, near Matjesfontein, *Goldblatt 3215*
Roggeveldia fistulosa Goldbl.	S. Africa, Cape, Roggeveld Escarpment, *Goldblatt 4163*
New World Taxa	
Cipura paludosa Aubl.	Nicaragua, *Henrich 143*
Sisyrinchium convolutum Nocca	Nicaragua, *Henrich 152*
Subfamily Ixioideae	
Anomatheca viridis (Ait.) Goldbl.	S. Africa, Cape, Olifantskop, Langebaan, *Goldblatt 2335*
Freesia alba (G. L. Meyer) Gumbleton	S. Africa, Cape, Sandbaai, Hermanus, *Goldblatt 5293*
Watsonia brevifolia Ker	S. Africa, Cape, near Albertinia, *Goldblatt 4855*
Pillansia templemanii L. Bol.	S. Africa, Cape, Arieskraal, Caledon dist., *Powrie s.n.*
Lapeirousia verecunda Goldbl.	S. Africa, Cape, Spektakelberg, Namaqualand, *Goldblatt 2789*
Gladiolus virescens Thunb.	S. Africa, Cape, near Botrivier, *Goldblatt 5641*
Hesperantha bachmannii Baker	S. Africa, Cape, Wildepaardehoek, Namaqualand, *Goldblatt 5754*
Babiana virginea Goldbl.	S. Africa, Cape, Roggeveld, *Goldblatt s.n.*

genome but have not begun to divide. The high readings were consistently approximately twice the readings in the low range. Intermediate readings were disregarded. In all samples studied, readings showed a two-fold low to high range. Difficulty was experienced in obtaining measurements in Ixioideae. The nuclei were weakly stained and contrasted poorly with the background cytoplasm. Genome size in this subfamily is undoubtedly very low in comparison to maize and to the other species of Iridaceae studied. The percent error in our measurements for this group is very high, but the results are, nevertheless, of value for comparison with other Iridaceae.

RESULTS AND DISCUSSION

The results of our measurements of genome size relative to the maize standard are reported in Table 2, along with the standard deviation of the measurement. The haploid and basic chromosome number of each species, also included in the table, are taken from previously published accounts (Goldblatt, 1971, 1976, 1979, 1980) or from papers in preparation. This represents the only extensive set of measurements in Iridaceae of nuclear genome size, which, in non green cells, can be regarded as essentially equivalent to the total cellular DNA content. The only previous determinations of genome size in Iridaceae, according to Bennett's (1972) review of amounts of nuclear DNA in angiosperms, are two reports for *Gladiolus*. One, by Sparrow et al. (1965), for a cultivar, *Gladiolus* 'Friendship,' is an estimated value of 13.5 pg. In the other, Baetke et al. (1967) obtained 6 pg for *Gladiolus* 'Mansoor.' In both cases the material studied was reported to be tetraploid. This second report is in fairly close agreement with our own estimation of 3.2 pg for a diploid species of this genus. The much higher figure reported by Sparrow et al. must apparently be disregarded. The relatively low genome sizes established for *Gladiolus* seem characteristic for subfamily Ixioideae, in which a range of values from 1.1 to 4.9 pg have been determined for seven diploid species, each a different genus. The genome size in the tetraploid *Pillansia*, 5.4 pg, is also consistent with the range for Ixioideae. These results are consistent with karyotypic observations for Ixioideae (Goldblatt, 1971), in which small chromosomes are characteristic and there seems no substantial variation in the total amount of chromosome material, as estimated by linear chromosome measurement, in diploid members of a range of genera of this subfamily, from *Babiana* with a low $x = 7$ to *Gladiolus* with $x = 15$.

Subfamily Iridoideae provides a sharp contrast. Genome sizes range from 6.4 pg in *Galaxia fugacissima* to a high of 36.4 pg in *Moraea calcicola*, among diploid species in Southern Africa. A 65.1 pg genome was found in the Middle Eastern *Iris histrio*, a species possibly of tetraploid origin although it is not polyploid compared with closely related species. The figures reflect the large difference in total chromosome size of Old World Iridoideae vs. Ixioideae, pointed out by Goldblatt (1971). The results also seem to confirm Goldblatt's (1976) contention that cytological evolution in *Moraea*, diploid species of which have haploid numbers of $n = 10, 9, 8, 7, 6$, and 5, proceeded from a basic chromosome number of $x = 10$ to a derived $x = 5$ by aneuploid decrease. Representatives of the three primitive subgenera of *Moraea*, *M. ciliata* (subgenus *Moraea*), *M. inconspicua* (subgenus *Visciramosa*), and *M. anomala* (subgenus *Monocephalae*), all $x = 10$, have genome sizes of 22 to 23 pg. Species of the derived subgenus *Vieusseuxia*, all $x = 6$, have genomes ranging from 23.4 pg in *M. bipartita* to 33.1 in *M. atropunctata* and 36.4 pg in *M. calcicola*. Two tetraploid species of *Moraea*, *M. villosa*, and *M. tulbaghensis*, have genomes of 72.4 pg of DNA, a value remarkably close to twice the 36.4 pg value obtained for the nearly allied *M. calcicola*.

There is some evidence in *Moraea* subgenus *Vieusseuxia* of the C-value paradox (Walbot & Goldberg, 1979). Related species of the same subgenus and section, and with similar karyotypes have unexpected differences in genome size (Table 2). The difference between the genome size of *M. unguiculata* and either *M. atropunctata* or *M. calcicola* is of the order of 50%. In genera allied to *Moraea* such as *Homeria* this paradox is also evident. In *Homeria*, most species of which have a basic $x = 6$ and very similar karyotype, *H. pendula* has a genome size of 22.5 pg, while *H. bifida* has 29.2 pg and the tetraploid *H. flaccida*, 41.2 pg. *Sessilistigma*, an undescribed monotypic genus closely related to *Homeria*, has a genome size of 31.6 pg, a figure consistent with the range found here in *Homeria*.

Hexaglottis, a genus also probably allied to *Homeria* has a genome size of 20.6 pg. This is low in comparison with *Homeria* but consistent with cytological observations which indicate a chromosome complement very similar, but slightly smaller than in *Homeria*. In examples of two other genera of Iridoideae, *Gynandriris* has a genome size of 24.1 pg, and *Roggeveldia* has 16.5 pg. Of the species studied here, these two genera are probably most closely related to *Moraea bipartita*, the genome size of which is 23.4 pg. The genome size data tend to support the hypothesis that there is a reasonably close relationship between *M. bipartita* and *Gynandriris*, their genomes being very similar in size. *Roggeveldia*, which seems related to this group (Goldblatt, 1979), presumably has lost a substantial amount of DNA in the course of its evolution if its relationships are, in fact, with these species.

Of the two New World taxa examined, *Sisyrinchium convolutum* (an octoploid with $n = 36$) has a genome size of 10.9 pg and *Cipura paludosa* (a tetraploid form with $n = 14$) has 19.5 pg. Basic genome size in *Sisyrinchium* would accordingly be of the order of 2.7 pg. This is comparable with Ixioideae rather than with Iridoideae, to which *Sisyrinchium* is usually allied. *Cipura* on the other hand has a basic genome size of the order of

TABLE 2. Mean genome size (C-value) for 30 species of Iridaceae with standard deviation (s.d.), haploid chromosome number (*n*) and basic chromosome number (*x*), arranged by subfamily.

Species	C-value	s.d.	*n*	*x*
SUBFAMILY IRIDOIDEAE (Including SISYRINCHIOIDEAE)				
OLD WORLD TAXA				
Iris histrio L.	65.1	±1.6	10	10
Dietes grandiflora N. E. Br.	13.5	0.2	10	10
Galaxia fugacissima (L. f.) Druce	6.4	0.8	9	9
Moraea anomala Lewis	22.0	1.3	10	10
M. inconspicua Goldbl.	23.0	1.3	10	10
M. ciliata (L. f.) Ker	22.7	0.9	10	10
M. fugax (de la Roche) Jacq.				
population 1	19.9	1.2	6	10
population 2	19.9	0.7	6	10
M. atropunctata Goldbl.	33.1	1.9	6	6
M. calcicola Goldbl.	36.4	2.5	6	6
M. tulbaghensis L. Bol.	72.4	3.4	12	6
M. villosa (Ker) Ker	72.4	1.3	12	6
M. unguiculata Ker	26.2	3.4	6	6
M. bipartita L. Bol.	23.4	0.6	6	6
Gynandriris setifolia (L. f.) Foster	24.1	1.2	6	6
Roggeveldia fistulosa Goldbl.	16.5	0.3	6	6
Hexaglottis namaquana Goldbl. ined.	20.6	0.7	6	6
Homeria bifida L. Bol.	29.2	1.7	6	6
H. pendula Goldbl.	22.5	1.6	6	6
H. flaccida Sweet	41.2	2.5	12	6
Sessilistigma radians Goldbl. ined.	31.6	1.9	6	6
NEW WORLD TAXA				
Cipura paludosa Aubl.	19.5	1.4	14	7
Sisyrinchium convolutum Nocca	10.9	0.6	36	9
SUBFAMILY IXIOIDEAE				
Anomatheca viridis (Ait.) Goldbl.	1.9	0.9	11	11
Freesia alba (G. L. Meyer) Gumbleton	3.7	0.3	11	11
Watsonia brevifolia Ker	1.6	0.5	9	9
Pillansia templemanii L. Bol.	5.4	2.2	20	10
Lapeirousia verecunda Goldbl.	4.9	0.5	8	10
Gladiolus virescens Thunb.	3.2	0.3	15	15
Hesperantha bachmannii Baker	1.1	0.3	13	13
Babiana virginea Goldbl.	3.5	0.4	7	7

9.8 pg, much larger than *Sisyrinchium,* and a difference clearly reflected in the karyology (Goldblatt, 1981). The genome size accords well with the Old World Iridoideae, although it is somewhat on the small side for the subfamily, and there is no doubt that *Cipura* is a member of Iridoideae.

The reasons for the often large differences in genome size among genera and species of Iridaceae are obscure. All members of the family are, with minor exceptions, long lived, geophytic perennials so that differences in life cycle (Bennett, 1972) cannot be used to explain genome size differences. In particular, the Old World taxa studied here all have a similar life cycle and similar environmental and edaphic requirements. The reasons for the primary difference in the genome size between Iridoideae and Ixioideae thus appear rooted in the evolutionary history of these subfamilies. The secondary differences within Iridoideae, between closely allied genera and within genera, apart from polyploidy, are equally difficult to explain and we can offer no reasonable explanation for the genomic differences in the taxa studied here. It is clear that if the primitive genus *Dietes* (Goldblatt, 1981) is regarded as having close to the basic genome for Iridoideae, then trends for both a decrease (in *Galaxia*) or an increase (in *Moraea, Homeria,* etc.) in genome size have taken place during the evolution of the subfamily.

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A SURVEY OF SEED SURFACE MORPHOLOGY IN *HESPERANTHA* (IRIDACEAE)[1]

WARREN L. WAGNER[2] AND PETER GOLDBLATT[3]

ABSTRACT

Seeds of a range of species of *Hesperantha* were examined with light and scanning electron microscope (SEM) and compared with three species of the most closely related genus, *Geissorhiza.* A turbinate to globose shape with a persistent funicle and a testa of uncontorted epidermal cells with smooth surfaces is apparently the basic seed type. Modifications of the basic type include increasing compression and a triangular or more or less irregular shape, sometimes accompanied by wrinkling and crumpling of the epidermal cells, and the development of dual tails and wings. This is most marked within *Hesperantha* sect. *Radiata* (but not *H. marlothii* of the section), where these modifications are accompanied by reduction in seed size. Wing-like structures are also developed within sections *Hesperantha* (*H. spicata* and *H. cedarmontana*) and *Concentrica* (*H. fibrosa*) but in both of these groups without accompanying crumpling of the epidermal cells, which coincidentally have developed rough surfaces.

Hesperantha Ker is a genus of some 55 species of corm bearing perennials of Iridaceae subfamily Ixioideae. It is centered in Southern Africa, but a few species occur in the montane areas of tropical Africa, extending as far north as Cameroon and Ethiopia. The genus has recently been revised for the winter rainfall area of South Africa by Goldblatt (1982, 1984) and is being studied in eastern Southern Africa by Hilliard and Burtt (1979, 1982). This study of seed morphology in *Hesperantha* was made in conjunction with the revisionary work, now completed or in progress.

Seed morphology of Iridaceae is in general poorly known and thus seldom has been of taxonomic value below the generic level. Differences in seeds between genera are, however, sometimes striking and may provide important generic characteristics. Good examples are the circumferentially winged seeds of *Gladiolus* and its close allies, the two winged seeds of *Watsonia,* and the inflated seeds with spongy testa of *Tritoniopsis* and *Anapalina.* This study was thus undertaken in the hope that some characteristics of taxonomic use would be found in *Hesperantha* at species and generic level. Seventeen species of *Hesperantha,* including examples from all four sections (Goldblatt, 1982), as well as three species of the related genus *Geissorhiza* Ker were assembled for light and scanning electron microscope examination. This represents a large sample for a monocot genus such as *Hesperantha,* in which seeds are typically produced after flowering and are seldom collected and consequently poorly known.

Seeds of *Hesperantha* have not previously been studied in detail, but SEM studies of seed morphology have been made in a few other genera of subfamily Ixioideae, in conjunction with the systematics notably in *Syringodea* (de Vos, 1974) and in *Crocus* (Baytop et al., 1975; Mathew, 1976). In *Crocus* some interesting seed surface features including trichomes and papillae have been found to be of taxonomic significance. In systematic studies of other genera of Ixioideae, seed morphology is occasionally of limited taxonomic use, as in *Tritonia* (de Vos, 1982: 113) where one or two species stand out from their allies in having unusual seed modifications.

The extensive study of Huber (1969) on the seed morphology of the monocotyledons deals largely with internal seed structure, and not at all with detailed surface microstructure such as is observed with the SEM. His observations on *Hesperantha* are very general and relate primarily to tribal and familial classification.

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MATERIALS AND METHODS

The seeds of 16 species of *Hesperantha* (about a third of the genus) were examined by scanning electron microscopy (SEM). Sufficient viable seeds were studied to document the variation present within each population. Four to ten seeds were generally adequate. Three additional species of the closely related genus *Geissorhiza* were also examined as out-groups in the hope that this would aid in the establishment of character polarity (Table 1). One population only of all species except *H. marlothii* was examined with the SEM. The variation in seed size in *H. marlothii* was such that two populations were studied, covering the extremes encountered in the species. Samples of several populations of *H. falcata* and *H. radiata* were also examined under the light microscope to determine whether material studied was typical of the species. In all cases they matched closely the samples studied. One more species, *H. pauciflora* (sect. *Hesperantha*) was also examined under the light microscope and since it had seeds exactly like those of *H. falcata* (also sect. *Hesperantha*), it was not examined further.

The number of populations examined may appear to be too small to gauge the variation within species but as indicated in the introduction, seed samples are difficult to obtain in *Hesperantha* in which plants are seldom collected in fruit. The material studied here therefore represents an unusually large assemblage. Where more than one population was available, as in *H. falcata* and *H. radiata,* the seed was examined with the light microscope and found to match the seed of the population studied with the SEM. Thus as far as it is possible to estimate, the single populations studied appear to be representative of the species. Several of the species examined (*H. elsiae, H. purpurea, H. brevifolia, H. cedarmontana*) are known from one or very few populations and are so restricted in their distributions that the material studied here represents a good sampling of the species. Among the widespread species, several populations were checked in *H. falcata* and *H. radiata* while only single samples were available in *H. bachmannii* and *H. pilosa.*

Viable seeds were attached with water soluble white glue to aluminum stubs, coated with 500–700 Å of gold in a sputter coater, and examined in a Hitachi S-450 SEM at 15 kV and 60–80 μA. Photomicrographs were made with Type 55 P/N Polaroid film. Contact prints were made on Illford No. 2 paper. Surface features are presented at two magnitudes of magnification: 35×–90× to show overall seed shape and surface topography, and 1,000× to resolve the microsculpture of the epidermal cell surface.

DESCRIPTION OF SEED FEATURES

The variation in the seeds of *Hesperantha* species is often limited to relatively minor modifications that produce large differences in seed shape, sometimes even within one capsule. There are, however, certain patterns of variation that appear, at least from the small samples available, to be characteristic of particular species. The variation within *Hesperantha* as well as that found in a sample of three species of the closely related genus *Geissorhiza* is presented in Figures 1–29. Only 13 of the 16 species of *Hesperantha* examined are illustrated. The additional species studied add no significant information to the observed pattern of variation. The variation is described in the following pages in sections dealing with shape, size, color, surface morphology, and microsculpturing.

Shape. The basic shape of *Hesperantha* seeds is turbinate to turbinate-globose. The embryo containing portion is globose to ovoid and this is modified to a turbinate shape by the persistent funiculus present on the seeds of many of the species (e.g., Figs. 1, 3, 5, 8). The same basic shape is evident in *Geissorhiza* (Figs. 16, 17). The more regular globose shape, illustrated here by *H. erecta* (sect. *Concentrica*) and *H. falcata* and *H. luticola* (both sect. *Hesperantha*) (Figs. 1, 5, 8), occurs in species of all sections of *Hesperantha* except sect. *Radiata,* as well as in *Geissorhiza* (*G. humilis*). The seed is more abruptly constricted to the persistent funiculus in these species.

The basic turbinate to globose shape is modified in a number of the species. The modifications can be grouped into three different types. An irregularly wrinkled surface occurs in several species of *Hesperantha* distributed in several sections (e.g., *H. bachmannii,* Fig. 4; *H. muirii,* Fig. 13) and in *Geissorhiza burchellii* (Fig. 18).

In contrast, seeds with irregular shape, a strongly wrinkled or crumpled surface coupled with the presence of two tails (one is the funiculus), and/or longitudinal wings characterize four of the five species of sect. *Radiata*; *H. muirii, H. elsiae* (Fig. 14), *H. radiata* (Fig. 11), and *H. brevifolia* (Fig. 12). The latter species appears to be the most specialized in this respect. These fea-

TABLE 1. Voucher information for the species of *Hesperantha* and *Geissorhiza* studied here. Species of *Hesperantha* are arranged taxonomically according to the sectional classification proposed by Goldblatt (1982). All collections are from the Cape Province, South Africa.

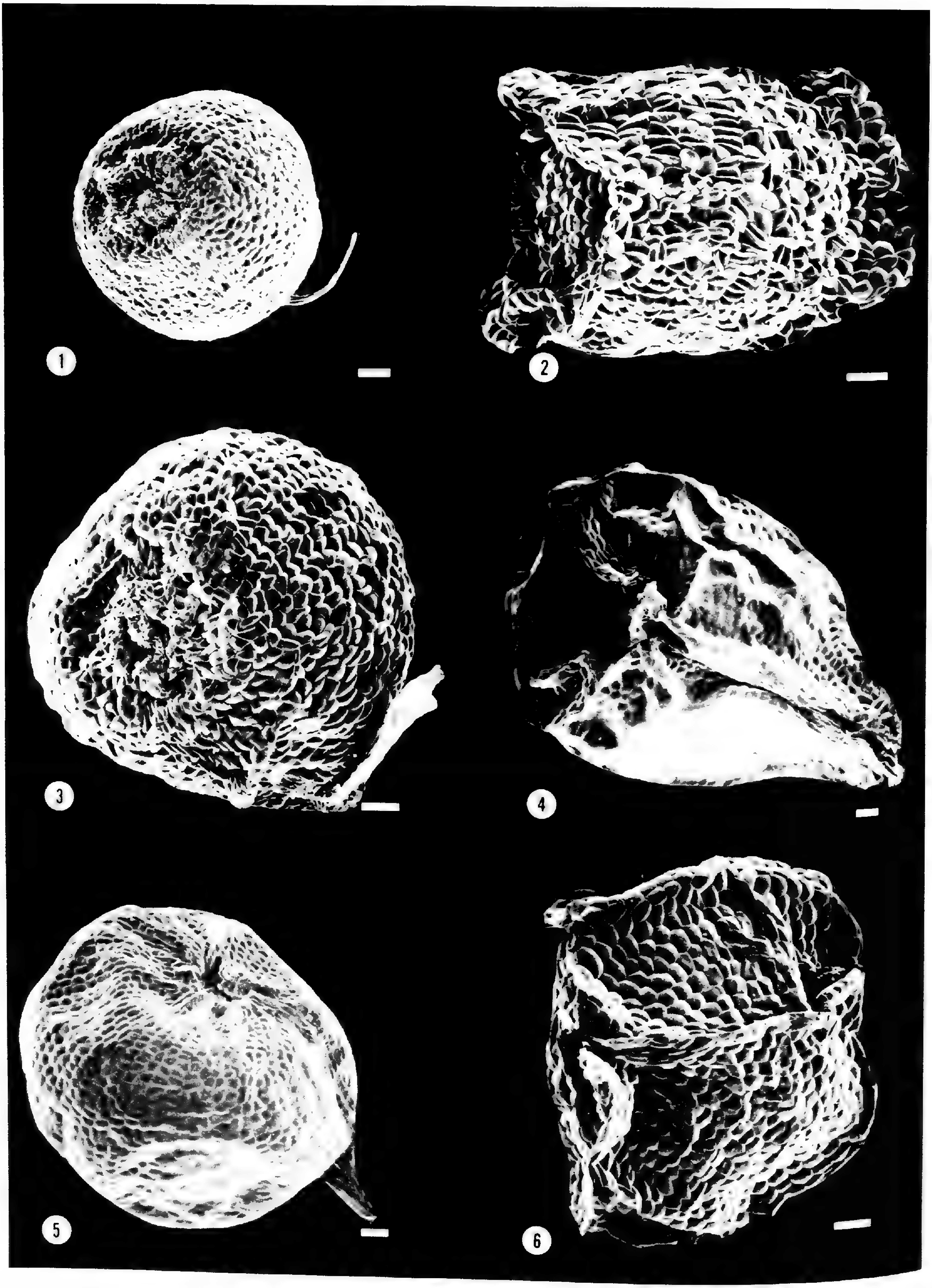
Species	Collection Data
	Hesperantha
	Sect. *Concentrica*
H. erecta (Bak.) Benth. ex Bak.	Saldanha distr., Donkergat, Posberg, *Goldblatt 4095* (MO).
H. fibrosa Bak.	Commonage S of Caledon, *Goldblatt 5899* (MO).
H. flexuosa Klatt	Wildepaardehoek Pass, *Goldblatt 5755* (MO).
H. montigena Goldbl.	Worcester distr., Mt. Brodie, *Esterhuysen 35307* (MO).
H. pilosa (L. f.) Ker	Caledon Zwartberg, *Goldblatt s.n.*, no voucher.
	Sect. *Imbricata*
H. bachmannii Bak.	N of Hankey, *Goldblatt 4937* (MO).
H. purpurea Goldbl.	Perdekraal, Calvinia distr., *Goldblatt 6246* (MO).
	Sect. *Radiata*
H. brevifolia Goldbl.	Piketberg, Zebrakop, *Esterhuysen 35320* (MO).
H. elsiae Goldbl.	Cedarberg, top of Krom River Kloof, *Goldblatt 5331* (MO).
H. marlothii Foster	Calvinia–Middelpos Rd. near Blomfontein, *Goldblatt 5813* (MO)—population 1; Nieuwoudtville escarpment, *Goldblatt 5835A* (MO)—population 2.
H. muirii (L. Bol.) Lewis	Hills W of Riversdale, *Goldblatt 5437* (MO).
H. radiata (Jacq.) Ker	N end of Cold Bokkeveld, *Goldblatt 5343* (MO).
	Sect. *Hesperantha*
H. falcata (L. f.) Ker	Bulshoek, Olifants R. Valley, *Goldblatt s.n.*, no voucher.
H. cedarmontana Goldbl.	Cedarberg, Middelberg Plateau, *Goldblatt 5130* (MO).
H. pauciflora Lewis	Kamiesberg, Welkom, *Goldblatt s.n.*, no voucher.
H. luticola Goldbl.	Calvinia–Middelpos Rd. near Blomfontein, *Goldblatt 5814* (MO).
H. spicata subsp. *graminifolia* (Sweet) Goldbl.	Cape Peninsula, near Cape Pt. Reserve, *Goldblatt 5263* (MO).
	Geissorhiza
G. burchellii Foster	Langeberg near Swellendam, *Esterhuysen 35604* (MO).
G. humilis (Thunb.) Ker	Cape Peninsula, near Cape Pt. Reserve, *Goldblatt 5263* (MO).
G. heterostyla L. Bol.	Near Humansdorp, *Goldblatt 6211* (MO).

tures are not present elsewhere in the genus. They do not, however, characterize all species of sect. *Radiata*. Population 2 of *Hesperantha marlothii* (Fig. 5) has the generalized turbinate shaped seed that is characteristic of the genus while the other population of *H. marlothii* studied has seed of a nearly pyramidal shape (Fig. 10). This is probably linked to the large seed size in this population and is presumably caused by the pressure of seed packing in the capsules. Dual tails and wings are not always present on all seeds examined (e.g., *H. elsiae*, Figs. 14, 15), but at least most seeds in each sample have these features. Again, this lack of uniformity is presumably due to the effects of seed packing.

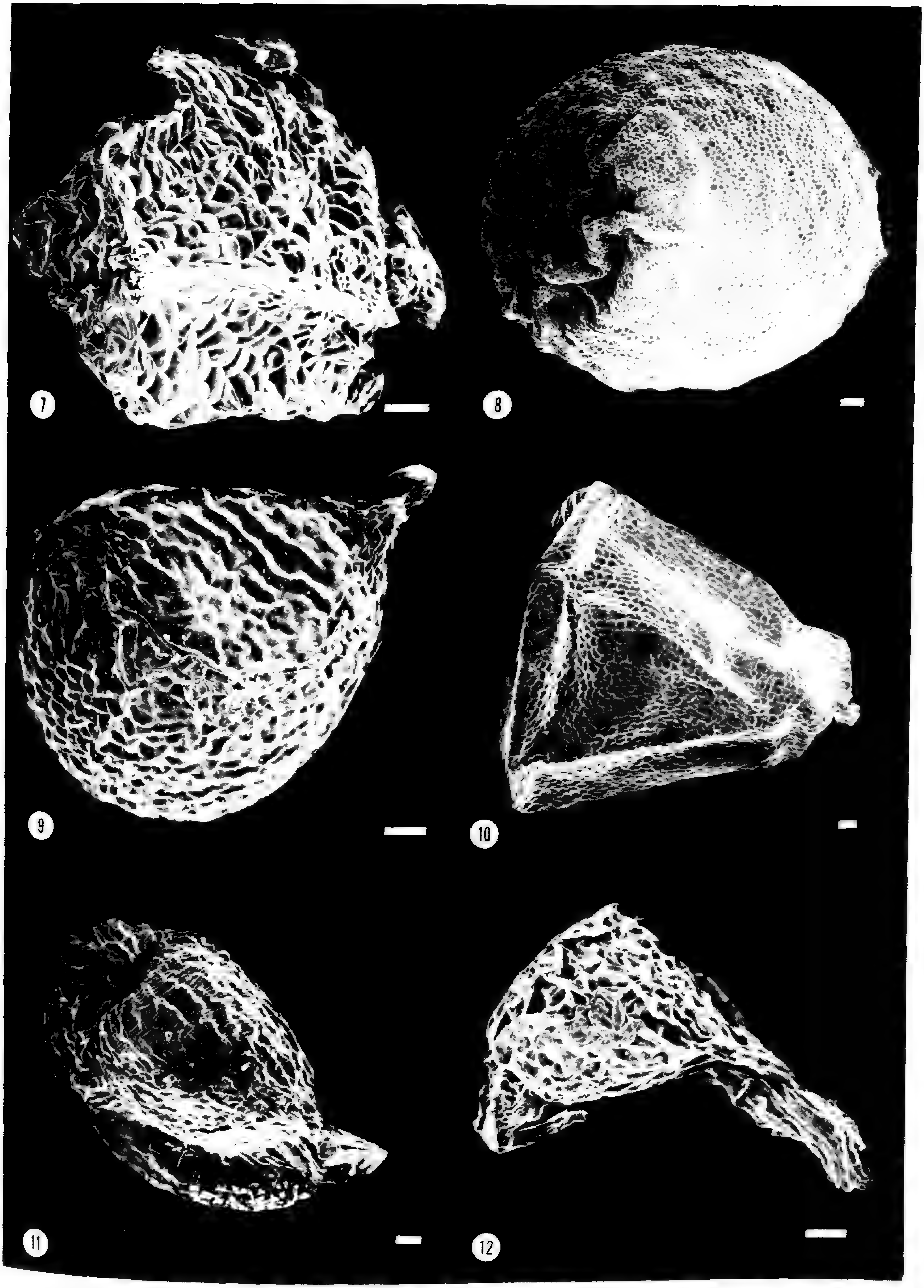
Finally, *Hesperantha fibrosa* (sect. *Concentrica*) (Fig. 2) and two species of sect. *Hesperantha*, *H. spicata* (Fig. 6) and *H. cedarmontana* (Fig. 7), have ellipsoid to irregularly shaped seeds with narrow longitudinal and apical wings and little or no contortion of the epidermal cells.

At the distal end of the raphe of many species of *Hesperantha* there is a porelike depression of the testa (Figs. 1, 3, 5). This is sometimes less conspicuous as in *H. marlothii* (Fig. 9) or very prominent as in *H. luticola* (Fig. 8). Several species have a broader depression at the distal end (Figs. 2, 4, 11, 13, 14) or the seeds are merely truncate (Figs. 6, 7, 10).

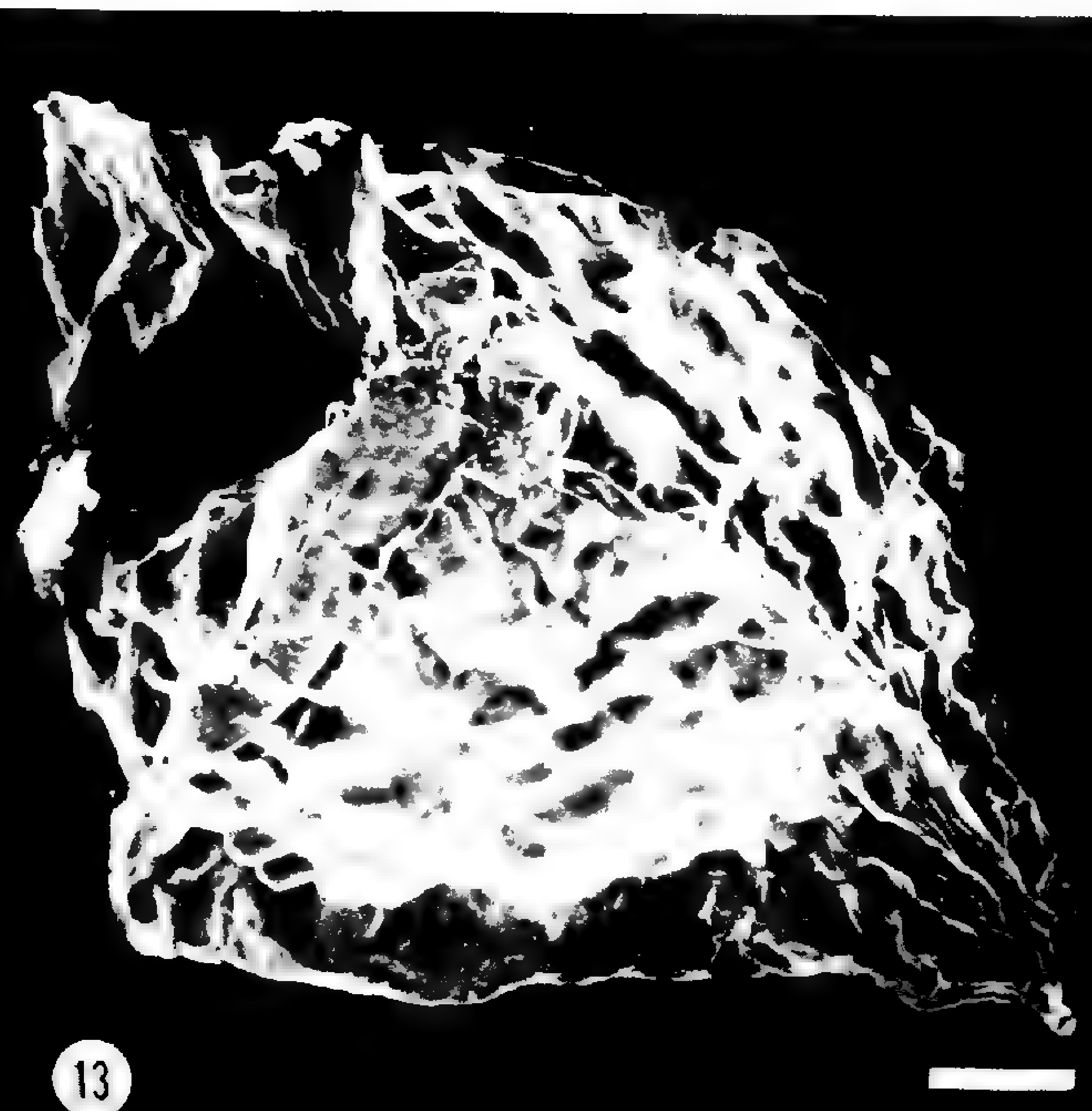
The raphe is often conspicuous and appears as



FIGURES 1–6. Scanning electron micrographs of seeds of *Hesperantha* species (Figs. 1, 2, sect. *Concentrica*; 3, 4, sect. *Imbricata*; 5, 6, sect. *Hesperantha*).—1. *H. erecta*.—2. *H. fibrosa*.—3. *H. purpurea*.—4. *H. bachmannii*.—5. *H. falcata*.—6. *H. spicata*. White bar = 100 μm.



FIGURES 7–12. Scanning electron micrographs of seeds of species of *Hesperantha* (Figs. 7, 8, sect. *Hesperantha*; 9–12, sect. *Radiata*).—7. *H. cedarmontana*.—8. *H. luticola*.—9. *H. marlothii* (population 1).—10. *H. marlothii* (population 2).—11. *H. radiata*.—12. *H. brevifolia*. White bar = 100 μm.



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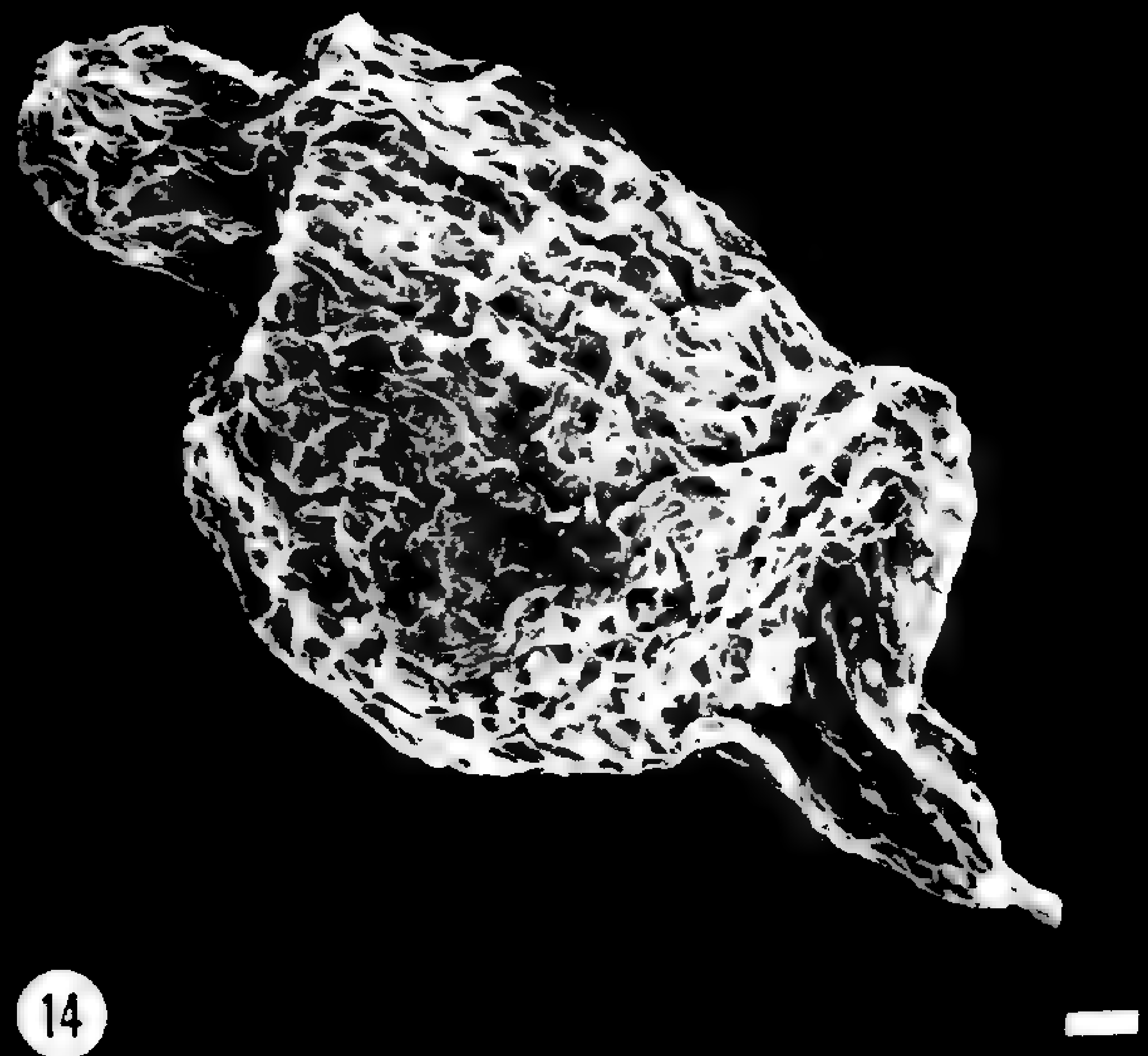

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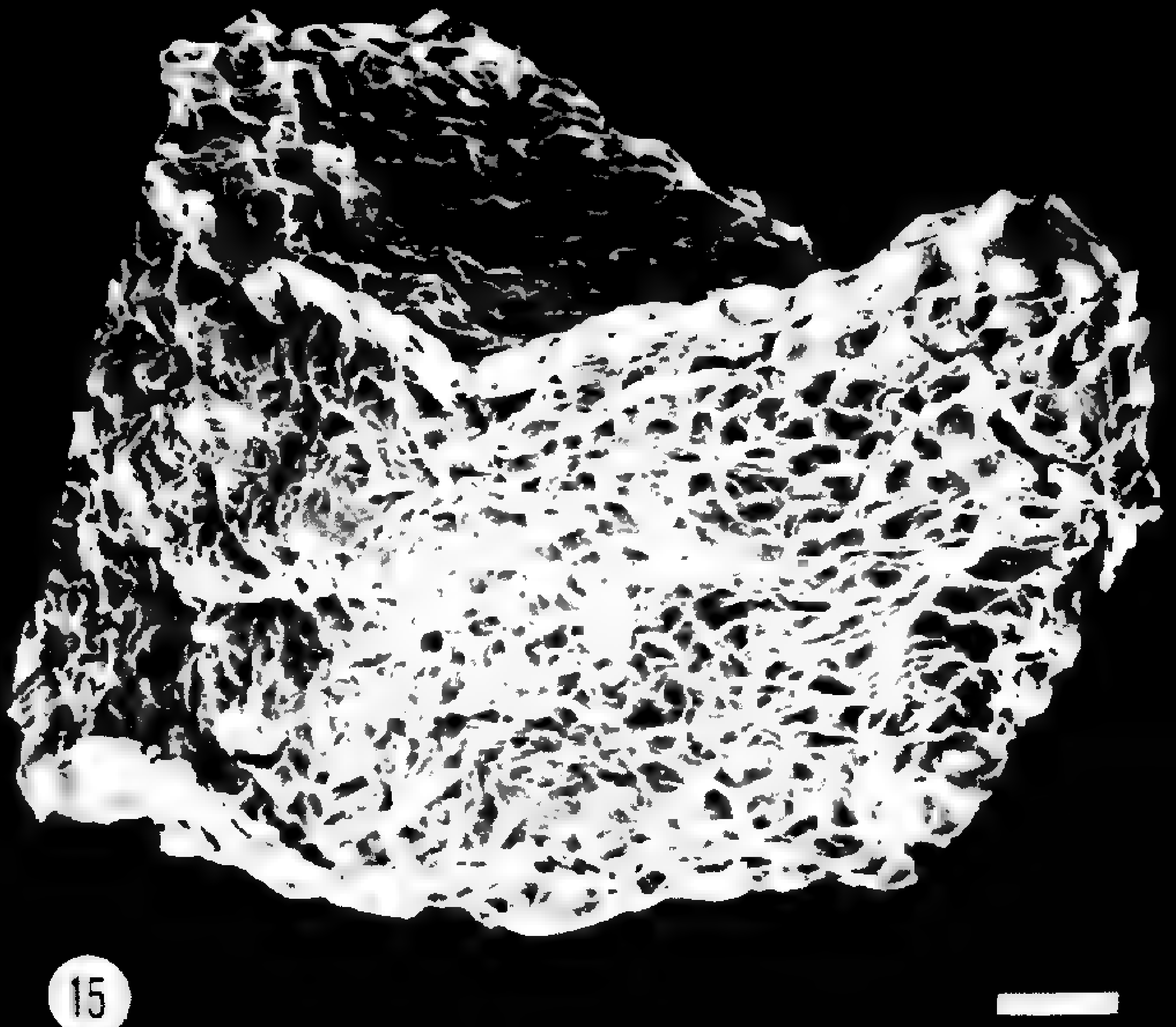

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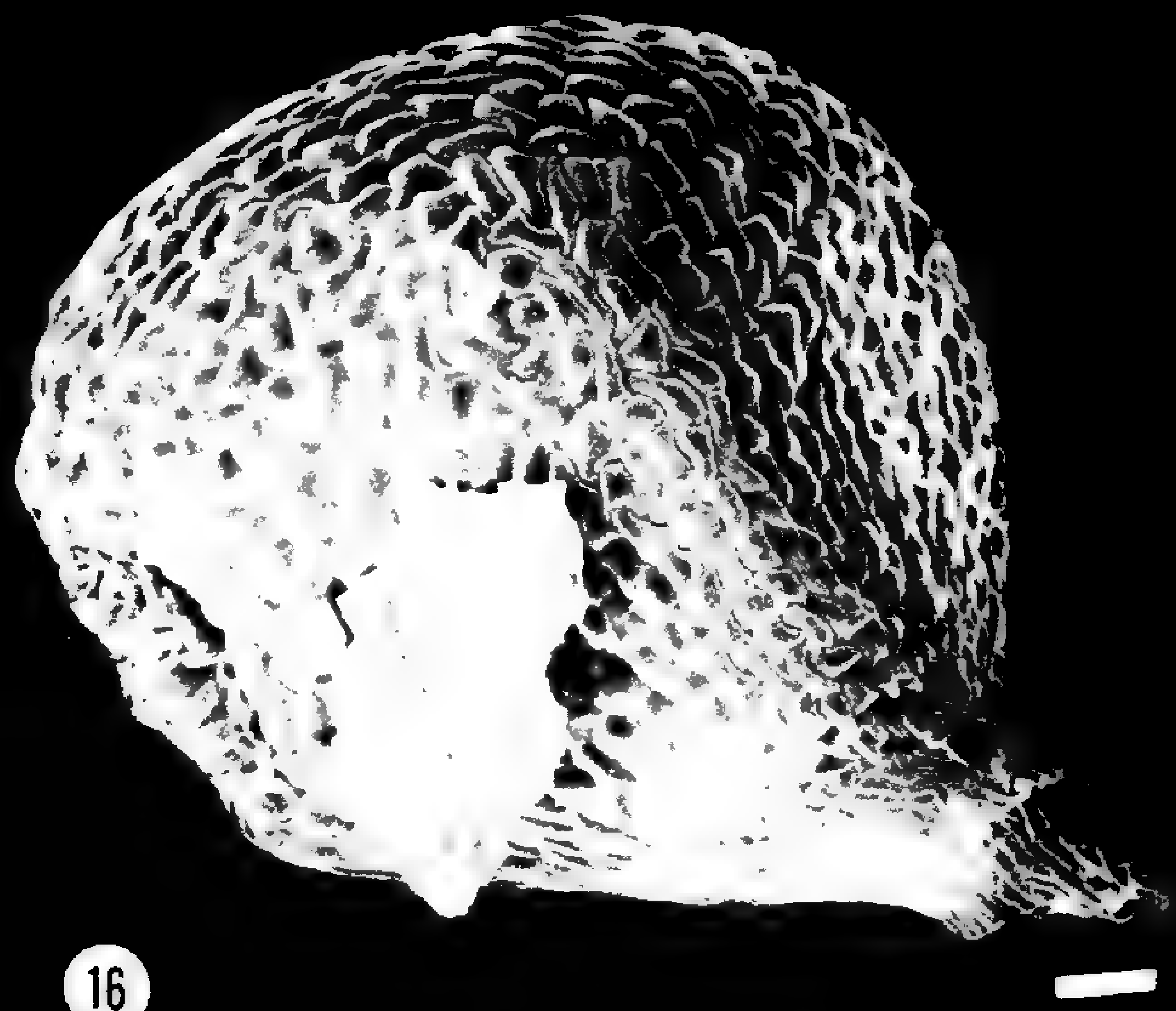

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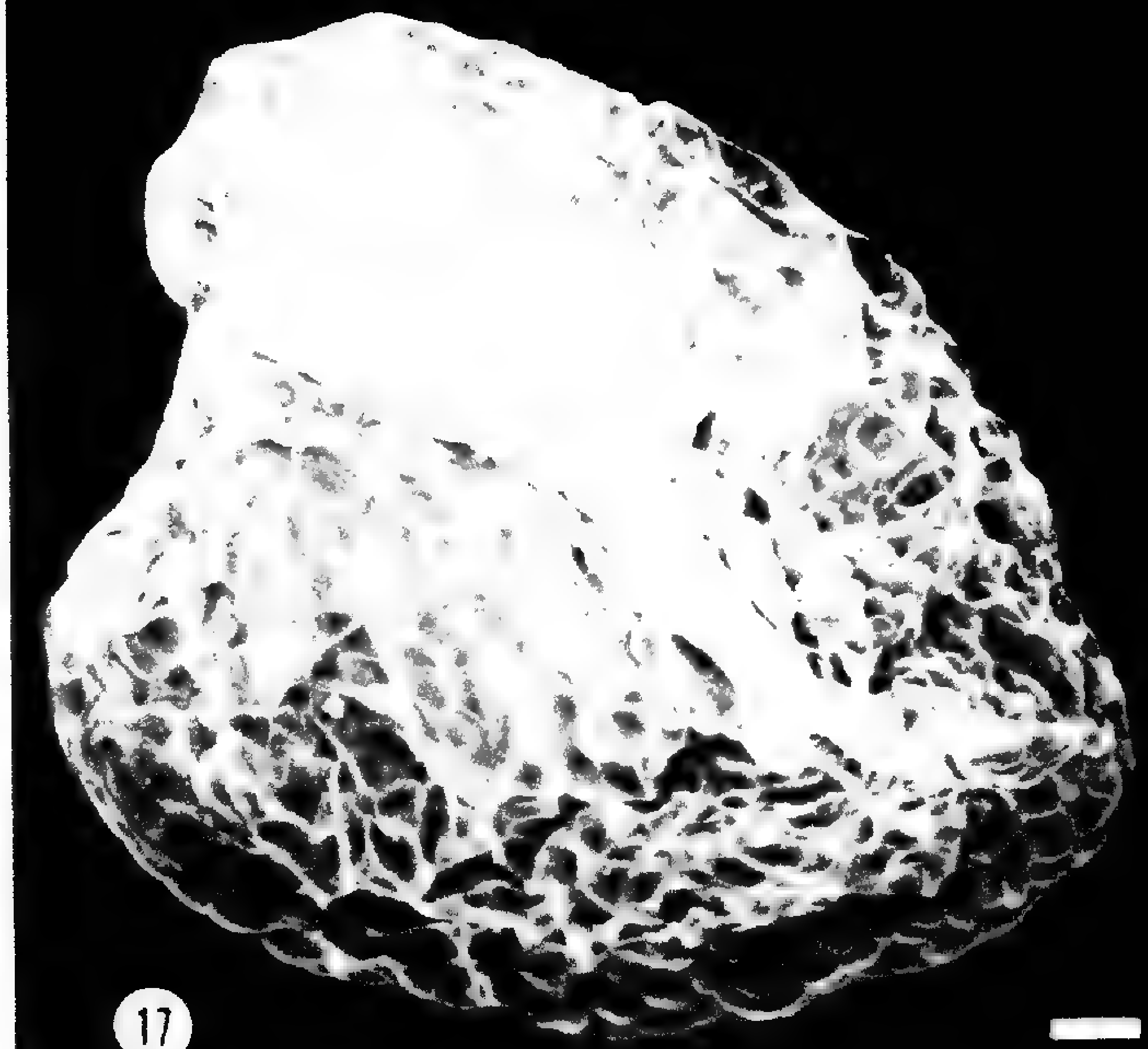

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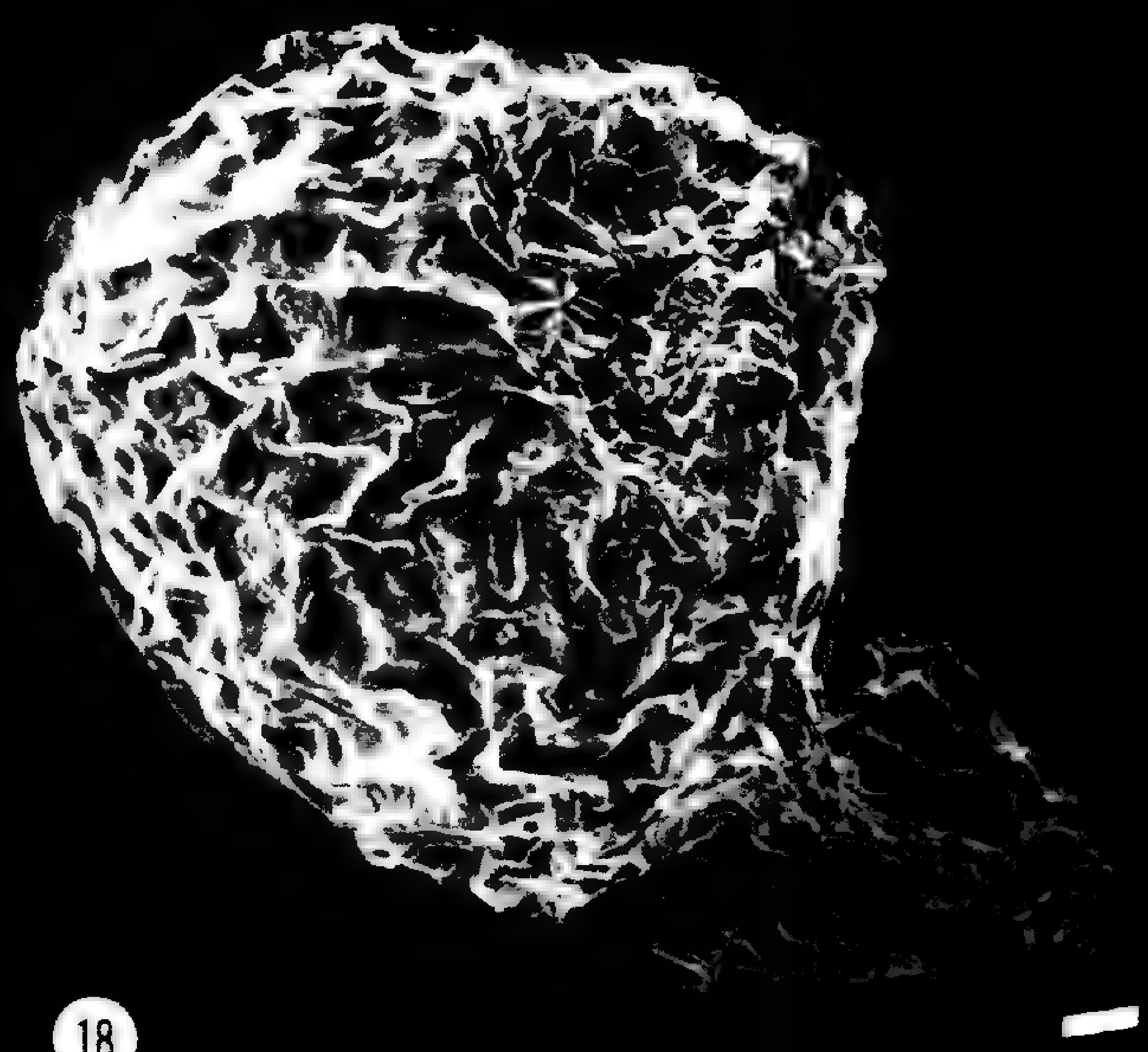

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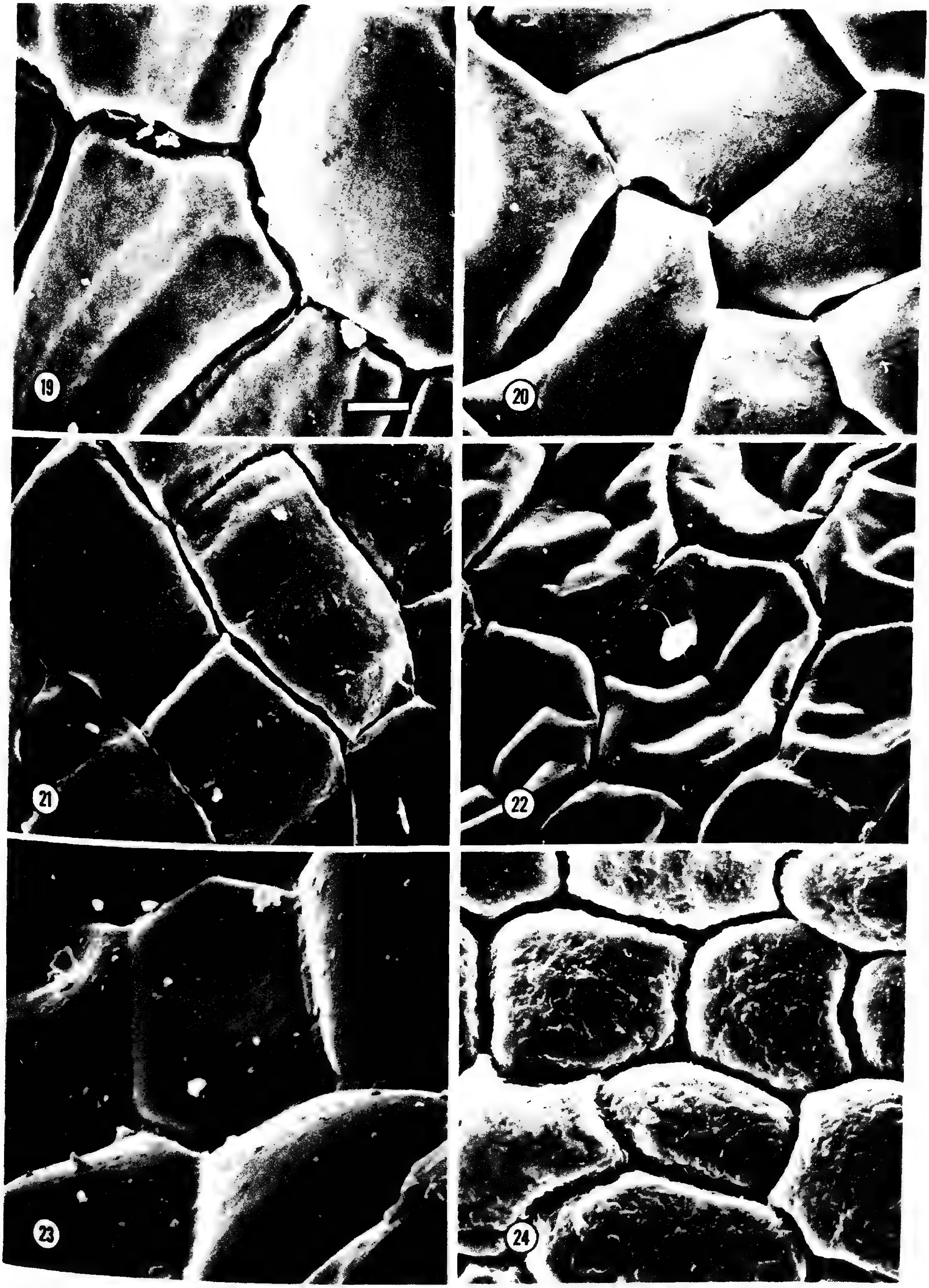
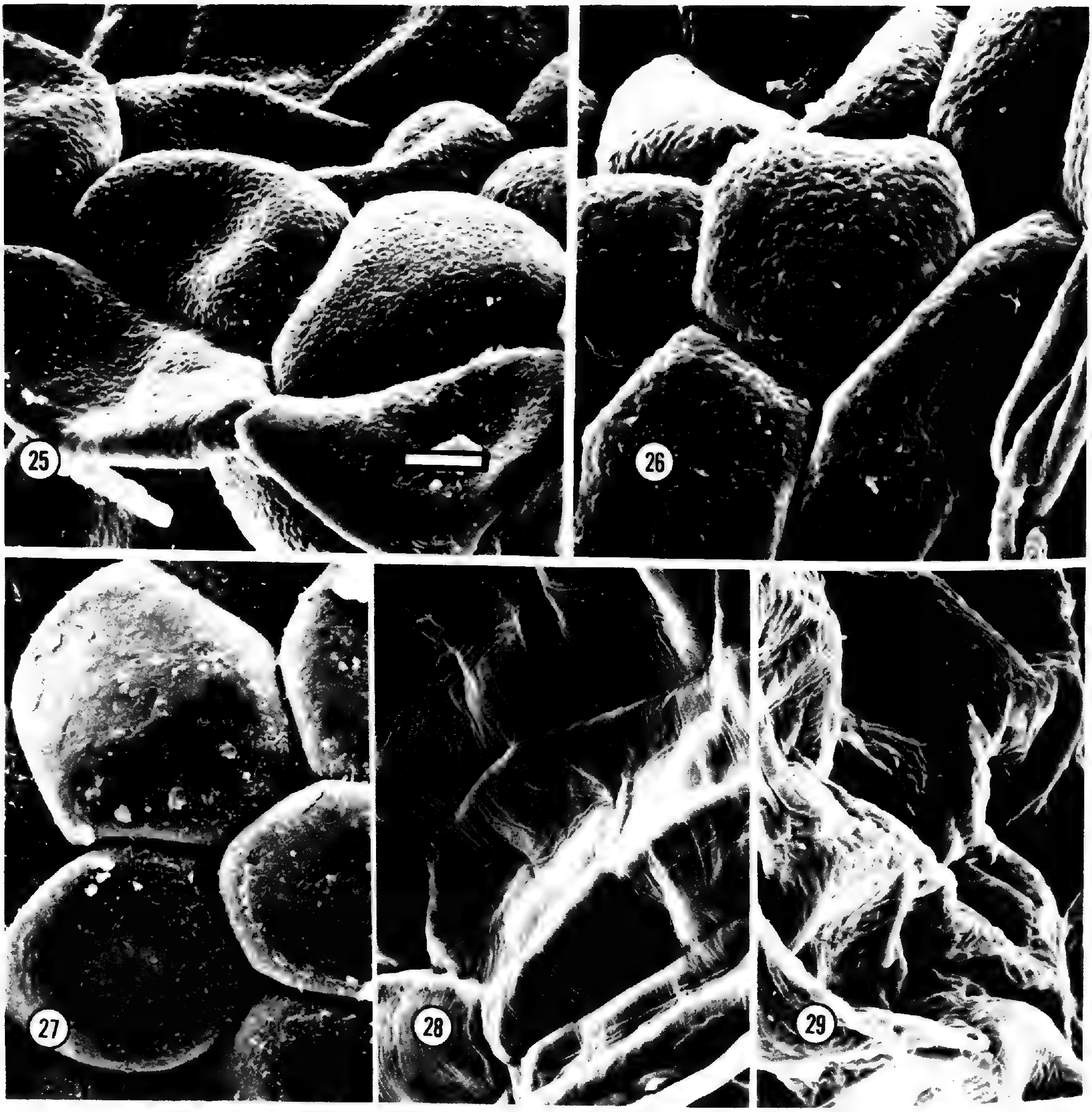
FIGURES 13–18. Scanning electron micrographs of seeds of species of *Hesperantha* sections *Radiata* and *Geissorhiza*.—13. *H. muirii*.—14,15. *H. elsiae*.—16. *G. humilis*.—17,18. *G. burchellii*. White bar = 100 μm.



FIGURES 19–24. Scanning electron micrographs of epidermal cell surfaces of seeds of species of *Hesperantha* and *Geissorhiza*.—19. *H. erecta*.—20. *H. purpurea*.—21,22. *H. radiata*.—23. *G. heterostyla*.—24. *G. humilis*. White bar = 10 μm. Scale same for all Figures.



FIGURES 25–29. Scanning electron micrographs of epidermal cell surfaces of seeds of species of *Hesperantha*.—25. *H. cedarmontana*.—26. *H. spicata*.—27. *H. luticola*.—28. *H. brevifolia*.—29. *H. elsiae*. White bar = 10 μm.

a flat or raised area of the testa where the epidermal cells are elongated along the longitudinal axis of the seed (e.g., Figs. 1, 3, 6, 7). The species of *Geissorhiza* sampled have seeds with similar raphe and distal depressions (Figs. 16, 18).

Size. Most species of *Hesperantha* have relatively small seeds typically from 0.8 to 1.5 mm long. The seeds of *Geissorhiza* species examined also have a similar size range. Four species, *H. montigena* (sect. *Concentrica*), *H. bachmannii* (sect. *Imbricata*), *H. marlothii* (sect. *Radiata*) (Fig. 10), and *H. luticola* (sect. *Hesperantha*) (Fig. 8), have larger seeds, ranging from 1.3 to 2 mm long or to 2.5 mm long in one of the two populations of *H. marlothii* studied (population 1). In contrast, three species of sect. *Radiata*, *H. brevifolia* (Fig. 12), *H. muirii* (Fig. 13), and *H. elsiae* (Figs. 14, 15), have particularly small seeds, 0.5–0.7(–0.8) mm long.

Color. The seeds of both *Hesperantha* and *Geissorhiza* are light to dark brown except those of *H. flexuosa*, *H. radiata*, and *H. luticola*, each in a different section, which are reddish brown. The seeds of most species are moderately lustrous but some are much more so, such as *H. bachmannii* (sect. *Imbricata*) and *H. marlothii* (population 1) (sect. *Radiata*). Seeds of *G. heterostyla* are similarly lustrous. Only *H. fibrosa* of sect. *Concentrica* and *H. luticola* of sect. *Hesperantha* have an unusually dull seed coat surface. The whitish color with a brown background of the seeds of *H. spicata* is a unique feature among the species sampled.

Surface morphology. The seed surfaces of both *Hesperantha* seeds and of those species of *Geissorhiza* sampled are composed of variable shaped epidermal cells (Figs. 19–29). Most cells are more or less isodiametric, but on ridges, wings, or contorted areas, the cell shape is usually altered (e.g., Fig. 20). The exposed periclinal cell wall is typically flat (Fig. 19) to slightly convex (Fig. 23). They are also often modified over parts of the seed surface to undulate (Fig. 21), convex (Fig. 22), irregular (Figs. 28, 29), or more spherical (Fig. 27). These modifications are either unique to one species such as the more spherical cells of *H. luticola* or are distributed sporadically in several sections, such as the three other types mentioned. The epidermal cell boundaries are distinct and fairly uniform among species of *Hesperantha* (Figs. 19, 21, 22, 25, 26) and appear similar to those of *Geissorhiza* (Figs. 23, 24). The boundaries are occasionally obscured by portions of the exposed periclinal walls that overlap (Fig. 20). Sometimes the boundaries are in full view but are not conspicuous (Figs. 28, 29). All three of these modifications appear to be minor and may be linked to the wrinkling or contortion of the testa surface as a result of packaging or desiccation.

Microsculpturing. The surface of the epidermal cells is generally smooth in both the *Hesperantha* and the *Geissorhiza* seeds surveyed. One species, *Geissorhiza humilis*, has an irregularly roughened surface. Within *Hesperantha* there are three species with roughened surfaces, *H. fibrosa* (sect. *Concentrica*), *H. cedarmontana*, and *H. spicata* (both sect. *Hesperantha*) (Figs. 25, 26). These roughened surfaces in *Hesperantha* are similar to one another but different from that of *Geissorhiza humilis* (Fig. 24). The similarity of the roughened surfaces of these three *Hesperantha* species suggests the possibility of a close relationship among them. Other species of *Hesperantha* have irregularly wrinkled cell surfaces (Fig. 29). This type of surface is closely linked to the contortion of the surface or portions of the surface in many species (e.g., Fig. 4). The very specialized seeds of *H. brevifolia* have a wrinkled cell surface unique among the species examined (Fig. 28).

DISCUSSION

The basic seed shape in *Hesperantha* seems to be turbinate to more or less globose with a persistent funiculus and an epidermis of isodiametric cells with unwrinkled surfaces. A more globose shape may be due to either looser packing of the seeds in the capsule or a relatively simple modification that has occured several times independently. In any case this variation apparently has nothing to contribute to our understanding of species relationships.

There appear to be no seed characters restricted to *Hesperantha* and none have been identified that differentiate *Hesperantha* from *Geissorhiza.* Seeds of certain species such as *H. marlothii* (population 2) are virtually indistinguishable from those of some species of *Geissorhiza.* Moreover, there is limited variation among species of *Hesperantha.* The most conspicuous variations, like contorted and wrinkled seed coats, appear to be relatively minor changes and may be a consequence of the density of seed packing in the capsules or to desiccation or a combination of the two.

Wrinkled seed coats and globose seed shape have a sporadic distribution in the various sections of *Hesperantha* as well as in *Geissorhiza,* in the case of wrinkled seed coats, and they presumably have no taxonomic utility. Modifications that are apparently consistently reproduced (as far as it is possible to judge from the sampling), such as triangular seeds in *H. marlothii* (population 1), oddly wrinkled surfaces of the epidermal cells of *H. brevifolia,* or the more spherical epidermal cells and large seeds of *H. luticola,* appear restricted to only one species or form, and thus are also not useful in determining species relationships. The only exception to this is in sect. *Radiata,* where seeds with irregular shapes, strongly wrinkled or crumpled surfaces, a tendency for small size, and dual tails and/or wings support the belief in the close relationship of *H. radiata, H. muirii, H. brevifolia,* and *H. elsiae* based on gross morphology. *Hesperantha juncifolia* and *H. longicollis,* the other species of the section, were not available for study, while *H. marlothii,* evidently closely allied to *H. radiata* (Goldblatt, 1984), does not have this distinctive seed type.

The similarity between the seeds of *H. fibrosa* (sect. *Concentrica*) and *H. cedarmontana* and *H.*

spicata (sect. *Hesperantha*), all of which have seeds with narrow wings, little or no contortion of the epidermal cells, and roughened cell surfaces, in contrast seems fortuitous as there seems to be no support from gross morphology to suggest that *H. fibrosa* may be allied to the species of sect. *Hesperantha* with these same characteristics.

From the relatively small sample of 17 species examined here, it appears that the main pattern of evolution in seed structure in *Hesperantha* has been one of change from a basic turbinate shape with uncontorted, smooth surfaced epidermal cells to increasing compression and a triangular or more or less irregularly angular shape (perhaps a result of dense packing within the capsule) sometimes accompanied by wrinkling and crumpling of the epidermal cells, and the development of dual tails and wings. This is most marked within sect. *Radiata* (but not in *H. marlothii* of this section), where these modifications are accompanied by reduction in seed size. However, narrow wings are also developed within sections *Hesperantha* (*H. spicata* and *H. cedarmontana*) and *Concentrica* (only in *H. fibrosa* of the species examined) but in both of these groups without accompanying crumpling of the epidermal cells, which have distinctive rough surfaces, apparently developed coincidentally.

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A FLORISTIC STUDY OF VOLCÁN MOMBACHO DEPARTMENT OF GRANADA, NICARAGUA[1]

JOHN T. ATWOOD[2]

ABSTRACT

Volcán Mombacho is a moderate sized (1,345 m elev.), quiescent volcano with one of two cloud forests in southwestern Nicaragua. Of 457 species listed, 80 are pteridophytes and 87 are orchids. The species richness of these groups may be accounted for by their high fecundity and dispersibility. This study has revealed only one endemic species. Since Mombacho is the apparent northern range limit of several orchid species, it is suggested that the flora of the cloud forest has most of its affinities with Costa Rica. The lack of several wide ranging species on Mombacho which are known only as far south as northern Nicaragua further supports this contention. As with most of tropical America, the cloud forests of Mombacho are threatened by exploitation of their natural resources.

Volcán Mombacho (Fig. 1) is a quiescent, much eroded, and well vegetated volcano located near the city of Granada, Nicaragua. "Mombacho" is a modification of the Nahuatl "Mopachotepetl" meaning "inclined mountain" (Mantica, 1973). It is located at 11°50′N latitude, 85°59′W longitude (see map, Fig. 2), and is the fifth largest of the quaternary volcanos in western Nicaragua forming a chain from El Salvador to Costa Rica (Mooser et al., 1958). With a maximum elevation of 1,345 m, Mombacho is somewhat lower than several other Nicaraguan volcanos, the highest of which is 1,745 m. It is, however, perhaps the most massive with a basal diameter of about 7 km. Its U-shaped crater rim is 1.5 km in diameter and the crater floor is about 750 m lower than the highest peak. The lowest point on the crater rim is 1,080 m.

Besides the highest peak of the southeast crater rim, there is a second peak on the northwest rim with an elevation of 1,222 m. Adjacent to this peak is a large flat area appropriately called "Plan de las Flores." Within this area are two small vegetated craters each of unknown depth and about 200 m in diameter. Eastward from Plan de las Flores lies a trough-shaped valley over 1.5 km across extending northeast from the crater rim for a distance of 3.5 km.

Aerial photographs reveal a number of lava flows extending down the sides of Mombacho, but these features have been obscured in the northeast valley and the open south side of the crater rim by later seismic events. The lava flows are for the most part fully vegetated, and their basal limits are sharply defined where they meet pastured savannas.

Certain areas, notably the flanks of the crater rim and the sides of the valley extending northeastward, are precipitous. These areas, often with a slope well over 100 percent, are mostly vegetated, but frequent landslides have left conspicuous scars and a jagged crater rim.

Very few permanent streams can be found on Mombacho, although stream beds occur in various ravines filled only during times of heavy precipitation. Most of the precipitation seeps down through the loose volcanic substrate, leaving little runoff. Because of the porous substrate, the two craters at Plan de las Flores do not contain lakes.

Viewed from Granada, Mombacho appears as a rich green, broadly truncated, and much eroded volcanic cone. It is most impressive in cloudless late afternoons, when the various physical features cast shadows pointing up the rough topography. A number of cut-over areas mar the slopes

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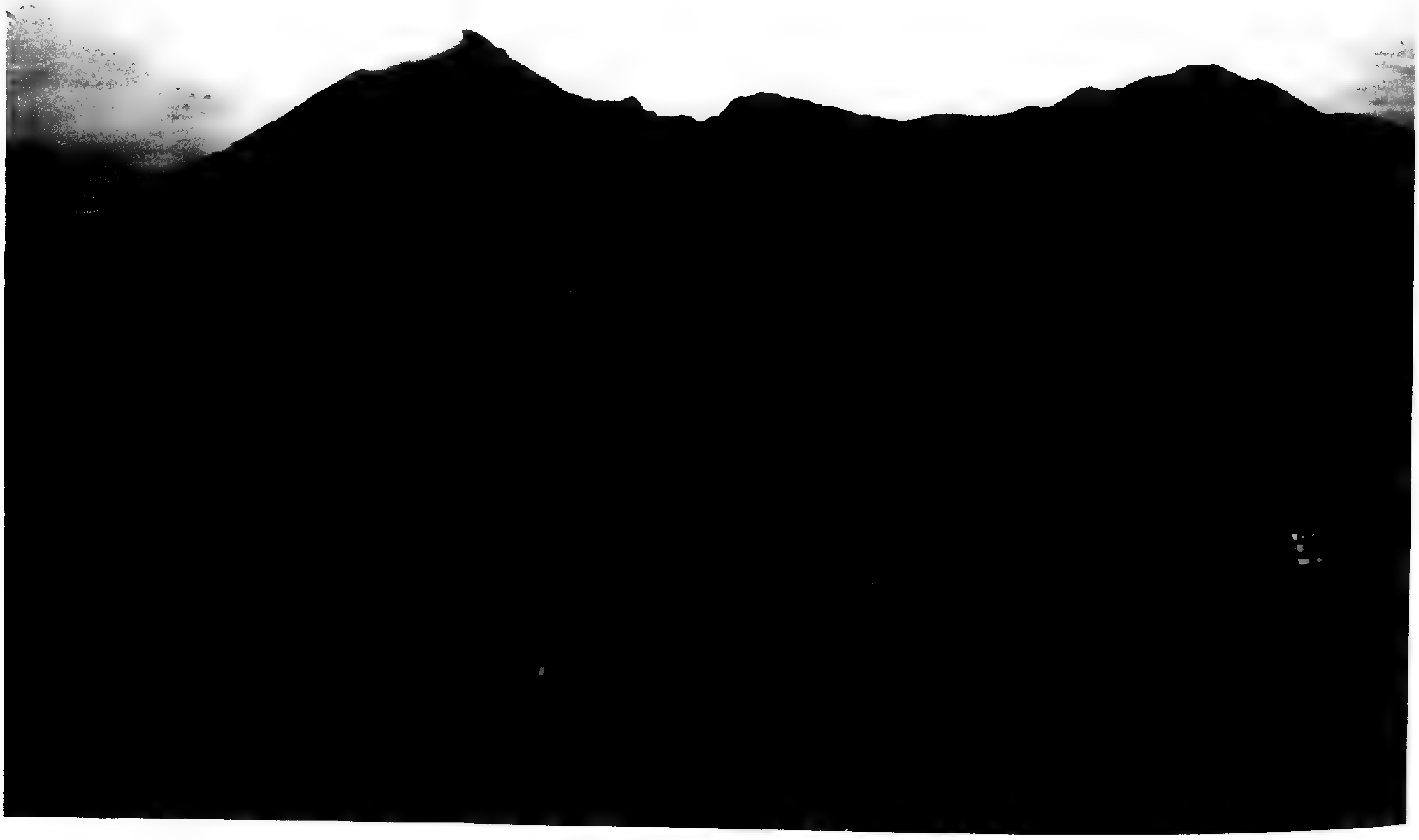

FIGURE 1. Profile view of Mombacho from the north.

and much of the lower areas have been deforested or severely disturbed.

Everywhere in the tropics the mountain forests are disappearing at alarming rates. It is hoped that interest in the flora of this mountain will help bring an awareness by government officials that the development of the Nicaraguan cloud forests is not in their best interests.

Volcán Mombacho was selected partly because it contains a substantial amount of extant virgin forest and, because being close to urban areas, it has educational, recreational, and economic potential. For these reasons it seemed that a survey of the flora of this volcano would be a greater contribution than a similar work on a more remote mountain. Collections made specifically for this work were made during the months of May through July 1975 and February and March 1977. The most complete set of voucher specimens has been deposited in the Beal-Darlington Herbarium of Michigan State University.

GEOLOGICAL HISTORY

Mombacho's violent past is reflected in the size of the crater and the general topography. Little is known of its geological history, but a few seismic events have been documented since the time of the Spanish conquest.

As a member of the west Nicaraguan volcanic chain Mombacho is probably not older than two million years and may be considerably younger. Mooser et al. (1958) reported that the most recent authenticated eruption occurred in 1560, but this report is not supported by Incer (pers. comm.). Incer (1973) indicated that during the same century the south crater rim avalanched away, causing the destruction of the south flank and an Indian village of 400 inhabitants. Crawford (1902) reported that an eruption occurred in 1850, but Mooser et al. (1958) also indicated that a small parasitic cone called "Pilas" formed on the north flank of Mombacho in 1850, but this report is probably confused with the eruption of a mountain north of Lake Nicaragua by the same name. However, a small cone northeast of Mombacho may have been active in historic times.

The uniform texture of the crater walls suggests that in its early development Mombacho was built up primarily from ash rather than lava flows. The ash probably formed a volcanic cone similar

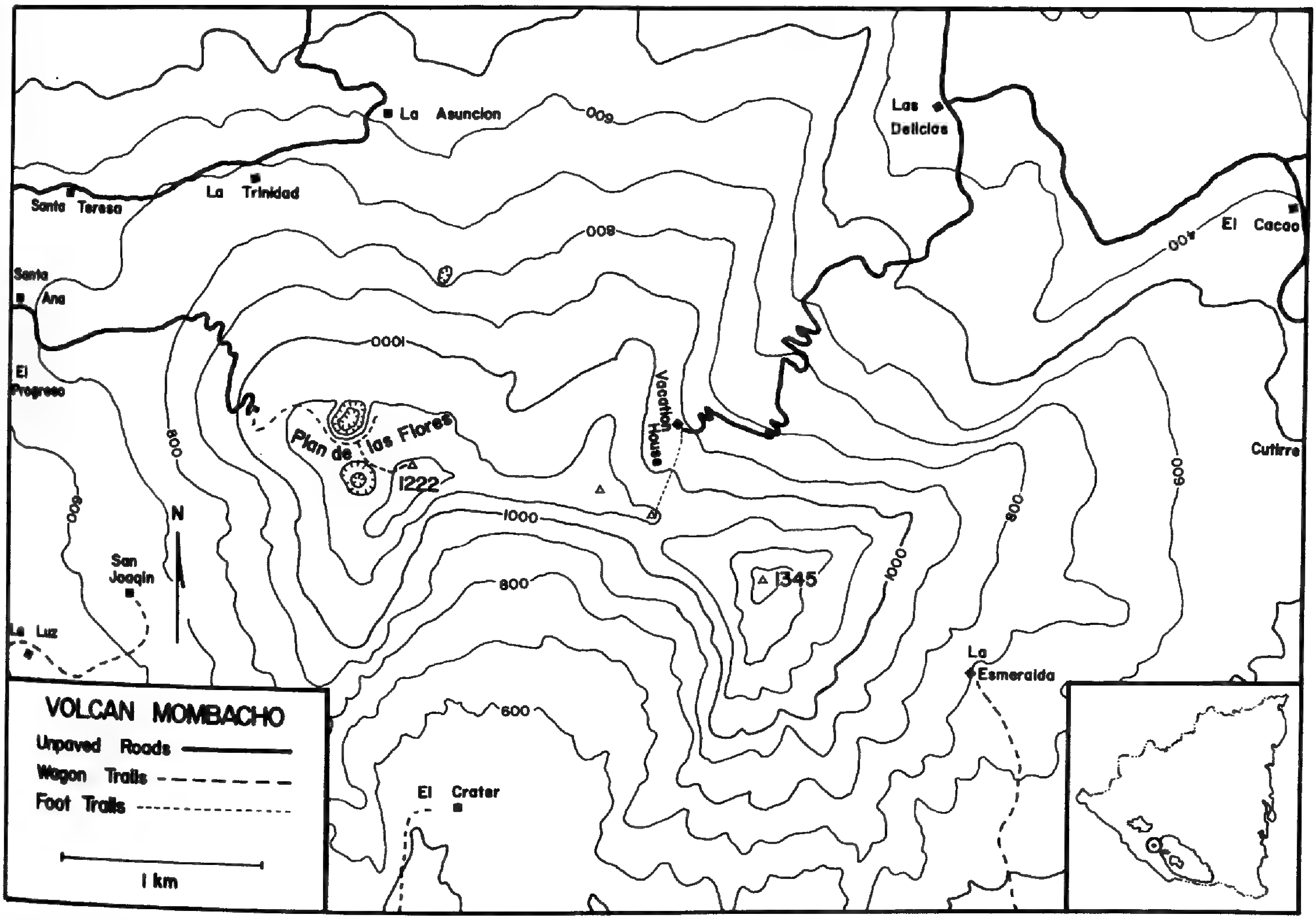

FIGURE 2. Map of Volcán Mombacho (after Hoja 3051 III and Hoja 3051 IV published by Instituto Geografica Nacional and Servicio Geodesico Interamericano, 1972 edition, scale 1 : 50,000).

to Mombotombo to the north and Concepción to the south. If lines following the existing flanks of Mombacho are projected upward, they meet at about 2,000 m (Incer, 1973), a possible elevation that Mombacho may have attained in its geological past. Apparently the more recent volcanism was manifested as lava flows, which seem to nearly cover the surface of the mountain.

It is not clear exactly how the crater was formed, but the very steep sides suggest that an internal collapse occurred, caused by subsiding lava not by an explosion similar to that which took place on Krakatoa. The two craters at Plan de las Flores apparently were formed by collapse (Incer, pers. comm.).

Exactly which events took place in the sixteenth century causing the destruction of the south crater wall is not clear, but it is known that a lake once occurred within the crater (Incer, 1973). Apparently the loose substrate collapsed under its own weight and pressure from the crater lake, but the ultimate avalanche was probably precipitated by an earthquake. A similar event probably occurred much earlier on the northeast flank, leaving a trough shaped valley. Since the sixteenth century, Mombacho has remained relatively quiet, but the rough topography and fumaroles of the crater rim attest to its violent past.

CLIMATE

The climate of lowland Pacific slope Nicaragua and the lower slopes of Volcán Mombacho may be described as "tropical dry." No single mean monthly temperature below 17.1°C has been determined at stations reported by Incer (1973). The widest range of variation of monthly means for any station is less than 4°C. However, Incer (1973) indicated that the daily temperature at Managua (with an annual mean of 26.3°C) may deviate at least 7.3°, because a temperature of 19°C in January has been recorded. The temperature therefore fluctuates little throughout the year. After the rains cease in December a dry season ensues with essentially no rainfall in the lowlands until May. This period of drought roughly corresponds to the winter season of the north. Because rainfall is much more abundant, the climate of the summit is moister and cooler, with swift gusty winds as attested by frequent blow-downs.

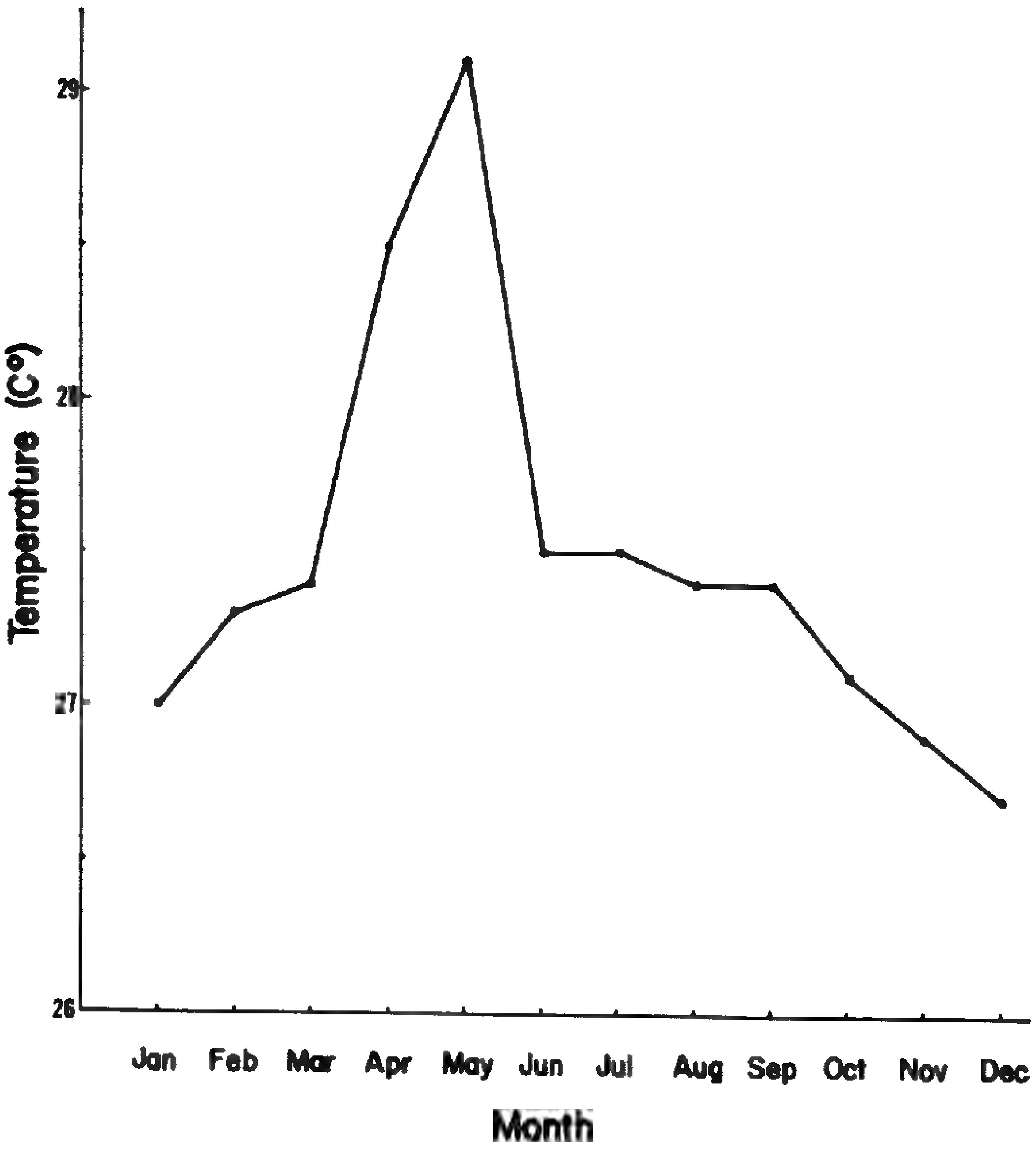

FIGURE 3. Mean monthly temperatures at Nandaime (data from Incer, 1973).

No temperature data were available for Volcán Mombacho, but data were taken from the nearby village of Nandaime (Incer, 1973), which lies 12 km southwest of the volcano at 150 m elevation (Fig. 3). To estimate the mean annual temperature of Mombacho's summit (ca. 1,200 m elev.) the mean dry and wet adiabatic rates were applied to the data from Nandaime. If the dry adiabatic rate of 1°C per 100 m (Strahler, 1973) is applied to the mean annual temperature at Nandaime (27.5°C), the mean annual temperature at the level of 1,200 m could be depressed 10.5° to a minimum 17°C. The wet adiabatic rate of 0.6°C per 100 m would depress the mean annual temperature 6.3°C to 21.2°C. Thus the calculated range of mean annual temperature falls between 17°C and 21.2°C. To estimate the minimum temperature at 1,200 m the dry adiabatic rate can be applied to the minimum temperature at Managua (19°C at 50 m elev.). The estimated temperature difference between the two elevations is 11.5°C, therefore the temperatures at Mombacho's summit could drop to 7.5°C. Clearly, if frost ever occurs at the summit, it must be a rare event.

The forests become increasingly wet with elevation. Not only is there more convectional and orographic rainfall, but also the dense vegetation behaves as a screen, filtering moisture from passing fog, as has been noted on other mountains (Oberlander, 1956; Twomey, 1957; Vogelmann et al., 1968; Vogelmann, 1973). Oberlander (1956) noted that significant condensation occurs only where trees are tall and fog-laden winds are strong. Baynton (1969) indicated that precipitation from fog in elfin forest vegetation at Pico del Oeste, Puerto Rico, comprised only ten percent of the total rainfall. This low percentage may reflect the shorter height of the vegetation and the subsequent lesser screening effect. Observations of Mombacho's weather are consistent with Baynton's more detailed considerations. Owing to the effects of nearby Lake Nicaragua, Volcán Mombacho probably receives more precipitation than do the volcanos to the north.

Figure 4 is a graph of the monthly precipitation at La Asunción (580 m elev.), on the north flank of Mombacho. Clearly the dry season is evident from December to April. The rainy season from April to December includes two peak months, June and September, with a "mini" dry season in July. Although the mean monthly rainfall at Mombacho's summit is undoubtedly higher, the shape of the rainfall curve is expected to have the same shape as the rainfall curve at La Asunción.

Rainfall undoubtedly varies locally with the slope. Clouds on the windward side move parallel with the slope, but move vertically when approaching essentially vertical cliffs. With vertical air movement a corresponding higher local precipitation is expected.

Figure 5 includes histograms of monthly evaporation at La Asunción. It shows that the period from March to May is the driest, corresponding to the period of maximal temperature at Nandaime.

The rapid changes of climatic factors at the summit are striking. Rapidly moving fog can disappear, revealing the full force of the sun only for the pattern to be repeated with a sudden blanket of fog. Such changes in the weather may have a considerable effect on the vegetation.

A BRIEF ACCOUNT OF THE VEGETATION

For purposes of this study it seems most natural and convenient to divide Mombacho into three altitudinal vegetation zones. For the lowest zone continuous throughout western lowland Nicaragua the term "deciduous seasonal forest" of Beard (1942, 1944) seems most appropriate, reflecting the deciduous nature of the vegetation as affected by seasonal rainfall. The second zone

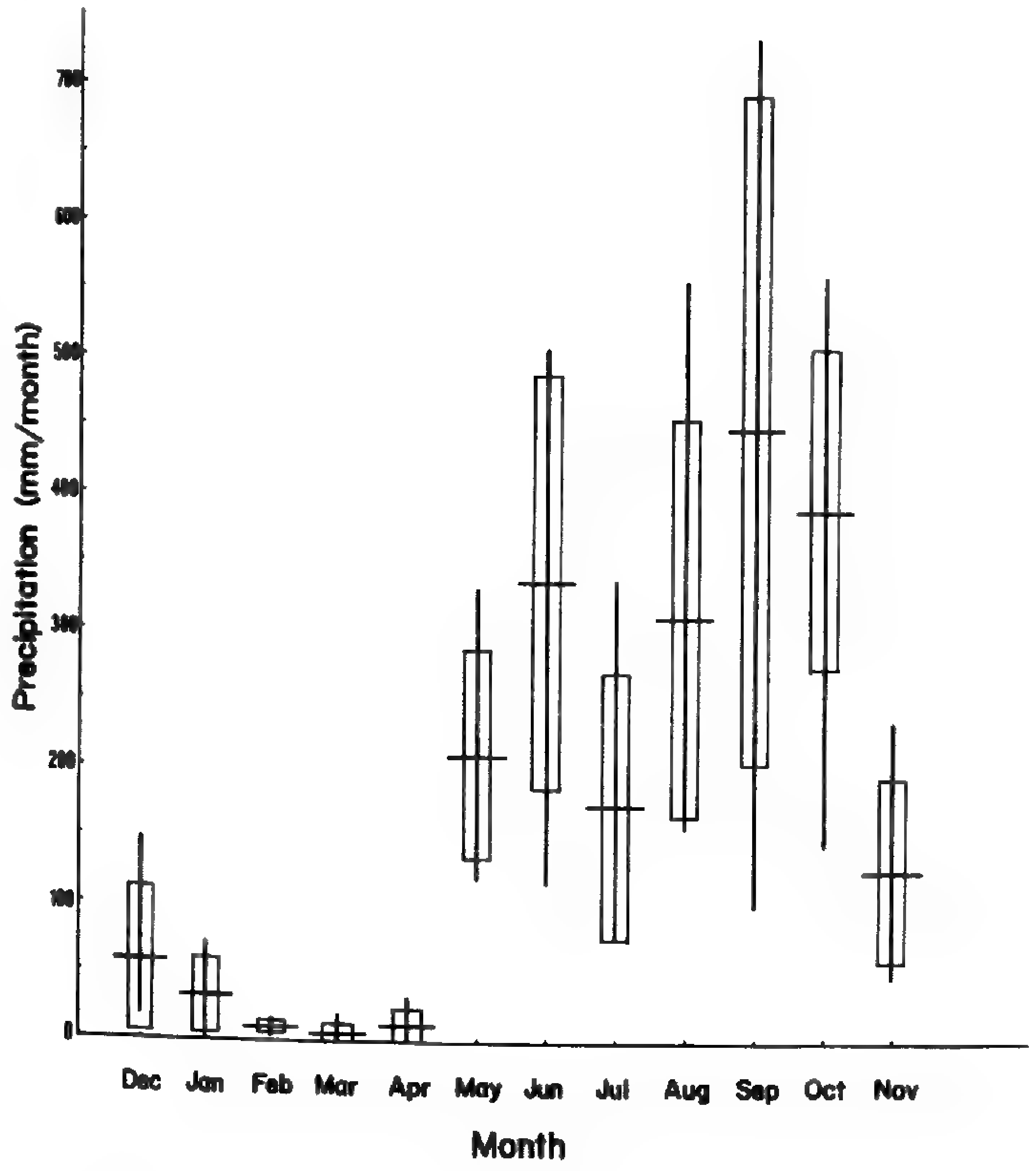

FIGURE 4. Monthly precipitation at La Asunción on Volcán Mombacho (elev. 580 m). The data span a four year period from December 1972 to November 1976. The vertical bars, horizontal bars, and rectangles represent the range, mean, and one standard deviation from the mean respectively (data provided by Empresa Nacional de Luz y Fuerza).

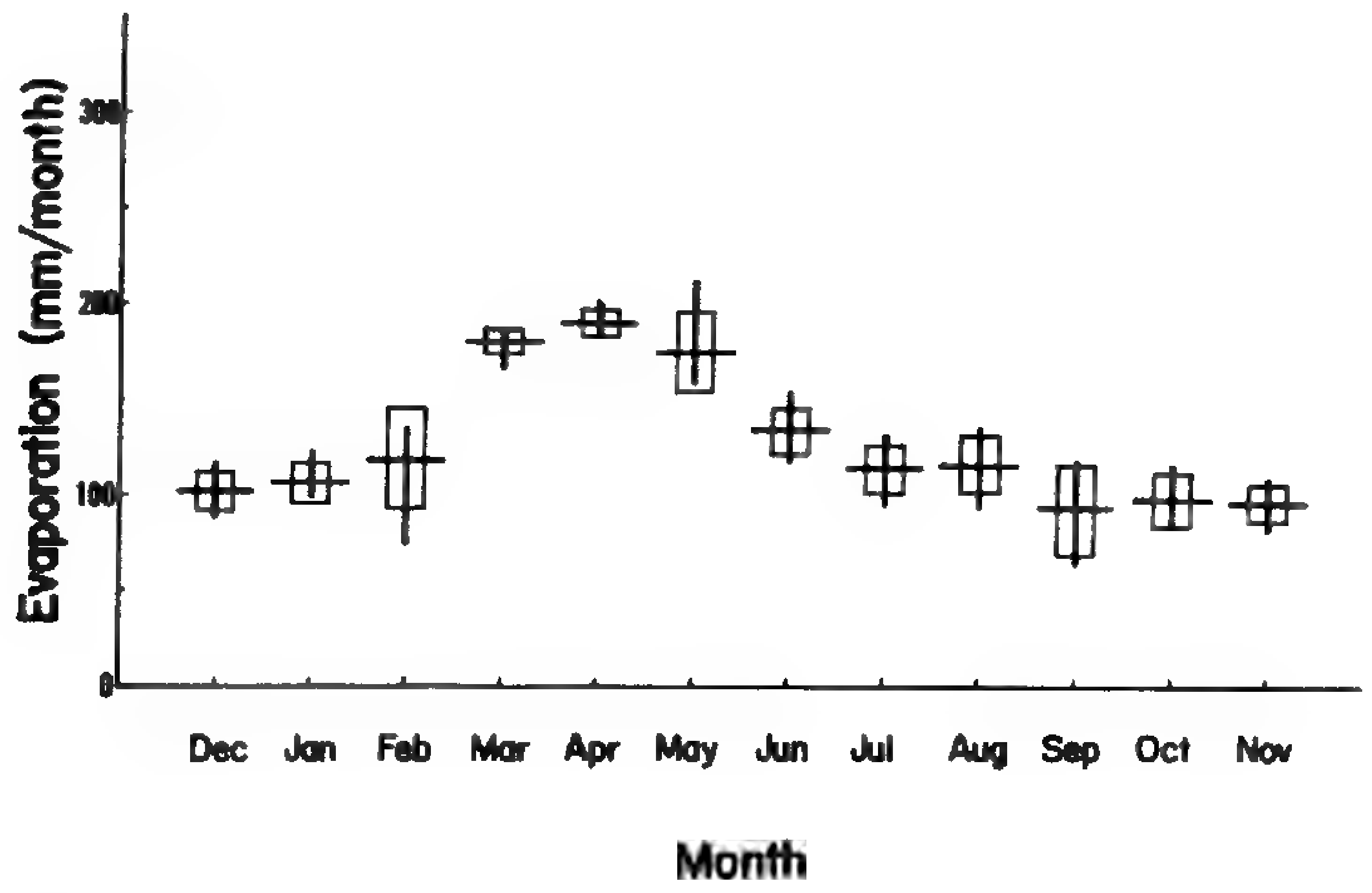

FIGURE 5. Monthly evaporation at La Asunción on Volcán Mombacho (elev. 580 m). The data span a four year period from December 1972 to November 1976. The vertical bars, horizontal bars, and rectangles represent the range, mean, and one standard deviation from the mean respectively (data provided by Empresa Nacional de Luz y Fuerza).

is here termed the "cloud forest." The cloud forests of Mombacho are evergreen and distinct from the deciduous forest. The third and highest vegetational zone, also often beclouded, is the "elfin forest" characterized by stunted trees to about 8 m tall.

The deciduous seasonal forest during the rainy season is very similar in appearance to the tropical rain forest. Even the stately emergent *Ceiba* is common to both forests in Nicaragua, although it usually does not gain its greatest stature in the deciduous forest. When the rains cease in December the forest becomes leafless, and several genera initiate flowering (*Plumeria, Byrsonima, Cochlospermum*), lending color to the otherwise drab landscape.

The shrubby layer includes *Casearia, Karwinskia*, and several vines of the families Convolvulaceae, Bignoniaceae, Solanaceae, Aristolochiaceae, Cucurbitaceae, and Vitaceae. This layer is usually torched by landowners to rid grazing areas of undesirable weeds and ticks. Because of the great demands made upon the deciduous seasonal forest by man, very little can be found in a natural state, and essentially none on Volcán Mombacho. Most of the forests surrounding Mombacho were probably converted to agriculture by native Americans long before the Spanish conquest.

Mombacho contains one of two cloud forests in southwestern Nicaragua; the other occurring on Volcán Maderas. The Mombacho cloud forest extends from approximately 400 m elevation on the east-northeast flank nearly to the summit. It begins considerably higher on the south-southwest flank, owing to the rain shadow. The cloud forest is characterized by evergreens and generally lush vegetation, a manifestation of the abundant precipitation. The many shades of green of the cloud forest indicate a complex aggregation of species, but this diversity diminishes with increasing elevation.

The tallest trees are to be found in the lower cloud forest, and the forest becomes shorter with elevation until the dwarfing effect culminates at the elfin forest.

Characteristic of the cloud forest is the presence of masses of epiphytes representing a number of plant groups. Many epiphytic ferns of several families occur as do members of the angiosperm families Bromeliaceae, Gesneriaceae, Piperaceae, Araceae, Lentibulariaceae, and Ericaceae, but by far the most species rich family is the Orchidaceae, although it is low in biomass.

The herbaceous flora of the cloud forest is characterized by pteridophytes. A grass, *Oplismenus* was observed to occur in areas of moderate shade in the upper cloud forest, but never in deep shade. Several composites occur, mostly in disturbed habitats. Two species of *Dieffenbachia* are found; one in the lower, the other in the upper cloud forest. Terrestrial orchids are found locally. *Tropidia polystachya,* supposedly abundant and widespread in much of the New World tropics, was found on two occasions. *Goodyera* cf. *bradeorum* is more often found in the upper cloud and elfin forests, as are two species of *Malaxis.*

In the lower cloud forest both vascular and non-vascular epiphytes are relatively uncommon on the lower portions of trees but occur in large numbers in the canopy. Most epiphytes were collected from trees that had fallen or were felled, but undoubtedly many more species remain uncollected. Several bromeliads and orchids in this area, such as *Guzmania lingulata, Tillandsia schiediana, Trigonidium egertonianum, Nidema boothii,* and *Encyclia fragrans,* are also common to lowland rain forests of the Zelaya Department. Two common epiphytic aroid species, *Anthurium scandens* and *A. cubense* are most abundant in this zone, the latter occurring in the marginal areas with the deciduous forest.

The shrub layer of the lower cloud forest includes the urticaceous *Urera,* but probably the Piperaceae is best represented here. *Pothomorphe* was collected with various species of *Piper* in disturbed areas, but other species of *Piper* were found in the darkest understory. In the lower cloud forest of the east slope, *Carica papaya* was observed to assume a dominant position in the understory.

A number of pioneer and adventive species were collected in disturbed areas, and many were undoubtedly dispersed by man. Among the more attractive is *Mirabilis jalapa,* a common weed of coffee plantations.

The lower cloud forest is the most disturbed zone of evergreen vegetation, and the little remaining primary forest is threatened. The best examples of extant lower cloud forest seem to be in the northeast facing valley above Finca Las Delicias. However, agriculture here is showing its effects because most of the primary lower cloud forest has either been removed or severely disturbed.

The upper cloud forest is characterized by a low, few-layered canopy lacking distinct crowns. The trees are often conspicuously covered with vascular and non-vascular epiphytes even to the base of their trunks, and the light intensity at the ground level is much higher than that of the lower cloud forest. Three commonly observed tree species of the upper cloud forest were *Hedyosmum montanum, Clusia salvinii,* and *Senecio arborescens,* but the latter never assumes the stature of the higher surrounding trees. The herbaceous flora is rich and includes several terrestrial orchids, two locally abundant species of *Carex,* and occasional composites as well as numerous ferns.

The upper cloud forest seems to be less threatened by agriculture than the lower cloud forest. However, its restricted size renders it vulnerable to complete and rapid destruction. The tell-tale tracks of wandering cattle were noted above Finca Las Delicias near the crater rim. Expansion of a coffee plantation was once tried but failed at Plan de las Flores, but further attempts in the remaining forest seem inevitable.

In the elfin forest precipitation is abundant, wind velocities are high and gusty, and the forest is usually beclouded. Elfin forest has been studied by a number of investigators. Brown (1919) investigated an elfin forest (mossy forest) on Mount Maquiling on the island of Luzon, Philippines. Beard (1942, 1944) studied elfin forests in the Antilles, and Steenis (1972) noted the elfin forests of Java. Detailed investigations have been conducted at Pico del Oeste, Puerto Rico by Howard (1968, 1969) and Gill (1969). Alvarez del Castillo (1976) contributed an ecological and floristic work on an elfin forest on Volcán San Martin Tuxtla, Veracruz, Mexico.

Beard (1944) characterized the elfin forest of the Caribbean area as an "open woodland about 8 m high of stunted, gnarled trees, often stilt-rooted and with thick fleshy leaves, with long rambling branches pointing away from the wind. There may be an understory of dwarf palms and tree ferns. The whole is loaded with moss, lichens, and epiphytes, and forms a completely impenetrable thicket."

Viewed from the air, the elfin forest of Volcán Mombacho appears as an even, dense canopy pruned by the elements. The upper cloud forest lacks the pruned appearance, and the line delimiting the two forests is often distinct. The canopy consists of one stratum beneath which are occasional shrubs (especially *Psychotria* spp.), and numerous herbs. Nearly every branch is inhabited by bryophytes, and epiphytic vascular plants are common everywhere. The leaves of arborescent elfin forest species with few exceptions tend to be leathery, entire, and small to medium-sized.

Aerial photographs show that the elfin forests of Mombacho extend along all exposed ridges and pinnacles down to an elevation of about 900

m. It blankets even the roughest topography, including nearly vertical cliffs.

The arborescent stratum of the more protected elfin forest contains numerous species including *Clusia salvinii, Rapanea ferruginea, Freziera friedrichstaliana, Myrcianthes fragrans, Oreopanax xalapense, Viburnum hartwegii,* a number of Rubiaceae, and tree ferns of the genera *Cyanthea* and *Nephelea.* Concerning the elfin forest Beard (1944) noted that "pure stands of *Clusia* spp. constitute this formation in some of the lesser Antilles between 1,000 and 1,100 m . . . ." Pure stands of *Clusia* occur on Mombacho, but only along the most exposed ridges and pinnacles (Fig. 6). Ferns, bromeliads, and orchids are among the most numerous and diverse epiphytes encountered in the elfin forest. Among the genera of epiphytic ferns represented are *Elaphoglossum, Grammitis, Polypodium, Hymenophyllum,* and *Trichomanes.* Bromeliad genera include *Aechmea, Guzmania, Pitcairnia, Tillandsia,* and *Vriesia.*

The terrestrial herbaceous stratum is expectedly rich. In the shaded area of the mature elfin forest the terrestrial herbaceous flora consists largely of ferns. An absence of grasses was noted, but *Oplismenus hirtellus* forms mats in open areas. Three species of Cyperaceae, *Carex donnell-smithii, C. polystachya,* and *Uncinnia hamata,* occur frequently in the elfin forest, often along damp and exposed banks. The terrestrial orchid inhabitants include *Malaxis maxonii, M. tipuloides, Erythrodes* spp., *Goodyera bradeorum,* and *Psilochilus* cf. *macrophyllus.* One terrestrial gesneriad, *Kohleria spicata,* is commonly found along the access roads to Plan de las Flores.

The herbaceous flora of disturbed areas varies with locality. The herbs of the disturbed crater rim consist almost exclusively of *Isachne arundinacea* with a scattering of weedy composites. *Arundinella deppeana* is the most characteristic grass of disturbed Plan de las Flores. Other herbs including *Castileja arvense,* several composites, and the ferns *Phlebodium aureum* and *Ophioglossum reticulatum* occur in open areas.

It is noted that a shrubby layer is often lacking especially in the elfin forests dominated by *Clusia.* In the more diverse elfin forest are shrubby *Psychotria* spp. and a bristly melastome, *Clidemia* (?) sp. The diversity of shrubs of disturbed areas is much higher, except along the crater rim where *Rubus* is most abundant. At Plan de las Flores the open disturbed area once cleared for coffee growing consists of a large number of shrubs and herbs. Among the shrubby species are *Conostegia* spp., *Monochaetum deppeanum, Ardisia* sp., *Parathesis* sp., *Viburnum hartwegii,* and *Cestrum aurantiacum.*

FIGURE 6. View of the highest peak of Mombacho with *Clusia* thicket in the foreground.

At least four alien floristic elements were observed at Plan de las Flores. *Hippeastrum* sp. was observed and collected once. A row of *Hibiscus rosa-sinensis* was observed in the abandoned clearing as were *Coffea arabica* and occasional clumps of *Musa paradisiaca.* Among a large number of pioneer species and weeds found in the disturbed area of the cloud forest above Finca Las Delicias was a cultivated *Coccoloba uvifera.* None of the once cultivated elements found seemed to be reproducing and no juvenile individuals were observed. Occasional waifs from lower elevations, such as *Mormodes* sp. and *Jacquiniella globosa,* were found in the elfin forest.

HISTORICAL SKETCH OF BOTANICAL EXPLORATION ON VOLCÁN MOMBACHO

The first pioneer traveler and naturalist known to make collections on Volcán Mombacho was Emanuel Ritter Friedrichstal. His travels included the Antilles, Nicaragua, Guatemala, and the Yucatan, from 1837 to 1841 (Allgemeine Deutsche Biographie, 1878). It is probable that several Friedrichstal specimens attributed to Guatemala actually took their origin in Nicaragua, as may be the case with *Freziera friedrichstaliana* known only from Mombacho (Kobuski, 1941), and Honduras (Melina, 1975), and not from Guatemala (Standley & Williams, 1961).

Anders Sandøe Oersted visited Mombacho in December of 1847 (fide F. Seymour, pers. comm.). He also collected *Heliocarpus nodiflorus* (Lay, 1949) and it is probable that he collected many more specimens.

Kobuski (1941) noted that G. Wright collected

Freziera friedrichstaliana on Volcán Mombacho.

Paul Levy, a French engineer, resided in Granada and collected Nicaraguan plants between 1869 and 1885 (Hemsley, 1887; Chaudhri et al., 1972), but if he made collections from Mombacho none of his specimens have surfaced.

Charles Fuller Baker, graduate of Michigan Agricultural College in 1891 (Cattell, 1906) made collections on Mombacho in February of 1903 (from herbarium sheet, *Baker 2488,* MSC).

In 1909 the first of two volumes of "Flora Nicaraguense" by Miguel Ramirez Goyena was published, and to this day it remains the sole flora of the area. Goyena doubtless botanized Mombacho, but nothing is known of his collecting there. Unfortunately his work cites no specimens, and only a few localities, so its utility is limited.

W. R. Maxon, A. D. Harvey, and A. T. Valentine visited Mombacho in July 1923. They collected a new species of *Malaxis* that Oakes Ames named *M. maxonii* (Ames, 1923).

Verne Grant collected on Mombacho in 1940 and 1941 (fide F. Seymour & F. Almeda, pers. comm.).

In January 1967 L. O. Williams, Antonio Melina R., and A. H. Heller collected there during a three-day period (Heller, pers. comm.). A. D. Moore, D. A. Dudey, and Charles Nichols collected on the southeastern slope on January 9, 1969. Much of the material for this work comes from their collections.

On January 27 of the following year Edwardo Narvaez S. and I collected in the disturbed area around the vacation house above Finca Las Delicias.

On April 9, 1971, I collected about 30 numbers from the elfin forest on the northwest crater rim.

In May 1972 R. L. Wilbur, D. E. Stone, and F. Almeda made collections near the crater (F. Almeda, pers. comm.).

Frank C. Seymour made collections on July 25, 1972 and also on August 1 of the same year with Stuart B. Robbins.

David A. Neill, Stephan A. Marshall, and I collected around the north and northwest crater rim in December 1973 and January 1974.

THE FLORA

Many of the collections in the following checklist were difficult to determine owing to lack of revisionary work. As monographic treatments are produced for various genera, many names included here will be found to be incorrect. The checklist is complete to 1980, but additional species have since been collected by W. D. Stevens.

A set of specimens collected in 1975 and 1977 was left at Universidad Centroamericana (UCA) at Managua, but the principal set of 1975 collections is contained in the Beal-Darlington Herbarium (MSC) of Michigan State University. These latter collections are preceded by A (Atwood), N (Neill), or AN (Atwood & Neill). Most of the specimens collected before 1975 by F. Seymour, D. Dudey, D. Moore, C. Nichols, S. Robbins, E. Narvaez S., D. Neill, A. Marshall, and me were owned by Mr. Frank Seymour, who kindly provided me access to his herbarium. This collection is now incorporated at the Missouri Botanical Garden (MO).

The classification of the fern families adopted here is authored by Crabbe et al. (1975). The classification of the angiosperm families is basically that of Cronquist (1968).

A total of 457 species are represented in the checklist, including 80 species of pteriodophytes distributed among 15 families and 33 genera, and 377 species of angiosperms representing 90 families and 256 genera. No gymnosperms are known from Mombacho. The largest fern families are the Aspleniaceae and Polypodiaceae with 24 and 16 species respectively. The largest angiosperm families are the Orchidaceae and Compositae with 87 and 29 species respectively.

It is unwise to speculate on the phytogeographic significance of most floristic elements of Mombacho because the species and their ranges are poorly known. Nevertheless several observations concerning phytogeography seem justified.

The large numbers of pteridophyte and orchid species are probably in part accounted for by their high fecundity and dispersibility. However, it is curious that the Gesneriaceae, also highly fecund and supposedly easily dispersed, is represented by only three species.

Five epiphytic orchids find their northernmost limits on Mombacho or central Nicaragua. These include: *Epidendrum lacustre, E. selaginella, Mesospinidium warscewiczii,* and *Pleurothallis convallaria.* The northerly range limits of these orchids and the absence of *Carpinus, Liquidambar,* and *Pinus* suggest that the flora is Costa Rican.

One endemic and one near endemic species are noted for Volcán Mombacho. The first species is *Maxillaria mombachoensis* (Orchidaceae), an attractive orange orchid of the *Maxillaria cucullata* complex and the second, *Freziera friedrichstaliana* (Theaceae), known otherwise only from Honduras.

List of Species

FERNS AND FERN ALLIES

ADIANTACEAE

Adiantum concinnum Willd. *Robbins 6254,* 1 August 1972 (MO). Lower cloud forest.

A. lunulatum (Roxb.) Burm. f. *Atwood 77120a,* 8 February 1977 (MSC). Very local in lower cloud forest.

A. macrophyllum Sw. *Atwood A48,* 30 April 1975 (MSC). Common in lower cloud forest.

A. trapeziforme L. *Atwood 77105,* 8 February 1977 (FSU, MO, MSC). Local in lower cloud forest.

Pityrogramma calomelanos L. *Seymour 6099,* 25 July 1972 (MO). Locally abundant in cloud forest.

P. ferruginea (Kunze) Maxon. *Atwood 3899,* 27 January 1970 (MO). Apparently uncommon in cloud forest.

Pteris altissima Poir. *Atwood 3909,* 27 January 1970 (VT). Lower cloud forest.

Vittaria cf. *remota* Fee. *Atwood 7742,* 3 February 1977 (FSU, MSC). Common elfin forest epiphyte.

ASPLENIACEAE

Asplenium abscissum Willd. *Neill N40,* 29 April 1975 (MSC); *Atwood A170,* 15 May 1975 (MSC). Local on crater rim and at Plan de las Flores.

A. cristatum Lam. *Atwood & Neill AN197,* 16 July 1975 (MSC). Lower and upper cloud forests.

A. formosum Willd. *Dudey & Moore 1966,* 9 January 1969 (MO); *Atwood & Neill AN93,* 2 July 1975 (MSC). Rare lithophyte on border of deciduous forest and cloud forest at Finca Las Delicias.

A. cf. *fragrans* Sw. *Dudey & Moore 1966a,* 9 January 1969 (MO).

A. hoffmanni Hieron. *Atwood & Neill AN57,* 1 July 1975 (MSC). Lower cloud forest.

A. pteropus Kaulf. *Atwood A13,* 29 April 1975 (MSC). Near northeast crater rim in elfin forest. Growing as an epiphyte.

A. cf. *pulchellum* Raddi. *Atwood 3911,* 27 January 1970 (MSC). Lower cloud forest.

A. radicans var. *partitum* (Klotzsch) Hieron. *Atwood 7776,* 6 February 1977 (MSC). Rare epiphyte of upper cloud forest.

Bolbitis cladorhizans (Sprengel) Ching. *Dudey & Moore 1968,* 9 January 1969 (MO). Lower cloud forest above Finca Las Delicias.

Ctenitis hemsleyana (Baker ex Hems.) Copel. *Atwood 77157,* 15 February 1977 (FSU). Locally common in shaded understory of elfin forest.

C. subincisa (Willd.) Ching. *Atwood & Neill AN190,* 16 July 1975 (MSC). Upper cloud forest.

Diplazium cristatum (Desr.) Alson. *Atwood A304,* 5 June 1975 (MSC). Common in elfin forest.

D. shepherdii (Sprengel) Link. *Atwood 3907,* 27 January 1969 (VT). Lower cloud forest.

D. striatastrum Lellinger. *Atwood, Marshall & Neill 6727,* 16 December 1973 (MO). Cloud forest.

Dryopteris karwinskyana (Mett.) Kuntze. *Atwood 77156,* 10 February 1977 (FSU, MSC). Locally common in elfin forest.

Elaphoglossum furfuraceum Christ. *Atwood 5451,* 9 April 1971 (VT). Elfin forest.

E. palmense Christ. *Neill N41,* 29 April 1975 (MSC); *Atwood A308,* 5 June 1975 (MSC); *Atwood & Neill AN196,* 16 July 1975 (MSC). Local epiphyte of upper cloud and elfin forests.

E. tectum (H. B. ex Willd.) Moore? *Atwood, Marshall & Neill 6724,* 16 December 1973 (MO). Apparently uncommon epiphyte of upper cloud and elfin forests.

E. sp. *Atwood A30,* 29 April 1975 (MSC); *Atwood A302,* 5 June 1975 (MSC). Elfin forest epiphyte at Plan de las Flores. Other species of *Elaphoglossum* undoubtedly occur on Volcán Mombacho.

Peltapteris peltata (Sw.) Morton. *Atwood 3913,* 27 January 1970 (MO); *Atwood, Marshall & Neill 6707,* 15 December 1973 (MO).

Polybotrya cervina (L.) Kaulf. *Atwood & Neill AN200,* 16 July 1975 (MSC). Upper cloud forest on east flank.

Polystichopsis pubescens (L.) Morton. *Atwood 3908,* 27 January 1970 (MO).

Tectaria heracleifolia (Willd.) Underw. *Atwood 77109,* 8 February 1977 (MSC). Uncommon terrestrial of lower cloud forest.

T. mexicana (Fee) Morton. *Atwood 77144,* 10 February 1977 (MSC, SEL). Lower cloud forest.

BLECHNACEAE

Blechnum cf. *divergens* (Kunze) Mett. *Atwood A42,* 30 April 1975 (MSC). Upper cloud and elfin forest terrestrial. This may be the same as *B. ensiforme.*

B. ensiforme (Liebm.) C. Chr. *Atwood, Marshall & Neill 6731,* 16 December 1973 (MO); *Neill N39,* 29 April 1975 (MSC). Upper cloud and elfin forest.

B. fragile (Liebm.) Morton & Lellinger. *Atwood, Marshall & Neill 6730,* 16 December 1973 (MO). Upper cloud and elfin forest.

B. lehmannii Hieron. *Atwood A292,* 5 June 1975 (MSC). Common terrestrial in shade of elfin forest.

B. occidentale L. *Dudey & Moore 1965,* 9 January 1969 (MO). Frequent in cloud and elfin forest.

B. pyramidatum (Lam.) Urb. *Nichols 2005,* 9 January 1969 (MO).

B. unilaterale Sw. *Atwood 77168,* 15 February 1977 (MSC). Local on eroded banks of upper cloud forest.

CYATHEACEAE

Cyathea sp. *Atwood A298a,* 5 June 1975 (MSC). Tree fern common at Plan de las Flores.

Nephelea mexicana (Schlecht. & Cham.) Tryon. *Atwood A344,* 10 July 1975 (MSC). Tree of elfin forest. Common locally.

DAVALLIACEAE

Nephrolepis pectinata (Willd.) Schott. *Atwood A14,* 29 April 1975 (MSC). Locally common in upper cloud forest about 900 m.

GLEICHENIACEAE

Gleichenia bifida (Willd.) Sprengel. *Atwood A17,* 29 April 1975 (MSC). Common fern of disturbed areas of crater rim and elfin forest. Often produces nearly impenetrable entanglements.

HYMENOPHYLLACEAE

Hymenophyllum myriocarpum Hook. *Atwood 7770,* 6 February 1977 (US). Elfin forest epiphyte.

H. polyanthos (Sw.) Sw. *Atwood, Marshall & Neill 6708, 6723,* 15 December 1973 (MO).

Trichomanes capillaceum L. *Atwood 3902,* 27 January 1970 (MO). Cloud forest.

T. krausii Hook. & Grev. *Atwood 5468b,* 9 April 1971 (MO). Elfin forest.

T. pyxidiferum L. *Atwood 7769,* 6 February 1977 (US). Elfin forest epiphyte.

T. radicans Sw. *Atwood 3900,* 27 January 1970 (MO); *Neill N45,* 29 April 1975 (MSC). Common in elfin forest.

T. rigidum Sw. *Atwood, Marshall & Neill 6722,* 16 January 1972 (MO). Cloud and elfin forests.

LOPHOSORIACEAE

Lophosoria quadripinnata (Gmel.) C. Chr. *Atwood A297,* 5 June 1975 (MSC). Plan de las Flores.

LYCOPODIACEAE

Lycopodium callitrichifolium Mett. *Atwood 7774,* 6 February 1977 (US). Very rare epiphyte in elfin forest.

L. dichotomum Jacq. *Atwood & Neill AN65,* 1 July 1975 (MSC). Epiphyte of lower cloud forest.

L. linifolium L. *Atwood 7741,* 3 February 1977 (MSC). Occasional epiphyte of elfin forest.

L. taxifolium Sw. *Atwood 5454,* 9 April 1972 (MO). Epiphyte.

L. verticillatum var. *parvifolium* (Wercklé ex Nessel) Lellinger. *Atwood 7740,* 3 February 1977 (US). Very rare epiphyte in elfin forest.

MARATTIACEAE

Marattia interposita Christ. *Atwood & Neill AN188,* 16 July 1975 (MSC). Upper cloud and elfin forest.

OPHIOGLOSSACEAE

Ophioglossum reticulatum L. *Atwood A353,* 10 July 1975 (MSC). Very abundant at disturbed area of Plan de las Flores.

POLYPODIACEAE

Grammitis blepharodes (Maxon) Seymour. *Atwood 5453,* 9 April 1971 (MO); *Atwood, Marshall & Neill 6728,* 16 December 1973 (MO). Upper cloud and elfin forest epiphyte.

G. serrulata (Sw.) Sw. *Atwood A25,* 29 April 1975 (MSC). Upper cloud and elfin forest.

G. staheliana (Posth.) Lellinger. *Atwood 7773,* 6 February 1977 (US). Apparently a very rare epiphyte of elfin forest.

Microgramma lycopodioides (L.) Copel. *Neill N27,* 26 April 1975 (MSC). Common at Plan de las Flores.

Phlebodium aureum (L.) J. Smith. *Atwood A163,* 15 May 1975 (MSC). Common at Plan de las Flores.

Pleopeltis percussa (Cav.) Hook. & Grev. *Atwood & Neill AN63,* 1 July 1975 (MSC). Epiphytic in lower cloud forest.

P. revoluta (Sprengel ex Willd.) A. R. Smith (syn. *Polypodium astrolepis* Liebm.). *Atwood 7733,* 3 February 1977 (US).

Polypodium angustifolium Sw. *Atwood 7738,* 3 February 1977 (MSC). Very common epiphyte of elfin forest.

P. dissimile L. *Atwood 3906,* 27 January 1970 (MO); *Neill N43,* 29 April 1975 (MSC). Lower cloud forest on east flank. About 800 m.

P. cf. *fructuosum* Maxon & Weath. *Robbins 6251,* 1 August 1972 (MO). Probably also *Seymour 6098,* 25 July 1972 (MO). Lower cloud forest.

P. loriceum L. *Atwood, Marshall & Neill 6725,* 16 December 1973 (MO). Northwest crater rim. *Atwood A167,* 15 May 1975 (MSC). Plan de las Flores.

P. plebejum Schlecht. & Cham. *Atwood 3905,* 27 January 1970 (MO). Cloud forest inhabitant.

P. plesiosorum Kunze. *Seymour 6097,* 25 July 1972 (MO). Lower cloud forest.

P. plumula Humb. & Bonpl. ex Willd. *Atwood & Neill AN91,* 2 July 1975 (MSC). Growing on boulders in margin of cloud and deciduous forest.

P. polypodioides (L.) Watt var. *polypodioides. Atwood & Neill AN92,* 2 July 1975 (MSC). In margin of deciduous and lower cloud forest.

P. wiesbaueri Sod. *Atwood 5452,* 9 April 1971 (VT). Upper cloud forest.

SCHIZEACEAE

Lygodium venustum Sw. *Seymour 6096,* 25 July 1972 (MO); *Atwood & Neill AN86,* 2 July 1975 (MO). In lower cloud and deciduous forests.

SELAGINELLACEAE

Selaginella sp. *Atwood 7730,* 3 February 1977 (MSC). Prostrate species common in elfin forest.

THELYPTERIDACEAE

Thelypteris balbisii (Sprengel) Ching. *Baker 2449* (GH).

T. columbiana (C. Chr.) Morton. *Atwood A26,* 29 April 1975 (MSC). Upper cloud and elfin forests.

T. dentata (Forsk.) E. St. John. *Atwood AA44,* 30 April 1975 (MSC). Upper cloud forest.

T. mombachensis Gomez. *Atwood A304a,* 5 June 1975 (MSC); *Atwood, Marshall & Neill 6726,* 16 December 1973 (MO). Elfin forest at Plan de las Flores.

FLOWERING PLANTS

ACANTHACEAE

Aphelandra deppeana Schlecht. & Cham. *Dudey & Moore 1959,* 9 January 1969 (MO).

A. aurantiaca (Scheidw.) Lindl. *Atwood 77108,* 8 February 1977 (FSU, MO, MSC). Locally common in deciduous forest at Finca Las Delicias. Flowers canary yellow.

Blechum brownei Juss. *Atwood A156,* 15 May 1975 (MSC). Weed of disturbed elfin forest. This and the following may not be distinct.

B. pyramidatum (Lam.) Urb. *Nichols 2005,* 9 January 1969 (MO).

Dyschoriste skutchii Leonard. *Narvaez 3888,* 27 January 1970 (MO).

Ruellia inundata H.B.K. *Dudey & Moore 1960,* 9 January 1969 (MO). Lower cloud forest.

AMARANTHACEAE

Achyranthes aspera L. *Atwood A55,* 30 April 1975 (MSC). In disturbed area by vacation house.

Alternanthera williamsonii Standl. *Narvaez 3881,* 27 January 1970 (MO).

Chamissoa altissima (Jacq.) H.B.K. *Dudey & Moore 1977,* 9 January 1969 (MO). Disturbed cloud forest above Finca Las Delicias.

Cyathula achyranthoides (H.B.K.) Moquin. *Dudey & Moore 1979,* 9 January 1969 (MO).

Gomphrena decumbens Jacq. *Atwood & Neill AN89,* 2 July 1975 (MSC). In pastures and roadsides at Finca Las Delicias.

Iresine celosia L. *Dudey & Moore 1977,* 9 January 1969 (MO). Lower cloud forest. Locally abundant and often sold in markets for decoration.

ANACARDIACEAE

Mangifera indica L. *Atwood 3921,* 27 January 1970 (MO). An escape in deciduous forest areas.

APOCYNACEAE

Echites cf. *turrigera* Woodson. *Atwood & Neill AN71,* 2 July 1975 (MSC). Deciduous forest.

Plumeria rubra L. Not collected but often observed as a conspicuous element of the deciduous forest. This is the national flower of Nicaragua. The Mombacho plants have white flowers.

Rauvolfia littoralis Rusby. *Atwood & Neill AN84,* 2 July 1975 (MSC). Common herb in deciduous forest area near Finca Las Delicias.

Stemmodenia donnell-smithii (Rose) Woodson. *Atwood & Neill AN69,* 1 July 1975 (MSC). In deciduous forest.

AQUIFOLIACEAE

Ilex aff. *carpenterae* Standl. *Atwood A192,* 15 May 1975 (MSC). Collected at Plan de las Flores.

ARACEAE

Anthurium cubense Engl. *Atwood & Neill AN82,* 2 July 1975 (MSC). Common epiphyte in trees of upper deciduous forest areas around Finca Las Delicias. This species forms large rosettes.

A. scandens (Aubl.) Engl. *Atwood A50,* 30 April 1975 (MSC); *Neill N56,* 29 April 1975 (MSC). Lower cloud forest epiphyte common in coffee plantations at Finca Cutirre.

Dieffenbachia aurantiaca Engl. *Atwood & Neill AN206,* 16 July 1975 (MSC). Upper cloud forest ravine above Finca Las Delicias about 900 m.

D. seguine L. *Atwood A212,* 18 May 1975 (MSC). Common terrestrial in deep shade at about 600 m.

Monstera acuminata C. Koch. *Atwood & Neill AN66,* 1 July 1975 (MSC). Common liana flanking tall trees of lower cloud forest.

M. adansonii Schott. *Atwood AA2,* 27 April 1975 (MSC); *Atwood A172,* 15 May 1975 (MSC); *Neill N28,* 27 April 1975 (MSC); *Atwood A363,* 10 July 1975 (MSC). Common liana of cloud forests.

Syngonium podophyllum Schott. *Atwood & Neill AN90,* 2 July 1975 (MSC). Common in deciduous forest areas.

ARALIACEAE

Oreopanax xalapense (H.B.K.) Dcne. & Planch. *Atwood A299, A361,* 10 July 1975 (MSC). Frequent in upper cloud and elfin forests.

ARECACEAE

Chamaedorea sp. *Atwood A171,* 15 May 1975 (MSC). Cloud and elfin forests, mostly in disturbed areas.

Undetermined. *Atwood & Neill AN50,* 1 July 1975 (MSC). Lower cloud forest near Finca Cutirre.

ARISTOLOCHIACEAE

Aristolochia anguicida Jacq. *Atwood & Neill AN81,* 2 July 1975 (MSC). In deciduous forest near Finca Las Delicias, growing near the following species. Collection in fruit only.

A. cf. *maxima* Jacq. *Atwood & Neill AN77,* 2 July 1975 (MSC). Deciduous forest.

ASCLEPIADACEAE

Asclepias curassavica L. *Robbins 6260,* 1 August 1972 (MO). Lower cloud and deciduous forests.

Gonolobus sp. *Neill 1363,* 3 February 1977 (UCA). Vine of cloud forest.

BEGONIACEAE

Begonia filipes Benth. *Dudey & Moore 2004,* 9 January 1969 (MO). Cloud forest.

B. plebeja Liebm. *Dudey & Moore 1985,* 9 January 1969 (MO). Lower cloud forest.

BIGNONIACEAE

Arrabidaea mollissima Bur. & K. Schum. *Dudey & Moore 1957,* 9 January 1969 (MO). Probably collected in deciduous forest.

Cydista diversifolia (H.B.K.) Miers. *Atwood & Neill AN207,* 16 July 1975 (MSC). In deciduous forests below Finca Las Delicias.

BIXACEAE

Bixa orellana L. *Atwood & Neill AN67,* 1 July 1975 (MSC). Common in lower cloud forest above Finca Cutirre.

BOMBACACEAE

Ceiba sp. No collection made. Forms immense crowns supporting numerous epiphytes. Throughout deciduous forest.

Quararibea funebris (Llave) Vischer. *Neill 1008,* 3 October 1976 (FSU). Tree about 25 m tall. Lower cloud forest.

BORAGINACEAE

Cordia dentata Poir. *Atwood & Neill AN75,* 2 July 1975 (MSC). Finca Las Delicias in deciduous forest.

Heliotropium indicum L. *Atwood & Neill AN74,* 2 July 1975 (MSC). Deciduous forest near Finca Las Delicias.

BROMELIACEAE

Catopsis sp. *Atwood & Neill AN205,* 16 July 1975 (MSC). Cloud forest.

Guzmania angustifolia (Baker) Wittm. *Neill 7582,* 8 August 1976 (MO).

G. compacta Mez. *Neill 7583,* 8 August 1976 (MO).

G. lingulata var. *minor* (Mez) L. B. Smith. *Atwood & Neill AN203,* 16 July 1975 (MSC). Common epiphyte of cloud forest. Very attractive species with brilliant red bracts.

G. monostachia (L.) Rusby ex Mez. *Atwood & Neill AN204,* 16 July 1975 (MSC). Common epiphyte of cloud forests. The contrasting black veined lower bracts and red upper bracts distinguish this from other species of *Guzmania* on Mombacho.

G. nicaraguensis Mez & C. F. Baker. *Atwood & Neill AN306,* 30 July 1975 (MSC). Uncommon at crater rim. Elfin forest epiphyte.

Pitcairnia heterophylla Beer. *Atwood 7796,* 8 February 1977 (MSC). Epiphyte of deciduous forest.

P. imbricata (Brongn.) Regel. *Neill 7580,* 8 August 1976 (UCA). Common in elfin forest at Plan de las Flores.

Tillandsia bulbosa Hook. *Atwood & Neill AN58,* 1 July 1975 (MSC). Lower cloud forest.

T. fasciculata Sw. *Atwood 5459,* 9 April 1971 (VT). Cloud and elfin forest epiphyte.

T. festucoides Brongn. ex Mez. *Atwood & Neill AN56,* 1 July 1975 (MSC). Lower cloud forest.

T. leiboldiana Schlecht. *Neill 7529,* 7 August 1976 (MO).

T. monadelpha (E. Morr.) Baker. *Atwood & Neill AN52,* 1 July 1975 (MSC). Lower cloud forest.

T. schiediana Steud. *Atwood & Neill AN80,* 2 July

1975 (MSC). Most abundant in dry deciduous forest.

T. usneoides L. *Atwood 3916,* 27 January 1970 (MO). Common cloud forest epiphyte.

Vriesea pedicellata (Mez & Werckle) Sm. & Pitt. *Atwood A16,* 29 April 1975 (MSC). Elfin forest epiphyte.

V. sp. *Atwood A15,* 29 April 1975 (MSC). Upper cloud forest.

BURSERACEAE

Bursera simaruba (L.) Sarg. *Atwood & Neill AN214,* 16 July 1975 (MSC). Common tree of deciduous forest.

CAMPANULACEAE

Lobelia laxiflora H.B.K. *Atwood 5477,* 9 April 1971 (VT). Elfin forest.

CAPPARACEAE

Forchhammeria matudai Lundell. *Atwood 77116,* 8 February 1977 (MSC). Lower cloud forest tree.

CAPRIFOLIACEAE

Viburnum hartwegii Benth. *Atwood A200,* 14 May 1975 (MSC). In disturbed sites of elfin forest at Plan de las Flores.

CARICACEAE

Carica papaya L. Not collected but observed in lower cloud forest in deep shade.

CARYOPHYLLACEAE

Drymaria cordata (L.) Willd. ex Roem & Schult. *Neill 1003,* 3 October 1976 (UCA). Coffee plantation weed.

CHLORANTHACEAE

Hedyosmum montanum W. Burger. *Neill 408,* 28 May 1976 (MSC). Common elfin forest tree.

CHRYSOBALANACEAE

Chrysobalanus icaco L. *Robbins 6261,* 1 August 1972 (MO). Probably lower cloud forest.

COCHLOSPERMACEAE

Cochlospermum vitifolium Willd. *Atwood & Neill AN78,* 2 July 1975 (MSC). Common deciduous forest component, but found as high as 800 m.

COMBRETACEAE

Combretum fruticosum (Loeff.) Stuntz. *Dudey & Moore 1951,* 9 January 1969 (MO). Probably lower cloud forest.

COMMELINACEAE

Campelia hirsuta Standl. *Dudey & Moore 1974a,* 9 January 1969 (MO).

C. zanonia (L.) H.B.K. *Neill N50,* 29 April 1975 (MSC). Common in cloud forest.

Commelina erecta L. *Narvaez 3884,* 27 January 1970 (MO). Cloud and elfin forest.

Dichorisandra hexandra (Aubl.) Standl. *Atwood & Neill AN186,* 15 May 1975 (MSC); *Neill N49,* 29 April 1975 (MSC). Local in cloud forests.

Phaeosphaerion persicariaefolium (DC.) C. B. Clarke. *Atwood A168,* 15 May 1975 (MSC). On disturbed sites at Plan de las Flores.

Tripogandra cf. *cumanensis* (Kunth) Woodson. *Atwood A44,* 30 April 1975 (MSC). In disturbed sites at Plan de las Flores.

COMPOSITAE

Baccharis trinervis (Lam.) Pers. *Atwood A7,* 29 April 1975 (MSC); *Atwood A43,* 30 April 1975 (MSC). Disturbed areas near vacation house.

Bidens pilosa L. Reported by F. C. Seymour (pers. comm.).

B. riparia H.B.K. *Narvaez 3891,* 27 January 1970 (MO).

B. squarrosa H.B.K. *Atwood 3924,* 27 January 1970 (MO).

Chaptalia nutans (L.) Hemsl. *Seymour 6105,* 25 July 1972 (VT). Common in disturbed areas of cloud forest.

Chromolaena odorata (L.) King & Robinson. *Atwood A54,* 29 April 1975 (MO). Disturbed site at vacation house.

Cirsium mexicanum DC. *Atwood 5479,* 9 April 1971 (MO); *Atwood A46,* 30 April 1975 (MSC); *Neill N60,* 30 April 1975 (MSC). Disturbed cloud forest.

Clibadium leiocarpum Steetz. *Atwood A161,* 15 May 1975 (MSC). Small tree in elfin forest.

Conyza chilensis Sprengel. *Atwood A183,* 15 May 1975 (MSC). Disturbed site at Plan de las Flores.

Delilea biflora (L.) Kuntze. *Atwood 3923,* 27 January 1970 (MO). Disturbed cloud forest.

Erectites hieracifolia (L.) R. *Nichols 2014,* 9 January 1969 (MO). Disturbed cloud forest.

Erigeron bonariensis L. *Narvaez 3895,* 27 January 1970 (MO). Disturbed area in cloud forest above Finca Las Delicias.

Eupatorium araliaefolium Less. *Atwood 77142,* 20 September 1977 (MSC). Small tree of disturbed cloud forest on northeast flank.

E. sinclairii (Benth.) King & Robinson. *Narvaez 3894,* 27 January 1970 (MO). In disturbed area of cloud forest at vacation house.

Fleischmannia pratensis (Klatt) King & Robinson. *Atwood A155,* 15 May 1975 (MO). Disturbed site at Plan de las Flores.

Galinsoga cf. *ciliata* (Raf.) Blake. *Narvaez 3893,* 27 January 1970 (MO). Disturbed cloud forest.

Hebeclinium macrophyllum (L.) DC. *Neill 775,* 19 September 1976 (MSC). Deciduous forest weed.

Liabum cf. *discolor* (Hook. & Arn.) Benth. & Hook. ex Hemsl. *Atwood A188a,* 15 May 1975 (MSC). Rare in disturbed elfin forest.

Melampodium divaricatum (L. Rich. ex Pers.) DC. *Atwood & Neill AN85,* 2 July 1975 (MSC). Deciduous forest.

Melanthera nivea (L.) Small. *Dudey & Moore 1961,* 9 January 1969 (MO). Cloud forest.

Neurolaena lobata R. Br. *Atwood 77107,* 8 February 1978 (MSC). Weed of disturbed cloud forest.

Perymenium nicaraguense Blake. *Dudey & Moore 1991,* 9 January 1969 (MO).

Pseudelephantopus spicatus (Juss.) C. F. Baker. *Nichols 2011,* 9 January 1969 (MO). Weed of disturbed cloud forest.

Senecio arborescens Steetz in Seem. *Neill N38,* 30 April 1975 (MSC); *Atwood A21,* 29 April 1975 (MSC). Common tree in upper cloud forest.

Spilanthes americana (L. f.) Hieron. ex Sodiro. *Atwood A19,* 29 April 1975 (MSC); *Atwood A175,* 15 May 1975 (MSC). On crater rim and at vacation house.

S. ocymifolia (Lam.) A. H. Moore. *Narvaez 3892,* 27 January 1970 (MO).

Verbesina fraseri Hemsl. *Dudey & Moore 1963,* 9 January 1969 (MO).

Vernonia canescens H.B.K. *Atwood A181,* 15 May 1975 (MO). Common in disturbed elfin forest.

V. patens H.B.K. *Atwood & Neill 1567,* 14 March

1977 (FSU). Lower cloud forest weed at Finca Cutirre.

CONVOLVULACEAE

Ipomoea alba L. *Atwood 77112,* 8 February 1970 (MSC). Roadside vine at Finca Cutirre.

Merremia tuberosa (L.) Rendle. *Neill 1565,* 14 March 1977 (MSC). Collected by a local resident for decoration.

M. umbellata (L.) Hallier f. *Atwood 77146,* 10 February 1977 (MSC). Locally common lower cloud forest vine.

Quamoclit hederifolia (L.) G. Don. *Dudey & Moore 1956,* 9 January 1969 (MO); *Atwood 77145,* 10 February 1977 (MSC).

COSTACEAE

Costus cf. *sanguineus* Donn.-Sm. *Nichols 1998,* 9 January 1969 (MO).

CRUCIFERAE

Rorippa indica (L.) Hieron. *Narvaez 3886,* 27 January 1970 (MO). In disturbed cloud forest.

CUCURBITACEAE

Melothria pendula L. *Atwood A180,* 15 May 1975 (MSC). Common vine of disturbed cloud forest.

Momordica charantia L. *Atwood 77117,* 8 February 1977 (MSC). Weed of coffee plantations.

Rytidostylis ciliata (Oerst.) Monachino. *Atwood & Neill AN304,* 30 July 1975 (MSC). Disturbed forest areas.

CYPERACEAE

Carex cf. *donnell-smithii* L. H. Bailey. *Atwood A162,* 15 May 1975 (MSC). Common herb of elfin and cloud forests. Spikes seem a bit short for the above species.

C. polystachya Sw. ex Wahl. *Atwood, Marshall & Neill 6733,* 16 January 1973 (MO); *Atwood A197,* 14 May 1975 (MSC). Not uncommon in elfin forest.

Cyperus mutisii (H.B.K.) Griseb. *Robbins 6256,* 1 August 1972 (MO).

C. tenuis Sw. *Dudey & Moore 1973,* 9 January 1969 (MO). Common in disturbed areas at low and high elevations.

C. sp. *Atwood A182,* 15 May 1975 (MSC). In open areas at Plan de las Flores.

Rhynchospora polyphylla Vahl. *Atwood A179,* 15 May 1975 (MSC). Common in disturbed areas of elfin forest.

Uncinnia hamata (Sw.) Urban. *Atwood 5457,* 9 April 1971 (MO). Common in elfin and cloud forests.

ELAEOCARPACEAE

Muntingia calabrura L. *Seymour 6103,* 25 July 1972 (MO). Common tree of deciduous forest area.

ERICACEAE

Cavendishia crassifolia (Benth.) Hemsl. *Atwood A35,* 30 April 1975 (MSC); *Neill N24,* 26 April 1975 (MSC). Abundant in upper cloud and elfin forests.

Satyria warszewiczii Klotzsch. *Neill 1101,* 25 October 1976 (FSU). Elfin forest tree.

Sphyrospermum majus Griseb. *Atwood A11,* 29 April 1975 (MSC). Common epiphyte of upper cloud and elfin forests.

EUPHORBIACEAE

Acalypha diversifolia Jacq. complex. *Atwood 7744,* 3 February 1977. Locally common tree of elfin forest.

A. setosa A. Rich. *Atwood & Neill AN48,* 1 July 1975 (MSC). Common weed of coffee plantation.

Croton cf. *pungens* Jacq. *Neill 1407,* 8 February 1977 (MSC). Tree of deciduous forest below Finca Las Delicias.

Euphorbia cf. *graminea* Jacq. *Narvaez 3883,* 27 January 1970 (MO). Common in disturbed cloud forest area.

Ricinus communis L. *Dudey & Moore 1952,* 9 January 1969 (MO). Below upper cloud forest level.

Sapium macrocarpum Muell. Arg. *Atwood 77147* (MSC). Common tree of cloud forest.

FLACOURTIACEAE

Casearia corymbosa Jacq. *Atwood & Neill AN213,* 16 July 1975 (MSC). Common shrub in deciduous forest near Finca Las Delicias.

GESNERIACEAE

Achimenes misera Lindl. *Atwood, Marshall & Neill 6736,* 16 December 1973. Apparently rare terrestrial on crater rim.

Columnea rubricaulis Standl. ex Yuncker. *Atwood 5476,* 9 April 1971 (MO). Common epiphyte of cloud and elfin forests.

Kohleria spicata (H.B.K.) Oersted. *Atwood 7737,* 3 February 1977 (MSC). Common terrestrial herb on disturbed embankments of access road on north flank.

GRAMINEAE

Arundinella deppeana Nees. *Atwood A40,* 30 April 1975 (MO). Common in disturbed areas at Plan de las Flores.

Eleusine indica (L.) Gaertner. *Dudey & Moore 1970,* 9 January 1969 (MO). Common herb of lower cloud forest.

Isachne arundinacea (Sw.) Griseb. *Atwood A10,* 29 April 1975 (MO, MSC). Vine forming impenetrable mats in elfin forest.

Lasiacis ruscifolia (H.B.K.) Hitchc. *Dudey & Moore 1948,* 9 January 1969 (MO). Common in disturbed areas of cloud forests.

Oplismenus burmannii (Retz.) Beauv. *Dudey & Moore 1972,* 9 January 1969 (VT); *Atwood A158,* 15 May 1975 (MSC). Locally common in upper cloud and elfin forests.

O. hirtellus (L.) Beauv. *Atwood A10a,* 29 April 1975 (MSC). Common in elfin forest.

Panicum sphaerocarpon Ell. *Neill 868,* 26 September 1976 (UCA).

P. trichoides Sw. *Dudey & Moore 1971,* 9 January 1969 (VT). Probably from lower cloud forest or deciduous forest.

Paspalum conjugatum Berg. *Robbins 6255a,* 1 August 1972 (MO).

P. paniculatum L. *Seymour 7521,* 6 August 1976 (MO). Frequently the dominant grass in upper cloud and elfin forests.

Setaria paniculifera (Steudel) Fourn. *Atwood A360,* 10 July 1975 (MSC). Common in disturbed elfin forest with *Arundinella* and *Epidendrum radicans.*

Sporobolus indicus (L.) R. Br. *Atwood A199,* 14 May 1975 (MO). Common in disturbed elfin forest.

GUTTIFERAE

Clusia salvinii Donn.-Sm. *Atwood A311,* 5 June 1975 (MSC); *Neill N222,* 7 June 1975 (MSC). Very common especially in forest where nearly solid stands are to be found along the most windswept ridges.

HAEMODORACEAE

Xiphidium caeruleum Aubl. *Neill 2922.* Common herb of disturbed embankments.

HELICONIACEAE

Heliconia cf. *collinsiana* Griggs. Observed near Finca Cutirre. Banana sized plant with pendulous inflorescences.

H. latispatha Benth. *Williams & Molina 200027* (F).

LABIATAE

Hyptis cf. *mociniana* Benth. *Atwood A185,* 15 May 1975 (MSC). Weed in open disturbed area of elfin forest.

H. verticillata Jacq. *Nelson 7596,* 8 August 1976 (MO).

Salvia occidentalis Sw. *Nichols 2006,* 9 January 1969 (MO). In disturbed areas of cloud forest.

LAURACEAE

Ocotea veraguensis (Meisnn.) Mez. *Baker 2493,* 20 February 1903 (MSC). "Small tree, 20–30 ft. high .... Flowers with strong and pleasant odor .... Occasional in high forests" (from Baker herbarium sheet).

LEGUMINOSAE

Cassia grandis L. f. *Neill 1561,* 14 March 1977. Deciduous forest.

C. spectabilis DC. *Neill 2723,* 12 October 1977 (MO, UCA).

Desmodium affine Schlecht. *Nichols 2001,* 9 January 1969 (VT).

D. aff. *costaricense* (Schindl.) Standl. *Atwood 7734,* 3 February 1977 (MSC). Occasional in disturbed areas of elfin forest.

D. cf. *incanum* DC. *Neill N227,* 6 June 1975 (MSC). Cloud forest.

D. sp. *Neill 1005,* 30 October 1976 (MSC). Lower cloud forest.

Gliricidia sepium (Jacq.) Steud. *Neill 1565,* 14 March 1977 (MSC). Tree cultivated for shade in coffee plantation.

Inga sapindoides Willd. *Neill 1406,* 8 February 1977 (FSU). Deciduous forest tree, perhaps planted.

Mimosa pudica L. Not collected. Common in open disturbed areas of cloud forest.

Mucuna argyrophylla Standl. *Neill 777,* 19 September 1976 (MSC). Cloud forest vine.

Schizolobium parahybum (Vell.) Blake. *Neill s.n.* (MSC). Tree of lower cloud and deciduous forest.

LENTIBULARIACEAE

Utricularia cf. *praetermissa* P. Taylor. Possibly a new species. *Atwood A351,* 10 July 1975 (MSC); *Atwood & Neill AN307,* 30 July 1975 (MSC). Locally abundant epiphyte in cloud and elfin forest.

LILIACEAE

Hippeastrum cf. *solandriflorum* Herb. *Atwood A364,* 10 July 1975 (MSC). Probably once cultivated. Plan de las Flores.

Hypoxis decumbens L. *Neill N226,* 5 June 1975 (MSC). Disturbed areas of cloud forest. Probably common.

MALPIGHIACEAE

Byrsonima crassifolia (L.) H.B.K. *Neill 2640.* Small tree of deciduous forest.

MALVACEAE

Hibiscus rosa-sinensis L. *Atwood A191,* 15 May 1975 (MSC). Once cultivated at Plan de las Flores but now abandoned.

Pavonia rosea Schlecht. *Neill 875,* 26 September 1976 (FSU).

Sida acuta Burm. *Robbins 6273,* 1 August 1972 (MO). Common weed of deciduous forest.

MARANTACEAE

Calathea macrosepala var. *macrosepala* K. Schum. *Atwood & Neill AN192,* 16 July 1975 (MSC). Common in forest edges of lower cloud forest.

Maranta arundinacea L. *Atwood A357,* 10 July 1975 (MSC). Common in coffee plantations on north flank, but probably more widespread in lower cloud forest.

MARCGRAVIACEAE

Marcgravia brownei (Tr. & Planch.) Krug & Urban. *Atwood A22,* 29 April 1975 (MSC); *Neill N223,* 7 June 1975 (MSC). Common vine of elfin forest.

MELASTOMATACEAE

Arthrostema ciliata R. & P. *Atwood A188,* 15 May 1975 (MSC). Uncommon vine of disturbed elfin forest.

Centradenia cf. *inaequilateralis* (Schlecht. & Cham.) G. Don. *Narvaez 3926,* 27 January 1970 (MO). Disturbed area of cloud forest above Finca Las Delicias.

Clidemia or *Henriettea*? Perhaps a new species. *Atwood A350,* 10 July 1975 (MSC). Common understory shrub of elfin forest. Very distinctive for its dense bristles distributed throughout the plant.

Conostegia oerstediana Berg ex Triana. *Neill N34,* 29 April 1975 (MSC); *Atwood A174,* 15 May 1975 (MSC). Small tree occasional at vacation house and Plan de las Flores.

C. subcrustulata (Beurl.) Triana. *Atwood & Neill AN209,* 16 July 1975 (MSC). In deciduous forest area below Finca Las Delicias.

Miconia laevigata (L.) DC. *Atwood & Neill AN53,* 1 July 1975 (MSC). Near Finca Cutirre in lower cloud forest.

M. minutiflora DC. *Atwood 3922,* 27 January 1970 (VT).

M. cf. *theazans* (Bonpl.) Cogn. *Neill N35,* 29 April 1975 (MSC). Above Finca Las Delicias in disturbed areas of cloud forest.

Monochaetum deppeanum (Schlecht. & Cham.) Naud. *Atwood A173,* 15 May 1975 (MSC). Common in open areas of elfin forest. This species ranges north to Mexico and southward to the island of Omotepe in Lake Nicaragua.

Ossaea micrantha (Sw.) Macf. *Neill 783,* 19 September 1976 (MSC). Cloud forest.

Tibouchina longifolia (Vahl.) Baill. *Atwood 7767,* 6 February 1977 (FSU). Common in disturbed elfin forest.

MELIACEAE

Trichilia glabra L. *Atwood 7745,* 8 February 1977 (MSC). Common at smaller crater rims at Plan de las Flores and deciduous forest.

MENISPERMACEAE

Cissampelos pareira L. *Neill 998,* 3 October 1976 (MSC). Deciduous forest vine.

MOLLUGINACEAE

Mollugo verticillata L. *Atwood & Neill AN88,* 2 July 1975 (MSC). Weed in open areas at Finca Las Delicias.

MORACEAE

Cecropia peltata L. *Atwood & Neill AN70,* 1 July

1975 (MSC). Common tree nearly everywhere in disturbed areas.

Ficus sp. Observed in lower cloud forest.

MUSACEAE

Musa paradisiaca L. Not collected but observed at Plan de las Flores. Undoubtedly planted.

MYRSINACEAE

Ardisia minor Standl. *Atwood 5475,* 9 April 1971 (MO). Elfin forest.

A. nigropunctata Oerst. *Neill 1331,* 21 November 1976 (FSU).

A. oblanceolata Standl. *Atwood 7749,* 3 February 1977 (MSC).

A. revoluta H.B.K. *Neill 1402,* 8 February 1977 (FSU). Lower cloud forest.

Rapanea cf. *ferruginea* Mez. *Atwood A159,* 15 May 1975 (MSC). Common elfin forest component.

MYRTACEAE

Eugenia oerstedeana Berg. *Neill 1403,* 8 February 1977 (UCA).

Myrcianthes fragrans (Sw.) McVaugh. *Neill N225,* 7 June 1975 (MSC). Common in elfin forest.

Psidium × *hypoglaucum* Standl. *Atwood A160,* 15 May 1975 (MSC). In disturbed area of elfin forest and probably cultivated.

Syzygium jambos (L.) Alston. *Neill N21,* 26 April 1975 (MSC); *Atwood AA43,* 30 April 1975 (MSC). Near Finca Las Delicias. Probably cultivated.

NYCTAGINACEAE

Cryptocarpus globosus H.B.K. *Dudey & Moore 1978,* 9 January 1969 (MO).

Mirabalis jalapa L. *Robbins 6528,* 1 August 1972 (MO); *Atwood A358,* 10 July 1975 (MSC). In shaded areas about coffee plantations.

M. violacea Heimerl. *Atwood & Neill AN87,* 2 July 1975 (MSC). In deciduous forests at Finca Las Delicias.

ORCHIDACEAE

Bletia florida (Salisb.) R. Br. *Atwood 77300,* March 1977 (Live collection). Occurs with *B. purpurea,* but no intermediates were observed.

B. purpurea (Lam.) DC. *Atwood 77160,* 15 February 1977 (SEL). Common in open dry areas at Plan de Las Flores.

Brassavola nodosa (L.) Lindl. Not collected but not uncommon in deciduous forest.

Catasetum maculatum L. C. Rich. *Atwood A32,* 30 April 1975 (MSC). In dry deciduous forests.

Caularthron bilamellatum (Rchb. f.) Schultes. *Neill 1566,* 14 March 1977 (SEL). Cleistogamous population in deciduous forests.

Clowesia russelliana (Hook.) Dodson. *Atwood 77135a,* 10 February 1977 (Live collection made, SEL). Uncommon in deciduous forests.

Cyrtopodium sp. Occasional epiphyte in deciduous forests below Finca Las Delicias. Living collection presently being grown for determination.

Dichaea graminoides (Sw.) Lindl. *Atwood A296,* 5 June 1975 (MSC). Occasional in elfin forest.

D. cf. *muricata* (Sw.) Lindl. *Atwood A28,* 29 April 1975 (MSC). Upper cloud and elfin forest.

D. aff. *rendlei* Gleason. *Atwood A347,* 10 July 1975 (MSC). Very similar to *D. panamensis,* but ovary is muricate. Elfin forest.

D. cf. *tuerckheimii* Schltr. *Atwood A207,* 14 May 1975 (MSC). Collection is sterile, but the small size suggests this species. Elfin forest.

Elleanthus cf. *aurantiacus* Rchb. f. *Neill N42,* 29 April 1975 (MSC); *Atwood A184,* 15 May 1975 (MSC). Very common epiphyte of elfin forest.

E. cynarocephalus (Rchb. f.) Rchb. f. *Atwood A301,* 5 June 1975 (MSC); *Atwood, Marshall & Neill 6742,* 17 December 1973 (MO). Abundant epiphyte in elfin forest.

E. graminifolius (Barb. Rodr.) Løjtnant. *Atwood, Marshall & Neill 6743,* 17 December 1973 (MO); *Atwood A165,* 15 May 1975 (MSC). Common in elfin forest.

E. hymenophorus Rchb. f. *Neill N32,* 30 April 1975 (MSC); *Atwood A186,* 15 May 1975 (MSC). Common in upper cloud and elfin forest.

Encyclia chacaoensis (Rchb. f.) Dressl. & Pollard. *Atwood A2,* 27 April 1975 (MSC). Common in lower cloud and deciduous forests.

E. cochleata (L.) Dressl. *Neill 1002,* 3 October 1976. Common epiphyte in lower cloud and deciduous forests.

E. fragrans (Sw.) Dressl. *Atwood A3,* 27 April 1975 (MSC). In deciduous and lower cloud forests, but to be expected in elfin forest.

E. gravida (Lindl.) Schltr. *Atwood A1,* 27 April 1975 (MSC). Uncommon in deciduous forest on southeast flank.

E. vespa (Vell.) Dressl. *Atwood 7756,* 3 February 1977 (SEL). Uncommon in elfin forest.

Epidendrum difforme Jacq. *Atwood 77128,* 10 February 1977 (MSC). Cloud forest.

E. lacustre Lindl. *Atwood, Marshall & Neill 6738,* 16 December 1973 (MO). Scattered throughout the elfin forest.

E. laucheanum Rolfe. *Atwood 5470,* 9 April 1971 (MO). Elfin forest inhabitant.

E. pansamalae Schltr. *Neill 885,* 26 September 1977 (SEL).

E. physodes Rchb. f. According to files of the late A. H. Heller (now at SEL) this occurs on Mombacho.

E. polyanthus Lindl. *Atwood g-62.* Collected May 1975.

E. pseudoramosum Schltr. *Atwood & Neill 7058,* 20 January 1974 (MO). Common in elfin forest.

E. radicans Pavon. *Atwood A164,* 15 May 1975 (MSC). Common in grassy areas of Plan de las Flores. A few yellow forms were observed, but most are red with a yellow labellum.

E. ramosum Jacq. *Atwood, Marshall & Neill 6744,* 17 December 1973 (MO). Common in elfin forest.

E. selaginella Schltr. *Atwood A206,* 14 May 1975 (MSC). Rather common locally at Plan de las Flores.

E. turialvae Rchb. f. *Neill 7589,* 8 August 1976 (SEL). Rare in cloud forest.

Goodyera bradeorum Schltr. *Atwood, Neill & Marshall 6741,* 16 December 1973 (MO). Local terrestrial of upper cloud and elfin forests.

Hexadesmia lindeniana R. & C. *Atwood 5462,* 9 April 1971 (MSC). Occasional in lower cloud forest.

H. micrantha (Lindl.) Ames & Correll. *Atwood A4,* 27 April 1975 (MSC). Common in lowland deciduous forests.

Isochilus cf. *major* Schlecht. & Cham. *Atwood &*

Neill 7045, 15 January 1974 (MO). Common in cloud forests.

Jacquiniella globosa (Jacq.) Schltr. *Atwood 77166,* 15 February 1977 (SEL). Occasional inside drier crater rim.

J. teretifolia (Sw.) Britt. & Wils. *Atwood 5460,* 9 April 1971 (MO). Common epiphyte on lower flanks of mountain in deciduous forests, but found also in protected areas of elfin forest.

Kegeliella sp. *Atwood A211,* 8 May 1975 (SEL). Rare in elfin forest (plant sterile).

Lepanthes sp. No. 1. *Atwood 77161,* 15 February 1977 (SEL). Local in elfin forest. Close to *L. turialvae,* but lip lacks midlobe.

L. sp. No. 2. *Atwood 77143,* 10 February 1977 (SEL). Upper cloud forest. Leaves are orbicular, as with species No. 3, but petals are differently shaped.

L. sp. No. 3. *Atwood 77165,* 15 February 1975 (SEL). Cloud forest.

Lockhartia hercodonta Rchb. f. ex Krzl. *Atwood 5468,* 9 April 1971 (MO). Locally common in cloud forests.

Lycaste aromatica Lindl. Live collection made (SEL). Local in cloud forest on north flank.

L. macrophylla (Poepp. & Endl.) Lindl. *Atwood g-65,* 16 December 1973 (SEL). Upper cloud forest. Uncommon.

Malaxis maxonii Ames. *Atwood A6,* 29 April 1975 (MSC). Common in cloud and elfin forests where it sometimes is encountered as an epiphyte. Mombacho is the type locality of the species.

M. tipuloides (Lindl.) Kuntze. *Atwood A345,* 10 July 1975 (MSC). Upper cloud forest inhabitant. This may be the northernmost limit of the species.

Masdevallia chontalensis Rchb. f. *Atwood & Neill AN305,* 30 July 1975 (MSC). Common in cloud and elfin forests.

M. simula Rchb. f. *Atwood & Neill 7042,* 15 January 1974 (MO). Apparently rare in upper cloud and elfin forests.

Maxillaria brunnea Linden & Rchb. f. *Atwood 7781,* 5 February 1977 (SEL). Uncommon in cloud forest.

M. crassifolia (Lindl.) Rchb. f. *Atwood 7798,* 8 February 1977 (SEL). Epiphyte of lower cloud forest.

M. mombachoensis Heller ex Atwood. *Atwood 7757,* 3 February 1977 (SEL). Common epiphyte in elfin forest. Apparently endemic to Volcán Mombacho.

M. neglecta (Schltr.) L. O. Wms. *Atwood 7782a,* 5 February 1977 (SEL).

M. aff. *reichenheimiana* Rchb. f. *Atwood 77159,* 15 February 1977 (SEL).

M. tenuifolia Lindl. *Atwood & Neill AN59,* 1 July 1975 (MSC). Lower cloud forests.

M. uncata Lindl. *Atwood & Neill 7038,* 15 January 1974 (MO). Localized in areas of cloud forests.

M. variabilis Batem. ex Lindl. Plants observed in cloud forest in December 1973.

Mesospinidium warscewiczii Rchb. f. *Atwood 7778,* 5 February 1977 (SEL). Uncommon epiphyte in shade of upper cloud forest.

Mormodes sp. No collection made. Rare in deciduous forest, living on rotting branches.

Nidema boothii Schltr. Uncollected, but occasional epiphyte of lower cloud forest.

Oncidium ascendens Lindl. *Atwood 3917,* 27 January 1970 (MO). In deciduous forest around Finca Las Delicias.

O. stenotis Rchb. f. *Atwood 77101,* 8 February 1977. Uncommon in lower cloud forest.

Platystele compacta Ames. *Atwood & Neill 7043,* 15 January 1974 (MSC). Not uncommon in cloud forest.

Pleurothallis blaisdelii S. Wats. *Atwood & Neill 7040,* 15 January 1974 (MO). Uncommon in upper cloud and elfin forest.

P. convallaria Schltr. *Atwood, Marshall & Neill 6745,* 17 December 1973 (MO). Flowers white and dark red-purple. Found only in elfin forest on northwest flank.

P. cf. *erinacea* Rchb. f. *Atwood & Neill 7063,* 20 January 1974 (SEL). Rare epiphyte in cloud forest.

P. foliata Griseb. *Atwood A12,* 29 April 1975 (MSC); *Atwood A300,* 5 June 1975 (MSC). Locally abundant, but an inconspicuous epiphyte of cloud and elfin forests.

P. guanacastensis Ames & Schweinf. *Atwood & Neill 7044,* 15 January 1974 (SEL). In elfin forest. This is an apparent range extension from Costa Ricca.

P. pruinosa Lindl. *Atwood 77100,* 8 February 1977 (FSU). Lower cloud forest on trees above Finca Cutirre.

P. racemiflora Lindl. ex Hook. *Atwood g-63* (MSC). Common in lower cloud forest where it often forms great masses. Also in deciduous forest.

P. ruscifolia (Jacq.) R. Br. *Atwood 77126,* 10 February 1977 (SEL).

P. sertularioides (Sw.) Sprengel. *Atwood & Neill AN54,* 1 July 1975 (MSC). Collection made north of Finca Cutirre at about 550 m.

P. tribuloides (Sw.) Lindl. *Atwood, Marshall & Neill 7046,* 15 January 1974 (MO). Local cloud forest inhabitant. This species is distinctive for its bright red flowers and echinate ovaries.

Polystachya masayensis Rchb. f. *Atwood & Neill AN60,* 1 July 1975 (MSC). In deciduous forests at Finca Cutirre.

Ponera cf. *striata* Lindl. *Atwood 5463,* 9 April 1971 (MO). Upper cloud forest.

Prescottia stachyodes (Sw.) Lindl. *Atwood 77155,* 15 February 1979 (SEL). Uncommon in elfin forest.

Psilochilus cf. *macrophyllus* (Lindl.) Ames. *Atwood & Neill AN308,* 30 July 1975 (MSC). Rare along crater rim above vacation house.

Scaphyglottis behrii (Rchb. f.) Benth. & Hook. ex Hemsl. *Atwood 7794,* 8 February 1977 (MSC, SEL). Local in lower cloud forest.

Sobralia hawkesii A. H. Heller. *Atwood & Neill 7059,* 20 January 1974 (MO). Common epiphyte of trees and nearly vertical cliffs.

Spiranthes acaulis (J. E. Sm.) Cogn. *Atwood 77115,* 8 February 1977 (MSC, SEL). In lower cloud forest of Finca Cutirre.

S. elata (Sw.) L. C. Rich. *Atwood 77148,* 10 February 1977 (SEL). Rare in cloud forest. Only collected once.

Stanhopea wardii Lodd. ex Lindl. *Atwood 77122,* 20 September 1977 (MSC). Uncommon in cloud forest.

Stelis cucullata Ames. *Atwood A194,* 14 May 1975

(MSC). Common in upper cloud and elfin forests. Other species of *Stelis* undoubtedly occur on Mombacho.

Trevoria glumacea Garay ? *Atwood A209*, 18 May 1975 (MSC). One budded plant found on southeast flank near top of highest peak. Known from Costa Rica and Omotepe.

Trichopilia sp. Observed in cloud forest, but not flowering or fruiting.

Trigonidium egertonianum Batem. *Atwood & Neill AN61*, 1 July 1975 (MSC). Common epiphyte in upper deciduous and lower cloud forests. The above collection is sterile, but undoubtedly represents this species.

Tropidia polystachya (Sw.) Ames. *Atwood & Neill 7041*, 15 January 1974 (MO). Cloud forest on southeast slope. Uncommon terrestrial.

Xylobium elongatum (Lindl.) Hemsl. *Atwood & Neill 7061*, 20 January 1974 (MO). Not uncommon in upper cloud forest.

OXALIDACEAE

Oxalis neaei DC. *Atwood A34*, 30 April 1975 (MSC). Weed of disturbed area around vacation house. This may be the same as the following.

O. yucatensis Kunth. *Nichols 2002*, 9 January 1969 (VT).

PAPAVERACEAE

Bocconia arborea S. Watson. *Atwood 7743*, 3 February 1977 (MSC). Upper cloud forest tree.

PASSIFLORACEAE

Passiflora biflora Lam. *Atwood A33*, 30 April 1975 (MSC). In disturbed area at vacation house.

P. edulis Sims. *Neill 7506*, 6 August 1976 (MO). Probably escaped.

P. sexiflora Juss. *Neill 1095*, 25 October 1976 (FSU).

PEDALIACEAE

Sesamum indicum L. *Atwood & Neill AN208*, 16 July 1975 (MSC). Deciduous forest escape.

PHYTOLACCACEAE

Petiveria alliacea L. *Dudey & Moore 1980*, 9 January 1969 (MO). Disturbed areas of cloud forest.

Phytolacca rivinoides Kunth & Bouché. *Neill N48*, 29 April 1975 (MSC). Weed in disturbed area of vacation house.

Rivina humilis L. *Dudey & Moore 1981*, 9 January 1969 (MO). Cloud forest.

PIPERACEAE

Peperomia cyclophylla Miq. *Atwood & Neill AN94*, 2 July 1975 (MSC). Epiphyte of lower cloud forest on margin with deciduous forest.

P. deppeana Schlecht. & Cham. *Nichols 2207*, 9 January 1969 (MO).

P. hylophila C. DC. *Neill N26*, April 1975 (MSC); *Neill N52*, 30 April 1975 (MSC). Rather common in cloud forests.

P. cf. *obtusifolia* (L.) A. Dietrich. *Atwood 7746*, 3 February 1977 (MSC). Epiphyte of elfin and cloud forest.

P. serpens (Sw.) Loud. *Neill N36*, 29 April 1975 (MSC). Cloud forest epiphyte.

Piper aduncum L. *Neill N22*, 26 April 1975 (MSC). Upper deciduous or lower cloud forest on southeast flank.

P. amalago L. *Atwood A312*, 5 June 1975 (MSC). Small tree at Plan de las Flores.

P. auritum H.B.K. *Atwood & Neill AN301*, 30 July 1975 (MSC). In ravine of lower cloud forest above Finca Las Delicias.

P. pseudofuligineum C. DC. *Atwood A41*, 30 April 1975 (MSC); *Atwood & Neill AN211*, 16 July 1975 (MSC). Disturbed areas of lower cloud forest.

P. cf. *umbricola* C. DC. *Atwood A8*, 29 April 1975 (MSC); *Neill N33*, 29 April 1975 (MSC). Disturbed area of cloud forest above 900 m.

Pothomorphe umbellata (L.) Miq. *Atwood & Neill AN49*, 1 July 1975 (MSC). Weedy and common in disturbed areas of cloud forest.

PLUMBAGINACEAE

Plumbago scandens L. *Atwood & Neill AN83*, 2 July 1975 (MSC). Common deciduous forest herb.

POLYGALACEAE

Monnina xalapensis H.B.K. *Atwood 5472*, 9 April 1971 (MO); *Atwood A352*, 10 July 1975 (MSC). In disturbed areas at Plan de las Flores.

POLYGONACEAE

Coccoloba uvifera (L.) Jacq. *Atwood A45*, 1 July 1975 (MSC). Cultivated plant at vacation house.

PORTULACEAE

Talinum cf. *paniculatum* (Jacq.) Gaertn. Not collected, but observed in deciduous forest areas.

RHAMNACEAE

Karwinskia cf. *humboldtiana* (R. & S.) Zucc. *Atwood & Neill AN212*, 16 July 1975 (MSC). Common shrub in deciduous forest below Finca Las Delicias.

ROSACEAE

Rubus aff. *hadrocarpus* Standl. & Steyerm. *Atwood A9*, 29 April 1975 (MSC); *Atwood A36*, 30 April 1975 (MSC). Common shrub of disturbed areas of crater rim, elfin forest, and cloud forest. The determination is questionable because of the glabrous drupelets.

RUBIACEAE

Borreria laevis (Lam.) Griseb. *Robbins 6266*, 1 August 1972 (MO). Common weed of disturbed area of vacation house.

Coccosypselum hirsutum Bartling ex DC. *Atwood A256*, 10 July 1975 (MSC). Elfin forest component at Plan de las Flores.

Coffea arabica L. *Robbins 6267*, 1 August 1972 (MO). Introduced and cultivated, but expected to escape.

Guettarda crispifolia Vahl. *Neill 407*, 28 May 1976 (UCA).

Hamelia patens Jacq. *Atwood A53*, 30 April 1975 (MSC). Common and perhaps dominant shrub of disturbed area above Finca Las Delicias.

H. rovirosae Wernh. *Robbins 6268*, 1 August 1972 (MO).

Hemidiodia ocymifolia (Willd.) K. Schum. *Seymour 7516*, 6 August 1976 (MO).

Hoffmannia oreophila L. O. Wms. *Neill N53*, 29 April 1975 (MSC). Upper cloud forest.

Manettia reclinata L. *Neill 1102*, 25 October 1976 (MSC). Elfin forest.

Palicourea angustifolia H.B.K. *Hall & Bockus 7541*, 7 August 1976 (MO). Cloud forest.

P. galeottiana Mart. *Atwood A346*, 10 July 1975 (MSC). Small tree at Plan de las Flores. Rather common. Other species of *Palicourea* undoubtedly occur on Mombacho.

Psychotria graciflora Benth. ex Oerst. *Atwood A293,* 5 June 1975 (MSC). Elfin forest component at Plan de las Flores.

P. cf. *minarum* St. & St. *Atwood, Marshall & Neill 6735,* 16 December 1973 (MO). Shrub in shade of upper cloud forest.

P. molinae Standl. *Hall & Bockus 7542,* 7 August 1976. Cloud forest.

P. oerstediana Standl. *Hall & Bockus 7572,* 8 August 1976 (MO). Upper cloud forest.

P. aff. *trichotoma* Mart. & Gal. *Atwood A57,* 29 April 1975 (MSC); *Atwood A212b,* 18 May 1975 (MSC). Shrub or small tree of cloud forest.

P. uliginosa Sw. *Atwood A23,* 29 April 1975 (MSC); *Atwood A291,* 5 June 1975 (MSC); *Atwood & Neill AN189,* 16 July 1975 (MSC). Upper cloud and elfin forest. Purple flowered shrub of elfin forest.

P. sp. *Atwood & Neill AN216,* 16 July 1975 (MSC). Roadside in deciduous forest area below Finca Las Delicias.

Richardia scabra L. *Seymour 7517,* 6 August 1976 (MO). Deciduous forest weed.

SAPINDACEAE

Paullinia clavigera Schlecht. *Atwood & Neill AN210,* 16 July 1975 (MSC). Deciduous forest inhabitant.

Serjania sp. *Neill 1401,* 6 February 1977 (FSU). Deciduous forest vine.

SAPOTACEAE

Manilkara sp. *Neill 1563a,* 8 February 1977 (UCA). Shade tree of coffee plantation.

SCROPHULARIACEAE

Castilleja arvensis Schlecht. & Cham. *Atwood A154,* 15 May 1975 (MSC). Local in disturbed area of elfin forest.

Schlegelia parviflora (Oerst.) Monachino. *Atwood 7747,* 3 February 1977 (FSU, MSC). Common elfin forest tree.

SIMAROUBACEAE

Picramnia teapensis Tulasne. *Neill 1399,* 8 February 1977 (MO). Lower cloud forest.

SOLANACEAE

Cestrum aurantiacum Lindl. *Atwood A354,* 10 July 1975 (MSC). Shrub at Plan de las Flores.

C. cf. *racemosum* R. & P. *Atwood 77110,* 8 February 1977 (MSC). Tree of lower cloud forest.

Jaltomata procumbens (Cav.) J. L. Gentry. *Neill 988,* 3 October 1976 (UCA). Lower cloud forest.

Physalis cordata Mill. *Neill 998,* 3 October 1976 (MSC). Weed of lower cloud forest.

Solanum americanum Mill. *Robbins 6263,* 1 August 1972 (MO).

S. canense Rydb. *Neill 1567,* 14 March 1977 (MSC). Deciduous forest.

S. nigrescens M. & G. *Narvaez 3927,* 27 January 1970 (MO). Disturbed areas in cloud forest.

S. torvum Sw. *Atwood A38,* 29 April 1975 (MSC). Disturbed area near vacation house.

Witheringia cf. *meiantha* (Donn.-Sm.) A. T. Hunziker. *Atwood A58,* 30 April 1975 (MSC). In disturbed cloud forest.

W. solanacea L'Herit. *Atwood A59,* 30 April 1975 (MSC). Disturbed areas near vacation house.

STERCULIACEAE

Byttneria aculeata Jacq. *Neill 774,* 19 September 1977 (UCA).

Melochia nodiflora Sw. *Dudey & Moore 1953,* 9 January 1969 (VT).

Sterculia apetala (Jacq.) Karst. *Atwood & Neill AN76,* 2 July 1975 (MSC). Deciduous forest tree.

THEACEAE

Freziera friedrichstaliana (Szysz.) Kobuski. *Atwood A166,* 15 May 1975 (MSC). Elfin forest component. Known only from Honduras and Volcán Mombacho.

TILIACEAE

Apeiba tibourou Aubl. *Atwood & Neill AN215,* 16 July 1975 (MSC). Deciduous forest inhabitant.

Heliocarpus donnell-smithii Rose. *Baker 2490* (MSC). Reported by Lay (1949).

H. nodiflorus Donn.-Sm. & Rose. *Oersted 14829.* Cited by Lay (1949). Tree of secondary growth.

Luehea sp. *Baker 2311* (MSC). Probably in deciduous forest.

Triumfetta dumetorum Schlecht. *Dudey & Moore 1955,* 9 January 1969 (MO). Cloud forest.

ULMACEAE

Trema micrantha (L.) Blume. *Neill 1366,* 3 February 1977 (FSU). Deciduous forest tree.

UMBELLIFERAE

Eryngium foetidum L. *Robbins 6259,* 1 August 1972 (MO). Common in disturbed areas of lower cloud forest.

Spananthe paniculata Jacq. *Atwood 5474,* 9 April 1971 (MO). Lower cloud forest in disturbed areas.

URTICACEAE

Fleurya aestuans (L.) Gaud. *Dudey & Moore 1975,* 9 January 1969 (MO). Common herb in coffee plantations.

Urera sp. Not collected but common in coffee plantations.

VALERIANACEAE

Valeriana scandens var. *candolleana* (Gard.) Muell. *Atwood A47,* 30 April 1975 (MSC). Weed of coffee plantations and disturbed cloud forest on north flank.

VERBENACEAE

Cornutia grandiflora (Schlecht. & Cham.) Schau. *Atwood & Neill AN79,* 2 July 1975 (MSC). In deciduous forest areas at Finca Las Delicias.

Lantana glandulosissima Heyek. *Dudey & Moore 1958,* 9 January 1969 (VT).

L. maxima Hayek. *Seymour 6104,* 25 July 1972 (MO). Lower cloud forest.

L. trifolia f. *hirsuta* Moldenke. *Atwood A355,* 10 July 1975 (MSC). Roadside in lower cloud forest.

Lippia cardiostegia Benth. *Nelson 7510,* 8 August 1976 (MO). Lower cloud forest.

L. controversa var. *brevipedunculata* Moldenke. *Atwood A202,* 14 May 1975 (MSC). Collected on north flank of Mombacho above Finca Asunción.

Priva lappulacea (L.) Pers. *Dudey & Moore 1983,* 9 January 1969 (MO). Cloud forest weed.

VIOLACEAE

Hybanthus attenuatus (Humb. & Bonpl.) G. K. Schulze. *Atwood & Neill AN73,* 2 July 1975 (MSC). Common in upper deciduous forest and lower cloud forest.

VITACEAE

Vitis tiliifolia Humb. & Bonpl. Sterile vines observed in lower cloud forest areas, south side of Mombacho.

ZINGIBERACEAE

Renealmia aromatica (Aubl.) Griseb. *Atwood, Marshall & Neill 6711,* 15 December 1973 (MO). Only one plant found in elfin forest.

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AN INDEX TO THE FAMILIES IN ENGLER AND PRANTL'S "DIE NATÜRLICHEN PFLANZENFAMILIEN"[1]

THOMAS MORLEY[2]

While teaching a course in the families of flowering plants over a period of many years much use was made of Engler and Prantl's publication, "Die Natürlichen Pflanzenfamilien." Ultimately it was found useful to compile an index to both editions of this great work. Families of non-flowering plants were added with the thought of making the index of general utility. The index is complete for the first edition and includes all presently published numbers of the second, namely: Band 1b, 2, 3, 5aI, 5bVIII, 6, 7a, 8, 10, 11, 13, 14a, 14d, 14e, 15a, 16b, 16c, 17aII, 17b, 18a, 19a, 19bI, 19c, 20b, 20d, and 21. According to Dr. F. A. Stafleu (pers. comm.), further progress with edition two is very slow and it is not at all certain if any other treatments will ever appear. Therefore it seems worthwhile to bring out this index at the present time.

The following abbreviations are used in the first edition: T = Teil (major division); Ab = Abteilung (division, sometimes also further subdivided); and N = Nachträge (supplement). N 1, N 2, N 3, and N 4 are the four supplements to T 2–4. The following abbreviation is used in the second edition: Bd = Band (volume).

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Craspedomonadaceae	T 1, Ab 1a:123.	
Crassulaceae	T 3, Ab 2a:23; N 1:180; N 2:28; N 3:138; N 4:108.	Bd 18a:352.
Cribrariaceae	T 1, Ab 1:18	Bd 2:320.
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Cruciferae	T 3, Ab 2:145; N 1:175; N 2:27; N 3:130; N 4:97.	Bd 17b:227.
Crossosomataceae	N 1:185.	
Cryphaeaceae	T 1, Ab 3:736, 1214	Bd 11:75.
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Cucurbitariaceae	T 1, Ab 1:408.	
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Cypheliaceae	T 1, Ab 1*:83	Bd 8:98.
Cyrillaceae	T 3, Ab 5:179; N 1:214	Bd 20b:1.
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Moriolaceae	T 1, Ab 1*:52	Bd 8:63.
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Mucedinaceae	T 1, Ab 1**:416	see Bd 5aI.
Mucoraceae	T 1, Ab 1:123	see Bd 5aI.
Mucorineae	T 1, Ab 1:119.	
Musaceae	T 2, Ab 6:1; N 1:88; N 2:12; N 3:51	Bd 15a:505.
Musci	T 1, Ab 3:142.	
Mycoideaceae	T 1, Ab 2:101, 160.	
Mycoporaceae	T 1, Ab 1*:77	Bd 8:92.
Mycosphaerellaceae	T 1, Ab 1:421	see Bd 5aI.
Myoporaceae	T 4, Ab 3b:354; N 1:309.	
Myriangiaceae	T 1, Ab 1:319.	
Myricaceae	T 3, Ab 1:26; N 3:93.	
Myriotrichiaceae	T 1, Ab 2:214; N to T 1, Ab 2:161.	
Myristicaceae	T 3, Ab 2:40; N 1:161; N 3:121	Bd 17aII:177.
Myrothamnaceae	T 3, Ab 2a:103	Bd 18a:262.
Myrsinaceae	T 4, Ab 1:84; N 1:270; N 3:269; N 4:235.	
Myrtaceae	T 3, Ab 7:57; N 1:262; N 2:49; N 3:247; N 4:214.	
Myuriaceae		Bd 11:123.
Myurococcaceae	N to T 1, Ab 2:39	Bd 3:80.
Myxomycetes	T 1, Ab 1:1	Bd 2:304.
Myxogasteres	T 1, Ab 1:8.	
Myzodendraceae	T 3, Ab 1:198; N 1:140	Bd 16b:92.
Najadaceae	T 2, Ab 1:214; N 1:37; N 3:8.	
Naviculaceae		Bd 2:272.
Neckeraceae	T 1, Ab 3:775	Bd 11:178.
Nectrioidaceae	T 1, Ab 1**:382.	
Nemastomaceae	T 1, Ab 2:521; N to T 1, Ab 2:254.	
Nemataceae	T 1, Ab 3:916	Bd 11:215.
Nepenthaceae	T 3, Ab 2:253; N 2:28; N 4:106	Bd 17b:728.
Nidulariaceae	T 1, Ab 1**:326	Bd 7a:56.
Nidularineae	T 1, Ab 1**:324	Bd 7a:52.
Nilssoniaceae		Bd 13:97.
Nitzschiaceae		Bd 2:293.
Noctilucaceae		Bd 2:47.
Nolanaceae	T 4, Ab 3b:1.	
Nostocaceae	T 1, Ab 1a:70	Bd 1b:177.
Nostochopsidaceae		Bd 1b:131.
Nyctaginaceae	T 3, Ab 1b:14; N 1:154; N 3:105; N 4:83	Bd 16c:86.
Nymphaeaceae	T 3, Ab 2:1; N 1:157; N 2:22; N 3:107.	
Nyssaceae	N 4:213.	
Ochnaceae	T 3, Ab 6:131; N 1:245; N 3:219; N 4: 203.	Bd 21:53.
Ochromonadaceae	T 1, Ab 1a:163.	
Octoknemaceae	N 4:75	Bd 16b:42.
Octoknemataceae—see Octoknemaceae.		
Oedipodiaceae	T 1, Ab 3:508	Bd 10:332.
Oedogoniaceae	T 1, Ab 2:108; N to T 1, Ab 2:107	Bd 3:244.
Oenotheraceae	N 3:249.	
Oicomonadaceae	T 1, Ab 1a:118.	

Olacaceae	T 3, Ab 1:231; N 1:144; N 2:18; N 3:98, N 4:74.	Bd 16b:5.
Oleaceae	T 4, Ab 2:1; N 1:281; N 3:290; N 4:243.	
Oliniaceae	T 3, Ab 6a:213.	
Olpidiaceae	T 1, Ab 1:67	see Bd 5aI.
Onagraceae	T 3, Ab 7:199; N 1:268; N 2:50; N 4:216.	
Onygenaceae	T 1, Ab 1:309	see Bd 5aI.
Oocystaceae	N to T 1, Ab 2:52	Bd 3:113.
Oochytriaceae	T 1, Ab 1:81.	
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Ophiocytiaceae	N to T 1, Ab 2:49	Bd 3:399.
Ophioglossaceae	T 1, Ab 4:449, 472.	
Ophiostomataceae		see Bd 5aI.
Opiliaceae	N 1:142; N 4:74	Bd 16b:33.
Opuntiales		Bd 21:592.
Orbiliaceae		see Bd 5aI.
Orchidaceae	T 2, Ab 6:52; N 1:97; N 2:12; N 3:75; N 4:42.	
Orobanchaceae	T 4, Ab 3b:123; N 1:299; N 3:316.	
Orthotrichaceae	T 1, Ab 3:456, 1198	Bd 11:10.
Oscillatoriaceae	T 1, Ab 1a:61	Bd 1b:193.
Osmundaceae	T 1, Ab 4:372, 380.	
Ostreopsiaceae		Bd 2:96.
Ostropaceae	T 1, Ab 1:271.	
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Oxytoxaceae		Bd 2:97.
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Pandaceae	N 4:151.	
Pandanaceae	T 2, Ab 1:186; N 1:35; N 2:2; N 3:6, N 4:6.	
Pannariaceae	T 1, Ab 1*:178	Bd 8:175.
Pantostomatineae	T 1, Ab 1a:111.	
Papaveraceae	T 3, Ab 2:130; N 1:174; N 2:27; N 3:129; N 4:96.	Bd 17b:5.
Paratheliaceae	T 1, Ab 1*:71	Bd 8:84.
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Parkeriaceae	T 1, Ab 4:339.	
Parmeliaceae	T 1, Ab 1*:207	Bd 8:229.
Pascherinemataceae		Bd 1b:99.
Passifloraceae	T 3, Ab 6a:69; N 1:253; N 3:243	Bd 21:470.
Patellariaceae	T 1, Ab 1:221.	
Pedaliaceae	T 4, Ab 3b:253; N 1:304; N 3:320; N 4:283.	
Peltigeraceae	T 1, Ab 1*:190	Bd 8:187.
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Penicilliaceae		see Bd 5aI.
Pentaphylacaceae	N 1:214; N 3:197	Bd 20b:13.
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Peridineae		Bd 2:3.
Peridiniaceae	T 1, Ab 1b:9	Bd 2:88.
Peridiniales	T 1, Ab 1b:1	Bd 2:79.
Peripterygiaceae		Bd 20b:397.
Perisporiaceae	T 1, Ab 1:333	see Bd 5aI.
Perisporiales	T 1, Ab 1:325.	
Peronosporaceae	T 1, Ab 1:112	see Bd 5aI.
Peronosporineae	T 1, Ab 1:108.	
Pertusariaceae	T 1, Ab 1*:195	Bd 8:217.
Pezizaceae	T 1, Ab 1:178	see Bd 5aI.
Pezizineae	T 1, Ab 1:173.	
Phacidiaceae	T 1, Ab 1:256	see Bd 5aI.
Phacidiineae	T 1, Ab 1:243.	
Phaeophyceae	T 1, Ab 2:176.	

Phalansteriaceae	T 1, Ab 1a:129.	
Phallaceae	T 1, Ab 1**:289	Bd 7a:96; see Bd 5aI.
Phallineae	T 1, Ab 1**:276	Bd 7a:76.
Philydraceae	T 2, Ab 4:75; N 1:70	Bd 15a:190.
Phrymaceae	T 4, Ab 3b:361; N 1:309.	
Phycomycetes	T 1, Ab 1:63.	
Phyllogoniaceae		Bd 11:174.
Phyllopsoraceae	T 1, Ab 1*:138	Bd 8:200.
Phyllopyreniaceae	T 1, Ab 1*:68	Bd 8:81.
Phyllosiphonaceae	T 1, Ab 2:125, 160; N to T 1, Ab 2:133	Bd 3:334.
Phymatosphaeriaceae	T 1, Ab 1:242.	
Physaraceae	T 1, Ab 1:32	Bd 2:325.
Physarales		Bd 2:325.
Physciaceae	T 1, Ab 1*:234	Bd 8:256.
Phytodiniaceae		Bd 2:102.
Phytolaccaceae	T 3, Ab 1b:1; N 1:154; N 4:82	Bd 16c:135.
Phytomyxinae	T 1, Ab 1:5.	
Pilacraceae	T 1, Ab 1**:86.	
Pilocarpaceae	T 1, Ab 1*:116.	
Pilotrichaceae	T 1, Ab 3:912	Bd 11:216.
Pinaceae	T 2, Ab 1:28; N 1:21; N 2:2; N 3:4; N 4:4.	Bd 13:271.
Piperaceae	T 3, Ab 1:3; N 2:16; N 3:92; N 4:62.	
Piptocephalidaceae	T 1, Ab 1:132.	
Pirolaceae	T 4, Ab 1:3; N 1:269.	
Pisocarpiaceae		Bd 7a:35.
Pisolithaceae		Bd 7a:35.
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Platanaceae	T 3, Ab 2a:137.	
Plectascineae	T 1, Ab 1:290.	
Plectobasidiineae	T 1, Ab 1**:329.	
Pleosporaceae	T 1, Ab 1:428.	
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Pleurocapsales		Bd 1b:79.
Pleuromoiaceae	T 1, Ab 4:754.	
Pleurococcaceae	T 1, Ab 2:54, 160; N to T 1, Ab 2:35	Bd 3:99.
Pleurophascaceae	T 1, Ab 3:774	Bd 10:219.
Plumbaginaceae	T 4, Ab 1:116; N 1:271; N 3:286; N 4: 239.	
Podaxaceae	T 1, Ab 1**:332	Bd 7a:116.
Podaxineae		Bd 7a:109.
Podocarpaceae		Bd 13:211.
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Podostemonaceae	T 3, Ab 2a:1; N 1:179; N 3:135; N 4:107	Bd 18a:3.
Podostemonales		Bd 18a:1.
Polemoniaceae	T 4, Ab 3a:40, 377; N 1:289; N 3:305; N 4:261.	
Polygalaceae	T 3, Ab 4:323; N 1:209; N 2:19; N 3:190; N 4:163.	
Polygonaceae	T 3, Ab 1a:1; N 1:151; N 2:19; N 3:101; N 4:80.	
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Polypodiaceae	T 1, Ab 4:139, 473.	
Polyporaceae	T 1, Ab 1**:152	Bd 6:169; see Bd 5aI.
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Pontederiaceae	T 2, Ab 4:70; N 1:70; N 2:9	Bd 15a:181.
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Protopityaceae		Bd 13:22.
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Pterobryaceae		Bd 11:125.
Pterospermataceae		Bd 3:94.
Ptychodiscaceae		Bd 2:70.
Ptychomitriaceae		Bd 11:6.
Ptychomniaceae	T 1, Ab 3:1217	Bd 11:102.
Pucciniaceae	T 1, Ab 1**:48	Bd 6:48.
Pulvinulariaceae		Bd 1b:118.
Punicaceae	T 3, Ab 7:22.	
Pyrenidiaceae	T 1, Ab 1*:76	Bd 8:89.
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Pyrenomycetineae	T 1, Ab 1:321.	
Pyrenopsidaceae	T 1, Ab 1*:158	Bd 8:153.
Pyrenothamniaceae	T 1, Ab 1*:61	Bd 8:73.
Pyrenotrichaceae		Bd 8:91.
Pyrenulaceae	T 1, Ab 1*:62	Bd 8:74.
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Pyrophacaceae		Bd 2:96.
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Quiinaceae	T 3, Ab 6:165	Bd 21:106.
Rafflesiaceae	T 3, Ab 1:274; N 1:151; N 2:19, N 3:100; N 4:78.	Bd 16b:243.
Ralfsiaceae	T 1, Ab 2:240; N to T 1, Ab 2:166.	
Ranunculaceae	T 3, Ab 2:43; N 1:167; N 2:22; N 3:121; N 4:91.	
Rapateaceae	T 2, Ab 4:28; N 1:61; N 3:41	Bd 15a:59.
Resedaceae	T 3, Ab 2:237; N 3:134	Bd 17b:659.
Restionaceae	T 2, Ab 4:3; N 1:61; N 2:9; N 3:35	Bd 15a:8.
Reticulariaceae	T 1, Ab 1:25	Bd 2:316.
Rhacopilaceae	T 1, Ab 3:975	Bd 11:50.
Rhamnaceae	T 3, Ab 5:393; N 1:229; N 2:41; N 3:210; N 4:192.	Bd 20d:7.
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Rhizomastigaceae	T 1, Ab 1a:113.	
Rhizophidiaceae		see Bd 5aI.
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Rhizophyllidaceae	T 1, Ab 2:527.	
Rhodochaetaceae	T 1, Ab 2:317.	
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Rhodophyllidaceae	T 1, Ab 2:366; N to T 1, Ab 2:221.	
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Rivulariaceae	T 1, Ab 1a:84	Bd 1b:162.
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Salvadoraceae	T 4, Ab 2:17; N 1:281	Bd 20b:232.
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Saprolegniaceae	T 1, Ab 1:96	see Bd 5aI.
Saprolegniineae	T 1, Ab 1:93.	
Sarraceniaceae	T 3, Ab 2:244; N 1:179; N 2:28; N 3:134	Bd 17b:704.
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Saururaceae	T 3, Ab 1:1; N 3:92.	
Saxifragaceae	T 3, Ab 2a:41; N 1:180; N 2:29; N 3:141; N 4:108.	Bd 18a:74.
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Simarubaceae	T 3, Ab 4:202; N 2:36; N 3:187; N 4:158	Bd 19a:359.
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Solanaceae	T 4, Ab 3b:4; N 1:292; N 2:69; N 3:309; N 4:271.	
Soleniaceae		Bd 2:230.
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Sordariaceae	T 1, Ab 1:390.	
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Sparganiaceae	T 2, Ab 1:192; N 1:35; N 2:2; N 3:8.	
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Spermophthoraceae		see Bd 5al.
Sphacelariaceae	T 1, Ab 2:192; N to T 1, Ab 2:146.	
Sphaerioidaceae	T 1, Ab 1a:349.	
Sphaeriaceae	T 1, Ab 1:394	see Bd 5al.
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Sphaerobolaceae	T 1, Ab 1**:346	Bd 7a:51; see Bd 5al.
Sphaerococcaceae	T 1, Ab 2:382; N to T 1, Ab 2:223.	
Sphaerophoraceae	T 1, Ab 1*:85	Bd 8:100.
Sphaeropleaceae	T 1, Ab 2:121; N to T 1, Ab 2:123	Bd 3:296.
Sphaeropsidales	T 1, Ab 1**:349.	
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Sphenophyllaceae	T 1, Ab 4:515.	
Spiridentaceae	T 1, Ab 3:765	Bd 10:474.
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Squamariaceae	T 1, Ab 2:532; N to T 1, Ab 2:54.	
Stachyuraceae	T 3, Ab 6:192; N 1:253	Bd 21:457.
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Stemonitaceae	T 1, Ab 1:26	Bd 2:322.
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Sterculiaceae	T 3, Ab 6:69; N 1:240; N 2:43; N 3:214; N 4:201, 328.	
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Stictidaceae	T 1, Ab 1:245.	
Stigmateaceae		see Bd 5al.
Stigonemataceae	T 1, Ab 1a:80	Bd 1b:121.
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Stilophoraceae	T 1, Ab 2:230; N to T 1, Ab 2:165.	
Strasburgeriaceae		Bd 21:87.
Striariaceae	T 1, Ab 2:204; N to T 1, Ab 2:159.	
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Styracaceae	T 4, Ab 1:172; N 1:281; N 3:290; N 4:241.	
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Synchytriaceae	T 1, Ab 1:71	see Bd 5al.
Taccaceae	T 2, Ab 5:127; N 1:80; N 3:49	Bd 15a:434.
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Thelotremaceae	T 1, Ab 1*:118	Bd 8:136.
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Thuidiaceae		Bd 11:309.
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Tilletiineae	T 1, Ab 1**:15	Bd 6:16.
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Trichothyriaceae		see Bd 5aI.
Trigoniaceae	T 3, Ab 4:309; N 1:209; N 4:163.	
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Triuridaceae	T 2, Ab 1:235; N 1:38; N 2:3; N 4:8.	
Trochodendraceae	T 3, Ab 2:21; N 1:158; N 2:22; N 3:110.	
Tropaeolaceae	T 3, Ab 4:23, 352; N 1:204; N 3:180	Bd 19a:67.
Tryblidiaceae	T 1, Ab 1:253.	
Trypetheliaceae	T 1, Ab 1*:69	Bd 8:81.
Tuberaceae		see Bd 5aI.
Tuberculariaceae	T 1, Ab 1**:498	see Bd 5aI.
Tuberineae	T 1, Ab 1:278	Bd 5bVIII.
Tubiferaceae		Bd 2:317.
Tulasnellaceae		see Bd 5aI.
Tulostomataceae	T 1, Ab 1**:342	Bd 7a:46; see Bd 5aI.
Turneraceae	T 3, Ab 6a:57; N 1:253	Bd 21:459.
Typhaceae	T 2, Ab 1:183; N 1:35; N 2:2; N 3:6.	
Ulmaceae	T 3, Ab 1:59; N 1:118; N 2:17; N 3:96; N 4:66.	
Ulothricaceae	T 1, Ab 2:79; N to T 1, Ab 2:70	Bd 3:157.
Ulvaceae	T 1, Ab 2:74; N to T 1, Ab 2:69	Bd 3:172.
Umbelliferae	T 3, Ab 8:63; N 2:51; N 3:256; N 4:221.	
Uredinales	T 1, Ab 1**:24.	
Urticaceae	T 3, Ab 1:98; N 1:122; N 3:97; N 4:69.	
Usneaceae	T 1, Ab 1*:216	Bd 8:238.
Ustilaginaceae	T 1, Ab 1**:6	Bd 6:7.
Ustilaginales		Bd 6:24.
Ustilagineae	T 1, Ab 1**:6	Bd 6:6.

Valerianaceae	T 4, Ab 4:172; N 1:316; N 2:74; N 3:332; N 4:302.	
Valoniaceae	T 1, Ab 2:145; N to T 1, Ab 2:109	Bd 3:252.
Valsaceae	T 1, Ab 1:454	see Bd 5aI.
Vampyrellaceae		Bd 2:313.
Vaucheriaceae	T 1, Ab 2:131; N to T 1, Ab 2:131	Bd 3:326.
Velloziaceae	T 2; Ab 5:125	Bd 15a:431.
Verbenaceae	T 4, Ab 3a:132, 377; N 1:290; N 2:64; N 3:307; N 4:266.	
Verrucariaceae	T 1, Ab 1*:53	Bd 8:65.
Violaceae	T 3, Ab 6:322; N 1:252; N 2:45; N 3:232; N 4:205.	Bd 21:329.
Vitaceae	T 3, Ab 5:427; N 1:230; N 2:41; N 3:211; N 4:193.	Bd 20d:174.
Vochysiaceae	T 3, Ab 4:312; N 2:37.	
Volvocaceae	T 1, Ab 2:29; N to T 1, Ab 2:15	Bd 3:28.
Vuilleminiaceae		see Bd 5aI.
Warnowiaceae		Bd 2:51.
Weberaceae	T 1, Ab 3:662, 1210.	
Welwitschiaceae		Bd 13:419.
Winteranaceae	T 3, Ab 6:314; N 3:231.	
Wittrockiellaceae	N to T 1, Ab 2:95	Bd 3:225.
Woroninaceae		see Bd 5aI.
Xanthopyreniaceae		Bd 8:91.
Xylariaceae	T 1, Ab 1:480.	
Xyridaceae	T 2, Ab 4:18; N 1:61; N 2:9; N 3:37	Bd 15a:35.
Zingiberaceae	T 2, Ab 6:10; N 1:90; N 2:12; N 3:53; N 4:39.	Bd 15a:541.
Zygnemaceae	T 1, Ab 2:16.	
Zygnemataceae	N to T 1, Ab 2:10	Bd 3:362.
Zygomycetes	T 1, Ab 1:119.	
Zygophyllaceae	T 3, Ab 4:74, 353; N 1:207; N 3:187; N 4:155.	Bd 19a:144.

TECHNIQUES FOR COLLECTING AQUATIC AND MARSH PLANTS[1]

ROBERT R. HAYNES[2]

Aquatic and marsh plants are those species occurring in substrates saturated with water most or all of the year. These substrates may be inundated permanently or may have the water table at the substrate surface. This habitat often poses a barrier to the collector and special problems in specimen preparation. As a result, aquatic and marsh plants are often inadequately collected and, therefore, poorly represented in herbaria.

When collecting for aquatic or marsh species, I examine almost every wet spot, pool, lake, or stream I encounter and wade to the plants, if necessary. The substrate is often quite muddy and I may sink to the knees or deeper. When the water is too deep to wade, I prefer using a small boat and then dragging the substrate with a rake or grappling hook (one constructed from pipe ca. 20 cm long by 2 cm wide, coat-hanger, and rope ca. 10 m long is adequate). One can, of course, stand on shore and toss the grappling hook into the bed of plants, if the plants are fairly close.

It is important to make complete specimens, including stems, leaves, roots, and reproductive structures—preferably mature flowers and fruits—of aquatic and marsh plants. Both staminate and carpellate flowers should be collected for taxa with imperfect flowers, e.g., Hydrocharitaceae. Sterile specimens should be collected only for those taxa, e.g., Lemnaceae, that are so rarely seen in flower that the taxonomy is based upon vegetative features. Some persons believe that aquatic habitats are visited so rarely that it is better to collect a sterile specimen than none at all. However, if the specimen cannot be determined, it might as well be left in nature.

Label data are especially important with aquatic or marsh plants. Information other than normal locality data that should be included are depth of water; flow rate of water; range of leaf size; whether leaves are submersed, floating, or emergent; color of flower; odor of flower; time of day of flowering; whether flowers are submersed, floating, or emergent; and whether fruits are submersed, floating, or emergent.

Care must be taken to prepare quality specimens of aquatic vascular plants. They normally do not need to be pressed immediately following collection. I usually wrap each collection in dry newspaper and store these wrapped collections in plastic bags or styrofoam chests. These bags or chests are kept in the shade to prevent overheating the plants. The moisture from the specimens is adequate to moisten the newspaper and to keep the specimens fresh and pliable for several hours. The plants can be pressed later that day when one has ample time to do the task carefully.

Several taxa, e.g., *Heteranthera* and *Utricularia,* have delicate flowers that are destroyed or from which the corolla falls off in the bag or press. Two or three flowers of these taxa should be preserved in 50% aqueous methyl or ethyl alcohol solution. Plastic 20 ml vials are excellent for this. Also, the "duckweed press," which is discussed later, works well for pressing these flowers.

Many species of aquatic and marsh plants have fairly large bulky stems, leaves, and subterranean parts. These large organs pose special problems when pressing. First, all parts of a specimen, other than the bulky structures, will have inadequate pressure in the press; as a result, they shrink during the drying process. This shrinking can be corrected by placing layers of newspaper on the flatter parts while the plant is in the press. Second, these bulky organs tend to have large amounts of water and, therefore, dry slowly—so slowly, in fact, they may completely decay while in the press. This decaying can be eliminated by splitting the large structures before pressing and by changing the corrugates and blotters of the press each day.

Delicate aquatic plants, especially those that

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grow submersed, need to be floated (see explanation below) onto a sheet of paper prior to pressing. I prefer to float the specimens onto half sheets of newspaper. These sheets are then placed between folded newspaper—the "pressing paper"—for pressing. I float and field press these delicate specimens at the time of collecting, rather than in the evening, so that I may use the body of water in which they were growing for floating. This procedure eliminates the need to take a pan for specimen floating on collecting trips.

The specimens are floated by placing the plant in water with the half sheet of newspaper below. After the plant is positioned properly on the paper, it is held in place to the top of the paper by the thumb as the newspaper is slowly lifted from the water. The paper is lifted in a manner so that water flowing from the paper separates the leaves, and the specimen adheres to the wet paper.

Some plants often have mucilages, either produced by the plant itself or by epiphytic algae, and, as a result, will stick to the half sheet and pressing paper upon complete drying. To prevent this sticking, I place the folded pressing paper between two sheets of blotting paper with minimal pressure and leave them for four to six hours at ambient temperature. This time period allows excess water to be absorbed by the blotting paper but does not allow adequate time for complete drying of the specimen. The specimens are then carefully removed from the pressing paper (including the half sheet), placed between unused, dry, folded newspaper, and pressed as usual. This transfer is done at the end of the collecting day when all other pressing is accomplished. Specimens rarely stick to the paper following this treatment. This procedure works quite well with such delicate species as those of *Utricularia.* Taxa that are extremely mucilaginous, e.g., *Brasenia,* may still stick to the paper even after this procedure. My students and I have found that these specimens are less likely to stick if they are pressed in folded nylon screen (available at local hardware stores) rather than paper. The screen is then placed between two blotters of the press. This screen should be used only with rather coarse taxa because it will damage delicate tissue.

If there is no time to change the paper, then one may wish to place waxed paper on one side only of the specimen to prevent it from sticking to the top sheet of the pressing paper. I do not use this technique, since the specimen will stick to the sheet used for floating. If the waxed paper technique is utilized, then the collector must float the specimen onto some good quality paper, such as bond typing paper or herbarium paper. Waxed paper works quite well with vegetative parts, but it will stick to delicate corolla lobes, such as those of *Utricularia.* These corolla lobes, however, do not stick to newsprint. Thus, a small section of the waxed paper should be torn off so that the waxed paper will not cover the corolla.

When pressing plants with whorled, dissected leaves, e.g., *Myriophyllum,* it is useful to section one node and float that node onto a small portion of paper. The number of leaves per whorl, as well as the number and arrangement of segments per leaf, are often important in these dissected-leaved plants. A single node floated onto a small section of paper makes observing these characteristics much less difficult.

The shape of stems or petioles may be important for identification of aquatic or marsh plants. These structures have large lacunae and, as a result, may collapse during pressing. Therefore, cross sections of stems and petioles should also be pressed to indicate the shape.

Specimens of Lemnaceae are often *very* poorly prepared. Wads of these plants—as well as snails, insects, small sticks, and other debris—are often smashed between folded newspaper during usual pressing. One obtains, from such a preparation, a mass of individuals seemingly welded together. Duckweeds are much better prepared by storing them in 50% methyl or ethyl alcohol in the field and by pressing them later in the laboratory. I take into the field 25–30 plastic bottles, each with a capacity of ca. 250 ml. At least one-third of these bottles is filled with absolute methyl or ethyl alcohol. When a population of Lemnaceae is located, the plants are collected by skimming a tea strainer or dip net (available at aquarium stores) along the surface of the water. I fill a bottle about half full with the plants. Then an aqueous solution of ca. 50% (v/v) methyl or ethyl alcohol is prepared and the bottle is filled with this solution. I use the water in which the plants were growing to prepare the solution. The plants will remain without deterioration for several weeks. The chlorophyll, of course, will be bleached out, but all important characteristics will remain. Once back in the laboratory, and following identification, the specimens are sorted by taxon onto standard index cards and are pressed. Special "duckweed presses" (designed by Howard Clark) can be made from pressing corrugates that are cut into sections the same size as the index cards. I do not use blotters or newspaper, but if they are used, they would be cut to sizes equal to the index cards. Neither frames nor straps are used with the press. Instead, one rubber band (ca. 7 mm wide and 75 mm in diameter) is placed around the press in the short direction for pressure. This rubber band gives enough pressure to keep the plants flat but not so much that the plants are welded to the paper. When the specimens are dried, two or three cards of each taxon prepared by this technique are placed inside a packet constructed from 100% rag typing paper and the packet is glued onto an herbarium sheet.

Members of the Nymphaeaceae and Nelumbonaceae are mostly large and difficult to press. Since flowers and fruits are important in the taxonomy of these taxa, these structures should be pressed open or split lengthwise so that the internal structure can be observed. One or two leaves are all that need be pressed for each specimen.

Michaelis (1981) has proposed using 50% glycerol (v/v aqueous) as a storage medium for all aquatics prior to pressing. I can see no value to such an approach because it would necessitate, for prolonged trips, transporting large amounts of glycerol. Also, specimens carefully processed by usual pressing techniques are equal to or better in quality than those prepared with the glycerol technique. This technique might be of value when one wishes to save some of the material in the three-dimensional form for teaching purposes, however.

LITERATURE CITED

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WOOD AND STEM ANATOMY OF *BERGIA SUFFRUTICOSA*: RELATIONSHIPS OF ELATINACEAE AND BROADER SIGNIFICANCE OF VASCULAR TRACHEIDS, VASICENTRIC TRACHEIDS, AND FIBRIFORM VESSEL ELEMENTS

Sherwin Carlquist[1]

Abstract

Bergia suffruticosa Fenzl provided sufficient lower stem and upper stem material to compare wood and stem anatomy to those of putatively related families: Clusiaceae (including Hypericaceae), Frankeniaceae, Lythraceae, and Haloragaceae. Of these, only Clusiaceae proves close; resemblances to *Bergia* include presence of simple perforation plates, presence of tracheids as the imperforate tracheary element type, presence of vasicentric tracheids and fibriform vessel elements, predominance of uniseriate rays with some biseriates, vertical orientation of scalariform vessel-ray pitting, absence of intraxylary phloem, abundance of brownish compounds in parenchyma cells, and occurrence of druses and solitary crystals. Other features such as seed anatomy confirm the relationship of Elatinaceae and Clusiaceae. The presence and nature of vasicentric tracheids in *Bergia suffruticosa* and Clusiaceae prompts an examination of this cell type. *Vascular tracheids* are defined here as: (1) present in latewood only (except for some genera in which all wood is like latewood); (2) not always present near vessels; (3) characteristic mostly of drought-deciduous shrubs; (4) about the same length as vessel elements in any wood in which they occur; (5) with pits like those of the vessel elements; and (6) present in families so specialized that the imperforate tracheary element type is the libriform fiber (rarely the fiber-tracheid). *Vasicentric tracheids,* in contrast, are (1) distributed in earlywood as well as in latewood and can occur in diffuse porous; (2) always occur near vessels; (3) are wider, somewhat shorter, and more densely pitted than associated imperforate tracheary elements although they always bear pits like those of vessels; (4) may be associated with fiber-tracheids (with various types of pitting) or libriform fibers, depending on the species; and (5) occur in trees or shrubs that may be evergreen or winter-deciduous, but tend to be unlike the shrubs (predominantly from families in which herbaceous species are frequent or preponderant) in which vascular tracheids occur. Vascular tracheids as defined here do not have vestigial perforations; cells with such perforations are regarded as vessel elements by definition. Fibriform vessel elements (perforate but intermediate in size and shape between tracheids and wide vessel elements) have been reported in other groups, notably vines, where fibriform vessel elements may result from vessel dimorphism (lateral enlargement of narrow vessels preempted by the great widening of a few vessels). Fibriform vessel elements may also occur in some nonvining families, such as Hydrophyllaceae, however.

Although some data are available on stem anatomy (mostly primary stem) of *Bergia suffruticosa* (Metcalfe & Chalk, 1950), the nature of secondary xylem has not been described for this species, the only species of Elatinaceae that could be considered at all woody. The material kindly provided me by Dr. Peter H. Raven included stems and some small roots. Roots were not large enough to make study of root wood feasible. No material of leaves or flowers was provided, and those structures are therefore not included in the present study.

Although wood anatomy is often not decisive in delineating relationships of dicotyledon families, wood anatomy of *Bergia suffruticosa* proves unusually valuable in indicating the probable relationships of Elatinaceae. The affinities of Elatinaceae have been claimed by various authors to include such families as Clusiaceae (including Hypericaceae), Frankeniaceae (and the allied family Tamaricaceae), Lythraceae, and Haloragaceae (C. D. Cook in Heywood, 1978). These four groups are located in four disparate orders, respectively—Theales, Tamaricales (near Cistales), Myrtales, and Cornales—according to the system of Thorne (1976). Opinions are not equally divided on which of these groups is most closely related to Elatinaceae. A few authors have favored placement near Frankeniaceae and Tamaricaceae (e.g., Wettstein, 1935). Hutchinson

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(1959) claimed affinity of Elatinaceae with Caryophyllaceae. However, more recent phylogenists opt unanimously for placement of Elatinaceae in Theales near Clusiaceae (Cronquist, 1981; Dahlgren, 1980; Takhtajan, 1980; Thorne, 1976). The families Clusiaceae and Hypericaceae are very close and are treated as a single family by most authors, such as the four just cited. I will follow that treatment in my discussion, and I will use the name Clusiaceae for the combined family.

The wood of *Bergia suffruticosa* demonstrates an unusual near-continuum in morphology between wide vessel elements, fibriform vessel elements, and tracheids. This phenomenon proves referable to concepts variously designated by particular terms. The concepts of vascular tracheids, vasicentric tracheids, fibriform vessel elements, and vessel dimorphism are compared and contrasted. The functional nature of these phenomena is also explored. Further work to refine definitions of these cell types is needed.

MATERIALS AND METHODS

Of the liquid-preserved specimens of *Bergia suffruticosa* placed at my disposal, one series, vouchered by the specimen *B. C. Daramo 6* (MO), was selected because xylem accumulation was maximal and straight stem portions suitable for sectioning were present. This material was collected from a shrub 90 cm tall growing near the Numan Bridge on the Benu River near Numan, Gongola, Nigeria. The liquid-preserved material was provided as bottles labeled "stems" and "roots" respectively. However, sections of the latter revealed presence of pith and endarch xylem. Therefore these segments have been designated "lower stems," and those labeled as stems have been designated as "upper stems" in the descriptions that follow. *Bergia suffruticosa* is branched from near the base; the "lower stem" is below most of this branching whereas the upper stems, much smaller in diameter, are taken from above most of this branching.

The lower stems of *Bergia suffruticosa* have wide vessels (Fig. 1). Upper stems are small in diameter, and have a thin but tough cylinder of secondary xylem (Fig. 10). These features would lead to fragmentation of vessel walls and of sections with ordinary rotary microtome or sliding microtome techniques. Such small stems are, moreover, difficult to handle with a sliding microtome. Therefore a new method in which infiltration and embedding in paraffin are preceded by treatment of the material in ethylene diamine (Carlquist, 1982) was used. The softening action of the ethylene diamine was hastened by placing the material being treated in a paraffin oven (60°C) for four hours. Sections were stained with a safranin–fast green combination.

Macerations were prepared from pickled material with Jeffrey's Fluid. Macerations were stained with safranin.

For comparison with *Bergia suffruticosa,* wood of several species of Clusiaceae was sectioned. These wood samples are part of the Rancho Santa Ana Botanic Garden wood sample collection, but are designated by serial numbers of the U.S. National Museum, which contributed them to that collection. This material did not require special softening techniques and was sectioned on a sliding microtome and stained with safranin. Macerations were prepared with Jeffrey's Fluid and stained with safranin.

ANATOMICAL DESCRIPTIONS

Lower stem (Figs. 1–9). Growth rings absent; larger vessel elements tend to be progressively wider in diameter (Fig. 1). Vessel elements range up to 230 μm in diameter. Perforation plates are simple. Cells that appear to be imperforate tracheary elements as seen in transection include both fibriform vessel elements (Fig. 3) and tracheids. Fibriform vessel elements are more numerous than the tracheids but grade into them, as well as into the wider vessel elements. Because there is a complete intergradation among classes of tracheary elements, none of these classes can be isolated for the purposes of measurement, and only extremes can be quantified. Wider vessel elements are about 320 μm long, tracheids are about 600 μm long. Wall thickness of wider vessels is 7 μm, wall thickness of tracheids, 3 μm. Intervascular pitting of vessels is composed of alternate pits that can be polygonal in outline where crowded (Fig. 7), otherwise circular in outline or somewhat laterally widened (Fig. 6); pits average about 6 μm in diameter. Vessel-ray pitting is composed of circular or elongate pits, the latter often elongate parallel to the long axis of the stem (Fig. 6), a kind of scalariform pattern. Vessel-ray pitting is bordered on the vessel side, simple on the ray cell side. Axial parenchyma is in strands of two cells. Axial parenchyma is often beside larger vessels (Fig. 4), but can also be scattered among other tracheary elements (Fig. 5). Because the fibriform vessel elements are so abundant, virtually all axial parenchyma may be adjacent to vessel elements and is therefore paratracheal. Rays are uniseriate to multiseriate (Fig. 2), wide multiseriate rays are infrequent. Rays mostly have lignified walls, a few have thin nonlignified walls (Fig. 2). Ray cells are mostly erect or square; a few procumbent cells are present, but these are only a little longer radially than tall axially. Some ray cells are idioblastic and bear tanninlike compounds (Figs. 2, 4). Secretory canals are absent from rays. Wood is nonstoried. Druse-bearing cells and tannin-bearing cells occur idioblastically in both cortex and pith (Figs. 8, 9). Starch grains are frequent in parenchyma cells in both cortex and pith. Protophloem fibers are present (Fig. 8) and tend to be scattered in groups rather than as a continuous cylinder around the stem.

Upper stem (Figs. 10–12). Widest vessels about 70 μm in diameter (Fig. 10). Perforation plates simple. Vessels are quadrangular in transectional outline near pith, as claimed by Metcalfe and Chalk (1950), but rounded in outline otherwise, suggesting that very little secondary xylem was present in the material studied by Metcalfe and Chalk. Length of wider vessel elements is about 400 μm; length of tracheids is about 530 μm. Fibriform vessel elements are present, somewhat less abundant in comparison to wider vessel elements and tracheids than they are in the lower stem. Pits on vessel elements are alternate, about 5 μm in diameter. Fully bordered pits are present on tracheids (Fig. 12). Axial parenchyma is sparse. Rays are mostly uniseriate (Fig. 11), but some biseriate rays are present. Very few rays are more than two cells wide (a maximum of four cells wide was seen). Ray cells are erect only, no square or procumbent cells were seen. Secretory canals are absent in rays. Wood is nonstoried. Druses are present in pith and cortex; solitary crystals are present as chambered crystals in strands of phloem parenchyma. Tanninlike compounds are present in idioblastic cells in both cortex and pith, also in xylem parenchyma. Protophloem fibers are present, forming a nearly complete cylinder inside the cortex.

RELATIONSHIPS OF ELATINACEAE

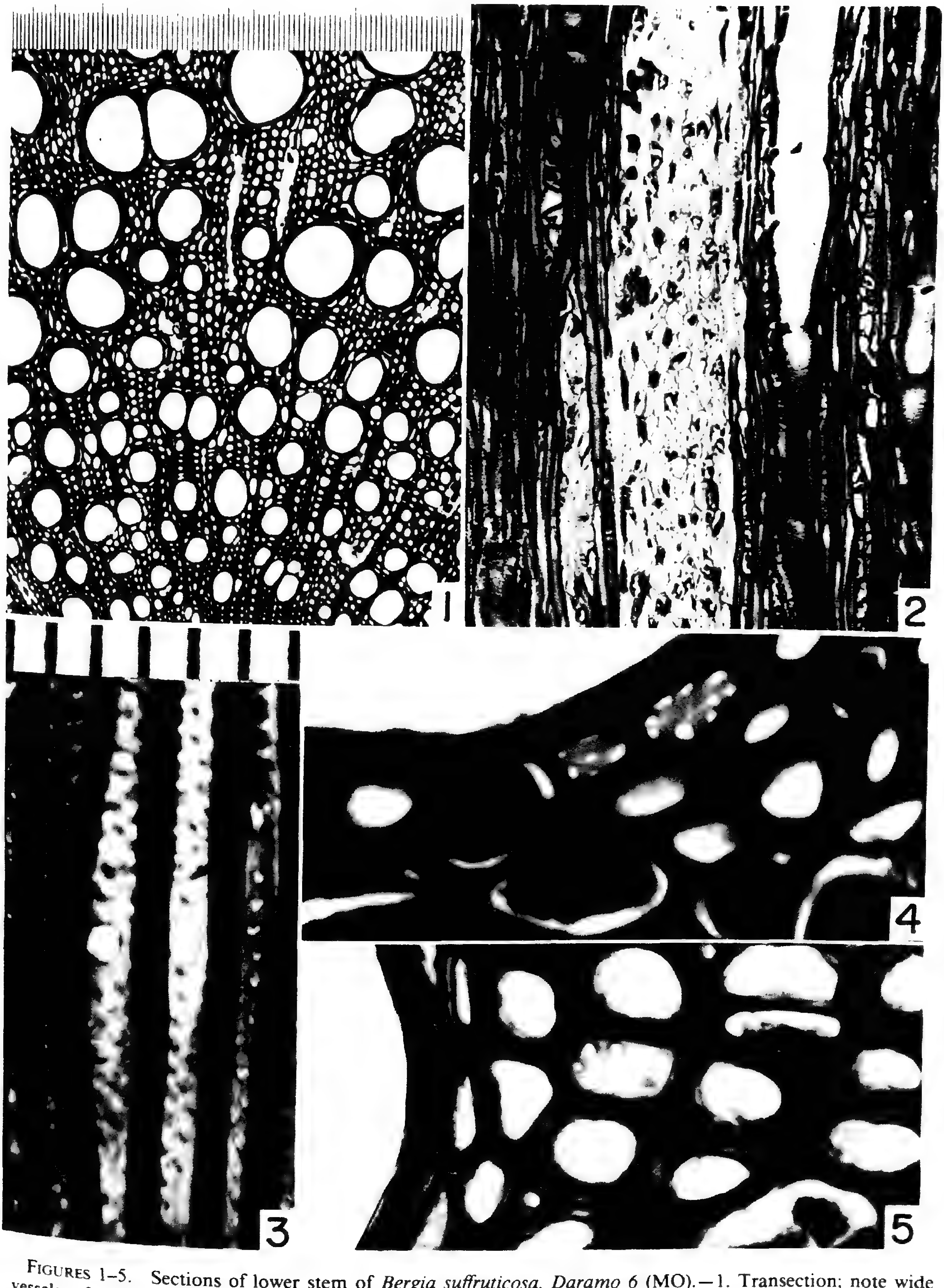
One can consider Clusiaceae, Tamaricaceae–Frankeniaceae, Lythraceae, and Haloragaceae as comprising the four groups to which Elatinaceae is compared in the present paper. All of these families except Clusiaceae have libriform fibers with simple pits, in contrast to Elatinaceae, in which tracheids bearing fully bordered pits are present (Fig. 12). While this discrepancy does not absolutely rule out a relationship, most families of dicotyledons do not have a wide range of pitting in imperforate tracheary elements.

Myrtalean affinity of Elatinaceae seems ruled out additionally because Elatinaceae lacks intraxylary phloem and vestured pits, features present in Lythraceae (Baas & Zweypfenning, 1979).

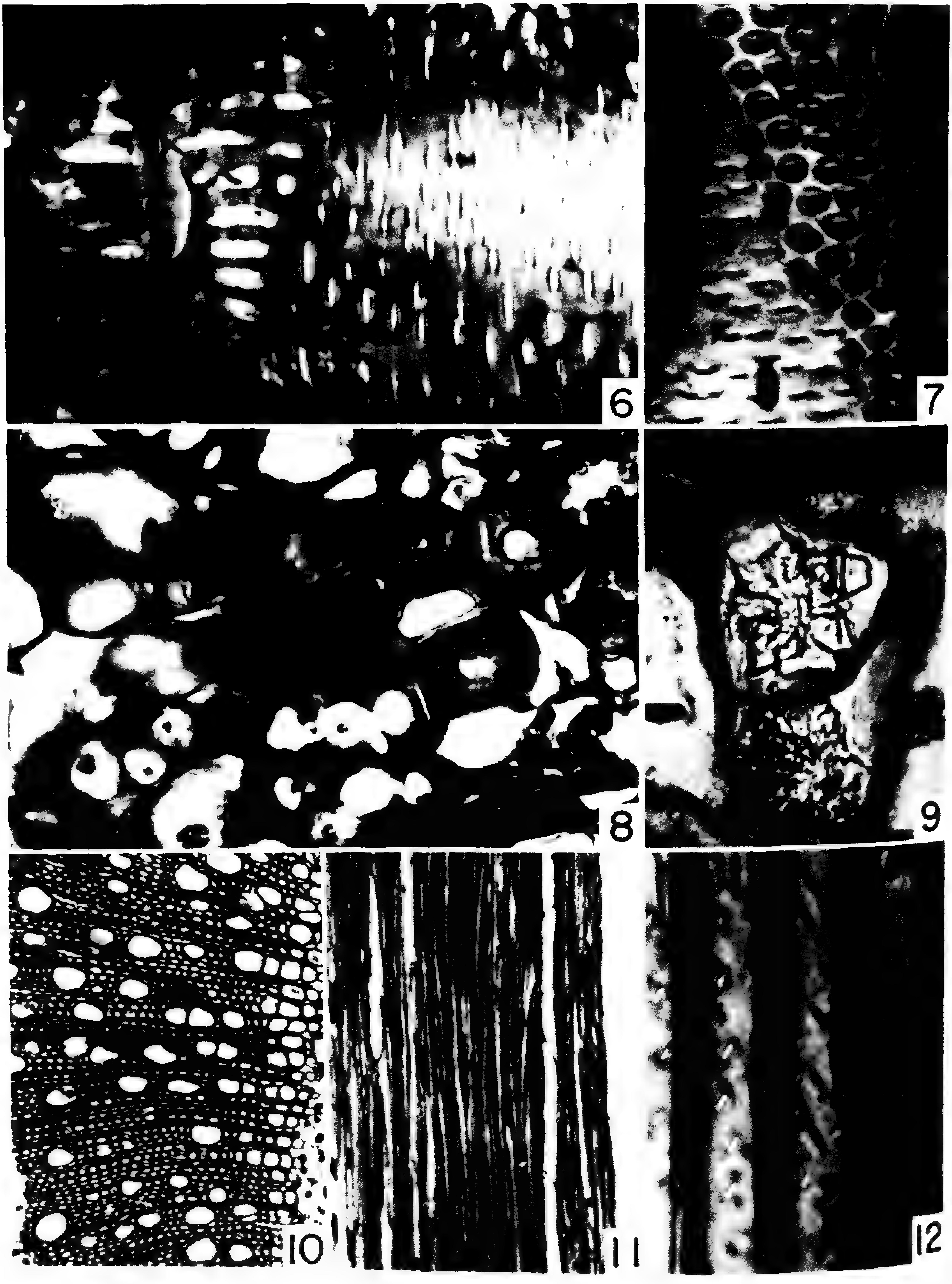
An undetermined Australian species of *Frankenia* represented in my wood slide collection has rayless wood, a feature not present in *Bergia suffruticosa. Tamarix* has unusually wide rays (10–25 cells wide), but has few or no uniseriate rays according to Metcalfe and Chalk (1950). Tamaricaceae has storied wood. Thus Frankeniaceae and Tamaricaceae contrast with Elatinaceae.

Although wood of Haloragaceae does not differ sharply from that of Elatinaceae except in having simple pits in imperforate tracheary elements, other differences in stem anatomy may be found. For example, Haloragaceae have crystals in trichomelike cells in the cortex; such cells are absent in Elatinaceae. The distribution of protophloem fibers in Haloragaceae (where such fibers are rare) is unlike that of Elatinaceae.

Affinity of Elatinaceae with Clusiaceae, the relationship claimed for Elatinaceae by recent phylogenists, can be supported by numerous wood features, in contrast with the above comparisons. Imperforate tracheary elements with fully bordered pits (Figs. 15, right; 16, right; 19, right) exactly like those on vessel elements (and thus tracheids) occur in both families. The occurrence of a tracheary element type intermediate in morphology between tracheids and wide vessel elements, termed fibriform vessel elements above, can be seen in *Hypericum* (Fig. 19, left) as well as in *Bergia suffruticosa* (Fig. 3). The occurrence of vasicentric tracheids in *Calophyllum* and other Clusiaceae is an allied phenomenon discussed below. Rays in Clusiaceae are most often uniseriate or biseriate (Figs. 14, 15), although somewhat wider rays have definitely been reported. The presence of a few wide rays in the lower stem of *Bergia suffruticosa* (as compared to the upper stem) may be an interpolation related to starch and water storage, and probably does not represent any remnant of any hypothetical wider-rayed condition. The predominant erectness of



FIGURES 1–5. Sections of lower stem of *Bergia suffruticosa, Daramo 6* (MO).—1. Transection; note wide vessels.—2. Tangential section. Wide multiseriate ray, center; other rays are mostly uniseriate or biseriate.—3. Portion of radial section, showing two tracheids (left) and three fibriform vessel elements with small perforation plates (right).—4. Transection; ray cells filled with tanninlike deposit.—5. Transection. Axial parenchyma cells near center and adjacent to vessel, lower left. Figures 1, 2, magnification scale above Figure 1 (finest divisions = 10 μm). Figures 3–5, magnification scale above Figure 3 (divisions = 10 μm).



FIGURES 6–12. Sections of *Bergia suffruticosa*, *Daramo 6* (MO). 6–9. Sections of lower stem.—6. Portions of vessel from radial section (long axis of vessel oriented left to right). Note vertically elongate vessel-ray pitting left.—7. Vessel wall from radial section; pits are alternate, polygonal to rounded in outline.—8. Portion of stem transection, cortical cells with tannin and starch, left; protophloem fibers, right.—9. Druse from cortex of stem transection. 10–12. Sections of upper stem.—10. Transection of secondary xylem, pith margin at right.—11. Tangential section, rays very narrow.—12. Portions of tracheids from radial section; pits fully bordered. Figures 6–9, 12, magnification scale above Figure 3. Figures 10, 11, magnification scale above Figure 1.

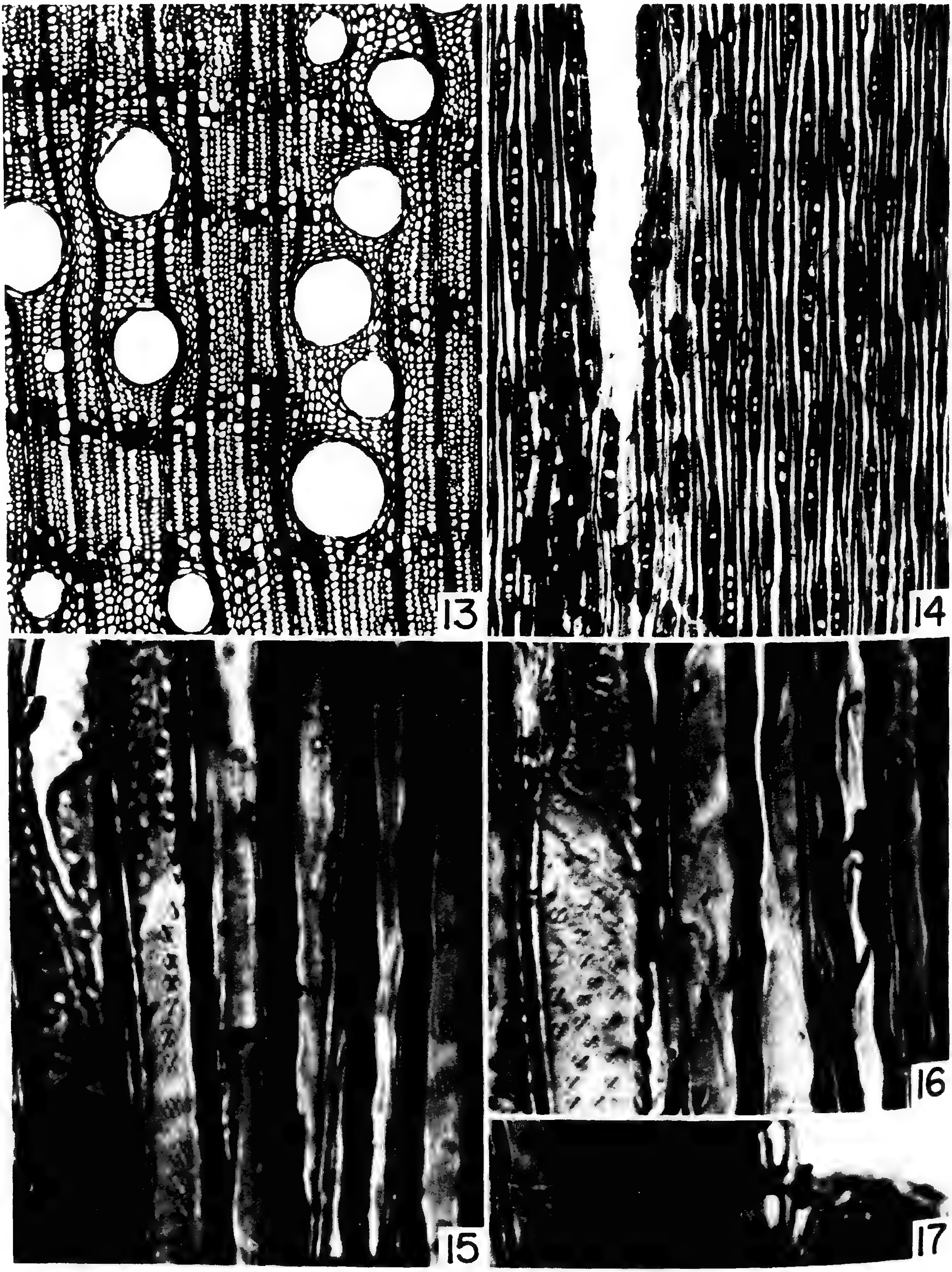
ray cells in *Bergia suffruticosa* is doubtless related to its stature as an herb, judging from characteristics of herbs and herblike plants discussed earlier (Carlquist, 1962). Diffuse parenchyma, as in Elatinaceae, can be found in a few Clusiaceae, such as *Mammea* (Metcalfe & Chalk, 1950), but a wide range in parenchyma types exists in Clusiaceae, ranging from apotracheal bands, as in *Calophyllum* (Figs. 13, 18) to absent, as in *Hypericum* (Fig. 20), or paratracheal (as can be claimed for *Bergia*) in *Tovomitopsis* (Metcalfe & Chalk, 1950). Vessel-ray pitting in *Bergia suffruticosa* may be scalariform, the pits elongate vertically (Fig. 6); this can be found in Clusiaceae also (Fig. 17). Presence of brown-colored compounds, presumptively regarded as tanninlike above, is widespread in dicotyledons, but these are very abundant in *Bergia suffruticosa* and in Clusiaceae. Secretory canals are absent in rays of *Bergia*, but they are absent in many Clusiaceae also. Druses and solitary crystals are widespread in dicotyledons; both types occur both in Elatinaceae and in Clusiaceae, however. The major reasons for allying Elatinaceae with Clusiaceae lie in gross morphology, the more important wood features outlined above, and in seed anatomy (Corner, 1976). Because of parallel aneuploidy in Clusiaceae and in Elatinaceae, chromosome number similarities may be inconclusive (Raven, 1975).

VASCULAR TRACHEIDS, VASICENTRIC TRACHEIDS, FIBRIFORM VESSELS, AND VESSEL DIMORPHISM: DEFINITIONS AND SIGNIFICANCE

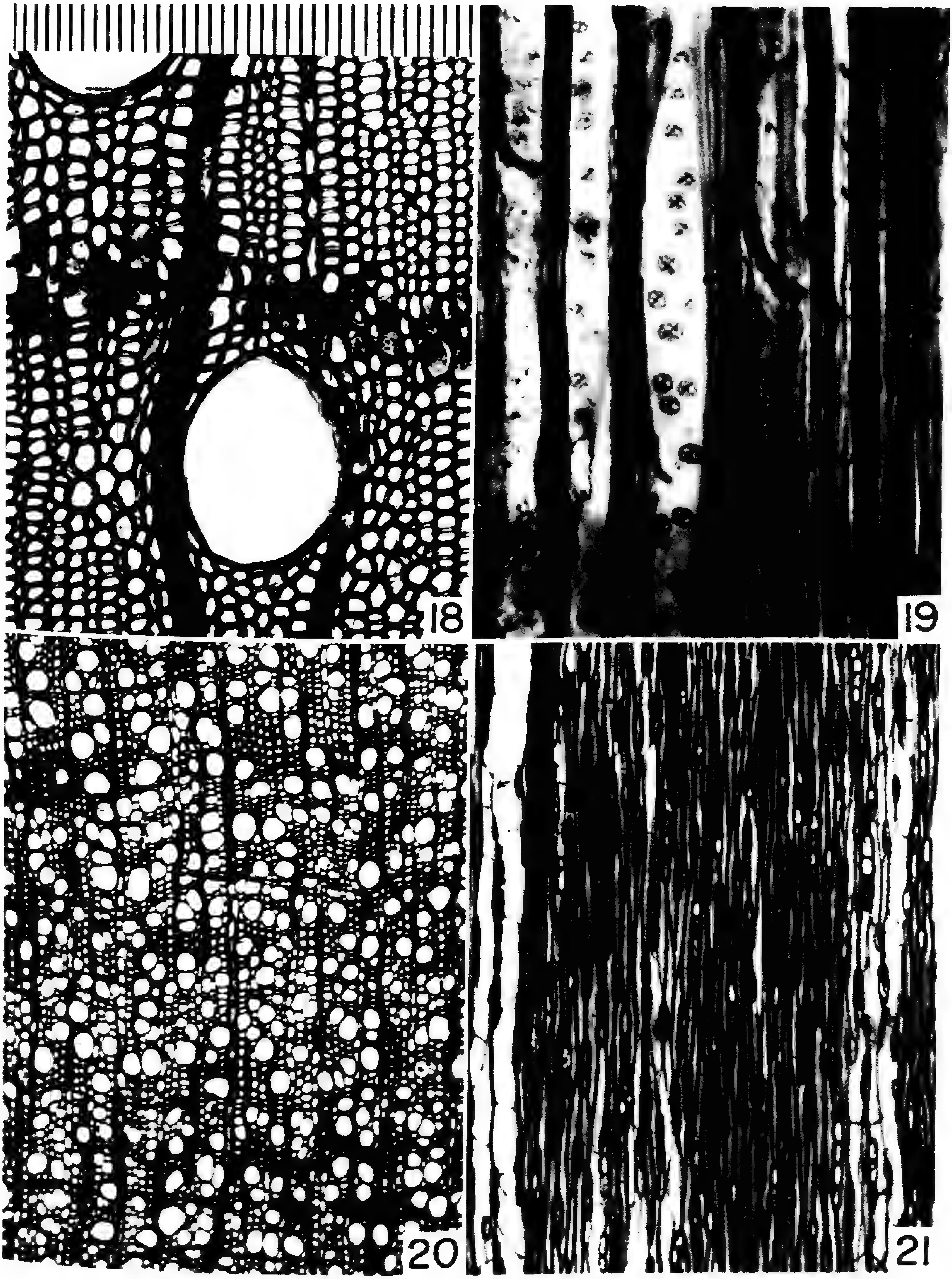
Among the anatomical features for which listings of families are given by Metcalfe and Chalk (1950, 1983) is presence of vasicentric tracheids. This feature, however, seems not to have received extensive comment in any paper. Vasicentric tracheids may be closely allied to other types of tracheary elements. Consequently, definitions and discussion are offered here. This discussion may be regarded as preliminary, and refinements and modifications are to be expected.

Vascular tracheids. Vascular tracheids are vessel elements so narrow that they lack perforation plates. Criteria for their recognition include the following. (1) They occur in woods that have sharply demarcated growth rings, and the vascular tracheids always occur in latewood only. Exceptions to this may be found in woods that represent such a high degree of xeromorphy that all wood in those species is comparable to latewood, as in *Loricaria thuyoides* (Carlquist, 1961) or globular cereoid cacti (Gibson, 1973). (2) Vascular tracheids are known only in highly specialized wood in which imperforate tracheary elements have simple pits only and therefore are libriform fibers. A minor exception is formed by Calycanthaceae, in which fiber-tracheids (with quite vestigial borders, however) are present and in which vascular tracheids easily distinguishable from the fiber-tracheids occur (Carlquist, 1983). (3) Vascular tracheids tend to be the same length as the vessel elements in any given sample, but are appreciably shorter than the libriform fibers with which they are associated. When comparing vascular tracheids to vasicentric tracheids (below), distribution within the wood is the most important of the above criteria. Thus, although Calycanthaceae are listed by Metcalfe and Chalk (1950, 1983) as having vasicentric tracheids, the family actually has vascular tracheids, formed only in the latewood of growth rings. The drawing of a transection of *Chimonanthus fragrans* wood by Metcalfe and Chalk does not include any indication of vasicentric tracheids (which are denoted by a special pattern in drawings of the woods that do have vasicentric tracheids elsewhere in their book). Vascular tracheids are found in such families as Asteraceae (Carlquist, 1960), Cactaceae (Gibson, 1973), and Scrophulariaceae (Michener, 1981). Functionally, vascular tracheids offer the safety of true tracheids under drought conditions in that air embolisms cannot spread from one vascular tracheid into another, whereas air bubbles can spread from one vessel element into numerous vessel elements subadjacent or superadjacent. Tracheary elements like vascular tracheids but with vestigial or pitlike perforations are not admitted as vascular tracheids here, but are considered vessel elements if any perforation occurs. Vascular tracheids probably occur most commonly in drought-deciduous shrubs; their occurrence is not familiar to those who study wood of trees exclusively.

Vasicentric tracheids. Judging from systematic occurrence (Metcalfe & Chalk, 1950: 1351; 1983: 205), vasicentric tracheids must have arisen more than once in dicotyledons, and therefore may not represent a uniform phenomenon. However, the following criteria may be used to identify and define vasicentric tracheids. (1) Vasicentric tracheids are imperforate cells that bear fully bordered pits like the pits of vessel elements in the woods in which they occur. (2) Vasicentric



FIGURES 13–17. *Calophyllum vitiense, USw-16369,* wood sections.—13. Transectional vessels are solitary; apotracheal banded parenchyma visible because of dark-staining contents.—14. Tangential section. Rays uniseriate, biseriate, rich in dark-staining contents.—15, 16. Portions of radial section; in each, vasicentric tracheids at left, fiber-tracheids at right, showing character of these two cell types and their bordered pits.—17. Portion of radial section; vessel-ray pitting at center, pits vertically elongate forming a scalariform pattern. Figures 13, 14, magnification scale above Figure 1. Figures 15–17, magnification scale above Figure 3.



FIGURES 18–21. Wood sections of Clusiaceae.—18. *Calophyllum vitiense*, *USw-16369*, transection; vasicentric tracheids are visible as cells larger in diameter than ordinary tracheids, to left of lower vessel and below upper vessel. 19–21. *Hypericum galioides*, *USw-14006*, wood sections.—19. Radial section; perforation plate visible in fibriform vessel, left; other cells at right are vasicentric tracheids.—20. Transection; vessels very narrow, numerous.—21. Tangential section; rays are mostly uniseriate. Figure 18, magnification scale above Figure 18 (divisions = 10 μm). Figure 19, magnification scale above Figure 3. Figures 20, 21, magnification scale above Figure 1.

tracheids are distributed around vessels and vessel groups. (3) Vasicentric tracheids tend to be at least somewhat longer than vessel elements in any given wood. (4) Vasicentric tracheids are not distributed with relation to growth rings and are present in earlywood as well as in latewood. Vasicentric tracheids may occur in woods without growth rings (e.g., *Calophyllum*, Fig. 13). The diffuse porous woods in which they occur are not so highly xeromorphic that the entirety of the wood may be regarded as a kind of latewood, a phenomenon true of the wood of cacti, cited above, in which vascular tracheids occur. (5) Vasicentric tracheids tend to be wider than the remaining imperforate tracheary elements in woods in which they occur (Figs. 15, left; 16, left; 18). (6) Vasicentric tracheids tend to be more densely pitted than the remaining imperforate tracheary elements in woods in which they occur (Figs. 15, left; 16, left; 19).

Vasicentric tracheids may grade from cells very similar to the imperforate tracheary elements in the woods in which they occur to very unlike the imperforate tracheary elements they accompany. If a wood has true tracheids, vasicentric tracheids would be indistinguishable from true tracheids, and by definition we can say that vasicentric tracheids are absent in woods with true tracheids. *Calophyllum* (Figs. 13–18) has what may be termed fiber-tracheids that are more slender, longer, and more sparsely pitted than the vasicentric tracheids in that wood. This situation may also be found in *Asclepias albicans* Watson. On the other hand, *Connarus* has vasicentric tracheids markedly different from the libriform fibers which form the ground tissue of wood in that genus (Dickison, 1972). I have observed association of vasicentric tracheids with libriform fibers in *Oceanopapaver neocaledonicum* Guillaumin, a member of Capparaceae.

Hypericum galioides (Figs. 19–21) has fiber-tracheids with bordered pits in addition to vasicentric tracheids. However, there are also elongate vessel elements that resemble tracheids but that have small perforation plates (Fig. 19). These may be termed fibriform vessel elements because they are narrow, long, and with pointed ends as compared with ordinary vessel elements. Presence of fibriform vessel elements is characteristic of *Bergia suffruticosa*, but in that species all imperforate tracheary elements must be termed tracheids, and therefore no vasicentric tracheids can be said to occur.

The functional significance of vasicentric tracheids seems potentially much like that of vascular tracheids. Vasicentric tracheids form an excellent subsidiary conductive system in case of occlusion of vessels by air embolisms, theoretically. Indeed, in many of the species with vasicentric tracheids, vessels are notably large and therefore vulnerable (*Calophyllum, Connarus, Quercus*). Other species with vasicentric tracheids occur in notably dry habitats (*Asclepias albicans, Oceanopapaver neocaledonicum*) so that a subsidiary conducting system composed of tracheids and thus safer than a system composed only of vessel elements plus presumptively nonconductive libriform fibers would have a positive selective value. However, vasicentric tracheids would be of high value, theoretically, precisely because of their distribution in wood: they surround vessels so that if the vessels are disabled, the three-dimensional conduction patterns are minimally rerouted. The potential significance of maintaining this network intact can be realized if one notes that libriform fibers (which presumably function little if at all in conduction) or ray cells frequently separate one vessel from another in a particular wood, so that a three-dimensional rerouting across such relatively nonconductive cells is not possible. This would seem an advantage of vasicentric tracheids over vascular tracheids until one takes into account that vascular tracheids are formed in large numbers and are often in association with very narrow vessels, which are relatively safer than wider vessels, so that rerouting of conduction in case of embolisms in narrow vessels is also likely to be minimal. Vascular tracheids and vasicentric tracheids may be successful for many of the same reasons, but probably occur in different kinds of plants.

Fibriform vessel elements. This term was originated by Woodworth (1935) to describe slender vessel elements, fusiform in shape and often longer than the ordinary vessel elements they accompany in any given wood in which they occur. Because the tips of these cells are pointed, the perforations are subterminal and often appear lateral thereby. Some fibriform vessel elements can be considered under the heading of vessel dimorphism below. Others, however, appear to have nothing to do with any kind of vessel dimorphism. In *Eriodictyon* (Carlquist et al., 1983) and other Hydrophyllaceae (Carlquist & Eckhart, 1984), fibriform vessel elements are present but vessel dimorphism cannot be said to occur: vessel elements intermediate in diameter are frequent. In the Hydrophyllaceae in which fibriform vessel elements occur, there is a continuum not merely in diameter of vessel elements, but between fibriform vessel elements and tracheids (or fiber-tracheids) in the genera *Eriodictyon, Turricula,* and *Wigandia.* There may be an adaptive value for production of the narrow fibriform vessel elements, for narrow vessels ought to be adaptive in plants of dry areas such as those occupied by *Eriodictyon* (Carlquist, 1966, 1975).

Vessel dimorphism. The term vessel dimorphism was used earlier (Carlquist, 1981) to denote the tendency in a vining family (Nepenthaceae) for vessels to be either very wide or else very narrow and fibriform with a small perforation plate (often only a little larger than a bordered pit). The latter class of vessel elements was, in that family, only slightly longer than the former. This tendency can be found in other vining families of dicotyledons, such as Convolvulaceae, in which Mennega (1969) termed the slender vessel elements "fibres" with "apertures" (= perforations) on their radial walls. These elements also have bordered pits and thus do not differ from the wide vessel elements except in their shape and size.

Probably the phenomenon of vessel dimorphism applies to virtually all vining families and genera. It can be regarded as a byproduct of the production of very wide vessels, which are adaptive in vining plants for reasons suggested elsewhere (Carlquist, 1975). In this hypothesis, the production of few but very wide vessels would preempt the widening of many vessel elements, which thereby are destined to become fibriform vessel elements. A slightly greater length for fibriform vessel elements as compared with the wide vessel elements they accompany in a particular wood may be expected simply because slender cells tend to retain greater intrusive capacities than wide ones. Fibriform vessel elements in a species with vessel dimorphism would theoretically form an effective part of the conductive system, albeit small in capacity when compared to the very great hydraulic capacities of the wide vessel elements.

Obviously the characteristics of vessel elements, vascular tracheids, and vasicentric tracheids may vary somewhat from any particular scheme, and thus generalizations are premature. Consequently, the listing of vasicentric tracheids given by Metcalfe and Chalk (1950, 1983) should be regarded as a starting-point for research, not as a summation.

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THE EVOLUTION OF DIOECY—INTRODUCTION[1,2]

GREGORY J. ANDERSON[3]

That flowers can be unisexual, and that pistillate and staminate flowers may be borne on separate plants of the same species (i.e., dioecy) has been recognized for some time. For example, dioecy was one of the 24 classes in Linnaeus's sexual system of classification (1737, *Genera Plantarum*), and Darwin discussed dioecy at length in his 1877 book, *The Different Forms of Flowers on Plants of the Same Species.* Almost 45 years later, C. and H. Yampolsky's broad survey of the angiosperms (1922, Biblioth. Genet. 3: 1–62) confirmed that dioecy is not an aberration among angiosperms but is indeed widespread. They reported that 37 of 51 angiosperm orders have at least one dioecious species. In spite of this, there was relatively little interest in dioecy through much of the following four decades. However, in recent years the study of pollination biology and reproductive biology in general—neo-natural history—have once again become popular scientific pursuits. With this reawakening, there have been many new studies, and controversy has arisen regarding the importance of dioecy and the evolutionary mechanisms promoting it. Some of these studies, and some of the controversy, are presented in the papers that follow.

One result of this renewed interest has been the recognition that dioecy is more extensive than Yampolsky and Yampolsky's original estimate of 3–4% of the angiosperm species. Estimates now range up to 28% for some regions (e.g., the Hawaiian flora, see paper by Baker & Cox, below), but overall, David Lloyd estimates that about 10% of the angiosperm species are dioecious (1982, Amer. Naturalist 120: 571–585). In fact, some of the species recently described as dioecious are not obviously so. For instance, my studies of *Solanum* (1979, Nature 282: 836–838; Anderson & Symon, "Dioecious species of *Solanum* from Australia," manuscript in prep.), and the short report included below by Bill Haber and Kamal Bawa, illustrate that there are a number of taxa that are functionally, if not morphologically, dioecious, and that this seemingly obvious breeding system can be overlooked.

In a similar fashion, renewed interest has led to reconsideration of the stability of sexual expression, a topic that is reviewed below by Carl Freeman, E. D. MacArthur, and K. T. Harper. Herbert Baker and Paul Cox consider another facet of the distribution of dioecy issue in a new analysis of the frequency of occurrence of dioecy in island floras. The study of islands has been of particular interest because some have been thought to have a very high percentage of dioecy (as indicated above).

There has also been an increase in interest in experimental analyses of the evolutionary and ecological consequences of dioecy. This approach is represented here by two papers. Spencer Barrett summarizes work from his lab on the influence of sex expression, population structure, and population distribution on mating success in two *Aralia* species. Tom Meagher uses *Chamaelirium luteum* as a case study to discuss the impact of the different resource allocation requirements of androecious and gynoecious plants on the evolution of life history characteristics of each sex individually and of the species as a whole.

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[1] The following six contributions constituted a symposium at the American Society of Plant Taxonomy annual meeting (with the Botanical Society of America and the American Institute of Biological Sciences) held at The Pennsylvania State University in August of 1982. The paper by Haber and Bawa was not presented at the symposium, and the other contributions have been modified from the oral presentations.

[2] I am grateful to the following for their careful reading of the manuscripts: K. Bawa, R. Bertin, J. Estes, C. Heiser, T. Lee, and T. Philbrick. I thank James Estes for helping set up the symposium and Nancy Morin for encouraging this publication and for the final editing of the papers. My work in reproductive systems and on this symposium was supported in part by the National Science Foundation (INT-7910959, BSR-8207125).

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FURTHER THOUGHTS ON DIOECISM AND ISLANDS[1]

HERBERT G. BAKER[2] AND PAUL ALAN COX[3]

ABSTRACT

Non-dioecious taxa are the floral majority, both in island floras and in those of the mainlands. This is true at all latitudes. Temperate zone islands have very low percentages of dioecious species. The percentages are somewhat higher in subtropical islands. Relatively high percentages of dioecism are found only in moist tropical islands or in floras that have had a moist tropical influence on their composition. Low islands in the tropics and rather arid islands in the sub-tropics and tropics have only small numbers of dioecious species in their floras. A multiple regression analysis shows that latitude and maximum height of islands together account for 82% of the variation in percentage of dioecism in our samples. Although autochthonous development of dioecism in an hermaphrodite immigrant cannot be ruled out yet, the percentage of dioecism in an island flora appears to be related to the percentage in a probable source flora in a comparable climatic zone. This equivalence could result from parallel evolution but probably depends more upon the long-distance dispersal, establishment, and radiation of taxa, including dioecious ones. This may be facilitated for the dioecious taxa by "leakage" in the dioecious breeding system, by dispersal of multiple-seed units, by longevity and vegetative propagation of perennial plants, and by an ability to utilize wind or unspecialized pollinators. In tropical regions, bird-dispersal of seeds particularly may have been involved in the stocking of forests on islands.

Lately, there has been increased interest in the breeding systems of seed plants and, more recently, this has been concerned with the role of dioecism in the origin and maintenance of adaptation to various environmental conditions (Ornduff, 1966; H. G. Baker, 1976; Freeman et al., 1976, 1980; Lloyd & Webb, 1977; Webb, 1979; Willson, 1979, 1982; Bawa, 1980, 1982; Bawa & Beach, 1981; Beach, 1981; Givnish, 1980, 1982; Lloyd, 1980, 1982; Cox, 1981, 1982, 1983; Thomson & Barrett, 1981; Ross, 1982).

Among these considerations has been the significance of dioecism in those flowering plants that make up the floras of islands (Bawa, 1980, 1982). Traditionally, it was temperate floras whose reproductive biology was studied, but as more attention is being given to islands in warmer climes, it is important that we do not go too far in the other direction and assume that tropical islands are typical of islands in general.

There is no difficulty in spotting dioecism or monoecism in wind-pollinated temperate zone trees and herbs, for the morphological differences between staminate and pistillate inflorescences are striking, being related to the very different functions of casting pollen into the wind and sieving pollen out from an aerial suspension, respectively. But making a quick diagnosis of the breeding system is not so easy with insect-pollinated species, particularly in the tropics. Because both staminate and pistillate flowers must attract the same visitors, they tend to be similar in appearance, sometimes even to the extent of having pistillate flowers that produce non-functional pollen grains (e.g., *Actinidia chinensis,* Schmid, 1978; *Solanum* spp., Anderson, 1979).

Some of the difficulty that this has produced in attempts to quantify the occurrence of dioecism in tropical floras is shown by estimates of dioecism in the Hawaiian flora. Carlquist (1965) judged it to be 27.7% while Gilmartin (1968), basing her analysis on the flora written by Hillebrand (1888), reported it to be only 5%—a striking discrepancy. Both authors claimed not to include gynodioecious and other deviant species in the percentage. Possibly the truth lies somewhere between these extremes, but we use the Carlquist figure because Gilmartin, herself, suggested that Hillebrand (1888) may have had difficulty in identifying dioecism from imperfectly preserved specimens or rarely collected species. Also, Carlquist (1965) made studies of many species and did not rely solely on the literature.

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TABLE 1. Percentages of Dioecism in Islands and Corresponding Mainlands.

Category	Island	Number of Species	% Dioecism	Comparable Mainland	Number of Species	% Dioecism
Cool temperate	Iceland	472	3	British Isles	1,489	3
Warm temperate	Azores	391	2	Portugal	2,183	2
	Bermuda	136	4	Carolinas	3,274	4
	San Clemente	221	2	California	3,727	3
	San Nicolas	92	6			
Subtropical	Guadalupe	116	3	Baja California	2,564	3
	Juan Fernandez	141	11			
	Norfolk Island	153	12			
	New Zealand	1,800	13			
Subtropical Dry	Easter	30	0			
Tropical Dry	Galápagos	439	3			
Tropical Low	Bikini Atoll	44	2			
	Leeward Islands	40	0			
	Aldabra	171	4			
	Chagos Arch.	71	1			
Tropical High						
Indian Ocean	Réunion	838	4			
	Mauritius	682	11			
	Seychelles	237	8			
Pacific Ocean	Tonga	404	16			
	Guam	279	13			
	Samoa	539	17			
	Hawaii	1,467	28			

DIOECISM AND ISLAND COLONIZATION

In a thoughtful and thought-provoking paper, Bawa (1982) suggested that "dioecious taxa may have been disproportionately more successful in colonizing the (Hawaiian) islands." This would seem to be out of accord with what Stebbins (1957) called "Baker's Law"—that taxa that successfully establish seed-reproducing populations after long-distance dispersal will usually be self-compatible (or apomictic) and, by implication, show relatively low levels of inbreeding depression following self-pollination (H. G. Baker, 1955, 1967). A convenient assumption in the past has been that the original colonists of isolated islands will have been hermaphrodites or monoecious and their dioecious descendants developed outcrossing breeding systems autochthonously (that is, after arrival on the island) (H. G. Baker, 1967; Carlquist, 1965, 1966, 1974; Gilmartin, 1968). However, Bawa (1982) and others have pruned the list of genera in which dioecism is most likely to have arisen after the Hawaiian islands had been colonized by hermaphroditic plants, by pointing to the existence of dioecious species in some of these genera outside of Hawaii. The subject is also discussed by Godley (1979) for the New Zealand flora.

Clearly, though, selection for outcrossing on islands could favor the evolution of dioecism since dioecism is more easily evolved than a functional self-incompatibility system. Mere alteration of the hormone system in a plant can produce separate staminate or pistillate flowers even on the same shoot (as in monoecious plants) without genetical difference. Consequently in the simplest case, dioecism could result through only a few genetic changes.

We believe that there is merit in considering the floras of a wider selection of islands than just the favorites—Hawaii and New Zealand. We have made use of floras written by specialists on the islands in question and have analyzed their species lists, with a special emphasis on "oceanic" islands that probably had no connection with a mainland since the origin of angiosperms.

We have been up against some difficulties because some published floras are little more than check-lists and, to some extent, it has been necessary to take the condition of a species elsewhere as indicative of its sexual condition in the flora in question. Even less satisfactory is the need to judge, in other cases, simply on the known characteristics of the genus. We have taken care to consider only species that are native to each particular island, thereby excluding human introductions that are especially numerous on such islands as Bermuda and other relatively densely populated places.

Monocots and dicots were treated separately in our analyses but their subtotals are combined here for an overall representation of the proportions of hermaphrodite and monoecious versus dioecious species in each flora. Hermaphrodite and monoecious species are lumped because the point at issue is the potentiality, or lack of it, for self-pollination—and monoecious plants have this to almost the same extent as do hermaphrodites. Hermaphroditic species, in these calculations, mean not only those species that have so-called "perfect" flowers, but also those in which hermaphroditic flowers are accompanied by staminate flowers (andromonoecism), by pistillate flowers (gynomonoecism) or a mixture of all three (polygamy). Even gynodioecious and androdioecious species are counted in with the hermaphrodites, the criterion being that the populations include at least some plants that can function both as pollen-donors and ovule-producers. This is in contrast to the species that are regularly dioecious. Needless to say, the uncertainties are greater for little-studied tropical islands than for those that are extra-tropical and well known. But, despite some inaccuracies because of restricted information, we feel that the statistics that have emerged are probably accurate enough for the genesis of some conclusions.

There exists an estimate of the proportion of dioecious species in the world, published in 1922 by Yampolsky and Yampolsky. This is very useful as a standard for comparison with local floras even though, as Bawa (1980) has pointed out, it is probably an underestimate because of the underrepresentation of tropical species in this venerable compilation. But it is most unlikely that anyone else will undertake the Sisyphean labor of producing an updated version, so, with our fingers crossed, we can use the 3–4% that the Yampolskys decided upon as a minimal estimate of the proportion of dioecious flowering plants in the world. All investigators are agreed that there is a positive partial correlation of dioecism with a woody habit (e.g., Bawa, 1980; Givnish, 1982), and this means that floras rich in trees and shrubs will tend to have a higher percentage of dioecious species.

ISLAND FLORAS

TEMPERATE ZONES

The temperate zone islands whose published floras we have analyzed (Table 1) are those of cool temperate Iceland (Löve, 1970) and the warm temperate Azores (Watson, 1870), Bermuda (Britton, 1918), San Clemente (Raven, 1963), and San Nicolas (Foreman, 1967). The last two islands are situated in the Pacific Ocean off the coast of California. Available lists of mainland floras that can be compared with these oceanic areas are, respectively, those of Great Britain (Clapham et al., 1962), Portugal (Pires de Lima, 1947), the Carolinas (Conn et al., 1980), and California (Jepson, 1928; Munz, 1963). We quote the number of species for California from Jepson (1928) but found the same percentage of dioecism by analyzing the flora by Munz (1963).

We find that the proportions of dioecious species (Table 1) are no greater on the islands than they are on the mainlands and they are as low as Yampolsky and Yampolsky's (1922) world standard.

SUBTROPICS

Although the tropics are delimited by the Tropic of Cancer in the northern hemisphere and the Tropic of Capricorn in the southern hemisphere, there is no convenient boundary for the subtropics. Consequently, our categorization of Guadalupe Island (Eastwood, 1929), off the coast of Baja California, as subtropical and the exclusion of San Clemente and San Nicolas Islands as warm-temperate is somewhat arbitrary. In this connection, it is notable that the percentage of dioecious species in the flora of Guadalupe does not show any difference from those of the temperate zones and Guadalupe has the same percentage of dioecious species as the Baja California mainland (Wiggins, 1980). The Juan Fernandez islands, off the coast of Chile, are also sub-tropical, although with tropical floristic affinities (Skottsberg, 1922a, 1922b, 1928b). Here, with 11%, there is a definite suggestion of increase in the percentage of dioecism.

New Zealand is difficult to categorize because of its wide latitudinal range, and, even though it is largely temperate in climate, many of its floristic affinities are with the more tropical islands to the north. This may have some responsibility for the rather large proportion of dioecious species in its flora (Godley, 1979) for, as we shall see, tropical islands that are large and mountainous are clearly richer in dioecious species than those of temperate regions.

Norfolk Island is interesting because it represents a sub-tropical island whose flora is probably derived from the same sources as the tropical or subtropical elements of the New Zealand flora, and, although the flora of Norfolk Island (Maiden, 1904) is smaller in number of species than that of New Zealand, its proportion of dioecious species is comparable—12%.

TROPICAL HIGH ISLANDS

In the tropics, floras of the islands that have mountains bearing moist forests have relatively high percentages of dioecious species (Table 1). This is shown by the floras of Samoa (Setchell, 1924; Christophersen, 1935, 1938), Hawaii (Hillebrand, 1888; Carlquist, 1965), Tonga (Yuncker, 1959), and Guam (Stone, 1970) in the Pacific Ocean and the Seychelles (Summerhayes, 1926), and Mauritius (J. G. Baker, 1877) in the Indian Ocean. Only the flora of Réunion (Cordemoy, 1895) in the Indian Ocean gives a surprisingly low percentage (4%).

However, this result for Réunion only accentuates an apparent slight difference between the percentages for the sampled islands of the Pacific and Indian Oceans, respectively. It may be that dioecious percentages are genuinely higher in Pacific Islands than in those of the Indian Ocean. This should be examined further and an attempt should be made to see if an explanation is to be found in the composition of the source floras or in the flyways of migratory birds. It has been suggested that other islands in the Indian Ocean east of Madagascar serve not as destinations but rather as "safety nets" for vagrant birds (Renvoise, 1971; Penny, 1971). Another possible explanation for the low proportion of dioecism in Réunion may be a relative overabundance of groups such as orchids and grasses which are rarely dioecious.

TROPICAL LOW ISLANDS

Unlike the high, forested islands, there are many small islands in the Pacific and Indian Oceans that are topographically low, and, in these islands, such as Aldabra (Hemsley et al., 1919), the Chagos archipelago (Willis & Gardiner, 1931), Bikini atoll (Taylor, 1950), and the Leeward Islands of the Hawaiian archipelago (Christophersen & Caum, 1931), the largest proportion of the flowering plant species occupy the littoral and strand zones. There is a striking lack of dioecious species on these islands (Table 1) and the same is probably true for the strand and littoral floras of high islands that also have interior forests (Long in Gilmartin, 1968).

The flora of the Aldabra islands, in the Indian Ocean, has been studied more completely than most low islands (Fosberg, 1971; Renvoise, 1971, 1975; Woodell, 1979; Wickens, 1979) and its relationships to the bird fauna have been commented upon by Renvoise (1971, 1975) and Woodell (1979). These authors agree that the littoral flora of Aldabra had probably arrived by rafting whereas the inland flora had been introduced by stray birds or fruit bats. Penny (1971) has noted that Aldabra is not a wintering ground for any migrant waders (which, anyway, would not be likely to be important agents of inland fruit and seed distribution).

TROPICAL AND SUBTROPICAL DRY ISLANDS

The Galápagos are discussed separately here because they are relatively dry for tropical "high" islands. Their flora (Wiggins & Porter, 1971) shows a very low percentage of dioecism. It is notable that Rick (1966) performed a series of bagging and pollination experiments on 18 species with hermaphrodite flowers in the Galápagos and found no evidence of self-incompatibility, suggesting that outbreeding mechanisms are not strongly represented in the Galápagos flora.

Easter Island, being extremely isolated at a distance of 2,300 miles from the coast of Chile, has a very small indigenous flora (Skottsberg, 1928a), even though it reaches a height of 1,969 feet (600 meters). The climate is subtropical, and, because of its volcanic rocks and steep slopes, the landscape of Easter Island is arid (Skottsberg, 1928a), so it qualifies as a subtropical counterpart to the tropical Galápagos islands. The flora is predominantly herbaceous. Of the 30 angiosperm species present, none is dioecious; this is in agreement with our results for the Galápagos.

TROPICAL WOODY FLORAS

The only analysis of a complete tropical mainland flora that we have for comparison with those of the islands is that by Croat (1978, 1979) for Barro Colorado Island, which, prior to the flood-

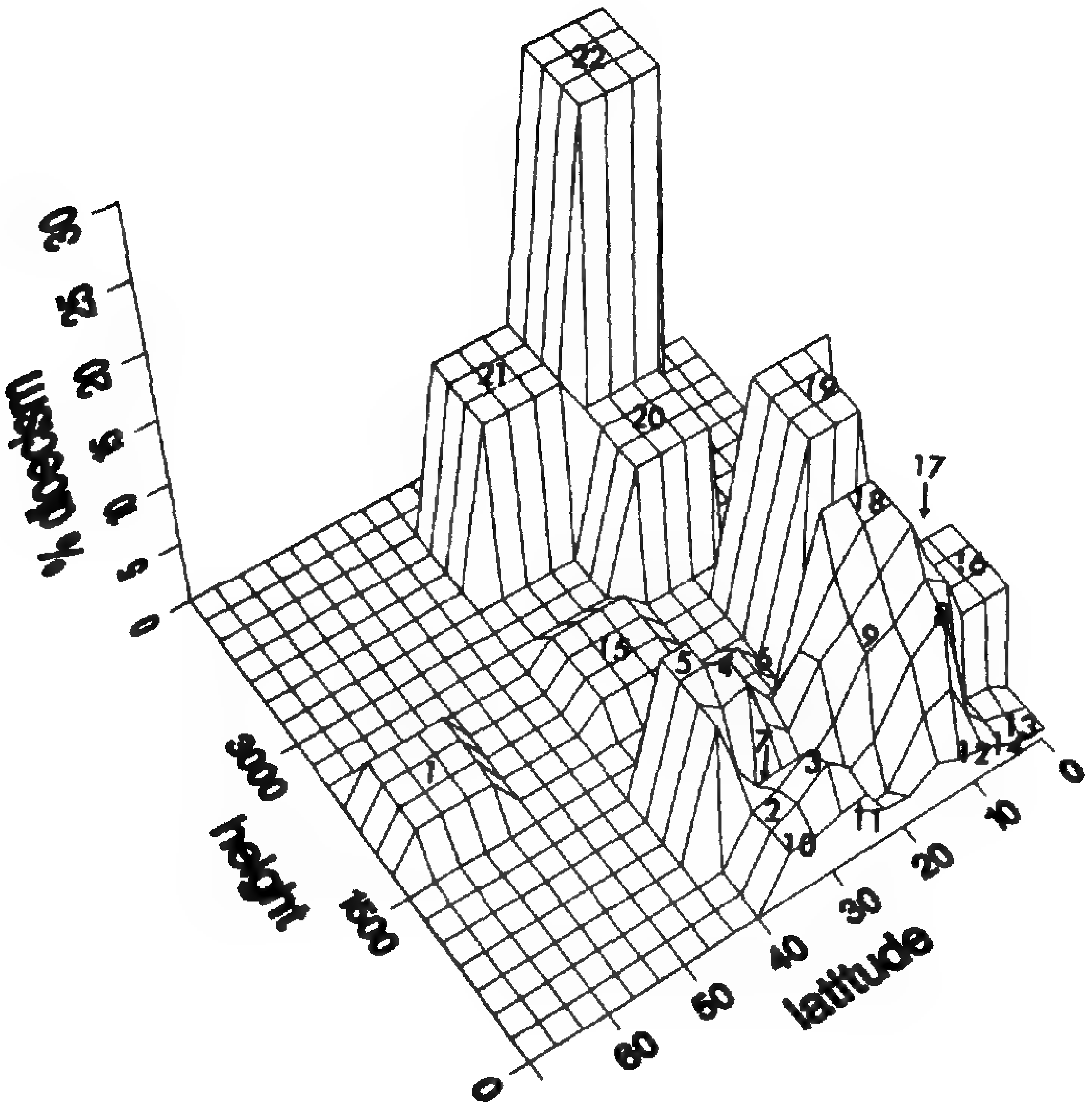

FIGURE 1. Graphical representation of percentage of dioecious angiosperms in island floras plotted against island height in meters and distance from the equator measured in degrees latitude for 22 different archipelagos or islands: (1) Iceland, (2) San Nicolas, (3) San Clemente, (4) Norfolk, (5) Juan Fernandez, (6) Guadalupe (Pacific Ocean), (7) Easter Island, (8) Guam, (9) Mauritius, (10) Bermuda, (11) Leeward Islands (Hawaii), (12) Bikini, (13) Aldabra, (14) Chagos archipelago, (15) Azores, (16) Seychelles, (17) Galápagos, (18) Tonga, (19) Samoa, (20) Réunion, (21) New Zealand, and (22) Hawaii.

ing of the Panama Canal from 1911 to 1914, was part of the mainland. Croat's (1979) calculation is that there are 9% of dioecious species in the Barro Colorado flora. Other calculations have been made for forest floras (in most cases just the trees) in mainland areas and they are summarized in Bawa (1980). Sobrevila and Arroyo (1982) have recently contributed a Venezuelan example. Percentages vary from 20 to 37%. This suggests that the tropical island forest floras have been derived from mainland sources that show a high percentage of dioecious species as Bawa (1982) and Givnish (1982) have already pointed out.

CORRELATIONS WITH ISLAND HEIGHT AND LATITUDE

The relationship between maximum island height and distance from the equator with the proportion of dioecious species can be seen in Figure 1. Through the use of multiple linear regression, we find that 82% of the variation in levels of dioecism between islands can be explained solely on the basis of maximum height of the island and its distance from the equator (as expressed in degrees of latitude) (Table 2). For the regression, percentage data were first transformed with an angular transformation ($\theta = \arcsin \sqrt{p}$, where p is the percentage expressed in decimal form). An analysis of variance of the regression indicates the regression to be very highly significant (P is very much less than 0.001), and F statistics computed for both partial coefficients of the regression show them to differ significantly from 0 (Table 2).

It is our belief that part of the remaining variation (18%) can be explained by the differing amounts of precipitation in the islands, but since this variable is not clearly independent of island height or latitude, nor is it uniform from year to year, we have not used it in our multiple regression.

DISCUSSION

In the 22 island floras we have studied, two important features are apparent: (1) the percentages of dioecious species in these islands do not generally differ from those in latitudinally comparable mainland floras, and (2) there is a very strong correlation between the level of dioecism and both the maximum island height and proximity to the equator.

Thus the contrast in the tropics between the low islands (and the dry islands), on the one hand, and the high forested islands, on the other, is clearly shown in statistics in Table 1 and in graphical form in Figure 1. This is very likely related to differences in the derivation of their floras from tropical mainland sources; that is, forests for high islands versus littoral vegetation for low islands. Island height may be thought of as a simple index of the potential habitat diversity of islands, particularly in the tropics.

Therefore, it is worth examining possible reasons why dioecism appears not to be such an impediment to the colonization of islands as might have been thought.

First, there may be the evolution of dioecism in a taxon that arrived at the island in the form of a self-compatible hermaphrodite. Carlquist (1974) listed 14 genera of flowering plants that appeared to be dioecious in Hawaii but are hermaphroditic or monoecious elsewhere. Bawa (1982) has pointed out that subsequent research has demonstrated that ten of these 14 genera are actually dioecious in certain non-Hawaiian locations as well. This, in itself, does not prove

TABLE 2. Analysis of Variance of Multiple Regression. Regression equation is: $\theta = 12.6 + 0.0036(\text{height}) - 0.123(\text{latitude})$ ($\theta = \arcsin \sqrt{p}$ where p = % dioecism in decimal form). Percentage of variation in transformed data explained by multiple regression = 1 − (50.3/274.8) = 82%. Both partial regression coefficients are significant at the 0.01 level.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	*F*
Regression	2	$\Sigma z^2 =$ 4,815.5	2,407.5	47.8***
Deviations	19	$\Sigma d^2 =$ 956.27	50.3	
Total	21	5,771.8	274.8	

that they have not evolved dioecism autochthonously in Hawaii, for they have demonstrated the genetic capability of becoming dioecious and could do so more than once. And there are still four genera (*Hedyotis* and *Canthium* in the Rubiaceae, *Santalum* in the Santalaceae, and *Wikstroemia* in the Thymelaeaceae) that may have developed dioecism only in the Hawaiian islands. There are also five endemic genera that are dioecious (Carlquist, 1974) and these could have developed dioecism in Hawaii (*Bobea* and *Straussia* in the Rubiaceae, *Broussaisia* in the Saxifragaceae, *Labordia* in the Loganiaceae, and *Touchardia* in the Urticaceae). So autochthonous evolution of dioecism cannot be ruled out entirely yet.

But it does seem that we should also be willing to allow that dioecious species can colonize islands in something like the same proportion that they show in mainland situations. And we need to explain why this is possible if they seem to need to be cross-pollinated to start the development of a seed-reproducing population. One possibility is that dioecism is not perfect in these species. Clearly, gynodioecious taxa should not be classed as dioecious, but it is also true that many taxa considered to be truly dioecious have occasional flowers of the opposite sex or of a hermaphrodite structure. Thus, there is the possibility of occasional seed setting, probably by self-pollination, in these taxa—especially as we know that in those cases that have been examined experimentally, hermaphroditic flowers in dioecious species are self-compatible (Baker, unpubl. data). This phenomenon, which we term "leaky dioecism," is the condition that prevails where hermaphroditism or bisexuality occurs at low levels in populations of otherwise dioecious species.

An example of leaky dioecism is found in Samoan populations of *Freycinetia reineckei*, a liana of the Pandanaceae. Traditionally, the Pandanaceae have been believed to be a classic case of a dioecious family (Hutchinson, 1973). However, a recent examination (Cox, 1981) of populations of *F. reineckei* in Western Samoa has revealed a consistent low level of bisexual plants (at levels ranging from 4 to 9%). The bisexual inflorescences borne by these plants produce viable pollen and also set fruit.

Working in the Philippines, B. Stone has also found a similar condition in *Freycinetia negrosensis* (see Cox, 1981), and Cammerloher (1923) noted it also in *F. strobilacea* in Indonesia. An *F. scandens* individual grown in the Royal Botanical Gardens in Sydney, Australia, from a single seedling from northern Queensland has been observed to produce staminate and pistillate spikes at the same time (Cox & B. Webster, unpubl. data). Although these levels of bisexuality may be low enough to be missed in herbarium studies, they may have been an important factor in the colonization of numerous isolated islands by the 190 species of this genus.

Other striking examples of leaky dioecism occur in the rubiaceous genus *Coprosma*. In the Juan Fernandez islands, Skottsberg (1922b) found a number of bisexual flowers on a branch of pistillate *Coprosma triflora*. In New Zealand, Godley (1979) reported hermaphrodite flowers on staminate plants of *C. robusta*. Fosberg (1937) reported pistillate inflorescences on a staminate bush of *C. cookei*, endemic to Rapa Island. A *C. pumila* bush growing in the University of California Botanical Garden in Berkeley produced some hermaphrodite flowers (Baker, unpubl. data).

Also in *Charpentiera* (Amaranthaceae) there is leaky dioecism (Sohmer, 1972). *Sanctambrosia* (Caryophyllaceae) is recorded as having leaky dioecism in the Desventuras Islands (Skottsberg, 1963). *Fragaria chiloensis* occasionally produces hermaphrodite flowers throughout its range along the Pacific Coast and the offshore islands of North and South America. Also, *F. chiloensis* is a hermaphrodite in Hawaii (Staudt, 1962).

Other examples of leaky dioecism occurring in New Zealand that have been noted by Godley (1979) include species in the genera *Cotula* (Compositae), *Clematis* (Ranunculaceae), *Pittosporum* (Pittosporaceae), *Dodonaea* (Sapindaceae), *Alectryon* (Sapindaceae), *Anisotome* (Umbelliferae), and *Astelia* (Liliaceae). *Fuchsia procumbens* has been made to produce seeds on staminate plants by hormonal treatments (Godley, 1979) and drought stress can result in the development of staminate flowers among the pistillate flowers in monoecious *Zea mays* (Moss & Downey, 1971). This listing could be greatly extended.

The late George Gillett, who knew the Hawaiian flora intimately, once said that he doubted whether there were any perfectly dioecious species in Hawaii—that there was always the possibility of an occasional seed being set by an abnormal flower on a staminate or pistillate plant.

Although it is not an island species, *Carica papaya* is an instructive example of a species with leaky dioecism (H. G. Baker, 1976). Staminate trees of this species are heterogametic as far as sex-determination is concerned (Storey, 1958, 1967). Consequently, when a staminate tree forms an occasional hermaphroditic flower that can be self-pollinated, the seeds produce plants of both sexes in the next generation. Thus, by leaky dioecism the dioecious condition is rederived from a single plant.

Another possible factor in the establishment of dioecious taxa after long-range dispersal is environmentally induced sex-lability, which has been demonstrated in several flowering plant genera (Freeman et al., 1976, 1980). It may be that on islands as well as mainlands, variations in environmental factors may trigger a change in sexual expression, resulting in the production of both pollen and eggs within an individual or a clone.

Another mechanism that might overcome the apparent disadvantage faced by a dioecious taxon upon arriving on an island by a single act of dispersal is the dispersal of multi-propagule units rather than single seeds (also mentioned by Wickens, 1979). Thus, more than one plant can be produced from a single immigration event. This is particularly likely to be the case with endozootic dispersal by birds of the seeds in berry fruits (which by definition are many-seeded).

It is notable that both Bawa (1980, 1982) and Givnish (1982) have drawn attention to the prevalence of endozootic dispersal of tropical forest tree seeds and have linked endozootic bird-dispersal of seeds with dioecism. They have suggested that potential dispersers will be more attracted to the greater fruit display that a pistillate tree can provide compared with the more resource-limited display of trees with hermaphrodite flowers and have proposed that the primary vectors of tree seed-dispersal to high tropical islands are such frugivores.

We simply bring these ideas together with the suggestion that endozootic dispersal, which promotes the defecation of several seeds as a group, could occasionally be effective in bringing staminate trees and pistillate trees onto islands in close proximity both in time and space. Thus, a seed-reproductive colony could develop. Although we believe that there is an abundance of multi-seed fruits in the tropics, it is notable that Flores and Schemske (1983) have shown an exceptional abundance of drupes in Puerto Rico. However, although drupes by definition are derived from a single, simple or compound pistil, they are not always one-seeded. A good example of a multi-seeded drupe is provided by the fruits of species of *Spondias* (Anacardiaceae).

Incidentally, endozootic dispersal is not the only mechanism by which multi-propagule units of dioecious taxa can be dispersed. For example, Lloyd (1972) has found in the genus *Cotula* in New Zealand that the achenes of these composites are dispersed individually in the monecious species, but in the dioecious species the entire head may be dispersed as a unit.

In this regard, evolution may have gone either way in any particular taxon. Thus, either dioecious species may have been selected for fleshy fruitedness or fleshy-fruited taxa may have been selected for dioecism. In any event, the correlation is the same.

As a side-light, it may be noted that dioecism has been linked with multi-propagule units in plants other than angiosperms. Thus, Schuster (1966) noted that the four spores resulting from meiosis remain united as a tetrad in almost all of the dioecious bryophytes, and this tetrad, rather than the individual spore, becomes the unit of dispersal. Because each tetrad in the dioecious taxa contains two "male" and two "female" spores, male and female gametophytes can develop in proximity to each other.

Another factor that mitigates the potentially deleterious effects of dioecism is a woody, perennial, iteroparous habit, often associated with strong powers of vegetative propagation (Bawa, 1980). Thus, a single plant of a dioecious species on an island may simply "wait" for the advent of a propagule of the opposite sex to grow to maturity nearby.

One has only to think of the Canadian pondweed, *Elodea canadensis,* which invaded Europe during the nineteenth century and succeeded in blocking waterways by purely vegetative production of ramets even though probably only a female plant was introduced (Clapham et al., 1962). An island example of this phenomenon can be seen on San Clemente Island, in the Pacific Ocean off the California coast. A single pistillate bush of *Baccharis viminea* was noted in 1900 by Trask (1904) and was still there when Raven (1963) saw it, although it had grown considerably during the interval. To the best of our knowledge it still remains there, although we hope that its lonely vigil has since been rewarded by the arrival of a staminate plant. Certainly it can continue to wait for a long time, in our human scale, but such a delay in the advent of a reproductive partner may not be long on the evolutionary time scale.

The picture of pollination biology on moist, high tropical islands appears to be in accord with another idea proposed by Bawa, who suggested (Bawa, 1980, 1982; Bawa & Opler, 1975) that many dioecious species in the tropics have flowers that are adapted to visitation by small generalist insects, particularly small bees and flies.

Because potential insect pollinator faunas on oceanic islands are frequently depauperate in number of species (Carlquist, 1974), and the insects are believed to be unspecialized in their choice of flowers to visit, dioecious plant species that do not require specialized pollinators may have a greater chance of establishment than those plants that require a specialized kind of visitor. Linsley et al. (1966) have shown that a high proportion of Galápagos plants are pollinated by a single carpenter bee (*Xylocopa darwinii*). Similarly, Woodell (1979) has demonstrated that a corresponding role is played on Aldabra by a beetle (*Maucoleopsis aldabrensis*).

This advantage of unspecialized pollination systems is not limited to entomophilous taxa, but occurs also in dioecious taxa with vertebrate pollination. Thus, the genus *Freycinetia,* which is widespread throughout the islands of the Pacific, is pollinated by a variety of opportunistic, non-coevolved vertebrates that range from large flying foxes and starlings to small white-eyes and endemic honeycreepers in Hawaii (Cox, 1982, 1983). A variety of bats, birds, and rodents has been recorded as visitors to the genus *Freycinetia* in various other places in the South Pacific (Cox, 1982).

Another case of unspecialized vertebrate pollination in dioecious taxa might be seen in the epiphyte genus *Collospermum* (Liliaceae), which may be pollinated by the endemic sheath-tailed bat in New Zealand (Daniel, 1976), but which is probably pollinated by a variety of other bats, birds, and possibly insects in other islands in the South Pacific.

All of these considerations that we have made have been directed to the demonstration that island floras usually bear a close resemblance in the percentage of dioecism to the mainland floras, from which they have been derived more or less by long-distance dispersal. And, if the mainland flora is a forest flora with a high proportion of dioecious taxa, it can be reproduced on the island without serious violation of Baker's Law. But we should be less than circumspect if we did not draw attention to another area in which investigation is needed. This is related to studies of the breeding systems of trees in dry and wet forests in Costa Rica (Bawa, 1974; Bawa & Opler, 1975) that have shown that a high proportion of the hermaphrodite-flowered tree species are self-incompatible. A similar result is reported from Venezuela (Sobrevila & Arroyo, 1982).

Is this picture of high levels of self-incompatibility also reproduced in the forests of large, high, moist tropical islands? Until the necessary experimental work is done, we cannot know. But, Godley (1979) and Pandey (1979a, 1979b) agree that while dioecism is strongly represented in the New Zealand flora, self-incompatibility appears to be rather rare, and we note the negative results of tests for self-incompatibility in the drier Galápagos flora conducted by Rick (1966).

However, there have been a few indications of self-incompatibility in the Hawaiian flora, e.g., *Plantago grayana* (Tessene as quoted in Carlquist, 1970), and we must wait for further experiments to show if we need to invoke "leaky self-incompatibility" as well as "leaky dioecism" to account for plant breeding systems in the islands!

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SEXUAL DIMORPHISM AND ECOLOGICAL DIFFERENTIATION OF MALE AND FEMALE PLANTS[1]

THOMAS R. MEAGHER[2]

ABSTRACT

The evolution of dioecy within a plant population introduces a situation in which there is divergent selection for means of achieving reproductive success. Male and female individuals play different roles in the reproductive biology of a dioecious species and hence have very different resource demands imposed upon them. The selection pressures presented by these different resource demands could in turn lead to the evolution of sexual dimorphism. Empirical studies of several dioecious plant species have shown that male and female plants differ in their resource allocation patterns. These differences between the sexes have also been shown to lead to sexual dimorphism in a wide range of life history characteristics in the dioecious perennial *Chamaelirium luteum*, including age at first reproduction, flowering schedules, size and size dynamics, and mortality rates. Quantitative genetic studies of resource allocation patterns for *C. luteum* suggest that the observed sexual dimorphism is probably the result of independent selection on the two sexes separately rather than the result of selection specifically favoring sexual dimorphism.

The establishment of a stable genetic polymorphism that results in separate male and female individuals is just the first step in the evolution of sexual dimorphism. The two sexes, by virtue of attaining reproductive success in different ways, play distinct roles in the biology of a species. Thus, a genetic polymorphism for sex expression is likely to have a wide range of ecological consequences, which in turn could result in selection pressures that may eventually lead to the evolution of secondary differences between the sexes. Secondary differences that have been observed between male and female individuals within dioecious species have included morphological, ecological, and behavioral attributes and are often referred to collectively by the phrase "sexual dimorphism."

Studies on animal species have shown that sexual dimorphism is evident in almost every aspect of their ecology and evolution (for reviews, see Selander, 1972; Maynard Smith, 1978; O'Donald, 1980). Traditional studies on sexual dimorphism in plants have been limited largely to floral characteristics (for review, see Lloyd & Webb, 1977); but, over the past few years, there has been a growing interest in broader manifestations of sexual dimorphism in plants (e.g., Lloyd & Webb, 1977; Grant & Mitton, 1979; Onyekwelu & Harper, 1979; Wallace & Rundel, 1979; Hancock & Bringhurst, 1980; Bullock & Bawa, 1981; Bullock et al., 1982; Meagher & Antonovics, 1982a, 1982b). This has included extensive discussion of various factors involved in the evolution of dioecy (e.g., Bawa & Opler, 1975; Lloyd, 1976, 1979; Charlesworth & Charlesworth, 1979), but there is still relatively little known about the evolution of sexual dimorphism in plants beyond differentiation of sex function.

Clearly the two sexes within a dioecious plant species perform very different functions in reproduction. As a consequence of these different functions, the two sexes may be subject to different sorts of resource demands (Lloyd, 1979; Charlesworth & Charlesworth, 1981; Charnov, 1982; Meagher & Antonovics, 1982a, 1982b) and, in turn, to divergent selection pressures, which will act to enhance the evolution of sexual dimorphism. In fact, observed cases of sexual dimorphism in traits related to life history and resource allocation (Lawrence, 1963, 1964;

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Bouwkamp & McCully, 1972; Putwain & Harper, 1972; Brockman & Bocquet, 1978; Lovett Doust & Harper, 1980; Gross & Soule, 1981; Meagher & Antonovics, 1982b) are presumably related to differential selection pressures that are imposed on male and female plants.

However, the extent of sexual dimorphism and the rate at which it is likely to evolve are subject to a variety of ecological and genetical constraints. For example, in order to remain a sexually reproducing species, male and female plants must maintain sufficient overlap in their ecological tolerances and life history characteristics to be able to interbreed effectively. This ecological limitation may be overcome by species with apomictic female plants (cf. Gustafsson, 1946–1947, cited in Grant, 1971). Genetical constraints arise because male and female individuals are members of the same species, and hence are limited in the extent that they can undergo genetically based divergence due to the overlap in genes in their respective genomes and the resultant genetic correlations (Lande, 1980). Thus the evolution of sexual dimorphism embodies the balance between factors acting to promote change and constraints tending to restrict change within populations.

The present paper addresses the processes and constraints involved in the evolution of sexual dimorphism in plants through an analysis of the dioecious perennial *Chamaelirium luteum* (Liliaceae). The population biology of this species has been well studied (Meagher, 1980, 1981, 1982; Meagher & Antonovics, 1982a, 1982b) and *C. luteum* has been shown to have extensive sexual dimorphism both in its overall morphology and in various life history characteristics. The discussion below will draw on investigations of four naturally occurring populations in the piedmont of North Carolina designated as *Natural Area, Seawell, Silver Hill,* and *Botanical Garden;* precise locations and site descriptions are given in Meagher (1980). Experimental analyses discussed below are based upon use of seed collected from three of these sites. Seed collected by common pistillate parent (halfsibship) were planted out and raised in the Duke University Phytotron. Altogether, 30 seedlings representing 30 halfsibships (900 total individuals) were planted. These plants were taken through a series of induction cycles (low temperature, short photoperiod) to promote flowering. The specific growth conditions and results of studies on the sex ratio are described in Meagher (1981).

The discussion that follows will focus on the following questions. How does sexual dimorphism influence the breeding structure of a population? What are the ecological consequences of sex differentiation? What are the genetic bases of sexual dimorphism and the probable selective forces that lead to the evolution of sexual dimorphism? Finally, what is the nature of ecological and genetic constraints imposed on the evolution of sexual dimorphism?

SEX RATIO AND SPATIAL DISTRIBUTION OF MALE AND FEMALE PLANTS

Aside from separation of the sexes into distinct individuals, there are other ways in which sex differentiation affects breeding relationships and the reproductive behavior of male and female plants. For example, the relative numbers of male and female plants, the sex ratio, has an influence on the effective population size (e.g., Ewens, 1969: 32–36). Also, if there is a strong numerical excess of one sex, the genetic contribution per individual of that sex will be correspondingly lower than that for individuals of the other sex. Finally, if differences between the sexes are sufficient to lead to noticeable differences in ecological tolerances, there may result a tendency for male and female plants to occur in different microhabitats, leading to increased spatial separation of the sexes.

A particularly striking feature of populations of *Chamaelirium luteum* is that the flowering sex ratios are extremely male biased (Meagher, 1981). If one observes the sex ratio among flowering plants during the breeding season in any given year, there is a large excess of male plants (Table 1). However, because only a relatively small percentage of the plants in a population flower in a given year, estimates of sex ratios based on a single flowering season could be biased by differences between male and female plants in their flowering schedules. There is a great deal of year to year variation in flowering sex ratios within any one site, showing that differential flowering behavior between male and female plants can have a dramatic effect on sex ratio estimates for any one season. In the present study, individual plants were monitored over a series of flowering seasons, so that for each successive year it was possible to obtain a cumulative estimate of the population sex ratio based not only on the plants

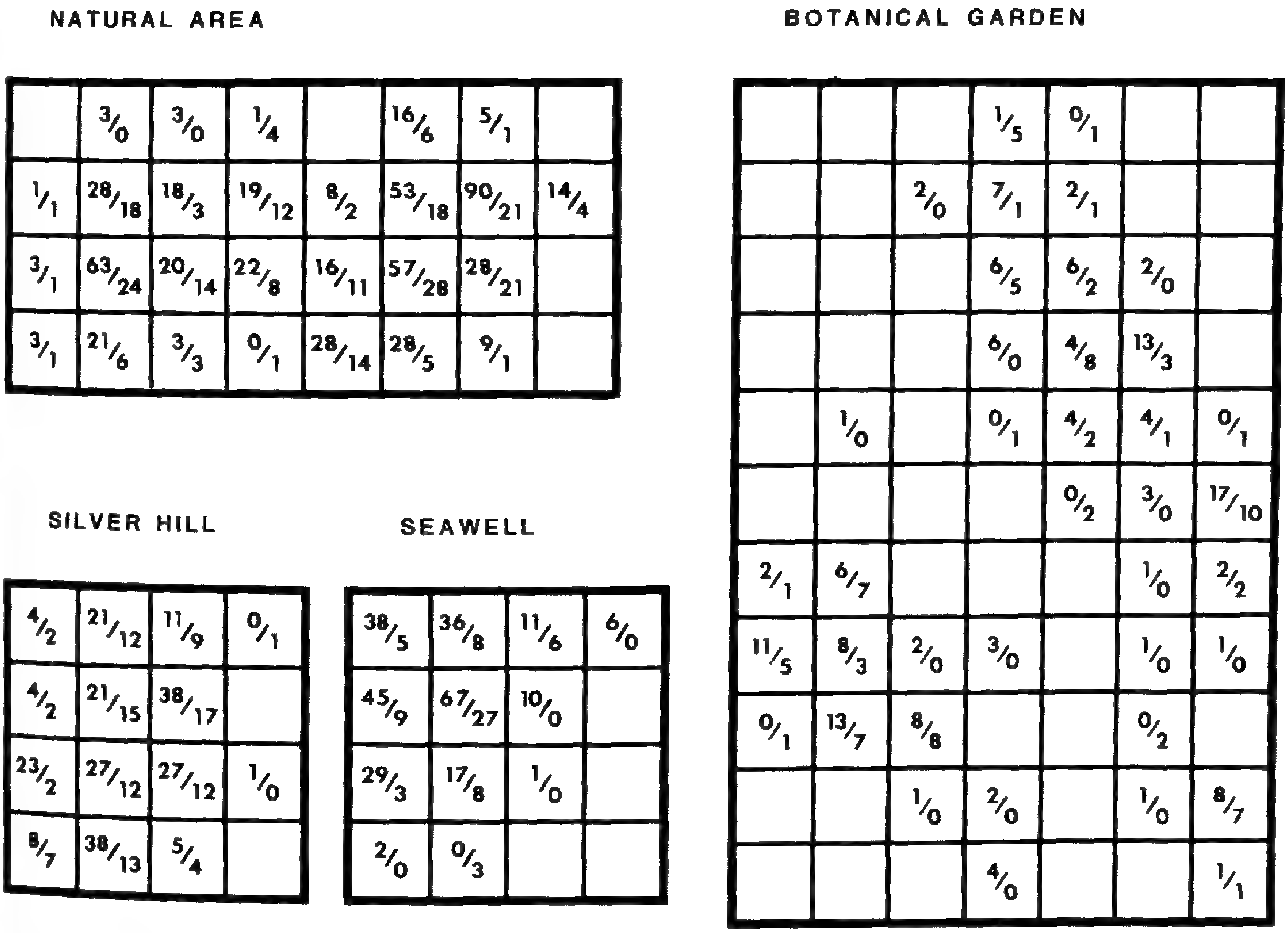
TABLE 1. Sex ratios in four populations of *Chamaelirium luteum* (from Meagher, 1981). Flowering sex ratios (male/female) are given for 1974–1979; G^2 (1 degree of freedom) test results for departure from a one to one sex ratio were statistically significant for all flowering sex ratios.

Site	Year	Percent of Population in Flower	Flowering Sex Ratio	Cumulative Sex Ratio Estimate
Natural Area	1974	9.7	4.51	
(N ≅ 2,200)	1975	10.6	3.07	
	1976	13.3	5.30	
	1977	19.9	3.41	2.47
	1978	6.7	4.52	
	1979	3.6	10.57	
	1980	11.0	3.90	
Seawell	1975	16.2	7.11	
(N ≅ 949)	1976	14.0	6.00	
	1977	14.6	4.79	3.37
	1978	9.5	6.50	
	1979	1.6	14.00	
	1980	25.0	4.39	
Botanical Garden	1975	25.1	2.80	
(N ≅ 450)	1976	19.1	3.47	
	1977	27.8	3.47	1.76
	1978	15.8	2.89	
	1979	15.6	3.38	
	1980	38.9	2.37	
Silver Hill	1975	12.5	3.18	
(N ≅ 1,103)	1976	9.0	3.71	1.74
	1977	19.1	2.52	
	1978	5.9	2.82	

in flower in a given year, but also on plants that had flowered previously. Inspection of such cumulative estimates showed a monotonic decline as the number of successive flowering seasons considered increased (Meagher, 1981). These cumulative estimates leveled off after the first several years and showed that the sex ratios for these four populations do show an overall excess of male plants (Table 1), even though this excess is generally not as dramatic as that observed within a single flowering season.

One can also look at the distribution of sex ratios over different microgeographic subunits of a population as a means of assessing the relative spatial distributions of male and female plants within a population. Tests of within population heterogeneity in sex ratio (Fig. 1) indicate that the sex ratio is not uniform within natural populations but rather varies from subunit to subunit, reflecting an underlying differential spatial distribution of male and female plants. Differences between male and female individuals of *C. luteum* in their relative spatial distributions within a population have been confirmed in a number of statistical analyses (Meagher, 1980; Meagher & Burdick, 1981).

The above discussion outlines a range of ecological consequences of dioecy. The differences between flowering sex ratios and cumulative estimates of the overall population sex ratios of *Chamaelirium luteum* suggest that male and female plants show different types of flowering behavior. The tendency toward differential distribution of male and female plants over different microsites, presumably the consequence of differential survivorship of the two sexes over these different microsites, provides evidence of ecological differentiation between the sexes. These phenomena are both related to the life history characteristics of the two sexes in terms of reproductive activity and survivorship. Therefore a comparative examination of the life histories of male and female plants provides a useful means for obtaining insight into such ecological side effects of sex differentiation.



NATURAL AREA

	3/0	3/0	1/4		16/6	5/1	
1/1	28/18	18/3	19/12	8/2	53/18	90/21	14/4
3/1	63/24	20/14	22/8	16/11	57/28	28/21	
3/1	21/6	3/3	0/1	28/14	28/5	9/1	

SILVER HILL

4/2	21/12	11/9	0/1
4/2	21/15	38/17	
23/2	27/12	27/12	1/0
8/7	38/13	5/4	

SEAWELL

38/5	36/8	11/6	6/0
45/9	67/27	10/0	
29/3	17/8	1/0	
2/0	0/3		

BOTANICAL GARDEN

			1/5	0/1		
		2/0	7/1	2/1		
			6/5	6/2	2/0	
			6/0	4/8	13/3	
	1/0		0/1	4/2	4/1	0/1
				0/2	3/0	17/10
2/1	6/7				1/0	2/2
11/5	8/3	2/0	3/0		1/0	1/0
0/1	13/7	8/8			0/2	
		1/0	2/0		1/0	8/7
			4/0			1/1

FIGURE 1. Within site heterogeneity in sex ratio (male/female) in *C. luteum* (from Meagher, 1980). G^2 test results indicated significant heterogeneity for the Natural Area ($P < 0.05$), Seawell ($P < 0.005$), and Botanical Garden ($P < 0.005$) sites (Meagher, 1980).

LIFE HISTORY DIFFERENCES BETWEEN MALE AND FEMALE PLANTS

The effect of sexuality on life history characteristics can be conveniently illustrated by moving temporally through the lifespans of the two sexes. The first aspect of life history considered here is the age at first reproduction (Fig. 2). These ages at first reproduction are based on the number of successive induction cycles to which a plant was exposed before it flowered for the first time among the cohorts of plants raised in the Duke University Phytotron. Clearly, male plants were inclined to begin flowering at an earlier age than female plants.

Various features of the sex ratio of *C. luteum* discussed above suggest that, among sexually mature individuals, male and female plants differ in their flowering schedules. The flowering schedules of male and female plants are compared here by considering the number of times plants of a given sex flowered over a span of years (Table 2). Male plants flowered more frequently than did female plants. An alternative way of stating these results is that female plants tend to have longer intervals between flowering episodes than do male plants.

Once an individual of *C. luteum* becomes established, its size, measured as the number of rosette leaves, plays an important role in determining its subsequent life history behavior (Meagher, 1982). The number of rosette leaves on female plants tends to be greater than the number of rosette leaves on male plants (Table 3), indicating that female plants are, on average, larger than male plants. Furthermore, the impact of flowering on the resource status of an individual is reflected in the year to year change in rosette leaf number. Percentage changes in the number of rosette leaves from the year before to the year after flowering were estimated for male and female plants (Table 4), and there was a significant reduction in size among plants that had flowered, suggesting that flowering imposed

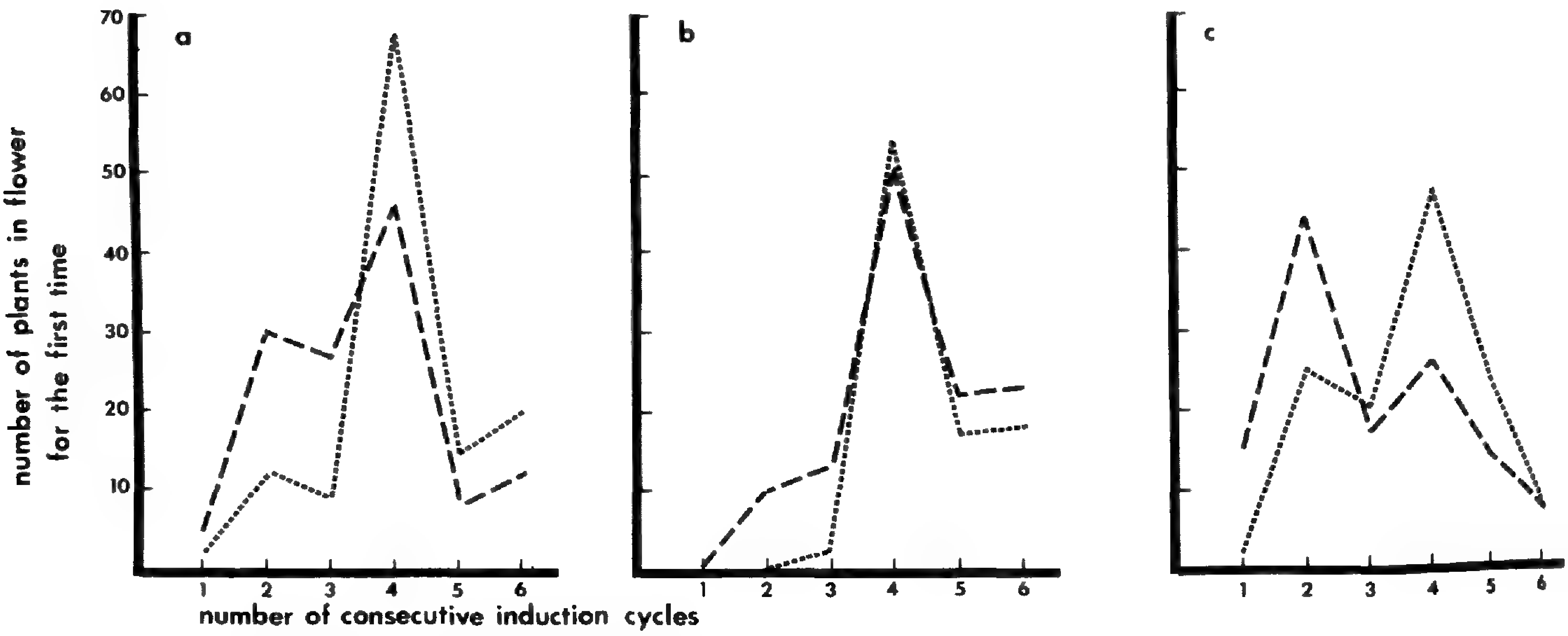


FIGURE 2. Age at first reproduction for male (dashed line) and female (dotted line) seedlings in the Duke University Phytotron; sites of origin for the seed are Natural Area (a), Silver Hill (b), and Botanical Garden (c).

a substantial drain on the resources of an individual. This effect was much more pronounced for female than it was for male plants.

The final stage in the life history to consider is death. Cumulative estimates of annual mortality rates for the two sexes (Table 5) show that female plants had a higher mortality rate than did male plants in two of three sites. For one of these two sites, the female mortality rate was significantly higher than the male mortality rate.

When these various life history characteristics of male and female plants are considered collectively, an overall pattern emerges that indicates a higher resource cost of flowering for female plants. With a later age at first reproduction and longer intervals between flowering episodes, female plants could be delaying flowering until they have assimilated a sufficient resource base to flower successfully. The tendency of female plants to be larger than male plants is also suggestive of a higher resource "threshold" that may be necessary for flowering to occur. In other words, female plants may delay flowering until they have achieved a greater size and are hence better buffered against the proportionately greater resource depletion that flowering represents for them. Finally, the extra costs and consequent resource depletion brought on by flowering for female plants could expose them periodically to a higher risk of mortality, resulting in a relatively higher mortality rate for female plants.

It seems quite reasonable that many of the observed life history differences between the sexes are causally related to the specific male and female resource demands and resource allocation patterns. From an evolutionary standpoint, therefore, one would expect that male and female plants would have very different types of selection pressures imposed on their resource allocation patterns. There may be divergent selection that favors male plants that put a relatively low proportion of their resources into flowering and that flower more frequently and that favors female plants that put a relatively high proportion of their resources per flowering episode into less frequent flowering.

RESOURCE ALLOCATION AND THE EVOLUTION OF SEXUAL DIMORPHISM

Traits or characters associated with sexual dimorphism, such as differences in resource allocation, are quantitative rather than qualitative in nature. The genetic basis of such characters is best defined by quantitative genetics models in which genetic variation is presumed to result from allelic variation at a large number of loci, each of which makes a small additive contribution to the overall expression of the trait under study (Falconer, 1981; Mather & Jinks, 1982). The genetic and evolutionary behavior of such quantitative variation can thus be studied by the application of appropriate statistical methods.

The phytotron studies described above were based on halfsibships of seedlings; information collected on quantitative characters from sets of halfsibships can be employed in the estimation of genetic parameters. Following the fourth in-

TABLE 2. The percentage of plants in flower in a given season that last flowered X years ago. These percentages represent averages over all consecutive years for which flowering data had been obtained through 1980 (see Meagher, 1981).

Site	X	Male Plants	Female Plants
Natural Area	1	37.4	1.6
	2	22.9	17.8
	3	12.0	19.0
	4	2.1	14.2
	5	2.2	6.0
	6	1.5	0.0
Seawell	1	30.1	0.0
	2	33.0	7.8
	3	18.3	8.3
	4	5.7	8.0
	5	7.3	11.4
Silver Hill	1	32.7	7.7
	2	34.1	17.2
	3	4.2	17.7

duction cycle in the phytotron, male and female plants within 22 of the 30 halfsibships were in flower for the first time and plants were harvested for dry weight measurements of three vegetative and three reproductive structures (Table 6). It is interesting to note that although male plants had a proportionately greater dry weight in their vegetative parts than did female plants, all of the structures on female plants had a higher absolute dry weight. Even though all plants were the same age, the female plants were on average larger than the male plants.

Dry weight values were log-transformed and percent dry weight values were subjected to arcsin square root transformations prior to statistical analysis because in both cases transformed values showed a better fit to a normal distribution.

In order to evaluate genetic components of variation from these data, a partially hierarchical analysis of variance involving population of origin and sex as main effects and halfsibships as a nested effect within populations was employed (Brownlee, 1960). The interactions of sex by population and of sex by halfsibship nested within population were also analyzed for each measurement. The effect of population of origin was taken into account because the halfsibships used were collected from three different populations, and differences among the populations made a significant contribution to the overall variation in eight of the 12 measurements analyzed.

In this analysis, there are two genetic components of variation that are relevant to the present discussion. The component of variation among halfsibships nested within populations is equal to one-fourth of the additive genetic vari-

TABLE 3. Rosette leaf number for male and female plants of *Chamaelirium luteum*. Values presented are from 1975–1979 pooled; cumulative numbers of observations for each sex are given in parentheses. Male and female means within each site were compared using an ANOVA (Sokal & Rohlf, 1969), and all three pairs of means are significantly different ($P < 0.0001$).

Site	Male Plants	Female Plants
Natural Area	4.1 (2,492)	4.4 (1,014)
Seawell	4.4 (1,025)	4.9 (260)
Silver Hill	4.9 (628)	5.3 (298)

TABLE 4. Percentage in rosette leaf number from the year before to the year after flowering (year 3–year 1); sample sizes are given in parentheses. Significance tests of departures from 0 were made using a t test (Sokal & Rohlf, 1969). Results from t tests comparing male transitions and female transitions were all statistically significant ($P < 0.001$).

Site	Male Plants	Female Plants
Natural Area	−17 (247)^{c}	−39 (133)^{c}
Seawell	−16 (118)^{c}	−29 (34)^{c}
Silver Hill	+2 (28)^{a}	−34 (12)^{b}

[a] Not significant.
[b] $P < 0.05$.
[c] $P < 0.001$.

TABLE 5. Annual mortality rates for male and female individuals of *Chamaelirium luteum*. Values presented are from 1975–1979 data pooled. Comparisons between male and female mortality rates are based on the log-likelihood ratio (Bishop et al., 1975). n.s. = not significant.

Site	Male Plants	Female Plants	Contrast
Natural Area	3.0	2.6	n.s.
Seawell	1.7	4.0	n.s.
Silver Hill	1.3	5.1	$P < 0.01$

TABLE 6. Mean dry weight and percentage of total dry weight for vegetative and reproductive plant parts for plants harvested in the phytotron experiment.

	Male (N = 57)		Female (N = 59)	
Character	Mean	% of Total	Mean	% of Total
Vegetative				
Rosette Leaves	2.64	46.9	2.98	39.5
Rhizome	1.53	29.3	1.75	24.4
Roots	0.72	14.3	0.99	14.2
Vegetative Total	4.89	90.5	5.72	78.1
Reproductive				
Inflorescence Leaves	0.06	1.3	0.30	4.4
Inflorescence	0.11	2.1	0.25	3.2
Stalk	0.31	6.1	1.01	14.3
Reproductive Total	0.48	9.5	1.56	21.9

ance, which is the portion of the overall variation that is most directly involved with response to selection (Falconer, 1981). In analyses of this type based on field collected progenies, one assumes that maternal effects on the characters measured are negligible and that the female plants have mated at random with male plants in the population. Because the characters assessed in the present study were measured on fully grown individuals, the assumption concerning maternal effects is probably reasonable. Violation of the second assumption would confound attempts to measure the actual level of additive genetic variance; but in the present study we are only concerned with whether or not such genetic variance exists, not with its actual magnitude.

The component of variation attributable to the interaction between sex by halfsibship nested within populations provides a means of evaluating genetic variation in the relative characteristics of male and female plants. In essence the sex by halfsibship interaction represents additive genetic variation for sexual dimorphism.

Analysis of variance (Table 7) showed a strong indication of sexual dimorphism in that differences between the sexes were significant for four of the six dry weight measurements and also for four of the six percentage dry weight measurements. Significant sex by population interactions for rhizome weight and for percent dry weight in rosette leaves and roots indicate that the extent of sexual dimorphism found, at least for vegetative characteristics, is not uniform over the different populations. The observed differentiation among populations suggests further that the extent of sexual dimorphism in resource allocation patterns may be subject to evolutionary modification within particular ecological contexts. However, the characters that showed evidence of additive genetic variation for sexual dimorphism, inflorescence weight, and percentage dry weight of rhizome and inflorescence, are not the same characters that showed a significant sex by population interaction. There were, however, significant levels of additive genetic variation found for rhizome weight, and percentage dry weight of rosette leaves, roots, and inflorescence stalk. The first three of these characters were the characters that did show a significant sex by population interaction. It therefore is reasonable to conclude that the among-population differentiation in the extent of sexual dimorphism is the outcome of the independent responses of male and female plants to site-specific selection pressures.

The manner in which response to selection on a trait in one sex will influence the expression of that trait, and hence the fitness, in the other sex depends on the nature of the genetic correlation that exists between the sexes for that trait. Traits that show a strong genetic correlation, whether positive or negative, between the sexes are not likely to show an independent response to selection on male and female plants because a genetic change that influences the fitness in one sex will also have an influence on the fitness of the other sex. Such genetic correlations have been proposed as a major factor limiting the evolution of

TABLE 7. F-ratio test results[e] from the partial hierarchical analyses of variance for plants harvested in the phytotron study.

A. Log Dry Weight

Effect	df	Vegetative: Rosette Leaves[f]	Vegetative: Rhizome[g]	Vegetative: Roots	Reproductive: Inflorescence Leaves	Reproductive: Inflorescence[f]	Reproductive: Stalk
Population	2	11.6^{c}	3.1^{d}	5.1^{a}	3.3^{a}	2.5^{d}	9.1^{c}
Sex	1	2.7	3.9^{d}	17.5^{c}	117.1^{c}	12.2^{c}	146.3^{c}
Sex * Population	2	2.7^{d}	4.9^{b}	0.1	0.2	1.4	2.5^{d}
Halfsibs within Populations	19	1.2	1.8^{a}	1.6^{d}	0.9	0.4	1.5
Sex * Halfsibs within Populations	19	1.6^{d}	1.2	1.1	1.0	1.8^{a}	1.2
Error	72						

B. Arcsin % Dry Weight

Effect	df	Vegetative: Rosette Leaves[g]	Vegetative: Rhizome[f]	Vegetative: Roots[g]	Reproductive: Inflorescence Leaves[f]	Reproductive: Inflorescence[f]	Reproductive: Stalk[g]
Population	2	2.5	7.2^{b}	3.0^{d}	2.0	1.0	0.4
Sex	1	35.9^{c}	26.6^{c}	0.1	73.6^{c}	9.9^{a}	122.9^{c}
Sex * Population	2	3.3^{a}	1.5	6.6^{c}	0.3	0.0	0.6
Halfsibs within Populations	19	2.5^{b}	1.2	2.1^{a}	1.1	0.3	1.8^{a}
Sex * Halfsibs within Populations	19	1.5	1.8^{a}	0.9	1.8^{a}	1.7^{d}	1.0
Error	72						

[a] $P < 0.05$.
[b] $P < 0.005$.
[c] $P < 0.001$.
[d] $P < 0.1$.
[e] Previously published F-ratios on these data (Meagher & Antonovics, 1982a) were based on non-transformed values of a subset of the data included in the present analyses.
[f] When the *sex * halfsibs within populations* mean square was significant, it was used as the denominator in F-ratio tests of *halfsibs within populations, sex * population,* and *sex* effects.
[g] When the *halfsibs within populations* mean square was significant, it was used as the denominator in the F-ratio test of the *population* effect.

sexual dimorphism (Lande, 1980). A small genetic correlation between the sexes for a given trait, however, would allow independent response to selection in males and females.

Genetic correlations between the sexes ($\hat{r}_g$) can be estimated from the analysis of variance discussed above using the method of Yamada (1962). For the present analysis,

$$\hat{r}_g = \frac{A - B}{A + B - 2C} \qquad (1)$$

where A, B, and C are the mean squares for halfsibships within populations, sex by halfsibships within populations, and error, respectively. Because the data set being analyzed was unbalanced, the estimate $\hat{r}_g$ for the total data set will be biased. In order to reduce this bias and also to provide a standard error of $\hat{r}_g$ for significance tests, the genetic correlations presented below were estimated using the jackknife method (Gray & Schucany, 1972; see also Rausher, 1984). For this method, estimates of $\hat{r}_{gi}$, i = 1, . . . , 22, were obtained by omitting the ith halfsibship and estimating $\hat{r}_g$ from analysis of the resultant subset of the overall dataset. The reduced bias estimate of $\hat{r}_g$ is then given by

$$\dot{r}_g = N.\hat{r}_g - (N - 1).\overline{\hat{r}_{gi}} \qquad (2)$$

with a standard error of

$$\text{s.e.} = [\Sigma_i(\hat{r}_{gi} - \hat{r}_g)^2/N(N - 1)]^{1/2} \qquad (3)$$

where N is the number of halfsibships.

Genetic correlations between the sexes were estimated for all of the measured traits that had significant levels of additive genetic variance (Table 8). Significance tests for rosette leaf and

TABLE 8. Genetic correlations (r_g) between the sexes for log dry weight and arcsin % dry weight in vegetative and reproductive structures. The estimates of the correlations and their standard errors were obtained using the jackknife method (Gray & Schucany, 1972); *t* test results for differences between the estimates and +1, 0, and −1 are also shown.

	Vegetative			Reproductive
	Rosette Leaves	Rhizome	Roots	Inflorescence
$\hat{r}_g$	0.16 ± 0.65	0.57 ± 0.68	−0.32 ± 1.18	−4.19 ± 5.25
t_{20} ($r_g = +1$)	1.3	0.6	1.1	1.0
t_{20} ($r_g = 0$)	0.3	0.8	0.3	0.8
t_{20} ($r_g = -1$)	1.8[a]	2.3[b]	0.6	0.6

	Vegetative			Reproductive		
	Rosette Leaves	Rhizome	Roots	Inflorescence Leaves	Inflorescence	Stalk
$\hat{r}_g$	0.50 ± 0.40	0.12 ± 0.33	0.97 ± 0.62	0.07 ± 0.58	−32.24 ± 29.43	0.45 ± 1.05
t_{20} ($r_g = +1$)	1.2	2.7[b]	0.0	1.6	1.1	0.5
t_{20} ($r_g = 0$)	1.2	0.4	1.5	0.1	1.1	0.4
t_{20} ($r_g = -1$)	3.7[c]	3.4[c]	2.9[c]	1.9[a]	1.1	1.4

[a] $P < 0.1$.
[b] $P < 0.05$.
[c] $P < 0.01$.

rhizome weight and for percent dry weight in rosette leaves, roots, and inflorescence leaves, indicated positive genetic correlations. The genetic correlation between the sexes for percent dry weight in rhizomes was significantly different from both +1 and −1 but not from zero, indicating a low genetic correlation for this trait. The other estimated correlations had such a high variance that no conclusions can be made as to their magnitude or direction.

The presence of positive genetic correlation between the sexes for some traits is hardly surprising; such results imply that the same genes are influencing these traits in both sexes. However, a small genetic correlation, as in the case of percent dry weight in rhizomes, indicates that there is relatively little overlap in the genes regulating that trait in male versus female plants. Therefore the two sexes are capable of independent responses to selection on this trait. The level of resources contained in the rhizome, which probably serves as a storage organ, may well have a direct physiological relationship to the life history differences observed within natural populations, particularly flowering schedules.

CONCLUSION

The ecological consequences of sexual dimorphism in plants are sometimes manifested in the form of partial spatial segregation between male and female plants along environmental (Freeman et al., 1976) or altitudinal (Grant & Mitton, 1979) gradients or over different microhabitats (Meagher, 1980). If such spatial segregation were taken to extremes, ultimately male and female plants might occur too far apart to effect sexual reproduction. Other ecological consequences of sexual dimorphism that have been observed for some plant species are differences between the sexes in life history characteristics and resource allocation patterns as cited above. Indeed spatial segregation is most likely the result of differential survivorship of male and female plants in different microhabitats (see Meagher, 1980 for review). Other life history dimorphism, such as differences in flowering schedules (Bullock et al., 1982; Meagher, 1981; Vernet, 1971; Valdeyron & Lloyd, 1979) or more specifically in the response to conditions that promote flowering (Meagher, 1981, 1984), might result in a further barrier to interbreeding between male and female plants. For example, such differences in flowering might reduce the probability of simultaneous flowering of male and female plants, or might result in greater spatial separation of simultaneously flowering plants of opposite sex. Yet, in order for a species or population to persist, of course, male and female plants must display sufficient overlap in spatial distribution or flowering behavior to allow reproduction to occur. This is particularly true for plants, which are nonmotile and incapable of the migration during breeding season that occurs in some sexually dimorphic animal species (e.g., Bartholomew, 1970). The limit to the extent of ecological differentiation a species can undergo and still persist thus constitutes an effective limitation on the evolution of sexual dimorphism.

The observed examples of sexual dimorphism in *Chamaelirium luteum* emphasize differences in spatial distribution, life history, and resource allocation, and provide a firm empirical basis for evaluation of the ecological consequences of sexual dimorphism. At the same time, these studies also represent a good start toward understanding ecological constraints on the evolution of sexual dimorphism.

Studies on the genetic basis for resource allocation patterns in the two sexes also provide insight into the evolution of sexual dimorphism. Significant differentiation between the sexes suggests that there has been in the past strong divergent selection on resource allocation patterns in the two sexes. However, male and female plants in a dioecious population share a common genetic heritage; autosomal genes that are present and exposed to selection in one sex will ultimately occur in progeny of the opposite sex. Because genetic changes, or responses to selection, which act to enhance fitness in one sex may conceivably prove to be deleterious to the other sex (Fisher, 1958; Lande, 1980; Yamada & Scheinberg, 1976), this genetic correlation between male and female plants could act to retard divergence between the sexes. Over evolutionary time, strong divergent selection on a particular trait could result in an accumulation of sex-limited gene expression for the genetic loci influencing that trait, thus countering the constraints imposed on the evolution of sexual dimorphism by genetic correlations between the sexes.

Interpretation of the evolution of a set of characters requires an understanding of both the genetic bases for those characters and of the ecological context within which those characters are expressed. Sexual dimorphism in dioecious populations provides an unusually clearcut situation within which to consider ecological and genetic properties of a set of characters simultaneously. By such consideration, we obtain an understanding not only of the type of selective forces acting to promote change in dioecious populations, but also of the nature of ecological and genetic constraints that act to regulate evolutionary change.

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THE ADAPTIVE SIGNIFICANCE OF SEXUAL LABILITY IN PLANTS USING *ATRIPLEX CANESCENS* AS A PRINCIPAL EXAMPLE[1]

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ABSTRACT

Experimental studies demonstrate that up to 20% of the individuals of *Atriplex canescens* and other species of the genus can alter their sexual state from one season to the next. Approximately 5% of the *A. canescens* individuals changed from an exclusively pistillate phenotype to an exclusively staminate phenotype or vice versa. Another 5% of the individuals changed their primary sexual emphasis, e.g., from an exclusively pistillate condition to a dominantly staminate, monoecious condition. In addition, 10% of the population changed from a unisexual state to a monoecious state in which staminate and pistillate flowers were approximately equal in number (or vice versa). In *Atriplex canescens,* sex change occurred in response to three stresses: an unusually cold winter, drought, and prior heavy seed set. When placed under stress, pistillate individuals are significantly more likely to change sex than staminate individuals. The ability to change sex appears to confer a survival advantage to the individual. Plants which change sex also appear to begin reproducing earlier than pistillate plants while producing as many seeds as pistillate plants do. Thus individuals that change sex appear to have some reproductive advantages in the population studied.

Recent ecological studies indicate that androecious (male) and gynoecious (female) individuals of several dioecious plant species exhibit partial niche separation; J. L. Harper has termed this pattern the Jack Sprat effect (Onyekwelu & Harper, 1979). The most commonly reported manifestation of the Jack Sprat effect is the segregation of androecious individuals and gynoecious individuals along strong environmental gradients. For example, Freeman et al. (1976) showed that the sexes of five dioecious plant species of the intermountain region of the western United States segregated along gradients of water availability or salinity. Androecious plants were proportionately more abundant at the stressful end of the gradient and gynoecious plants were proportionately more prevalent in favorable environments. In another study, Fox and Harrison (1981) demonstrated that slope exposure affected the sex ratio of *Hesperochloa kingii.* They typically found that androecious individuals of the species were more common in areas with low soil moisture whereas gynoecious individuals were usually more common in moister areas. Similar results have been observed by others (Davey & Gibson, 1917; Richards, 1975; Waser, pers. comm.). Cox (1981) showed that the sexes of *Trophis involucrata* and *Mercurialis perennis* segregate along gradients of phosphorus availability and pH, respectively, and Onyekwelu and Harper (1979) found differences in sex ratios of spinach in populations experiencing different intensities of intraspecific competition. In all of these cases, androecious plants were proportionately more abundant in the most stressful environments. Further evidence for partial niche separation between the sexes of dioecious plants comes from the studies of Putwain and Harper (1972), who showed that competition between members of the same sex was considerably more intense than competition between androecious and gynoecious plants of *Rumex acetosa* and *R. acetosella.*

A growing number of researchers have found physiological and morphological differences between the sexes of dioecious species (Heslop-Harrison, 1972; Adams & Powell, 1976; Lloyd

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& Webb, 1977; Valdeyron & Lloyd, 1979; Hancock & Bringhurst, 1979; Gross & Soule, 1981; Meagher & Antonovics, 1982). Such differences apparently arise as a result of natural selection operating differently on individuals of each sex. Selection appears to operate on differences in requirements for staminate and pistillate functions. For example, androecious and gynoecious plants growing on common sites experience different levels of water stress. Gynoecious plants of several species [*Atriplex hymenelytra* (Stark, 1970), *A. canescens, A. confertifolia, A. cuneata, A. corrugata* (Freeman & McArthur, 1982), *Hesperochloa kingii* (Fox & Harrison, 1981), *Simmondsia chinensis* (Hikmat et al., 1972), and *Spinacea oleracea* (Freeman, unpubl. data)] tend to be under greater water stress than androecious plants, particularly during midday in the fruiting season (Freeman & McArthur, 1982). Freeman and Vitale (unpubl. data) show that under severe water stress, the pistillate function in spinach was impaired to a greater degree than was the staminate function. In her studies of tropical orchids, Gregg (1973) has shown that shading more adversely influenced the pistillate than the staminate reproductive potential.

Whereas numerous studies indicate partial niche separation between the sexes of dioecious plants, little or no attention has been given to the evolutionary consequences of the Jack Sprat effect. Furthermore, few studies examine the selective forces that create staminate biased sex ratios in one environment and pistillate biased ratios in another.

If two species in physiological competition show partial niche separation, conventional theory would predict that the reproductive potential of those species would be unequal at some sites of coexistence, and that the physiological responses of the two species would differ significantly for at least some widespread and recurrent environmental stresses (Birch, 1953a, 1953b). In a similar fashion, if the sexes of dioecious plants do indeed display partial niche separation along a resource gradient, we would then expect androecious and gynoecious plants to respond differently to at least some environmental variables. In such cases, if patch size is small relative to the distance androecious plants can disperse pollen, androecious and gynoecious plants may not be equally fit in all environments.

Using sex allocation theory, Charnov and others (Charnov & Bull, 1977; Freeman et al., 1980; Charnov, 1982) have shown that if the sexes are not equally fit in all environments and the environments are highly heterogeneous in time and/or space, and if an individual has little control over which environment it will experience, then genes allowing environmental control of sex will be favored over genes imparting strict genetic control of sexual expression. Given these assumptions, in some environments or at some times individuals of a dioecious plant species that can alter sexual expression in response to environmental cues can increase their genetic contribution to future generations. That over 50 dioecious plant species are known in which individuals have been observed to change sex or to produce hermaphrodite or monoecious offspring supports the hypothesis that labile sexual expression imparts some selective advantage to individuals in at least some situations (Freeman et al., 1980).

Mathematical models developed by Charnov and Bull (1977) predict that if monoecious individuals were placed in a common environment where staminate and pistillate functions had unequal fitness, floral sex ratios would be locally altered to favor the more successful sex. That kind of a response appears to have occurred in *Acer grandidentatum* (Barker et al., 1982), *Juniperus osteosperma, Quercus gambelii,* and *Sarcobatus vermiculatus* (Freeman et al., 1981).

VARIABLE FITNESS OF ANDROECIOUS AND GYNOECIOUS INDIVIDUALS IN COMMON ENVIRONMENTS

Sex allocation theory predicts that labile sex expression may evolve where patch quality differentially affects staminate and pistillate fitness. To test that theory, the first question requiring attention is, "Are androecious and gynoecious plants equally fit in all environments?" Due to the difficulty of quantifying reproductive success of androecious plants, few studies have examined the influence of environment on relative fitness of androecious and gynoecious individuals of dioecious plant species. We are aware of only four studies that document differences in the environment and associated fitness of androecious and gynoecious plants (Gregg, 1973; Fox & Harrison, 1981; Freeman & Vitale, unpubl. data; Freeman et al., unpubl. data). If androecious and gynoecious individuals are not equally fit in all environments, a plant may enhance its fitness by changing sex; thus, sex change may be viewed as an adaptation to patchy en-

TABLE 1. The effect of environment on the fitness of androecious and gynoecious plants of four orchid species. Plants were grown in full or 50% of full sunlight. The fitness values were computed by dividing number of inflorescences in partial shade by the number produced in full sun (data from Gregg, 1973).

Species	Growing Condition	Relative Fitness	
		Androecious	Gynoecious
Cycnoches warscewiczii	Full sun	1.00	1.00
	Bright shade	17.50	1.00
Catasetum expansum	Full sun	1.00	1.00
	Bright shade	4.71	0.18
Cycnoches densiflorum	Full sun	1.00	1.00
	Bright shade	0.63	0.11
Cycnoches stenodactylon	Full sun	1.00	1.00
	Bright shade	0.42	0.06

vironments. If androecious and gynoecious individuals have equal fitness in all environments, nothing would be gained by changing sex. We will now examine the four studies that have noted differences in the environment and that report measures of staminate and pistillate fitness. We will consider whether fitness differences exist between the two sexes and whether those differences are correlated with environmental differences.

Gregg (1973) conducted manipulative experiments with four species of polygamous orchids. She grew plants in full sun and then in "bright shade" (50% full sun) and noted the sex expressed and the number of inflorescences per plant. In order to determine the relative performance of androecious and gynoecious plants, we have divided the number of inflorescences produced in the shade by the number produced in full sun for both sexes (Table 1). The data demonstrate that gynoecious plants produce relatively fewer inflorescences in shade compared with androecious plants. For two species, androecious performance was enhanced by shading. The results of her studies coupled with those of Dodson (1962), which demonstrated that androecious plants of some orchid species are proportionally more abundant in shady areas and gynoecious plants more common in light gaps, suggest a differential response of androecious and gynoecious plants to shading (partial niche separation).

Fox and Harrison (1981) compared the sex ratios of populations of *Hesperochloa kingii*, a dioecious grass, growing in mesic versus xeric environments. They found six to seven bar differences in soil water potential between xeric and mesic sites. As previously noted, they observed proportionately more androecious plants in the xeric environment. Fox and Harrison (1981) also used the number of inflorescences per individual as a measure of fitness. Because both sexes usually produced the greatest number of inflorescences in mesic environments, we report fitness of both sexes as 1.0 on those sites. To allow easy comparison, the inflorescences/plant ratios on xeric sites are given as a fraction of the number produced on the more moist paired site (Table 2). In three of the four cases considered, androecious plants were appreciably more fit than were gynoecious plants on xeric sites. The fourth case was puzzling to Fox and Harrison and is to

TABLE 2. The effect of environment on the fitness of androecious and gynoecious plants of *Hesperochloa kingii* (Fox & Harrison, 1981). See text for an explanation of fitness values.

Site	Description	Androecious Fitness	Gynoecious Fitness
A	Moist alluvial bench	1.00	1.00
	Dry sandy slope	1.00	0.57
B	Moist north-facing slope	1.00	1.00
	Dry south-facing slope	0.50	0.24
C	Moist grassy bottom land	1.00	1.00
	Dry south-facing slope	0.61	0.11
D	Moist sagebrush bench	1.00	1.00
	Dry west-facing slope	0.89	1.42
Overall Average	Moist	1.00	1.00
	Dry	0.75	0.59

us as well, because the fourth site shows the greatest difference in sex ratio between moist and dry microhabitats in the study, i.e., a slight pistillate biased sex ratio was observed in the wet environment (S/P = 0.69) whereas a significantly staminate biased sex ratio occurred in the dry environment (S/P = 3.76 and $\chi^2 = 24.39$, $P < 0.01$). Thus, data for sex ratios are in agreement with our predictions, but the relative fitness values obviously do not agree with our thesis. When we include the data from this aberrant site (D), the overall averages show that dry environments depressed pistillate fitness more than staminate fitness (Table 2) although the difference is not significant ($t = 0.69$, $P < 0.53$). When site D is excluded the difference is highly significant ($t = 5.6$, $P < 0.05$).

Freeman and Vitale (unpubl. data) germinated spinach seeds in a common environment and then randomly assigned seedlings to well watered, 'wet' treatment and a water stressed, 'dry' treatment. Plants in the 'wet' treatment received five times more water than stressed plants. The average number of viable pollen grains per anther multiplied by the average number of anthers per plant was used as the measure of staminate fitness. Pistillate fitness was taken as the average number of germinable seeds produced/gynoecious plant. Using Freeman and Vitale's data, we express staminate and pistillate fitness in stressed conditions as a fraction of that in the 'wet' treatment. Androecious plants in the 'dry' environment had a relative fitness of 0.77 while the relative fitness of gynoecious plants in the 'dry' environment was only 0.16.

Freeman et al. (unpubl. data) have compared the reproductive biomass of androecious and gynoecious individuals of *Atriplex canescens* growing on steep slopes versus alluvium at slope bases. Androecious reproductive biomass was taken as the weight of staminate catkins prior to dehiscence of exserted stamens. Gynoecious reproductive biomass was taken as the weight of fruits just before fruit abscission. Because gynoecious plants on alluvial soils produced more fruits than gynoecious plants on slopes, we calculated relative fitness of the latter by dividing their reproductive biomass by the comparable variable for gynoecious plants on alluvium. Relative fitness of slope and alluvium androecious plants was similarly computed. Relative fitness of 'slope' androecious plants was 0.82, but relative fitness of 'slope' gynoecious plants was only 0.33 ($t = 4.82$, $P < 0.001$).

In each of the foregoing cases, the relative performance of gynoecious plants on stressed sites was less than the relative fitness of androecious plants. Such a response would be predicted if the sexes actually showed partial niche separation as suggested by Freeman et al. (1976) and Onyekwelu and Harper (1979). However, we note that it is not necessary for gynoecious individuals to respond less well than androecious individuals under stress to validate the assumption of sex allocation theory. It is only necessary that fitness of androecious and gynoecious plants be unequal under some conditions. Some physiological, morphological, and anatomical studies of dioecious plants have shown differences between androecious and gynoecious plants, but in most cases there is little indication that the differences have ecological or evolutionary significance (Lloyd & Webb, 1977; Freeman et al., 1980). In contrast, the foregoing case studies suggest that the staminate and pistillate functions are unequal in common environments. Such results have obvious practical consequences, but they also suggest possible avenues for the evolution of at least some dioecious plant taxa and/or taxa capable of reversing sexual expression. Linking unequal fitness of male and female gametes at common sites to evolution of a dioecious species will require evidence that androecious plants in stressful environments sire more descendants by exporting pollen to more mesic sites than could be produced by nearby stressed gynoecious plants. If such a condition existed, plants with pistillate flowers in dry environments could increase their genetic contribution to future generations by producing staminate flowers instead. In the only experimental study known that attempts to evaluate the fitness of stressed and unstressed androecious and gynoecious plants, Freeman and Vitale (unpubl. data) show that androecious plants from a dry environment that sired three gynoecious plants there and one in a wetter environment would leave more offspring in the second generation, on average, in the moist than in the dry environment (54 in the moist versus 21 in the dry), because gynoecious plants were sixfold more fit in the moist than dry environments.

SEX CHANGES AND TERMINOLOGY

The foregoing evidence indicates that androecious and gynoecious individuals of at least some dioecious plant species are not equally fit in all environments. Because we know of no mechanism by which seeds can choose the environment in which they fall, some plant species satisfy the assumptions of sex allocation theory and would be predicted to be capable of switching sex by that theory. The question we now address is, "Do individuals of dioecious plant species change sex (or, in the case of annuals, show environmental sex determination)?" Also, do individuals of monoecious plant species alter their floral sex ratios in response to changes in environmental quality?

Dioecious species, by definition, contain only unisexual individuals. Obviously a plant that changes sex must be genetically bisexual and is not strictly speaking dioecious. The ecological and evolutionary significance of altered sex expression is equivalent to dioecy, however. We will refer to species that display environmental sex determination or change sex as subdioecious.

Typically, *Atriplex canescens* individuals are either unisexual (Gynoecious = G, or Androecious = A) or monoecious (Mo = having both staminate and pistillate flowers on the same individual). A plant that is exclusively gynoecious one year and exclusively androecious another has changed sexual expression. But what of a plant that changes from a unisexual phenotype to a monoecious phenotype? Has it changed sex? Clearly the change is one of degree and not of kind. We would agree that an exclusively gynoecious individual one year that displayed a single staminate flower among a myriad of pistillate flowers the next has not changed its primary sexual expression. Nevertheless, the plant has demonstrated a genetic capacity to produce staminate flowers. We will consider any gynoecious plant that later obtains an appreciable fraction of its fitness (say 20%) through pollen has changed its sexual state. For convenience, changes of less than 20% will be described as sexual inconstancy rather than change of the primary sexual state. We will call changes exceeding 20% sex change. When 20–80% of the flowers are of the sex not previously displayed, we will describe the plant as monoecious. If changes exceed 80%, we will refer to the situation as a change in primary sexual expression.

A number of researchers, most notably Lloyd and Bawa (in press), are willing to concede that sexual inconstancies occur but do not believe that individuals change their primary sexual expression. Furthermore, they argue that if plants do change primary sexual expression, the fraction of the population so affected is trivially small. We will present evidence suggesting that in the case of *Atriplex canescens,* the Lloyd and Bawa position is inconsistent with the data. If plants do track the environment as hypothesized in sex allocation theory, then small changes in ratios of staminate to pistillate flowers from year to year on monoecious plants would also be predicted and should be more frequent than large changes. Thus, plants that respond to modest environmental changes may appear to be only sexually inconstant. Absence of large changes in floral sex ratios of individuals would constitute strong evidence against sex allocation theory. If large changes can be documented, sex allocation theory would be strengthened.

SEXUAL STATES IN *ATRIPLEX CANESCENS*

In 1977, McArthur reported that some individuals of a half sib family of *Atriplex canescens* changed sexual expression. Work has continued with this population to the present. Several kinds of data on the sexual state of individuals now exist. Annually, all individuals have been classified as androecious (A), gynoecious (G) or monoecious (Mo). In Table 3, the kinds of changes observed are listed. As expected, the bulk of the changes were between gynoecious and monoecious or androecious and monoecious states; only 33 of 665 individuals changed from androecious to gynoecious or vice versa. An additional six plants were monoecious at one time in their life, exclusively androecious another year, and exclusively gynoecious in yet another year. Changes between androecious and gynoecious sexual states support sex allocation theory. However, gynoecious ↔ monoecious and androecious ↔ monoecious changes could represent either sexual inconstancies or major changes of sexual expression, depending on ratios of staminate and pistillate flowers of individual plants. These data by themselves are not sufficient to allow discrimination between sexual inconstancy and sex change without the addition of floral sex ratio data.

Fruits were collected from 14 of 35 plants that had been androecious and monoecious but never gynoecious. Fruit production of these monoecious plants was compared with average fruit set of gynoecious plants in the same year. Most of the androecious ↔ monoecious plants had a single episode of sexual change. In cases in which plants had multiple episodes, the year of largest fruit set was used. Plants producing less than 20% as much fruit by weight as the average gynoecious plant were classified as sexually inconstant. Plants

TABLE 3. Summary of floral phenotypes in the U103p family of *Atriplex canescens* over the period 1972–1978. The population is maintained at the Snow Field Station, Ephraim, Utah (McArthur & Freeman, 1982).

		Number of Plants					
				Changed Phenotypes (at least one year) to:			
Floral Phenotype[a]	1972	Died Without Changing Phenotype	Constant Phenotype Through 1978[b]	G	A	Mo[c]	Probability of Constant Phenotypes
G	372	40	149	—	22	161	0.51
A	228	39	155	11	—	23	0.85
Mo	34	2	1	12	13	6	0.09
0	31	8	1	3	6	13	0.29
Totals	665	89[d]	306	26	41	203	

[a] G = Gynoecious; A = Androecious; Mo = Monoecious; 0 = No flowers.

[b] G, A, and Mo, phenotypes considered constant if only departure was to 0 phenotype.

[c] Includes plants that were G or A some years in addition to being Mo for at least one year.

[d] Actually 101 plants died and seven were sacrificed for pathological study by 1978. The other 19, however, are accounted for under "changed phenotypes."

producing 20–80% as much fruit as an average gynoecious plant were considered to have changed from unisexual to a monoecious state, and those producing greater than 80% of the average fruit crop were considered to have changed their primary sexual expression. These data show that 36% of the 14 test plants were sexually inconstant, 43% were monoecious and 21% changed their primary sexual expression. Thus by our criteria, over 64% of the androecious ↔ monoecious plants made significant changes in sexual expression during the period of record. Had we counted multiple episodes of sex changes rather than only the year of largest fruit set, percentages for the sexual states would be: sexually inconstant, 42; functionally monoecious, 46; and changes in primary sexual expression, 12.

The foregoing results suggest that seven (21% × 35) of the androecious → monoecious plants changed their major sexual expression, whereas an additional 15 plants were monoecious for at least one year. Thus the total number of plants changing sexual emphasis should be increased by the seven plants that were staminate and became pistillate biased monoecious individuals.

In order to provide a complete inventory of individuals capable of sex change in the population, we must add plants that changed from pistillate to predominantly staminate biased monoecious individuals (80% or more staminate flowers) to the 46 plants noted above. We also collected fruit from plants displaying gynoecious and monoecious states but not the exclusively androecious phenotype. If such plants were simply sexually inconstant, only a slight reduction in fruit set would be expected when the plant was monoecious. We now compare fruit crop of gynoecious ↔ monoecious plants against average fruit crop of the same plants while they were functioning as exclusive gynoecious plants. If reduction in fruit crop was less than 20%, plants were classified as sexually inconstant. When fruit set reduction exceeded 80%, plants were considered to have had a change in primary sexual expression. Changes between 20 and 80% in fruit production were considered as possible changes to the monoecious condition. Again, we considered all changes and the largest change exhibited. Data exist for only 48 of the 173 plants. When all changes are considered, 46% were less than 20%, and 38% exceeded 80% reduction in fruit set. The remaining 17% of changes fell between 20 and 80% reduction in fruit set. When we consider only the largest changes, 33% of the changes were less than 20%, 52% exceeded 80%, and 15% exceeded 20% but were less than 80%. These data document a drastic reduction in fruit set as plants changed from strictly gynoecious to a monoecious condition. Two possible explanations for the results exist: (1) plants changed to a primarily staminate biased monoecious state, or (2) plants were only sexually inconstant but had low fruit production.

In addition to recording fruit production by plant, we have also subjectively rated overall reproductive potential (staminate plus pistillate functions) of monoecious plants. The rating scale ranged from 0 to 9 and was based upon the numbers of flowers of each sex. Although the subjective rating data are crude, they do give some indication of the importance of the male sexual functions on plants that have never displayed the exclusively androecious phenotype. Such data exist for 84 plants that displayed the gynoecious and monoecious phenotypes, but were never exclusively androecious. If these gynoecious monoecious plants were only slightly sexually inconstant while in the monoecious state, one would predict that their overall reproductive potential as androecious individuals would be slight. However, if primary sexual expression changed, one would expect high subjective ratings and a low fruit production. It is important to note that pollen was not limiting in this population (McArthur et al., 1978).

Plants were assigned to one of the ten categories of 'reproductive potential,' and the mean number of grams of fruit produced (and standard deviations) were computed for each category. For example, plants that displayed the gynoecious phenotype in 1975 and were given the rating of 1, produced, on the average, 1 g of fruit; plants given a rating of 9 in 1975 produced an average of 325 g of fruit. In 1974, gynoecious plants with a subjective rating of 9 produced an average of 499 g of fruit. Given the standards for plants with exclusively pistillate flowers, we can examine fruit set of monoecious individuals and assign each individual to a reproductive potential class solely on the basis of fruit set. For example, a plant that was phenotypically monoecious in 1975 and produced 60 g of fruit would be assigned to gynoecious reproductive class 4 on the basis of fruit production. If the plant had been rated as 4, we would conclude that the bulk of its reproduction was through the gynoecious function. If, on the other hand, a monoecious plant produced 60 g of fruit and received a rating of 9, one would conclude that a substantial fraction of the rating arose from production of staminate flowers. Thus, the important parameter was the difference in a plant's rating as a monoecious individual and its expected rating based solely upon fruit production. Individuals showing differences less than or equal to two classes were classified as sexually inconstant. If the difference was three or four classes, we considered the plant to have changed to a functionally monoecious state, and if the difference was greater than five, the plant was considered to have changed its primary sexual expression. The data show that 48 of the 84 plants (57%) were sexually inconstant, 25 plants (30%) changed from the gynoecious to functionally hermaphroditic state, and 11 plants (13%) changed sexual expression.

These data are consistent with conclusions drawn from Table 3, and suggest that both explanations for the reductions in fruit sets may be valid (i.e., some plants become predominantly staminate, whereas others become monoecious but produce little fruit). They also provide a conservative estimate of the number of plants that were gynoecious and changed to prevailingly staminate biased monoecious individuals. Multiplying 13% by the number of plants that were gynoecious or monoecious but never androecious (173), we obtain an estimate of 23 gynoecious plants that became prevailingly staminate biased bisexual plants. Adding this to the number of plants observed to change from androecious to gynoecious (33) plus the number of androecious plants that changed to pistillate biased monoecious individuals (7) plus the six plants that displayed all three phenotypes, gives a total of 69 plants that changed sex completely or changed their primary sexual expression (roughly 10% of the total of 665 individuals studied). This is still only part of the story, for we have not considered plants that changed from the unisexual to the monoecious state, for which 20 but less than 80% of their flowers were of the sex opposite to that previously produced. For the androecious to monoecious class, 26 plants are tallied (35 plants × 0.4615). For gynoecious to monoecious, the number would be 52 plants (173 × 0.2979). Thus, by our criteria 69 + 78 or 147 plants of 665 (21%) changed their sexual state. We consider this a conservative estimate for two reasons: (1) many sex changes were recorded during the drought of 1976–1978, but those data were not usable, because corresponding fruit set data were not taken, and (2) at least some plants considered sexually inconstant on the basis of available data have the potential to change sex under other conditions. The latter consideration is dramatized by plant #7–40, which, by the criteria employed here, was a sexually inconstant gynoecious individual. That plant was cloned into 24 ramets, seven of which have flowered. Five of the seven ramets produced only staminate flowers and produced as many flowers as the average ramet from pure

TABLE 4. The number of individuals changing sex in natural populations of five species of *Atriplex*. All populations consist of a sample of 200 individuals chosen at random, except for *A. lentiformis*. The *A. lentiformis* population included all 70 individuals. The observations cover the five years from 1978 to 1983.

Species	Type of Change in Sexual Morph	
A. canescens	G ↔ A or G ↔ Mo ↔ A	9
	G ↔ Mo	8
	A ↔ Mo	17
A. confertifolia (Desert Experimental Range Population)	G ↔ A or G ↔ Mo ↔ A	17
	G ↔ Mo	8
	A ↔ Mo	8
A. confertifolia (Purgatory Basin Population)	G ↔ A or G ↔ Mo ↔ A	6
	G ↔ Mo	0
	A ↔ Mo	2
A. corrugata	G ↔ A or G ↔ Mo ↔ A	12
	G ↔ Mo	9
	A ↔ Mo	54
A. cuneata	G ↔ A or G ↔ Mo ↔ A	6
	G ↔ Mo	26
	A ↔ Mo	11
A. lentiformis	G ↔ A or G ↔ Mo ↔ A	9
	G ↔ Mo	9
	A ↔ Mo	5
A. tridentata	G ↔ A or G ↔ Mo ↔ A	11
	G ↔ Mo	39
	A ↔ Mo	9

androecious plants. Clearly, this "sexually inconstant gynoecious plant" retained the genetic capacity to produce staminate flowers in abundance given the "right" circumstances.

The above data suggest that individuals of *Atriplex canescens* change sex. Some dismiss these results because they are derived from a population of half sibs descended from a single gynoecious plant. Data from Freeman and McArthur (unpubl. data), however, demonstrate sex change in natural populations of *A. canescens, A. confertifolia, A. corrugata, A. cuneata, A. lentiformis,* and *A. tridentata* (Table 4). In the majority of cases, individuals changed from a unisexual to a monoecious state, but complete changes were also observed in all species. Furthermore, extensive studies on natural populations and clones of *A. canescens* derived from natural populations are in agreement with these results. The half sib family of *A. canescens*, then, is not atypical for the genus; sex change seems deeply entrenched in species of *Atriplex* of the intermountain west of North America.

RELATED STUDIES IN SEX CHANGE

In addition to our own studies, well documented records of individuals that change sex under natural conditions have been reported for: *Juniperus australis* and *J. osteosperma* (Vasek, 1966), *Acer pensylvanicum* (Hibbs & Fischer, 1979), *Acer saccharinum* (Sakai, unpubl. data), and *Elaeis guineensis* (Williams & Thomas, 1970). In addition, there are voluminous data on *Arisaema triphyllum* and *A. dracontium*, sequential hermaphrodites (typically individuals begin by producing staminate flowers and change to production of pistillate flowers) that are widely acknowledged to change sex (see Gow, 1915; Pickett, 1915; Schaffner, 1922; Maekawa, 1924; Camp, 1932; Sokamoto, 1961; Policansky, 1981; Bierzychudek, 1982; Lovett-Doust & Cavers, 1982). In all of these species, some individuals are reported to change from the unisexual to a monoecious state. Unfortunately, however, there is a paucity of information concerning the percentage of staminate and pistillate flowers produced by monoecious plants of these species.

MECHANISMS AND CONSEQUENCES OF SEX CHANGE IN *ATRIPLEX CANESCENS*

The foregoing data suggest that the assumptions of sex allocation theory are valid for many plant species in a variety of distantly related families. The magnitude of change in several different populations demonstrates that sex change is not numerically trivial. At this point we are left with a number of unanswered questions: (1) What conditions induce plants to change sex? (2) Does changing sex enhance an individual's fitness? (3) By what mechanisms do plants change sex? (4) Is sex change compatible with the current understanding of the genetics of sex determination in plants?

In regard to the question of the conditions that induce plants to change sex, we have recorded the sexual expression of each individual in the half sib family of *Atriplex canescens* through the period 1968–1978. This includes a severe cold period (1972–1973) and a major drought (1976–1978). In both stressful periods, significantly more plants shifted away from femaleness (i.e., G → Mo or A, and Mo → A) than towards femaleness

TABLE 5. Direction of change in sexual state following severe external stress. The winters of 1973–1974 and 1974–1975, were normal for temperatures and precipitation. The winter of 1972–1973 was unusually cold, and the winter of 1975–1976 was much drier than normal. Magnitudes of difference in population changes in sexual expression in normal and stressful years are tested for significance by Chi-square analyses. G = Gynoecious; A = Androecious; Mo = Monoecious. The expected values are shown in parentheses.

	Type of Sex Change			
Year	G to Mo or A	Mo to A	Mo to G	A to Mo or G
1972–1973	85	10	7	12
	(48.8)	(10.6)	(28.5)	(26.1)
1973–1974	16	12	52	42
	(52.2)	(11.4)	(30.5)	(27.9)
	$\chi^2 = 98.2$		$P < 0.01$	
	G to Mo or A	Mo to A	Mo to G	A to Mo or G
1974–1975	13	6	10	8
	(25.5)	(1.5)	(4.8)	(5.2)
1975–1976	104	1	12	16
	(91.5)	(5.5)	(17.2)	(18.8)
	$\chi^2 = 34.1$		$P < 0.01$	

TABLE 6. In this table we examine the hypothesis that a heavy seed set in year X may influence the sex of individuals in year X + 1. Because not all individuals appear to be capable of changing sex, we selected those which could change sex and then classified them into two groups, i.e., those that changed in year X + 1 and those that did not. We then ranked the seed set of the individuals in year X into three categories, i.e., $x < 0.75\ \bar{x}$; $0.75\ \bar{x} < x < 1.25\ \bar{x}$; $1.25\ \bar{x} < x$.

	x < 75%	75% < x < 125%	125% < x
Did Not Switch	8	13	6
	(7.47)	(8.19)	(11.34)
Switched	23	21	41
	(23.53)	(23.51)	(35.66)

$\Sigma\ x^2 = 6.67$; $P < 0.05$.

(A → G or Mo and Mo → G) (Table 5). In addition to such obvious external stresses, we have examined the influence of prior year fruit production on sexual expression in the next year (Table 6). Plants that produced heavy fruit crops ($X > 125\%$ of the plant's annual longterm average crop) changed sex more readily than plants that had light ($X < 75\%$ of the plant's average crop) or normal fruit crops ($0.75\bar{x} < X < 1.25\bar{x}$).

We also observed that mortality was significantly greater among plants on the edge (43%) of the half sib family plantation than among individuals growing in the center (11%) of the population. We consider that edge plants are more stressed for water because of their greater exposure to light and wind. When the incidence of complete sexual changes (G ↔ A) are compared for plants occupying the edges versus those in the interior of the patch, significantly more changes occur in plants growing around the edges (Table 7).

We have emphasized temperature and water relations in the foregoing analyses, but the work of Gregg (1973), Cox (1981), Schaffner (1922, 1925, 1927) and others suggests that factors such as light intensity and mineral nutrient availability may also affect sexual expression of plants. Gregg (1973) showed that when gynoecious or large monoecious individuals of the tropical orchids she studied were placed in the shade, they produced staminate flowers. Androecious plants placed in full sunlight often produced pistillate flowers. Such effects of light on sexual expression suggest that studies of sexual expression of cohorts of dioecious tropical forest trees are needed during the period when individuals move from shaded forest floor and subdominant positions into the canopy. Are the mortality rates of androecious and gynoecious plants equal? Are androecious and gynoecious plants equally fit at all ages and in all positions within and below the canopy? Do individuals change sex? Studies on *Castilloa elastica* (summarized in Dzhaparidze, 1967) show that sequential hermaphroditism occurs in at least one tropical tree species.

Unfortunately, we currently have only indirect measures to predict whether sex change will enhance fitness. Cole (1954) was the first to emphasize the contribution of early reproduction to fitness. In this connection, we find that *Atriplex canescens* plants of variable sexual expression reproduce significantly earlier in life than constant gynoecious individuals but later than constant androecious individuals (Table 8). Results are based on 70 ramets from sexually labile individuals, 70 ramets of constant androecious plants and 61 ramets from constant gynoecious plants. Of the 70 androecious ramets, 69 flowered in the second year after cloning; 34 sexually

TABLE 7. Comparison of the distribution (edge versus the interior of the patch) of plants that have completely changed sex (A ↔ G) versus those that have never changed sex. Expected values are shown in parentheses.

	A G	Constant
Edge	28	108
	(18.0)	(118.0)
Interior	31	278
	(41.0)	(268.0)
$\chi^2 = 9.22$	$P < 0.01$	

	A G	Other Classes of Sex Change
Edge	28	68
	(19.7)	(76.3)
Interior	31	160
	(39.3)	(151.7)
$\chi^2 = 6.6$	$P < 0.01$	

TABLE 8. Incidence of flowering among two-year old ramets of *Atriplex canescens*. The analysis is of the number of plants in each category. Expected values in parentheses.

Plantation 1 (irrigated)	Androecious	Gynoecious	Sexually Labile
Flowering	69	6	34
	(36.86)	(35.28)	(36.86)
Nonflowering	1	61	36
	(33.14)	(31.72)	(33.14)
	$\chi^2 = 110.99$		$P < 0.001$

Plantation 2 (non-irrigated)	Gynoecious	Sexually Labile
Flowering	6	34
	(19.56)	(20.44)
Nonflowering	61	36
	(47.44)	(49.56)
	$\chi^2 = 25.99$	$P < 0.01$

labile ramets also flowered, but only six gynoecious plants had flowered by the end of the second growing season (Table 8). Of the ramets from sexually labile individuals that flowered, 11 were staminate, 21 were monoecious but prevailingly staminate, and two were exclusively pistillate.

In addition to the time of onset of reproduction, parental longevity and the number of offspring per reproductive event have an effect on the fitness of an individual (Cole, 1954). We have obtained two measures of longevity: the first is based on the average age at death of individuals in the half sib family; the second considers mortality through time in ramets of common age from constant staminate, constant pistillate, or sexually labile individuals. In the half sib population, the average gynoecious plant died at an earlier age than either androecious or sexually labile plants. Plants that changed sex lived significantly longer than either androecious or gynoecious plants (Table 9). In our second set of data, no mortality was observed among ramets from sexually labile individuals after seven years. Androecious plants exhibited 99% survivorship, but gynoecious survivorship was only 87% after seven years. The ability to change sex thus appears adaptive, at least as far as age at first reproduction and survivorship are concerned.

Finally, we examine fruit production of constant gynoecious plants and plants that vacillate between the gynoecious and monoecious states. We have no valid way of comparing reproductive output of androecious plants and sexually labile individuals, but we can compare fruit production of sexually labile plants and gynoecious plants. For the four years for which fruit production data are available, plants that changed sexual expression at some time in their life averaged 327 g of fruit per year, whereas constant gynoecious plants averaged 330 g per year. We point out, however, that the very highest fruit producers are constant gynoecious plants (McArthur et al., 1978). In addition, of course, the sexually labile individuals also reproduced via pollen in at least one year. For the period of record, it would appear that plants that change sex are not disadvantaged, but indeed may enjoy a fitness advantage in terms of offspring produced per year. A more complete demographic analysis is needed and is under way.

The third question posed earlier concerns the mechanism(s) by which plants change sex. Although we lack experimental data on how plants change sex, it is important at this stage that plausible models be formulated. Two fairly well studied models could account for our observations on *Atriplex canescens*. The first is derived from the work of Chailakhyan and Khryanin (1978). They have shown that in spinach (which, like *Atriplex*, is a member of the Chenopodiaceae) and hemp, the ratio of cytokinin to gibberellic

TABLE 9a. Age at death of *Atriplex canescens* individuals of different sexual morphs. All individuals are from the half sib population of McArthur (1977). All plants originated from seed germinated in 1968. The population is cultivated at the Snow Field Station, Ephraim, Utah.

Sexual Morph	Initial Number of Individuals	% Mortality 1972–78	Average Age at Death (years)[a]
A	190	21.6	4.85 ± 1.56
G	203	20.2	5.78 ± 1.82
Mo	261	8.0	7.71 ± 1.31

[a] All means differ significantly from each other.

TABLE 9b. Mortality among *Atriplex canescens* individuals of different sexual morphs. Ramets were taken from plants taken from a population native to the Book Cliff area of east central Utah.

Morph	% Survival After 7 Years
Mo	100
A	99
G	87

acid controls sexual expression. With cytokinin in excess, plants generally produce pistillate flowers. Itai and Vaadia (1970) have shown that under conditions of water stress, cytokinin is not transported to above ground parts from sites of synthesis in the root. Chailakhyan and Khryanin (1978) have shown that gibberillic acid continues to be synthesized in leaves when plants are stressed for water. Thus, should a plant experience severe water stress, cytokinin flow to stem tips appears to diminish, whereas gibberillic acid continues to be produced. Under such conditions, even a plant genetically predisposed to produce cytokinin in abundance, and thus produce pistillate flowers, might instead produce staminate flowers.

Pharis (1975) has shown that the ratio of polar to nonpolar gibberillic acids determines sex expression in some conifers. Polar gibberillic acids tend to yield microsporangiate forms while nonpolar forms tend to yield megasporangiate forms. Under water stress, polar gibberillic acids are not converted to nonpolar forms, and again, plants produce predominantly microsporangiate reproductive structures.

Lastly, we return to the question of genetic controls of sexual expression, a theme that two of us have previously discussed (McArthur, 1977; Freeman et al., 1980; McArthur & Freeman, 1982). It seems likely that not all dioecious or subdioecious plants are capable of changing sexual expression. In some species, sex appears to be rigidly controlled by genetics. Perhaps the most absolute case of such control occurs among the mistletoes (*Viscum*) in which gynoecious plants inherit a large translocation ring, a feature that androecious plants lack (Wiens & Barlow, 1979). Other rigid genetic systems are also known to occur (Westergaard, 1958; Lloyd & Bawa, in press). It is not clear how common such systems are. The problem is complicated because even in species such as *Atriplex canescens,* which are known to contain individuals with labile sexual expression, an appreciable fraction of the population does not seem capable of sex change and shows no form of sexual inconstancy. Sexual expression in such individuals is constant and indifferent to environmental fluctuations. We have observed thousands of plants over nearly a decade. Many have maintained a constant unisexual state throughout the entire period. When such constant androecious and gynoecious plants are cloned and placed in a variety of environments, sexual expression of ramets is always that of the parent plant. There is thus little doubt of a strong genetic component to sexual expression in *Atriplex,* particularly in *A. canescens.* Nevertheless, we also find many individuals of *A. canescens* and many other species with subdioecious individuals that express more than one sexual state in their life. The work already presented in this paper indicates that at least three sexual morphs occur: androecious, gynoecious, and labile. We recognize that the third sexual morph may require further subdivision when detailed genetic studies are made. We believe that all of the observed facts can be accommodated by known genetic mechanisms since sexual expression depends on both the quantities of and ratios among hormones, and hormone production is affected by both genetic and environmental factors. Given differential effects of environmental stress on hormones controlling sexual expression, tissue differentiation and flower morphs could be dramatically altered in kind or degree from year to year on the same individual. We thus fail to see any compelling reasons to interpret *A. canescens* as a two morph or diphasic model as do Lloyd and Bawa (in press). A variety of data for *A. canescens* argues for at least three sexual morphs with the labile morph capable of producing staminate flowers only, pistillate flowers only, or monoecious individuals having a variety of staminate to pistillate flower ratios. Our clonal studies, which will be summarized elsewhere, show that all of these phenotypes can be derived from a single sexual labile individual in a single year under common garden conditions.

Conclusions

The picture now emerging of sex expression in *A. canescens* is far more dynamic than most have previously believed. Some individuals appear capable of widely divergent floral sex expression in response to variable local environmental conditions and the individual's own physiological state. Modifications range from modest adjustments to complete changes of sexual expression. Such modifications appear to be adaptive. How such modifications are achieved, through interactions of environment, physiology, and genetics are subjects requiring further investigation. Likewise, mechanisms by which androecious, gynoecious, and sexually labile individuals persist in common populations remain to be identified.

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VARIATION IN FLORAL SEXUALITY OF DICLINOUS *ARALIA* (ARALIACEAE)[1]

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ABSTRACT

Spatial and temporal variation in floral sexuality of diclinous plant populations influence the mating system and reproductive success of individuals. Observations of the phenology of the sex condition in andromonoecious *Aralia hispida* and dioecious *Aralia nudicaulis* indicate non-random patterns of gender expression. In *A. hispida,* cycles of male and female function resulting from developmentally synchronized protandry within ramets restrict opportunities for self- and geitonogamous pollination as well as intensify competition among staminate flowers for ovules. A ramet's male reproductive success is negatively correlated with the degree of flowering synchrony between the ramet and the population. In species with developmental synchronization of dichogamy, the evolution of large clone size will disrupt synchrony of sexual function among ramets leading to increased inbreeding. This could provide unisexual mutants with an outbreeding advantage and favor the evolution of dioecism. Genet size in *Aralia nudicaulis* is very large, precluding investigation of their frequency and distribution. In forest habitats flowering staminate ramets occur at higher densities than pistillate ramets, particularly in shaded locations. This pattern is due to differences between ramets of the sexual morphs in the frequency of flowering, possibly as a result of differential reproductive costs. Previously published data on the flowering phenology of staminate and pistillate ramets are re-interpreted in light of information showing differences in the microdistribution of flowering ramets of the sexes. Large genet size in *A. nudicaulis* can result in the spatial isolation of flowering ramets of the sexes. However, no spatial effects on the fecundity of ramets were apparent in a one hectare forest plot. The percentage fruit set in *A. nudicaulis* was substantially higher than in four co-occurring self-incompatible, entomophilous, clonal herbaceous species. This pattern of fruit set is in accord with data collected from several other plant communities and may result from the absence of functionally staminate flowers in pistillate plants of dioecious species and their importance to total fitness in hermaphrodite plants.

The mating success of individuals in diclinous plant populations is strongly influenced by spatial and temporal variation in the sexual condition of flowers. The variation is manifested at various levels including individual flowers, inflorescences, ramets, and genets during a single day, part of the flowering season, or over several years. Observations of the reproductive behavior of diclinous populations have usually revealed non-random patterns of flowering in space and time of the sexual morphs or among staminate- and pistillate-functioning flowers (Lloyd, 1973, 1974, 1981; Jong, 1976; Webb, 1976; Cruden & Hermann-Parker, 1977; Lloyd & Webb, 1977; Bawa, 1980a; Lovett-Doust, 1980; Primack & Lloyd, 1980; Bullock & Bawa, 1981; Lovett-Doust & Cavers, 1982; Lindsey, 1982; Schlessman, 1982). This has led to the formulation of a variety of hypotheses that attempt to explain the adaptive significance of variations in floral sexuality. The hypotheses involve several inter-related concepts including outbreeding advantage (Charlesworth & Charlesworth, 1978, 1979; Maynard Smith, 1978; Thomson & Barrett, 1981a; Lloyd, 1982), sexual selection (Gilbert, 1975; Janzen, 1977; Willson, 1979; Bawa, 1980b; Givnish, 1980), optimal allocation of resources to maternal and paternal function (Charnov, 1979, 1982), and strategies for coping with environmental uncertainty (Thomson & Barrett, 1981b; Lloyd, 1982). Whereas the relative importance and degree of interdependence of these concepts for particular taxonomic and ecological groups are still under active debate, there is general agreement on the need for more detailed information on the factors influencing the sexual performance of individuals in natural populations.

Until recently the description and measurement of plant sexuality has lacked a quantitative basis. Inferences on the mating system of populations from observation of floral morphology alone can be particularly misleading in dichogamous species. Numerical indices of functional

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TABLE 1. Reproductive characteristics of *Aralia hispida* and *Aralia nudicaulis* populations from central New Brunswick. From Barrett and Helenurm (1981) and Thomson and Barrett (1981).

Characteristic	*Aralia hispida*	*Aralia nudicaulis*
Major Habitat	forest clearings and open, disturbed sites	forest understory
Clone Size	small	very large
Flowering Period	July	June
Major Pollinators	bumble bees especially *Bombus vagans* and *B. terricola*	bumble bees especially *Bombus vagans* and *B. ternarius*
Breeding System	andromonoecism with synchronized protandry and self-compatibility	dioecism
Average Number Flowers per Ramet	324	♀ 75.2, ♂ 120.0
Average Flowering Time per Ramet (days)	23.2	♀ 4.9, ♂ 7.4
Fruit	fleshy fruit with 5 seeds	fleshy fruit with 5 seeds

gender (Lloyd, 1979, 1980a; Thomson & Barrett, 1981b) emphasize the quantitative and dynamic nature of sexual performance, particularly in plants with hermaphroditic flowers. Although the indices make certain unrealistic biological assumptions, e.g., panmixia, they are useful in illustrating the great variation in which individuals can succeed as pollen or seed parents and in drawing attention to the basic dichotomy in plant sexuality between populations that are monomorphic in gender and those that are dimorphic (Lloyd, 1979). These theoretical developments in combination with the use of electrophoretic techniques for estimating mating system parameters such as ovule and pollen outcrossing rates (Brown & Allard, 1970; Horovitz & Harding, 1972; Ross, 1977; Clegg, 1980; Ritland, 1983) are likely to provide new opportunities for examining the sexual performance of individuals in plant populations. They also draw attention to the fact that many aspects of plant mating are frequency dependent phenomena (Ross, 1977, 1982; Ross & Gregorius, 1983). Hence the reproductive success of an individual at a certain time will depend on the frequency, sexual condition, and fertility of the remaining individuals in the population. Studies of mating systems can be investigated accurately, therefore, only at the population level, taking into account the spatial and temporal aspects of variation in reproductive behavior.

Detailed observations of flowering patterns and sexual performance of individuals in natural populations are available for relatively few diclinous taxa. Lloyd and Webb (1977) reviewed much of the data prior to the mid 1970s for sexually dimorphic taxa. More recent studies include Meagher (1980, 1981), Bullock and Bawa (1981), Lloyd (1981), Cox (1981, 1982), Policansky (1981), Bierzychudek (1982), Lovett-Doust and Cavers (1982). Our own studies of *Aralia* (Araliaceae) have involved an examination of flowering patterns in the sexually monomorphic *A. hispida* Vent. (Thomson & Barrett, 1981b; Thomson et al., 1982) and the sexually dimorphic *A. nudicaulis* L. (Barrett & Helenurm, 1981; Barrett & Thomson, 1982). Here I review some of these studies and make some attempt to explain the functional significance of variation in sex expression in light of various models of selection.

NATURAL HISTORY OF *ARALIA*

The four *Aralia* species of eastern North America are diclinous, perennial herbs or shrubs of wooded habitats. *Aralia nudicaulis* is dioecious, the remaining species (*A. hispida, A. racemosa,* and *A. spinosa*) are andromonoecious. Our work was undertaken in spruce-fir forests and associated habitats in central New Brunswick during the summers of 1978–1981. In this region *A. nudicaulis* is abundant in the understory of forests, whereas *A. hispida* is more com-

TABLE 2. Floral sexuality and fruit set (percentage of hermaphrodite flowers with mature fruit) in three andromonoecious populations of *Aralia hispida* from central New Brunswick. After Thomson and Barrett (1981).

Population (sample-size, ramets)	Total Flowers	Percentage		Fruit Set
		☿	♂	
A (N = 51)	7,407	30.0	70.0	95.8
B (N = 49)	11,893	26.6	73.4	92.2
C (N = 50)	8,926	35.0	65.0	97.2

monly encountered as a weed of disturbed sites such as forest clearings, roadsides, and burned areas. Where logging roads traverse the forest, the two species can be found growing together. Although these species share similar pollinators, their non-overlapping flowering periods preclude interspecific pollination (Table 1).

Many aspects of floral biology in *Aralia* species resemble those described for the related Umbelliferae (Müller, 1883; Ponomarev, 1960; Bell, 1971; Cruden & Hermann-Parker, 1977; Webb, 1979, 1981; Lovett-Doust, 1980; Lindsey, 1982; Schlessman, 1982). Flowers are small, whitish green, and aggregated into umbellate inflorescences. Hermaphroditic species are self-compatible and frequently exhibit complex patterns of synchronized protandry or protogyny (see below). Inflorescences of dioecious taxa occasionally contain hermaphrodite as well as staminate and pistillate flowers. However, our observations of *A. nudicaulis* in Canada and those of Bawa et al. (1982) in Massachusetts, indicate that variable sex expression of individuals is a rare condition in this species.

One of the most important ecological differences between *A. hispida* and *A. nudicaulis* is clone size. Clones (genets) of *A. hispida* are rarely larger than a few meters in diameter, with the majority being smaller. Genets are composed of one to ten ramets, most of which are reproductive. In contrast, clones of *A. nudicaulis* are very large and probably of considerable age. Field observations of isolated clones, excavation work, and mapping studies (reviewed below) suggest that in the forests studied by us genets may cover several hundred square meters, although unequivocal evidence for this is difficult to obtain. Large genets of *A. nudicaulis* are composed of hundreds of ramets, many of which are vegetative. The relative proportion of vegetative to reproductive ramets varies with local site conditions, particularly the light regime (see below). Characters such as size, inflorescence production, and flower number per ramet in *A. nudicaulis* do not display the high degree of phenotypic plasticity exhibited by *A. hispida.*

Bumble bees are major pollinators of both *Aralia* species. Because flowers are open, small, and with anthers and stigmas borne in similar positions, any visitor is a potential pollinator. Minor visitors include andrenid and halictid bees, and syrphid flies. Foraging bees preferentially visit umbels that contain a large number of flowers, and there is some evidence that staminate-phase inflorescences are preferred over pistillate in *A. hispida* (Thomson et al., 1982). Observations of marked bumble bees indicate that individual bees restrict their foraging to a limited number of plants that they visit in regular sequences or 'traplines.' Following pollination and fertilization, fruits of both *Aralia* species develop into large, black, vertebrate dispersed, sarcochores that usually contain five seeds.

GENDER ALTERNATION IN *ARALIA HISPIDA*

Aralia hispida exhibits synchronized protandry within and among different umbels. Individual ramets pass through alternating staminate and pistillate phases during their blooming period as each umbel order flowers. Controlled pollinations demonstrate that the period of stigmatic receptivity of hermaphrodite flowers does not overlap significantly with the staminate flowering period and the probability of geitonogamy is accordingly reduced. On average a ramet functions as a male for approximately three weeks and as a female for one week. Pollen release by hermaphrodite flowers within an umbel lasts for four to five days, whereas the pistillate phase is compressed into one to two days. The overall proportion of hermaphrodite flowers in a population is approximately one-third of the total flowers (Table 2) and their numbers decline in successive umbel orders or as the season progresses. A detailed account of the floral biology and phenology of flowering of *A. hispida* is given in Thomson and Barrett (1981b).

Alternation between staminate and pistillate function in ramets of *A. hispida* results in complex patterns of gender expression within populations. A wave form pattern of floral sex ratio was evident in a population of ramets censused throughout the flowering season (Fig. 1). This

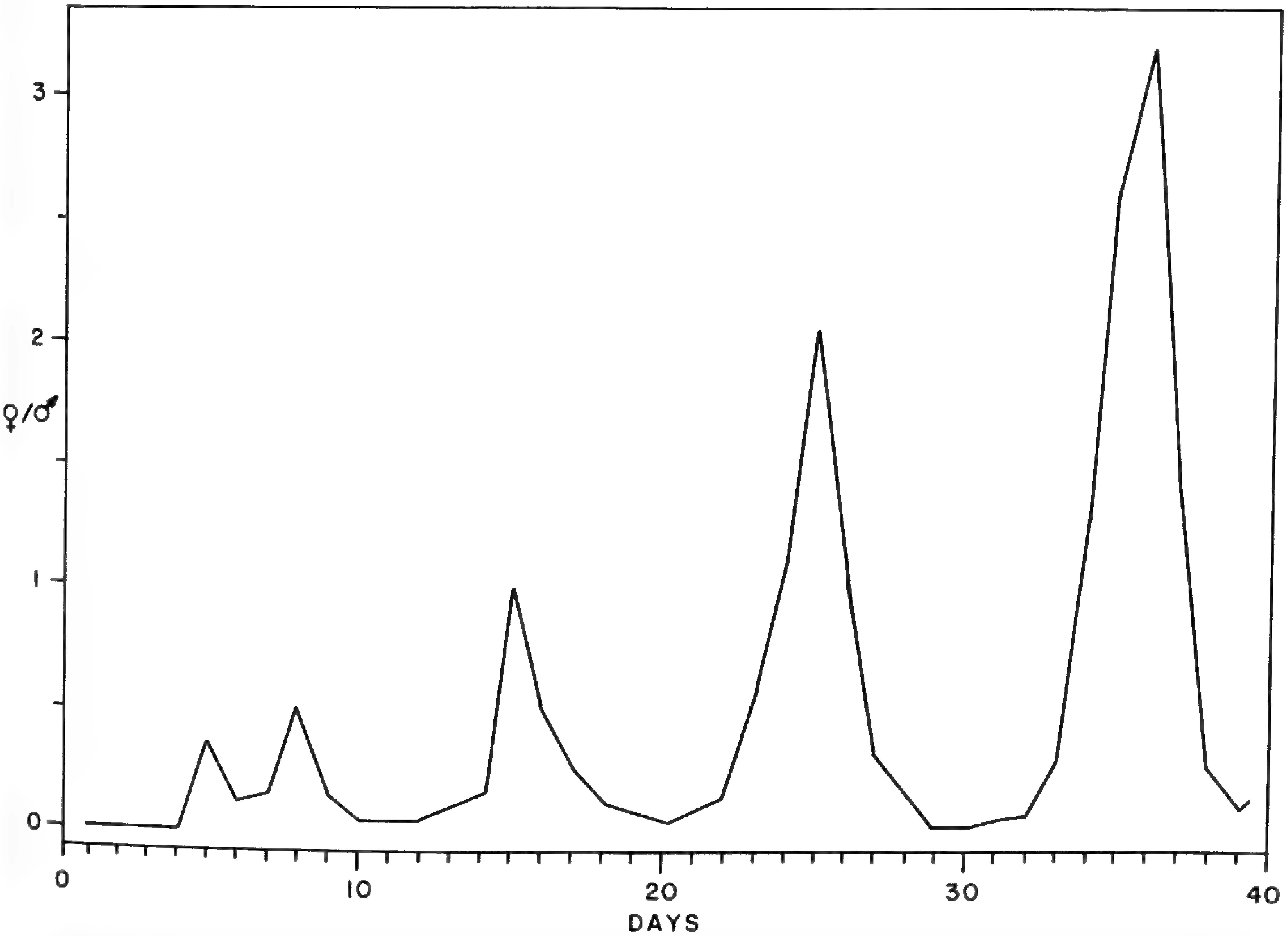

FIGURE 1. Wave form expression of gender in a population of *Aralia hispida*. The ratio of pistillate-functioning to staminate-functioning flowers is plotted daily throughout the flowering period of 48 ramets. After Thomson and Barrett (1981b).

arises, in part, from the relatively low variation among ramets in the commencement of flowering in comparison with the number of days between flowering peaks of different umbel orders. In addition, there is a marked tendency for ramets of a single genet to be developmentally synchronized with respect to umbel order and sexual condition. Intense competition for ovules among staminate-functioning flowers of different genets occurs at regular intervals during the blooming period corresponding to the troughs in Figure 1. Using estimates of functional gender one can examine the reproductive success of individual staminate- and pistillate-functioning flowers. In a population with this flowering behavior, male success is negatively correlated with the degree of synchrony between a given ramet's flowering pattern and that of the population. Ramets that produce staminate-functioning flowers at a time when most other individuals are in their pistillate phase will encounter little competition for mates. Figure 2 gives estimates of male reproductive success for a ramet which was closely synchronized with the remainder of the population.

Selection on the male component of fitness as well as the avoidance of inbreeding may explain the complex flowering behavior in *A. hispida*. Intrasexual competition among pollen donors may account for the extended staminate phase, in comparison with the pistillate phase, of individual ramets. The gradual release of pollen over a three week period is likely to maximize the number of insect visitors and hence the potential number of mates. Within the life span of an individual flower, pollen is released gradually by sequential anther dehiscence, and nectar secretion occurs throughout the day (Thomson et al., 1982). The extended staminate phase could also have been selected to reduce the likelihood of reproductive failure owing to environmental unpredictability (Thomson & Barrett, 1981b). Unfortunately, models that invoke sexual selection or 'bet-hedging' often make qualitatively

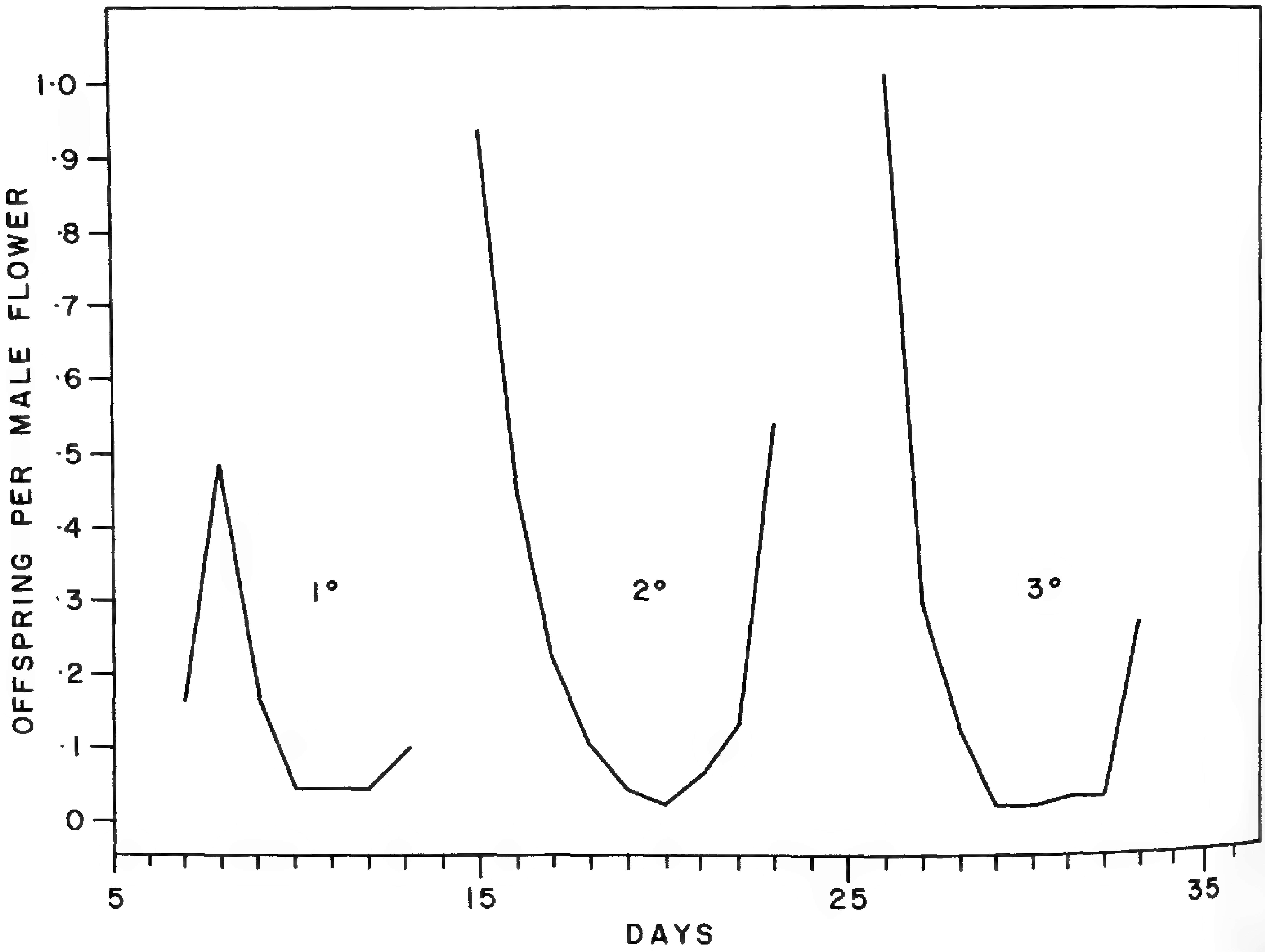

FIGURE 2. Estimate of mating success of staminate-functioning flowers of an *Aralia hispida* ramet throughout its flowering period. The flowers which are most successful are the earliest and latest within each umbel order. Breaks between the curves are days when the ramet functioned as a female. After Thomson and Barrett (1981b).

similar predictions about the evolutionary response of reproductive traits. Devising experiments to distinguish the relative importance and independence of these processes is a major challenge and reminiscent of the difficulties associated with various models of selection of self-fertilization (see Jain, 1976; Lloyd, 1980b).

Despite the protracted staminate phase of umbels, mating success via pollen tends to be concentrated at the beginning and/or end of the staminate flowering period of umbels, resulting in characteristic U- or J-shaped reproductive success curves (Fig. 2). In contrast female success is uniformly high throughout the flowering period (Table 2) and therefore there may be no selective advantage to a protracted pistillate phase. Tight flowering synchrony may be advantageous for pistillate-functioning flowers to compensate for their apparently reduced attractiveness to pollinators (Thomson et al., 1982).

Lloyd and Yates (1982) have developed ESS models to find the proportions of time that outcrossing, dichogamous, hermaphrodite flowers should spend in their staminate and pistillate phases to optimize total fitness. The models can be usefully applied to observations of flowering behavior in *A. hispida*. If paternal and maternal fitness are pollinator limited, fitness is maximized if flowers spend equal amounts of time functioning as males and females. However, where an increase in male fitness is limited by access to ovules and female fitness is limited by resources (Bateman, 1948), natural selection should favor prolongation of the staminate phase. The latter conditions fit well with the available data from *A. hispida*, in which pollinator levels are consistently high throughout the blooming period and fecundity is near maximum.

The developmental synchronization of protandry within and among umbels of *A. hispida* reduces the likelihood of self- and geitonogamous pollination and hence inbreeding. Thus the complex systems of dichogamy exhibited by the Araliaceae and Umbelliferae may be viewed as outbreeding mechanisms. They may have evolved as alternatives to physiological self-incompatibility which appears to be rare or perhaps absent from these families. In the absence of dichogamy or self-incompatibility, the aggregation of many, small unspecialized flowers in a single inflorescence would be particularly likely to result in high levels of selfing.

A different explanation for the synchronized patterns of sexual expression was proposed by Lovett-Doust (1980) based on his studies of Umbelliferae. He suggested that the separation of anther dehiscence and stigma receptivity represents a pattern of resource allocation that minimizes competition between male and female gamete production. This view has been questioned by Webb (1981) who suggested that intrasexual selection among plants in their staminate phase and outbreeding advantage may explain the occurrence of protandry and tight developmental synchronization, respectively, in the family. Clearly there is a need for experimental tests to distinguish between these competing hypotheses.

The effectiveness of synchronized protandry in reducing geitonogamous pollinations depends on the degree of developmental synchronization within and between ramets of a single genet. One of the major disruptive influences to developmental synchrony among the ramets of a genet is clonal expansion. Shifts in life history associated with radiation into more stable environments could select for increased clone size. Ramets in a large clone are likely to experience widely different environmental conditions, and it seems unlikely that mechanisms could exist to maintain sexual phase synchrony with the result that geitonogamy would increase. It is possible that under these circumstances the outbreeding advantage gained by a unisexual mutant could lead to its spread, with dioecism ultimately being selected. Such an explanation could account for the associations between patterns of sexuality and plant size observed in *Aralia*. It would be of interest to examine these relationships in the Umbelliferae in which dioecy and various forms of dichogamy co-occur. In addition, an examination of the relative effects of self- and cross-fertilization on offspring vigor and fertility in andromonoecious taxa would be useful for evaluating the plausibility of the outbreeding advantage model.

FLOWERING IN *ARALIA NUDICAULIS*

Populations of *Aralia hispida* are frequently composed of scattered colonies of flowering ramets, which on excavation proved to be genets. Expansion of clone size is often limited by disturbance or successional processes and hence the limits of individual genets can usually be estimated. In *A. nudicaulis* the size and complexity of the rhizome system makes identification of genets, as well as determining the sex of vegetative ramets, a difficult task. This problem is particularly acute in locally disturbed areas or where high flowering density occurs. As a result of these difficulties the unit of investigation in our studies has exclusively been the flowering ramet, composed of a single inflorescence and subtending leaf. The extent to which the behavior of ramets reflects that of the genet is unknown. In large clones it is possible that ramets separated by a considerable distance are physiologically independent (see Bawa et al., 1982).

TEMPORAL PATTERNS

The distribution of flowering ramets in *A. nudicaulis,* in time and space, was examined during the summers of 1979 and 1980. To avoid over-representation of individual genets, transects 1–2 km in length were adopted for sampling phenological patterns. Four transects were censused at one or two day intervals along a roadside and in forest habitats. Further details are given in Barrett and Helenurm (1981). In three of the four transects, pistillate ramets began flowering and reached peak flowering before staminate ramets. This difference was particularly evident in the two forest transects. In virtually all other studies of the flowering phenology of the sexes in dioecious species, the reverse pattern is evident (see Lloyd & Webb, 1977) and several adaptive explanations have been proposed. For example, Bawa (1980a) and Bullock and Bawa (1981) have suggested that early staminate flowering and late pistillate flowering in the small tree *Jacaratia dolichaula* (Caricaceae) may be attributed to intrasexual competition among staminate plants and mate choice by pistillate plants, respectively. Other explanations mainly associated with differential reproductive costs between the sexes are detailed in Lloyd and Webb (1977).

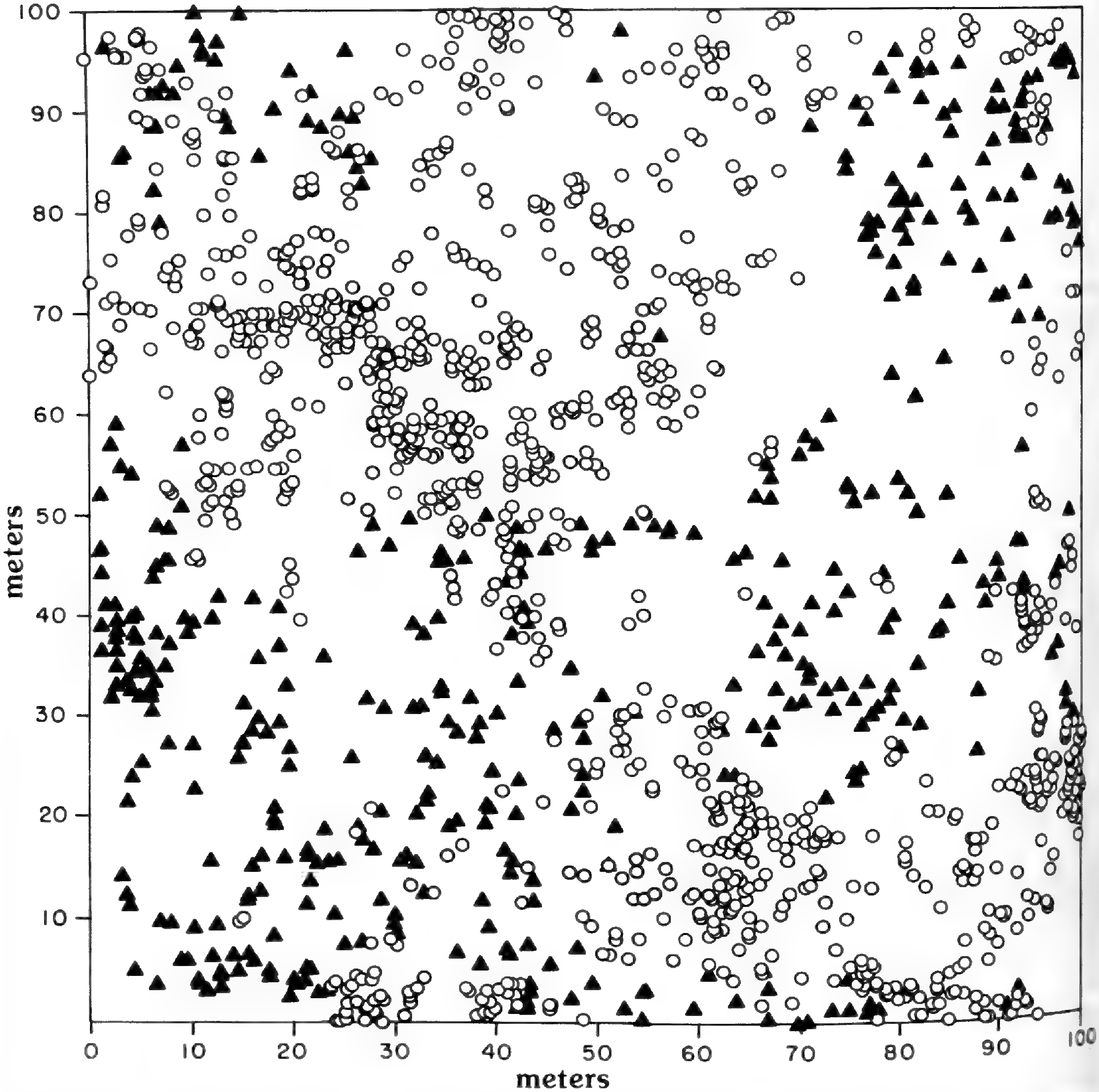

FIGURE 3. Distribution of staminate and pistillate flowering ramets of *Aralia nudicaulis* within a one hectare block of spruce-fir forest in central New Brunswick during the summer of 1979. Open circles are staminate ramets (N = 1,244), solid triangles are pistillate ramets (N = 449). After Barrett and Thomson (1982).

The flowering patterns in *A. nudicaulis* may not reflect genetic differences between the sexes in flowering time. The observed differences may result from the non-random distribution of flowering ramets of the sexes in the habitats sampled. Flowering in shaded areas tended to be delayed by several days relative to exposed sites. Examination of the spatial distribution of flowering ramets indicated that females were less likely to flower in shaded sites in comparison with males (Barrett & Thomson, 1982 and see below). In our forest transects it seems likely that the delayed flowering of staminate ramets may have resulted from differences in the relative proportions of staminate and pistillate flowering ramets in shaded areas. It is also possible that despite our efforts to avoid over-representation of single clones in our samples through the use of long transects, genetic differences between clones in flowering time, unrelated to sex, may have been involved. These problems in the interpretation of field data on flowering behavior in *A. nudicaulis* highlight the difficulties of evolutionary interpretation of variation patterns in large clonal plants where single genets may occupy a mosaic of environments. They also draw attention to the likelihood of interaction between spatial and temporal influences on reproductive behavior.

SPATIAL PATTERNS

The spatial relationships of flowering ramets were examined in a one hectare square block of spruce-fir forest during the summer of 1979 (for details see Barrett & Thomson, 1982). The distribution of all 1,743 flowering ramets is illustrated in Figure 3. It is tempting to suggest, based on visual inspection of the map, that several large clones of *A. nudicaulis* occupy most of the space within the forest block. A greater diversity of genetic markers than sex alone would, however, be required to distinguish individual clones. Electrophoretic studies, of the kind undertaken by Silander (1979) on *Spartina patens* would be valuable for examining the clonal structure of *A. nudicaulis* populations. Notwithstanding the difficulties of establishing the genetic aspects of population structure in the forest block, several valuable insights into the flowering behavior of *A. nudicaulis* were obtained.

By dividing the forest block into 100 10 m^2 by 10 m^2 plots, it was possible to examine associations between flowering ramets of the sexes at various spatial scales as well as with various environmental conditions. Throughout the block, as well as in other forest sites in New Brunswick (Barrett & Helenurm, 1981) and Massachusetts (Bawa et al., 1982), staminate flowering ramets outnumber pistillate. Flowering ramets of both sexes occurred more frequently in plots under an open canopy. However, there was a reduced likelihood of pistillate flowering in heavy shade in comparison with staminate ramets (Fig. 4). This may be associated with differences in the cost of reproduction in the sexes. Studies of resource allocation in *A. nudicaulis* indicate that reproductive effort in pistillate ramets is considerably higher than in androecious ramets, and that the male-biased sex ratio of flowering ramets may result from differences between the sexes in flowering propensity, particularly in forest sites (Barrett & Helenurm, 1981). Evidence to support this hypothesis was obtained by Bawa et al. (1982) from an examination of the flowering histories of staminate and pistillate ramets. Erect shoots in *A. nudicaulis* bear a series of scars left by the annual foliage leaf as well as by the inflorescence in years where flowering occurs. Hence it is possible to reconstruct the past history of flowering of a ramet by careful dissection of individual shoots. Bawa et al. (1982) found that staminate ramets were more likely to flower in consecutive years in comparison with pistillate ramets. In addition they also found no differences between the sexes in the recruitment or mortality patterns of ramets from field observations over a three year period. Thus it seems likely that the male-biased sex ratio of flowering ramets in *A. nudicaulis* is largely the result of sex specific differences in reproductive costs.

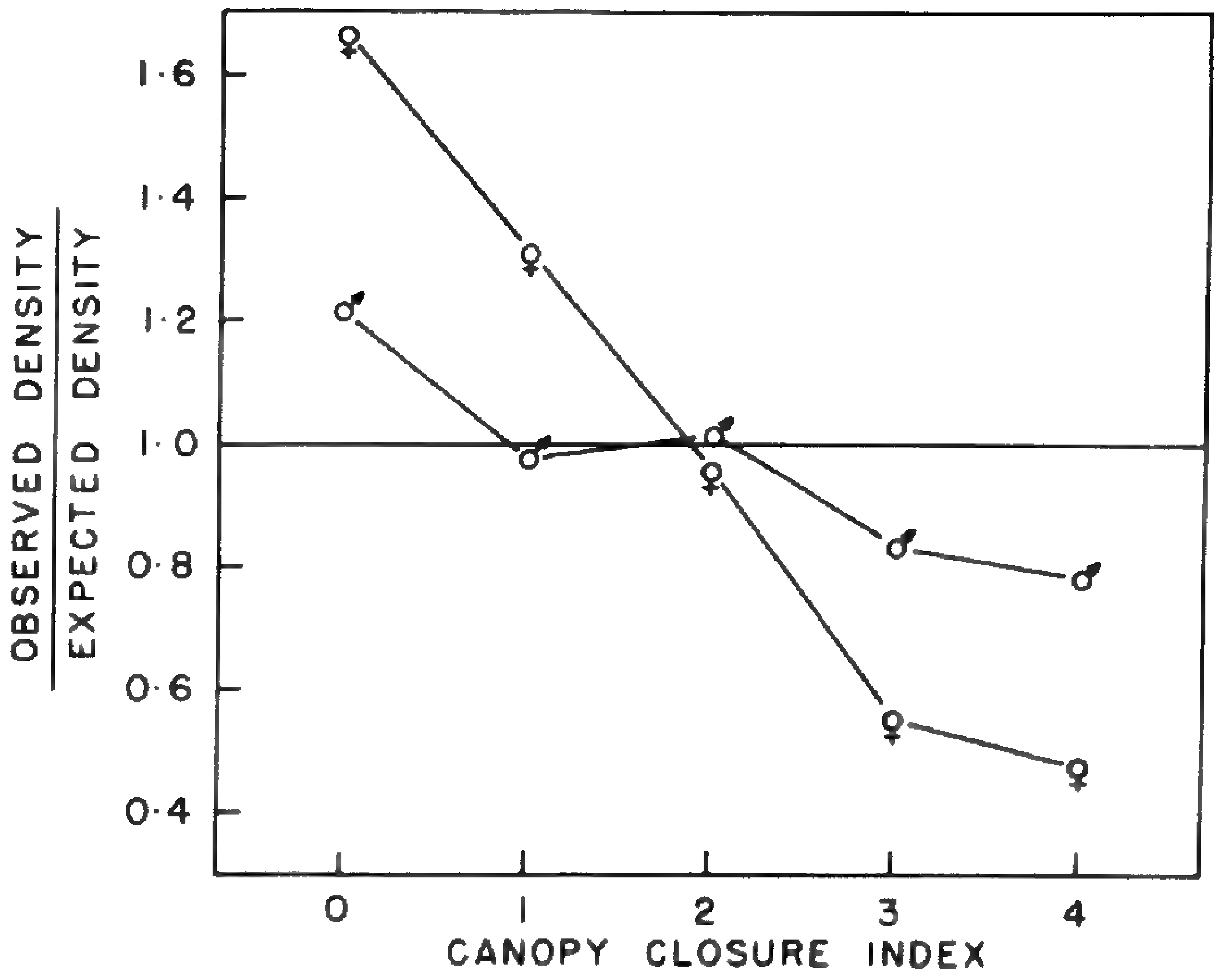

FIGURE 4. Density response of staminate and pistillate flowering ramets of *Aralia nudicaulis* to canopy closure. Closure index: 0 = most open canopy, 4 = most closed canopy. The female response is significantly stronger than the male response (G = 18.61, df = 4, $P < 0.001$). After Barrett and Thomson (1982).

FECUNDITY IN *ARALIA NUDICAULIS*

Inspection of Figure 3 indicates that considerable variation exists in the distance separating flowering ramets of the sexes of *A. nudicaulis.* Intersexual distance could be a potentially important influence on reproductive success. Barrett and Thomson (1982) investigated the relationships between the spatial pattern of ramets and fecundity within the forest block. Since the position of all flowering ramets in the block was known, it was possible to examine the relationships between the fruit set of pistillate ramets and the sexual composition of neighboring ramets at a range of spatial scales. No systematic variation in fecundity in relation to position was detected. At most of the biologically meaningful spatial scales, fecundity was uncorrelated with either staminate flowering density, pistillate

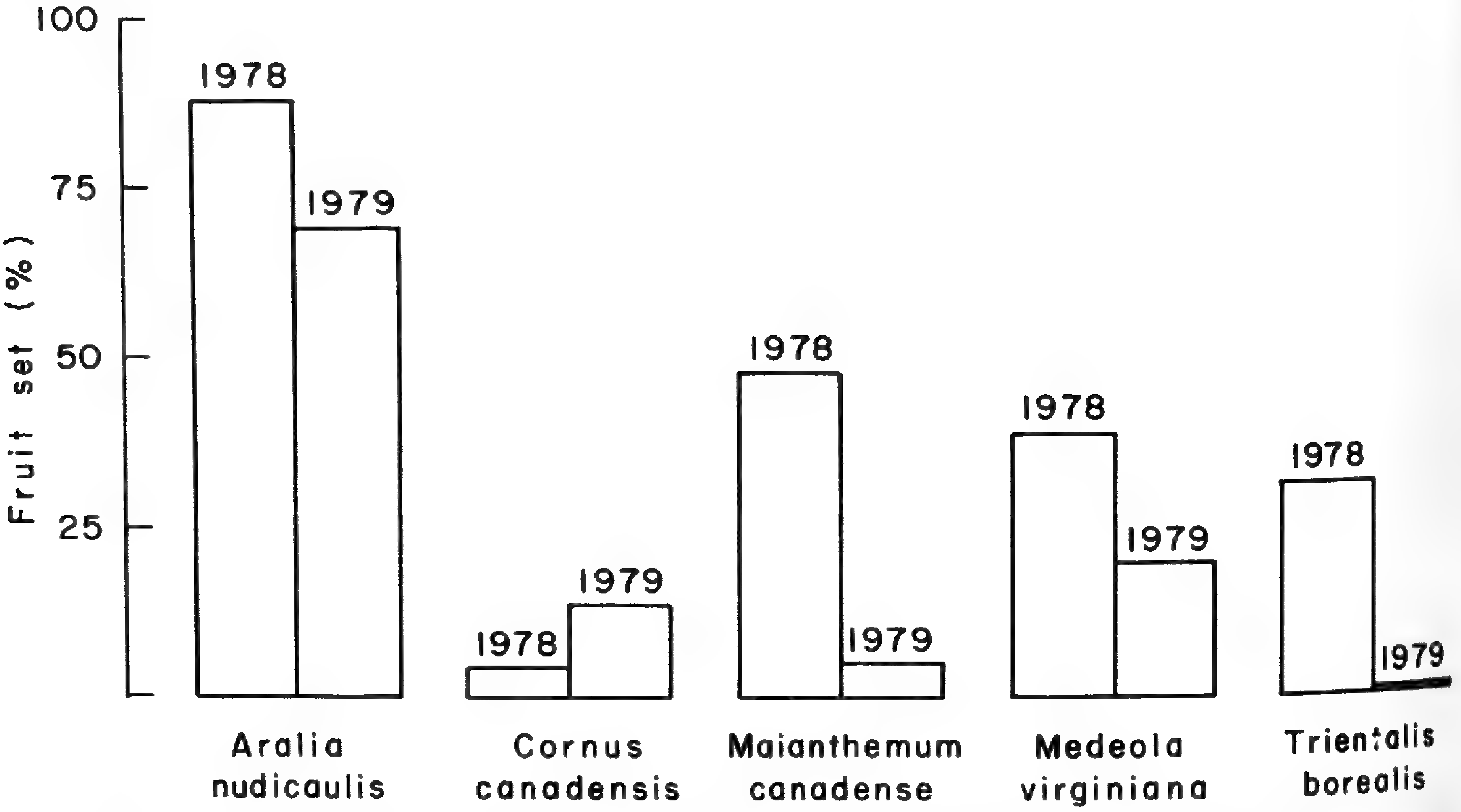

FIGURE 5. Natural levels of percentage fruit set in five entomophilous, clonal herbs from spruce-fir forests in central New Brunswick during summer 1978 and 1979. Sample sizes (flowers) for 1978 and 1979 are: *Aralia nudicaulis* 827, 20,078; *Cornus canadensis* 965, 5,069; *Maianthemum canadense* 101, 4,040; *Medeola virginiana* 63, 320; *Trientalis borealis* 69, 16. Barrett and Helenurm (unpubl. data).

flowering density or the local sex ratio of ramets. Barrett and Thomson (1982) suggested that the relatively long flight distance of bumble bees visiting the population, pollen carry over, and the predominance of staminate flowers at the site, all interact to reduce spatial effects on fecundity. Presumably at very low flowering densities isolation distances would be a more important influence on fecundity.

The fruit set of *A. nudicaulis* at the forest site averaged 68%, with the modal fecundity class 90–100%. This level was considerably higher than several other insect pollinated self-incompatible herbaceous species co-occuring with *A. nudicaulis* in this area. These species (*Cornus canadensis, Medeola virginiana, Maianthemum canadense,* and *Trientalis borealis*) share several common features with *A. nudicaulis.* All species are long-lived clonal perennials, three of the four (*C. canadensis, M. canadense,* and *T. borealis*) flower at the same time as *A. nudicaulis,* have relatively small white flowers and share a similar pollinator fauna (Barrett & Helenurm, unpubl. data). Of the five species only *T. borealis* does not possess fleshy fruits. The levels of fruit and seed set in *A. nudicaulis* were higher than the remaining species in the two years in which data were recorded (Fig. 5).

These results, although based on a small number of species, are in accord with predictions made by Bawa and Opler (1975) in their consideration of the pollination biology of zoophilous dioecious and self-incompatible plants. They argued that under certain conditions dioecism might be selected because it permits greater pollination success than would occur in a self-incompatible breeding system. Their arguments involve the likelihood of increased pollination efficiency in dioecious taxa as a result of the absence of 'pollen clogging' of incompatible stigmas (Shore & Barrett, 1984) as well as the increased inter-plant movement of pollinators visiting dioecious species owing to greater variation in floral rewards. Although experimental evidence to support these suggestions is limited, Bawa and Opler (1975) did report that the fruit set of dioecious species was generally higher than in self-incompatible taxa in a tropical deciduous forest in Costa Rica. A similar pattern was observed by Zapata and Kalin Arroyo (1978) in a study of breeding systems and reproductive efficacy of a secondary deciduous forest in Venezuela. More comparisons of fecundity in co-occuring dioecious and self-incompatible species are required before generalizations can be made. However, if a clear pattern emerges it may result from the fundamental differences in the nature of selection acting on inflorescences of plants with the two breeding systems. High flower/fruit ratios in outcrossing hermaphrodites may result from selection for increased inflorescence size to enhance pollen donation and male success (Willson & Rathcke, 1974; Willson & Price, 1977). Clearly these selective forces cannot occur in seed bearing individuals of a dioecious species. Accordingly low fruit set levels in self-incompatible plants, in comparison with dioecious species, may result from the maintenance of a significant number of hermaphrodite flowers which function solely as males in self-incompatible plants (see Sutherland & Delph, 1984).

CONCLUSIONS

Our studies of the reproductive behavior of diclinous *Aralia* species document spatial and temporal variation in sexual function and enable some evaluation of the ecological consequences of sexual dimorphism. They give only limited clues, however, to the potential selective forces that maintain flowering patterns. The longevity and size of many diclinous plants restrict detailed examination of the genetic dimension so vital to evolutionary interpretations. As a result we are forced to assume that the phenotypic variation in fitness components related to sexual performance that we measure in the field has a genetic basis. Most of the literature documenting genetic effects on sexuality in higher plants involves agricultural and horticultural crops. Many examples of genes with large effects (e.g., male sterility) are reported, but there is less information on the genetics of sex expression and allocation patterns to male and female reproductive function. The available data (reviewed in Charnov, 1982) suggest that genetic variance for sex differential fertility variation within plant populations does occur (see Ross, 1982; Ross & Gregorius, 1983). However, one suspects that the high plasticity of many plant characters, particularly those involving size and flower number, as well as environmental unpredictability will complicate attempts to elucidate major fitness components. How much of the observed variance in reproductive performance in diclinous plant populations can be assigned to genetic causes is a major unresolved question.

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EVOLUTION OF DIOECY IN *SAURAUIA* (DILLENIACEAE)[1]

W. A. HABER[2] AND K. S. BAWA[3]

ABSTRACT

Saurauia veraguensis in Costa Rica is morphologically androdioecious but functionally dioecious. Both staminate and pistillate flowers bear pollen. The pollen in the staminate flowers is tricolporate, and smaller than the inaperturate pollen borne by the pistillate flowers. The inaperturate pollen probably plays a role in pollination by serving as a reward, but it does not germinate on the stigmas and is therefore non-functional in fertilization. Dioecy in *Saurauia* may have evolved via androdioecy, although other evolutionary pathways such as via gynodioecy cannot be ruled out.

Saurauia Willd. (Dilleniaceae) is a large genus of small- to medium-sized trees with approximately 300 species distributed in tropical Asia and America (Willis, 1973). Approximately 65 species occur in the Western Hemisphere from central Mexico to Chile (Hunter, 1966). Taxonomic treatments of the genus imply that the species have perfect flowers (Hunter, 1966). However, Soejarto (1969), in a detailed study of herbarium specimens, found that several species in South America are sexually dimorphic. On the basis of pollen fertility and the size of pistils, he concluded that at least seven species are dioecious and one androdioecious. During the course of our ongoing studies of the reproductive biology of tropical forest plants in Costa Rica, we observed two distinct sexual phenotypes in *Saurauia veraguensis,* a species not studied by Soejarto. One phenotype appeared to bear only staminate flowers and the other only hermaphroditic flowers, indicating the occurrence of androdioecy. Because androdioecy is presumed to be extremely rare among angiosperms (Charlesworth & Charlesworth, 1978; Bawa, 1980) we investigated the reproductive biology of *S. veraguensis.* Here we describe the sexual system of *S. veraguensis* and discuss the evolution of dioecy in the genus.

STUDY SITE AND PLANTS

Saurauia veraguensis is a small tree, reaching up to 7 m in height. Our field observations were restricted to two populations; one was on the Pacific face of the Cordillera de Tilarán in the Monteverde cloud forest and the other on the Atlantic slopes of the Volcan Poás, both in northwest Costa Rica at an elevation of 1,500 to 1,600 m. Holdridge et al. (1971) characterized the vegetation of these areas as Lower Montane Moist Forest-Wet Forest Transition. Voucher specimens of the species investigated (*Bawa 3001* and *3002*) have been deposited in the herbarium of the California Academy of Sciences (CAS), San Francisco.

FLOWER MORPHOLOGY AND POLLINATION BIOLOGY

The inflorescences are axillary and thyrsiform. The average number of flowers in staminate inflorescences (34) is significantly greater than in 'hermaphrodite' inflorescences (18) ($t = 4.1, P < 0.01$; five inflorescences from each of five trees of each sex). Flowers in both flower morphs are up to 30 mm across. In both types of flowers, the petals are white, there are numerous (38–47) stamens, and a 5-locular ovary with five styles. In 'hermaphroditic' flowers, the styles (7 mm) extend well above the stamens, in contrast to staminate flowers in which styles are short (0.9–1.1 mm) and always obscured by the stamens (Fig. 1a–b).

The flowers are pollinated by medium-sized bees (especially *Melipona,* Meliponinae) that collect pollen from the stamens. Neither flower morph secretes nectar.

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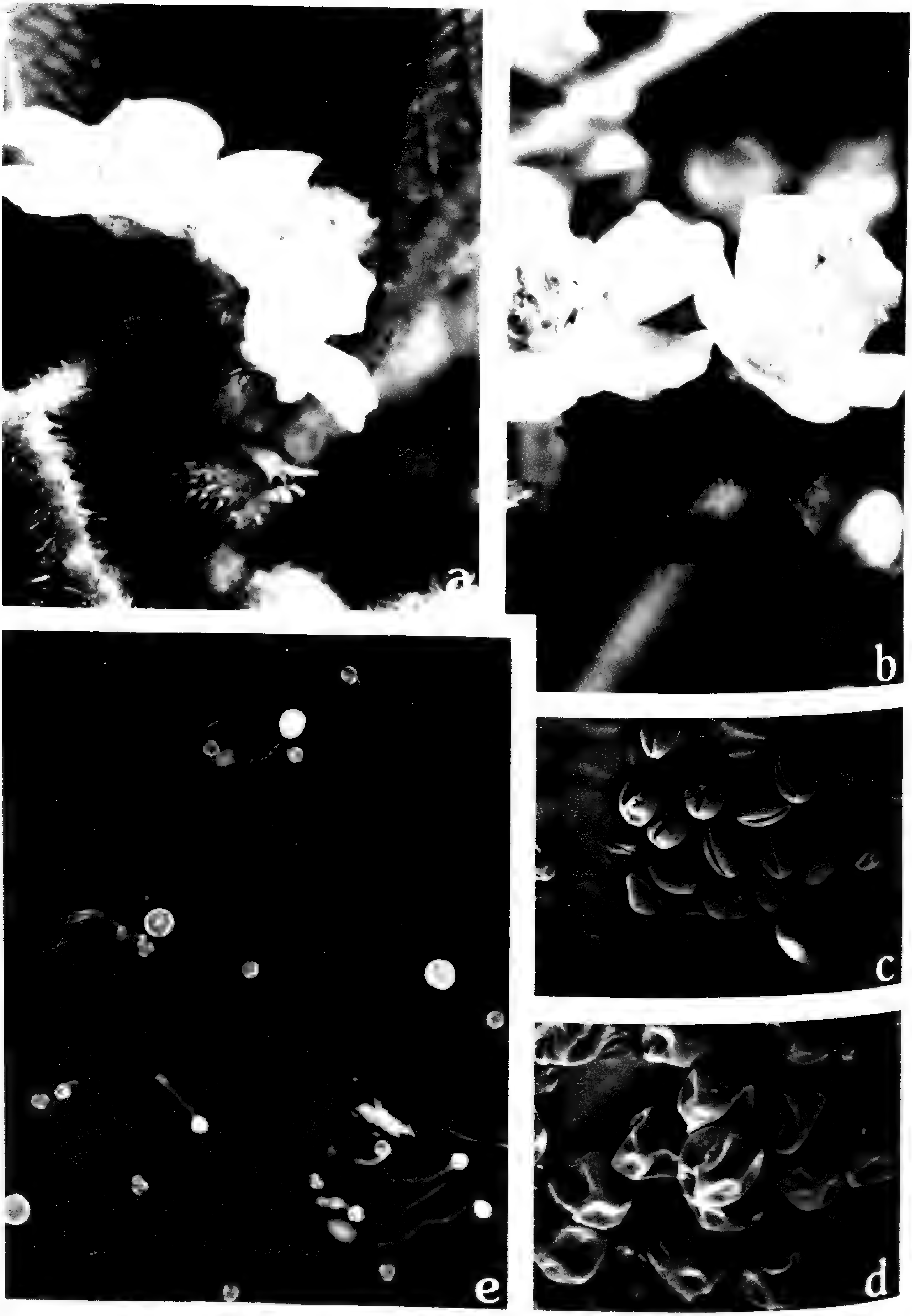
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DIMORPHIC POLLEN AND SEED SET

We found significant differences between the pollen of staminate and the apparently 'hermaphroditic' flowers (Fig. 1c–e). First, the pollen of staminate flowers is about two to three times smaller than that of the 'hermaphroditic' flowers. Second, the pollen of the staminate flowers is tricolporate, whereas pollen from 'hermaphrodite' flowers is inaperturate. Both types of pollen from fresh flowers stained well with lactophenol, but an SEM examination of pollen from herbarium specimens showed that of 'hermaphroditic' flowers to be collapsed (Fig. 1d). Furthermore, crossing experiments using the pollen of 'hermaphroditic' flowers, and an examination of stigmas of open-pollinated 'hermaphroditic' flowers [utilizing Martin's (1959) technique] showed that this inaperturate pollen generally does not germinate (Fig. 1e); out of the several hundred pollen grains examined on the stigmas of more than 20 flowers, tubes were observed from only five pollen grains and these tubes were very short.

Observations of more than 40 trees each of androecious and apparently 'hermaphroditic' trees revealed that staminate flowers do not produce fruits.

DISCUSSION

Clearly plants with staminate flowers transmit their genes via pollen and those with morphologically 'hermaphrodite' flowers function only as seed parents. Thus, *Saurauia veraguensis* is dioecious. This is not the first dioecious species found in the genus. Recall, Soejarto (1969) described seven dioecious and one androdioecious taxa from South America. Soejarto's conclusions were based on stylar dimorphism and pollen fertility as determined by stainability. Soejarto reported no differences in the size of pollen grains produced by the androecious (or hermaphroditic) and gynoecious plants. In the dioecious species, he noted that long style flowers have empty pollen grains, but in the androdioecious species such flowers contained up to 80% stainable pollen. It is possible that in the androdioecious species he studied the pollen grains borne by the hermaphroditic plants do not germinate. We also found that pollen grains of gynoecious *S. veraguensis* plants stain well; only their failure to germinate in crossability studies established their sterility. Nevertheless, reports of putative androdioecy in the genus are interesting and of considerable value in ultimately determining the evolutionary pathway to dioecy.

Hooker (1841), in his "Icones Plantarum," first suggested the possibility of dioecy in the genus. In reference to *Sauruja pedunculata* (= *Saurauia pedunculata*) Hooker commented: "The flowers which I examined appeared to be all male, having small abortive pistil, and very short, erect styles." Soejarto (1969) also referred to several earlier suggestions of dioecy in the genus. However, in the most recent revision of the genus, Hunter (1966) dismissed the possiblity of unisexuality despite the fact that he noted both pollen and stylar dimorphism. For example, Hunter stated: "Fifteen of the specimens examined had tricolporate pollen with no discernible surface ornamentation. Five of the specimens had much larger grains which were irregularly roughened. The irregularly roughened cells are not taxonomically significant, however, since two of the species in which they occur are also among the 15 specimens with tricolporate pollen . . . . These irregularly roughened cells may represent a developmental phase of the pollen, possibly the pollen mother cells, or they may be the final phase of an abortive pollen. Some species frequently have flowers in which the pistils are aborted. Such flowers have been interpreted as unisexual, but this condition may be merely a matter of maturation."

Elsewhere in the family, *Tetracera* has been described as androdioecious (Kubitzki & Baretta, 1969), but there is no empirical evidence for the transmission of genes via pollen by plants with hermaphrodite flowers. In fact, the androdioecy pathway to dioecy has not been fully documented for any species. Definite evidence for the existence of androdioecy has been presented

FIGURE 1. a–c. *Saurauia veraguensis.*—a. 'Hermaphrodite' or functionally pistillate flowers.—b. Staminate flowers; both × ¾.—c. Pollen from a staminate flower.—d. Pollen from a pistillate flower; both × 1,100.—e. Part of the stigma of an open-pollinated pistillate flower showing lack of pollen tubes from the larger pollen of pistillate flowers and the pollen tubes from the smaller pollen of staminate flowers, × 500.

so far for only one species: *Xerospermum intermedium* (Appanah, 1982). Even in this case, plants essentially function either as pollen donors or pollen recipients.

The sexual system of *Saurauia* is very similar to that of a dioecious *Solanum* species (Anderson, 1979) in which the pistillate flowers also produce non-germinating inaperturate pollen; however the pollen from the two sexes in *Solanum* does not differ in size, as it does in *Saurauia*. Interestingly, an earlier report based on morphological criteria alone also referred to the nine Australian dioecious species of *Solanum* as androdioecious (Symon, 1979). These have subsequently been determined to be functionally dioecious as well (G. J. Anderson & D. E. Symon, pers. comm.). The production and dispersal of inviable pollen by pistillate flowers has also been reported in the dioecious *Actinidia chinensis* of the Actinidiaceae (Schmid, 1978).

The evolutionary pathway to dioecy in *Saurauia* is uncertain. The vast majority of species in the Dilleniaceae are described as having perfect (bisexual) flowers, and dioecy is not particularly common in the order. Five evolutionary pathways to dioecy have been proposed (Bawa, 1980; Ross, 1982). Of these, evolution via gynodioecy or androdioecy is plausible in *Saurauia*. The morphological similarity to androdioecy does not, however, preclude the possiblity of evolution to dioecy via gynodioecy, that is, the establishment of a male-sterile mutant in the population was followed by replacement of hermaphrodites by female-sterile mutants.

The difficulty of androdioecy evolving in a population as a result of selective pressure for outcrossing is outlined by Lloyd (1975) and Charlesworth and Charlesworth (1978). It has been argued that in plants that can self-fertilize, the pollen of androecious plants is at a disadvantage compared to the pollen of hermaphrodites. This disadvantage disappears in outcrossing populations, but only if the androecious plants have a two-fold advantage in fitness via pollen over hermaphrodites (Charlesworth & Charlesworth, 1978).

Saurauia veraguensis is pollinated by bees. Pollen appears to be the only food reward offered to the pollinators, and this is probably one of the reasons why gynoecious individuals have retained the capacity to bear pollen, which of course does not germinate but is important in pollinator reward, as in *Solanum* (Anderson, 1979) and *Actinidia* (Schmid, 1978). The pollen produced by staminate flowers is much smaller than that of pistillate flowers, and staminate inflorescences also bear more flowers than the pistillate inflorescences. Although we have no data on the quantity of pollen produced by staminate and pistillate flowers in *Saurauia veraguensis*, in dioecious *Solanum* the amount of pollen produced by androecious plants is twice that of gynoecious plants (Anderson, 1979). It is conceivable that in the putative androdioecious ancestors of dioecious species, the androecious phenotypes might have become established because of their greater pollen production resulting from pollinator mediated sexual selection (Bawa, 1980; Bawa & Beach, 1981; Beach, 1981; see also Ross, 1982). Thus in such cases it may be unnecessary to invoke outcrossing as a selective force in the evolution of androdioecy.

Ultimately, the more than 300 species of *Saurauia* may hold the key to understanding the evolution of dioecy via androdioecy. A comparative study of the sexual systems should help in evaluating the importance of androdioecy and gynodioecy in the evolution of dioecy. The possible evolutionary pathway of androdioecy to dioecy in *Saurauia* and *Solanum* offers a more rewarding avenue of study than many other sexually dimorphic genera.

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THE EVOLUTION OF DIOECY—CONCLUDING REMARKS

K. S. Bawa[1]

Since the pioneer work of Darwin on the evolution of sexual systems in plants (Darwin, 1877a, 1877b) no sexual strategy in recent years has attracted as much attention as dioecy. First, a number of population genetic models were developed in the 1970s to trace the evolution of dioecy via different pathways (Lloyd, 1975, 1976, 1979; Ross, 1970, 1978, 1980, 1982; Charlesworth & Charlesworth, 1978a, 1978b). Almost concurrently, field studies highlighted the ecological consequences of dioecy (Bawa & Opler, 1975; Lloyd & Webb, 1977; Wallace & Rundel, 1979; Meagher, 1980, 1981; Bullock & Bawa, 1981). Then a resurgence of interest in the sexual selection theory led to a search for new selective pressures driving the evolution of dioecy (e.g., Willson, 1979). The finding that dioecy is associated with certain pollination and seed-dispersal syndromes further eroded the traditional view that outcrossing is the main selective force in the evolution of dioecy (Bawa & Opler, 1975; Bawa, 1980a; Givnish, 1980; Beach, 1981; but see Thomson & Barrett, 1981; Lloyd, 1982; for a balanced review, see Charnov, 1982). Here, I briefly consider the major unresolved problems in the evolution of dioecy, including some already discussed at length by the contributors to this symposium.

First, a fundamental problem concerns the extent to which sex expression in dioecious species is constant. Freeman et al. (this symposium) document in detail substantial sex reversals in *Atriplex canescens*. On the other extreme the dioecious lily, *Chamaelirium luteum*, studied by Meagher (this symposium) exhibits no change in sex expression. Furthermore, the two sexes in *C. luteum* show remarkable ecological divergence. Sexual dimorphism in many other dioecious species is also pronounced (Lloyd & Webb, 1977; Bawa, 1980b; Bawa et al., 1982; Bullock & Bawa, 1981; Bullock, 1982; Bullock et al., 1983). If indeed there is no constancy in sex expression, then we need models to explain how sex-linked divergence in morphological, behavioral, physiological, and biochemical traits might have evolved. Freeman et al. (1980, this symposium) mention many other species that presumably change sex, but as pointed out by Lloyd and Bawa (1984), patterns of gender modification in plants are varied and complex. In order to understand the origin of these complex patterns and their adaptive significance, it is necessary to distinguish, for example, extremes such as "sex choosers" (e.g., *Arisaema triphyllum*) and "sex adjustors" (e.g., many dioecious species, see Lloyd & Bawa, 1984). Only a precise quantitative description of gender may allow the resolution of various patterns of gender modification. For many species that are assumed to change sex, such information is simply not available (Lloyd & Bawa, 1984).

Second, the study of evolutionary pathways to dioecism remains an area of major importance. Dioecism has been presumed to have evolved via five distinct routes directly from hermaphroditism and via androdioecy, gynodioecy, monoecy, and heterostyly (Bawa, 1980a; Ross, 1982). It is not known if the ecological pressures favoring the evolution of dioecy are the same in each pathway. However, the population genetic models for almost all pathways assume selective pressure against inbreeding as the major driving force (Lloyd, 1982; Ross, 1982 and references therein). Field studies for specific taxa are badly needed to test the models. Another major problem in the understanding of evolutionary pathways is the uncertainty about the frequency with which dioecy has evolved directly from hermaphroditism or via androdioecy. In fact, the evolution and occurrence of androdioecy itself has been questioned (Charlesworth & Charlesworth, 1978a, 1978b, pers. comm.; and see Haber & Bawa, this symposium). Systems such as those in *Actinidia chinensis* (Schmid, 1978), *Saurauia* spp. (Haber & Bawa, this symposium) and *Solanum* spp. (Anderson, 1979) may prove to be useful in the search for general models for the evolution of dioecism via androdioecy.

Third, the importance of selection against inbreeding depression (see e.g., Willson, 1979; Bawa, 1980a, 1982a; Givnish, 1980, 1982; Thomson & Barrett, 1981; Beach, 1981; Char-

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nov, 1982; Lloyd, 1982) is, perhaps, the most outstanding of the unresolved issues in the evolution of dioecy because its resolution has the potential to fundamentally alter our overall view of the evolution of sexual systems in plants (Willson, 1979; Bawa & Beach, 1981).

Fourth, explanations for the recently discovered "ecological correlates" of dioecy (Bawa & Opler, 1975; Bawa, 1980a; Givnish, 1980) need to be empirically examined. Divergent opinions have been expressed to account for the association between dioecy and pollination by small bees or generalist insects and that between dioecy and fleshy fruits (Bawa & Opler, 1975; Bawa, 1980a; Beach, 1981; Givnish, 1980, 1982; Charnov, 1982; Lloyd, 1982; see also Bawa, 1982b; Herrera, 1982). In particular, for species pollinated by small bees or generalist insects, we need to know a) if an increase in male reproductive expenditure results in a disproportionate increase in male fitness (Bawa, 1980a; Beach, 1981), and b) if such species are particularly vulnerable to selfing or limited pollen dispersal and if the advantage of dioecy is that it results in outcrossing (Lloyd, 1982). Similarly in species with fleshy fruits dispersed by specialized frugivores, we need to know if an increase in investment in seed and fruit crops results in a disproportionate gain in fitness via enhanced seed dispersal (Bawa, 1980a, 1982; Givnish, 1980; Charnov, 1982; Herrera, 1982; Lloyd, 1982).

Fifth, the origin and evolution of sexual dimorphism—the morphological, physiological, biochemical, genetical, and ecological differences between sexes—is virtually an unexplored area (Lloyd & Webb, 1977; Wallace & Rundel, 1979; Bawa, 1980b; Meagher, 1980, 1981, 1982, this symposium; Meagher & Antonovics, 1982a, 1982b; Bullock, 1982; Bullock & Bawa, 1981; Bullock et al., 1983). As Meagher points out in his paper above, the study of sexual dimorphism is useful in providing insights into the type of selection that results in divergence as well as the ecological consequences of such divergence.

The differences in resource allocation for various functions in different sexual morphs remains a particularly interesting problem, especially the differences between male-sterile and female-sterile mutants and the hermaphrodites that they may eventually replace. Although it is obvious that the mutants, by the "law of compensation" (Darwin, 1877a), should allocate more resources to male or female functions than the hermaphrodites, we do not know the extent to which these differences are present when the mutant arises versus the extent to which the differences develop during the evolution of dioecy. Note that if, as argued by Lloyd (1982), the initial differences are not large, sudden gains in male and female reproductive success of the mutants may not be possible. Such gains would be especially difficult to make in the absence of inbreeding depression in the original population of hermaphrodites, a phenomenon required in Bawa's (1980a) and Givnish's (1980) hypotheses. In this context, comparative data on the reproductive ecology of various types of male- and female-sterile mutants that arise in a population are also needed. It is possible, and likely, that of the many types of mutants that arise, only a small fraction with appropriate reproductive traits become established to convert a monomorphic population into a sexually dimorphic population.

Ornduff (1983) has recently questioned the preoccupation of biologists with rare sexual systems such as dioecy. After all, approximately 90% of the angiosperms are estimated to be cosexual (Lloyd, 1982). But in asking why plants are dioecious, in many ways we are trying to determine why the vast majority of flowering plants are cosexual (see e.g., Charnov, 1982; Lloyd, 1982).

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FLORA OF THE VENEZUELAN GUAYANA—I

JULIAN A. STEYERMARK[1]

XYRIDACEAE

Aratitiyopea Steyerm. & Berry, gen. nov. TYPE: *Aratitiyopea lopezii* (L. B. Smith) Steyerm. & Berry.

Inflorescentia terminalis capitata late hemisphaerica multiflora expedunculata. Flores sessiles trimeri purpurei. Sepala 3, duobus conduplicatis valde carinatis, tertio nec carinato. Corolla purpurea fere actinomorphica gamopetala trilobata, tubo anguste cylindrico, lobis aequalibus linearibus rectis. Stamina 3, filamentis in parte suprema tubi corollae insertis. Ovarium 3-loculare superum. Stylus simplex basi appendicibus conspicuis carnosis reflexis subtentus. Stigmata 3 patuli fimbriati. Semina exalata ovoideo-elliptica turgida longitudinaliter 12–14-porcata, inter porcas valde alveolati. Herbae perennes, caulibus valde elongatis subhorizontalibus vel serpentibus.

Aratitiyopea from Cerro Aratitiyope, Territorio Federal Amazonas, Venezuela.

Aratitiyopea lopezii (L. B. Smith) Steyerm. & Berry, comb. nov. *Navia lopezii* L. B. Smith, Bot. Mus. Leafl. 15: 40. 1915; 16: 195. pl. 28. 1954. Fl. Neotrop. Monogr. 14: 465. fig. 163: L–M. 1974. TYPE: Brazil. Amazonas: Cerro Dimití, upper Rio Negro basin, on rocks, 800 m, May 12–19, 1948, *Schultes & López 9956* (holotype, US-1985318; isotype, US-1985319). Figure 1.

Stem trailing, subhorizontal to ascending at the apex, elongated to 2 m, rooting near the base, densely foliose, to 2.5 cm thick. Leaves rich green both sides, densely crowded towards the apex, deciduous lower down, many ranked, spreading-ascending, those immediately subtending the inflorescence ligulate-lanceolate, 10–14 cm by 2.5–3 cm, those lower down more elongated, 21–23 cm by 3.5–4 cm, firmly membranous, abruptly acuminate, entire; leaf sheaths lustrous, brown basally, 4 cm wide. Inflorescence sessile, epedunculate, broadly hemispheric, capitate, terminal, multiflorous, 10–12 cm diam., 7–9 cm high. Bracts surrounding inflorescence erect, purple, chartaceous-scarious, wine-red or reddish purple, lanceolate, acute, 3.2–3.3 cm by 0.6–1.1 cm, the outermost ones ovate-lanceolate, subacute, 2.2 cm by 1.1–1.2 cm. Bracts subtending flower similar in size to those subtending inflorescence. Sepals pale lilac, chartaceous-scarious, free to the base, linear-lanceolate, attenuate to an acute apex, 4.5–5.5(–6) cm long, 5–12 mm wide at base, 5 mm wide upward, two of them strongly keeled, the third not keeled. Corolla purple, straight or nearly so, actinomorphic or nearly so, 7–8.3 cm long, tube narrowly cylindric, 5–6.2 cm long, 4–4.5 mm wide; lobes 3, equal, straight, linear-ligulate, rounded or broadly obtuse at apex, 1.5–2.2 cm long, 3–4 mm wide. Stamens 3, epipetalous; filaments 8–12 mm long, attached 2–7 mm below base of sinus of corolla lobes in upper fourth of corolla; anthers golden, linear, 5–10 mm long, 1.5–2.5 mm wide, basifixed, slightly bilobate at base. Stigmas 3, purple, suborbicular-ovate, spreading, 3 mm long, 2 mm wide, fimbriate-penicillate. Style exserted, lavender, filiform, 8 cm long, 0.8–1 mm wide, 3-angled, provided at the base with 3 fleshy, ligulate-oblong glands 3–4.5 mm by 1.5–2 mm, the glands strongly reflexed, touching the apex of the ovary, obscurely crenulate at the truncate apex, and raised on 3 clavate stipes 3.5 mm by 1 mm closely appressed to the stylar base. Ovary pale green, 3-celled, placentas 6, axile; ovules numerous. Seeds dark brown-castaneous, ovoid-elliptic, rounded at each end, or slightly apiculate at one end, 1.1 mm long, 0.9–1 mm wide, longitudinally 12–14-ridged, alveolate with ca. 15 transverse ribs.

Distribution: Territorio Federal Amazonas of southwestern Venezuela, northwestern Brazil and southeastern Colombia (Vaupés).

Specimens examined. VENEZUELA. AMAZONAS: shaded moss- and sphagnum-covered crevasse in wet shade over rocks, Cerro Aratitiyope, 90 km SW of Ocamo, ascent of forested NW ridge leading to summit, 1,550–1,600 m, 28 Feb. 1984, *Steyermark, Berry & Delascio 130289* (MO, NY, US, VEN); *Saxofridericia-Brocchinia* thickets at base of laja, Cerro Aratitiyope, 90 km SW of Ocamo, 990 m, 24 Feb. 1984, *Steyermark, Berry & Delascio 130088* (MO, NY, US, VEN);

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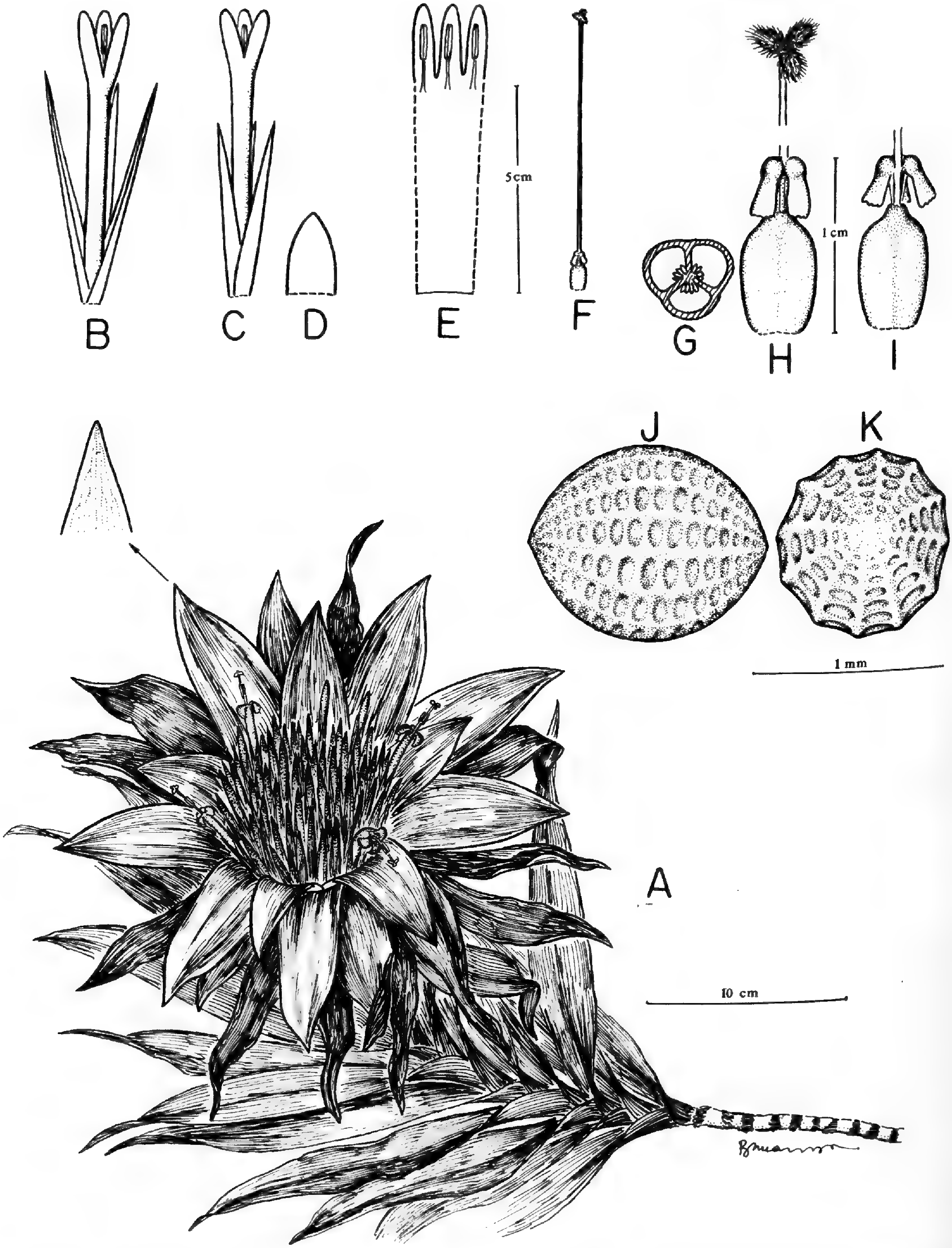

FIGURE 1. *Aratitiyopea lopezii.*—A. Habit.—B, C. Corolla with sepals, showing length variation of sepals.—D. One of the outermost bracts of inflorescence.—E. Interior of corolla with attached stamens.—F. Pistil, showing style, stigmas, stylar appendages at base, and ovary.—G. Cross-section of ovary.—H. Natural reflexed position of stylar appendages at apex of ovary and detail of stigmas.—I. Stylar appendages elevated, showing relation to base of style and ovary.—J. Seed, lateral view.—K. Seed, end view.

locally frequent in scrub forest on granitic dome on right bank of river, Río Siapa, just below Raudal Gallineta (about 110 river km from mouth), 600–700 m, 21 July 1959, *Wurdack & Adderley 43564* (NY, US, VEN); lower N escarpment, hanging on wet cliffs, Cerro Sipapo, 1,300 m, 27 Nov. 1948, *Maguire & Politi 29497* (NY, US, VEN); Cerro Sipapo, 1,500 m, 17 Dec. 1948, *Maguire & Politi 27742* (NY, US); 10 Jan. 1949, *Maguire & Politi 28276* (NY, US); summit of Cerro Avispa, Río Siapa, 10°30′N, 65°51′W, 1,510 m, 5 Dec. 1972, *Dunsterville & Dunsterville s.n.* (US, VEN, photo US).

Aratitiyopea lopezii var. **colombiana** (L. B. Smith) Steyerm. & Berry, comb. nov. *Navia lopezii* var. *colombiana* L. B. Smith, Bot. Mus. Leafl. 16: 195. 1954. Fl. Neotrop. Monogr. 14: 465. 1974.

Distribution: Vaupés of southeastern Colombia.

Specimens examined. COLOMBIA. VAUPÉS: Cerro Isibukuri, Río Kananari, 4 Aug. 1951, *Schultes & Cabrera 13342* (holotype, US; isotype, COL, GH); Cerro Isibukuri, Río Kananari, 4 Aug. 1951, *Schultes & Cabrera 13393* (US); 23–25 June 1952, *Schultes & Cabrera 15078* (COL, US).

When Dr. Lyman B. Smith (in Schultes, 1951: 40) originally published the description of this outstandingly beautiful plant, he wrote Dr. Schultes that "This species has flowers more than twice the size of any previously known *Navia,* and the rose-purplish color of the petals appears to be unique in the genus."

Unfortunately, when the species was described, the stamen number was apparently overlooked, since only three, rather than six, stamens are present in the flowers of *Navia lopezii.* A careful comparison of herbarium specimens of *Navia lopezii* with the newly collected material of *Aratitiyopea* leaves no doubt but that they are congeneric and conspecific. The sessile large heads with rose-purple bracts and purplish flowers of *Aratitiyopea* are identical with those found in *Navia lopezii.* Moreover, a careful examination of both fresh and pickled material of flowers of *Aratitiyopea,* and herbarium material of *Navia lopezii* identified by Dr. Lyman Smith reveals the presence of three prominent, reflexed, fleshy glands or appendages at the base of the style, together with three stamens, the same combination of characters duplicated in *Orectanthe,* a member of the Xyridaceae.

The relationship of the genus *Aratitiyopea* is most closely shown with the genus *Orectanthe,* in habit approaching the elongated caudex of *O. ptaritepuiana. Aratitiyopea* radically departs from *Orectanthe* in the completely different seeds, which are exalate, alveolate, prominently ridged, and symmetrically ovoid-elliptic in *Aratitiyopea* rather than broadly winged, non-alveolate, and non-ridged as in *Orectanthe,* in the equal, linear-ligulate lobes of the purple nearly actinomorphic corolla, and in the sessile, epedunculate inflorescence.

The stylar appendages in both *Aratitiyopea* and *Orectanthe* are strictly basal, the reflexed apex of the glandular appendages touching the apex of the ovary, whereas in *Abolboda* they are elevated above the ovary. Moreover, the glandular portion of the appendage in *Aratitiyopea* and *Orectanthe* is flattened, plate-like, oblong-ligulate, and much broader than the slender supporting stipe, whereas in *Abolboda* the glandular portion is very slender, scarcely or not at all broader than the filiform, supporting portion and does not touch the apex of the ovary. Additionally, the apex of the ovary in *Abolboda* is slightly split into three triangular or ovate-lanceolate, acute, usually indurate lobes, whereas in *Aratitiyopea* the ovary is entire and of the same texture throughout. The seeds of *Aratitiyopea* are symmetrical, whereas those of *Abolboda* are asymmetrical and suboblique, although the two are similar in having alveolate, striate surfaces. Although Maguire (in Maguire et al., 1958: 2–3. fig. 1: g, k, l) described and figured the style of *Orectanthe* as "crateriform, . . . undivided" and the stigma as "oblique terminati aliquantum fimbriato crateriformi," an examination of herbarium material provides evidence that the stigma is trifid as in *Aratitiyopea,* which in freshly preserved material definitely shows a trifid or deeply three-lobed fimbriate-penicillate stigma.

Dr. Joan Nowicke, palynologist of the Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C., has studied the pollen of *Aratitiyopea lopezii,* and has kindly supplied the following description based upon herbarium specimens preserved in 70 percent ethanol, with a double stain according to Alexander (1969). "Pollen spheroidal, 175–195 μm diam. (exclusive of projections), inaperturate, intectate, the wall 9–10 μm thick, the surface with a very thin layer of sparsely distributed granules (pila?) and with prominent knob-like projections 6–7 μm long.

Pollen of *Aratitiyopea* lacks the typically stratified angiosperm exine that consists of endexine, footlayer, columellae, and tectum. Only two parts of the wall absorbed the stain, the knob-like projections and a very thin surface layer of sparsely distributed granules. This suggests that they have similar composition, and being the outermost components suggests that both are ektexine. The remainder and vast majority of the wall was translucent. The most likely interpretation of the pollen wall in *Aratitiyopea* is that reduction of the exine has occurred. Judging from the staining pattern, the granules and knob-like projections are the only remaining components of exine; the thick, clear portion of the wall is probably intine. Since the exine is so thin, preformed openings (apertures) are not necessary.

The staining pattern of *Aratitiyopea* is similar to that reported by Carlquist (1960) for three xyridaceous genera, *Abolboda*, *Orectanthe*, and *Achlyphila*: an outer portion, the spines and ornamentation, which absorbed safranin red, and an inner portion which absorbed fast green. The pollen of *Aratitiyopea* is very similar to that of the above genera, all have large inaperturate grains with an outermost thin granular layer and spines or knob-like projections having widened bases. This distinctive pollen morphology reinforces the validity of the transfer of *Navia lopezii* from Bromeliaceae to Xyridaceae."

Among the characters Maguire used in differentiating *Orectanthe* (in Maguire et al., 1958: 2), the caulescent habit was given in his table of contrasts and comparisons between the known genera of Xyridaceae. However, when the two known species of *Orectanthe* are keyed out on the following page (in Maguire et al., 1958: 3), it is stated that *O. sceptrum* includes "plants essentially acaulescent," as contrasted with *O. ptaritepuiana* having "plants caulescent." This same inconsistency is repeated in Maguire's later key to the genera of Xyridaceae (in Maguire et al., 1960: 12).

Although Maguire at first believed that taxonomic evidence supported Erdtmann's suggestion that *Abolboda* and *Xyris* were not compatible familially (in Maguire et al., 1958: 1–2, 1960: 11) and that *Abolboda* should be referred to a separate family, Abolbodaceae (Nakai, Ordines, familial, tribus (etc.) in praelectionibus anni 1937), Maguire later conceded (in Maguire et al., 1960: 15) that all four genera known at that time pertain to a single family, Xyridaceae, and "mutually exclude them from any other monocotyledonous family or families."

The following key is provided to account for the additional genus, *Aratitiyopea*, of the Xyridaceae.

KEY TO THE GENERA OF XYRIDACEAE

1. Corolla gamopetalous; stylar appendages usually present 2
    2. Sepals 3; stylar appendages basal, at apex of ovary, the reflexed portion ligular-oblong, broader than the supporting stipe, and touching the apex of the ovary; apex of the ovary entire, of soft uniform texture 3
        3. Corolla lobes unequal in size and shape; corolla yellow or brownish yellow; inflorescence long pedunculate; seeds broadly winged, not alveolate nor ridged .... *Orectanthe*
        3. Corolla lobes equal in size and shape; corolla purple; inflorescence sessile; seeds exalate, alveolate, ridged .... *Aratitiyopea*
    2. Sepals usually 2; stylar appendages raised on the style above the apex of the ovary and not touching the apex, the reflexed portion filiform and about equalling width of the filiform-supporting stipe; apex of the ovary 3-toothed, undurate .... *Abolboda*
1. Corolla polypetalous; stylar appendages absent 4
    4. Rhizomatous caulescent herb; inflorescence open, the flowers pedicellate; sepals not keeled; staminodia lacking .... *Achlyphila*
    4. Non-rhizomatous, usually acaulescent herb, inflorescence capitate, the flowers sessile; 2 lateral sepals keeled; staminodia present .... *Xyris*

RAPATEACEAE

Stegolepis maguireana Steyerm., sp. nov. TYPE: Venezuela. Bolivar: Chímantá Massif, Acopán-tepui, around sandstone outcrops in wet savanna area, NW portion, 1,950 m, 14 Feb. 1984, *Steyermark, Luteyn & Huber 129962* (holotype, VEN; isotype, NY).

Herbae perennes, 2-metralis altae; vaginis conduplicatis 17 cm by 6 cm enervatis marginibus scarioso-membranaceis; laminis utrinque glaucis friabilibus valde 1-nervatis 1.5–2 m longis 2–3 cm latis; pedunculo axillari apice non dilatato foliis manifeste longiore 2–2.5 cm longo 5–6 mm diam.; inflorescentia hemisphaerica 3.2 cm longo 3.5–3.8 cm diam. multiflora; spiculis ovoideis occultis 8–9 mm × 4 mm; sepalis induratis non reflexis; petalis luteis parvis.

This species differs from the related *S. parvipetala* Steyerm. and subsp. *chimantensis* Maguire in the peduncles prominently longer than the leaves, the very brittle narrower leaves only 2–3 cm wide, the leaves glaucous on both sides, not silvery below with green stripes as in *S. parvipetala*, and in the yellow instead of orange petals.

Stegolepis terramarensis Steyerm., sp. nov. TYPE: Venezuela. Amazonas: Cerro Marahuaca, cumbre, extremo noreste, 3°50′N, 65°28′W, 2,580–2,600 m, 30 Mar.–1 Apr. 1983, *Steyermark & Delascio 129197* (holotype, VEN). PARATYPE: same locality and date, *Fernandez 66* (VEN).

Herbae perennes 0.5–1-metralis; vaginis valde conduplicatis 14–15 cm longis apice 2.5–3 cm latis, auriculis prominentibus ligulatis suborbicularibus apice rotundatis 1.5–1.8 cm longis 2.5–3.5 cm latis marginibus scariosis; laminis coriaceis lineari-ligulatis apice falcate rotundatis vel obtusis 47–54 cm × 3–3.5 cm, costa media nervis secundariisque tantum leviter manifestis haud prominentibus; pedunculis 6–7, valde costatis 25–55 cm longis 2–3 cm crassis infra spiculam 4–6 mm crassis; spiculis plerumque (1–)3–7, bracteolis tantum inclusis 1–1.5 cm longis; bracteolis lanceolato-oblongis obtusis vel subobtusis, exterioribus 4–5 mm longis, interioribus (superioribus) 8–10 mm × 2.5–3.5 mm; sepalis lanceolatis acutis 15 mm longis induratis; petalis 1.5–2 cm longis; antheris linearibus transverse rugosis 9–10 mm longis.

This species is related to *S. hitchcockii* Maguire, *S. pulchella* Maguire, and *S. membranacea* Maguire, but differs in the rounded to falcately obtuse leaf blades with more strongly developed ligulate auricles and obtuse broader bracteoles. In its 3–7(rarely 1–)-flowered inflorescences, it is more closely allied to *S. hitchcockii* but the latter has shorter anthers and broader leaf blades. From *S. membranacea* it may additionally be distinguished by the indurated, enervate, coriaceous leaf blades which are inconspicuously nerved, and in the broader apex of the peduncle, while from *S. pulchella* it further differs in the usually greater number of spikelets and the less conspicuously, coriaceous leaf blades.

Although Maguire (1982: 139) states that the bracteoles in *S. pulchella* and *S. membranacea* are "algo obtusas" or "obtusiusculis," an examination of these taxa, as well as *S. hitchcockii* and subsp. *morichensis*, indicates that they are all lanceolate or deltoid-lanceolate and narrowed to a subacute apex, whereas those of *S. terramarensis* are oblong-lanceolate and much broader towards an obtuse apex.

The species is named to commemorate the Fundacion Terramar, under whose auspices the expedition to Cerro Marahuaca was administered.

NOTE ON *SAXOFRIDERICIA SPONGIOSA* MAGUIRE AND *S. DUIDAE* MAGUIRE

In his description of the leaf width of *S. duidae* Maguire (1982: 94) states "2–3.5 cm de ancho" and that of *S. spongiosa* (Maguire, 1982: 97) as "7–10 cm de ancho." Measurements of material of *S. spongiosa* nevertheless indicate a more limited range of variation from 4–8 cm, with some specimens only 4–6 cm wide.

The peduncles of *S. spongiosa* are stated to be "abruptamente ensanchados y bulbosos debajo de la inflorescencia." Some specimens, such as *Wurdack & Adderley 4366* are not. The sponge-like texture of the sheath is characteristic.

On the other hand, *S. duidae* may exhibit a pronounced enlargement below the heads, as in *S. spongiosa*, although in his key Maguire (1982: 90) states that the peduncles are "ensanchados" only "gradualmente debajo de la inflorescencia."

Although *S. duidae* is included under the portion of the key (Maguire, 1982: 89) which states that the heads are "4 cm mas o menos ancho," nevertheless the text under *P. duidae* (Maguire, 1982: 94) gives greater dimensions of "inflorescencia 4.5–5.5 cm de diametro." There is intergradation in head size between these two taxa. *Huber 6182*, identified as *S. duidae*, is *S. spongiosa.*

IRIDACEAE

Trimezia chimantensis Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Piar, Macizo de Chimantá, sector centro-noreste del Chimantá tepui, cabeceras orientales del Caño Chimantá, 5°18′N, 62°09′W, 2,000 m, 26–29 Jan. 1983, *Steyermark, Huber & Carreño 128071* (holotype, VEN). PARATYPE: Macizo de Chimantá: sector SSE, altiplanicie suroriente del Acopán-tepui, cabeceras del Río Arauac, praderas húmedas y arbustales enanos sobre turberas, bosquecillos ribereños y vegetación sobre rocas abiertas, 5°11′N, 62°00′W, 1,920 m, 14–16 Feb. 1984, *Steyermark, Luteyn & Huber 129864* (VEN).

A *T. fosteriana* foliis angustioribus 3 mm latis utrinque viridibus haud glaucis, petalis minoribus 2 cm longis, spathae valvis 2.5–3.5 cm longis, antheris minoribus 3–3.5 mm longis recedit.

Cormous herb 0.8–1.2 m tall; leaves rich green both sides, narrowly linear, 0.7–0.8 m long, 3 mm wide; scape 0.7–1.2 m tall, equalling or exceeding the leaves, 3 mm wide, 2–3-bracteate; bracts linear, the lower ones 16–45 cm long, those in the upper third 4–8.5 cm long; spathes lanceolate, acuminate 2.5–3.5 cm long; perianth completely yellow, unspotted, the segments 2 cm long; anthers 3–3.5 mm long; style 6 mm long, branches 4 mm long.

This species differs from the related *T. fosteriana* Steyerm. in the generally narrower, completely green, non-glaucous leaves, shorter spathes and perianth segments, and smaller anthers. Originally described from specimens collected in the Gran Sabana of Estado Bolivar, *T. fosteriana* is also now known to occur on the summit of Chimantá Massif (*Steyermark, Huber & Carreño 128440* and *128798*).

SARRACENIACEAE

REALIGNMENT OF THE GENUS *HELIAMPHORA*

Introduction. One of the outstanding endemic genera of the Guayana Highland of Venezuela is *Heliamphora.* Thus far, it is known to be restricted to the summits of some of the sandstone table mountains of the Roraima formation of Estado Bolivar and Territorio Federal Amazonas of the Venezuelan Guayana and adjacent Sierra de Neblina and Pirapicu of northwestern Brazil. The genus also descends to the Gran Sabana of southeastern Estado Bolivar in Venezuela.

The original species, *H. nutans,* was collected by Robert Schomburgk from Roraima and described by Bentham in 1841. As a result of Tate's collections from the summit of Cerro Duida, Gleason described three additional species, *H. macdonaldae, H. tatei,* and *H. tyleri* in 1931. A fifth species was added by Gleason (in Gleason & Killip, 1939: 164) as a result of collections made by Tate and Cardona from the summit of Auyan-tepui. Subsequent to his expedition to Ptari-tepui in 1944, Steyermark (in Steyermark et al., 1951: 239) described a sixth species, *H. heterodoxa,* and presented a key to the known species, at that time commenting on the variation as demonstrated by *H. heterodoxa* as well as by the *H. tatei-tyleri-macdonaldae* group.

A review of the comparative morphology, foliar trichomes, and glands present on the species of *Heliamphora* known up to 1942 was published by F. E. Lloyd (1942: 9–16). His account was based partly on previous literature, as well as herbarium material and living plants of *H. nutans.* A popular article on the mechanism of the trap in the species of *Heliamphora* on Cerro de la Neblina appeared in 1973 by Charles Brewer-Carías. In 1978, Dr. Bassett Maguire published a review of the genus Sarraceniaceae (in Maguire et al., 1978: 36–62). In that treatment two new species, *H. ionasii* and *H. neblinae,* and four new varieties (two in *H. heterodoxa* and two in *H. neblinae*) were described, while *H. tyleri* was synonymized with *H. tatei,* and *H. macdonaldae* was reduced to a variety of *H. tatei.*

Present work. In an attempt to identify numerous specimens of *Heliamphora* collected by the writer on various expeditions to the Venezuelan Guayana during the past five years, Maguire's treatment of the genus was used. Unfortunately, due to the tremendous variation exhibited throughout the genus, it became evident that several characters employed in his key were inapplicable to distinguish various taxa. This has resulted in the present realignment in which a re-examination and evaluation has been made of various gross morphological characters available in differentiating the taxa.

Previous observations by Steyermark (in Steyermark et al., 1951: 240–242) stressed the morphological variations which occurred in *H. heterodoxa* and within the *H. tatei-tyleri-macdonaldae* group. Attention at that time was also called to the variation in pitcher size and shape induced by changes in wetter habitats. Observations on living plants as well as on extensive collections from expeditions made in 1953, 1955, and since 1960 to the present have further aided the writer in his realignment of the genus. An examination of the extensive collections of *Heliamphora* in the Herbarío Nacional of Venezuela (VEN), supplemented by duplicate material from NY, has been a basis for the following observations and a new key to the taxa.

Variation within the genus. It should be emphasized that all the taxa in *Heliamphora* exhibit a great amount of plasticity, varying to such an extent that scarcely a single character remains foolproof for their differentiation. Size and shape of pitchers, their appendages, height of flowering plant, contraction or elongation of the cauline axis, glabrity and length of pedicels, length and apex of the lowest floral bract, shape and size of tepals, number of flowers on the scape, relative length of the lowest floral bract as compared with length of the lowest pedicel, and presence or absence of a foliar bract on the scape below the inflorescence—each of these characters exhibits a certain degree of instability and intergradation, so that their role in distinguishing one taxon from another is indeed limited, if not completely unreliable. Although shape and size of pitchers, height of plant, and other characters may afford generally recognized differences between taxa, such characters may change under varied environmental conditions. Certain characters, however, have been found to be more or less constant and applicable, even though exhibiting some variation. I refer here to the relative number and length of the anthers, the relative total length of the upper pubescent zone of the interior surface of the pitcher in proportion to the length of the pitcher itself, and the density and relative length of the hairs of this upper pubescent zone. Each of the characters examined will be discussed in the following section of this study (see Table 1 for summary of these characters).

Androecium. The number of anthers within a flower has been found to be generally reliable in separating the main taxa of the Territorio Federal Amazonas from those of the Estado Bolívar, the latter varying from usually (4–)8–14(–15 or rarely 16), the former from 15–20. The taxa of Estado Bolívar include *H. minor* with stamens varying from 10–14, *H. heterodoxa* var. *heterodoxa* from 8–14 (rarely to 16 in *Steyermark & Wurdack 374* from Chimantá Massif) (VEN), *H. heterodoxa* var. *exappendiculata* from 7–10 rarely 4 in *Cardona 1523* from Chimantá Massif (VEN), 10–14 in *H. nutans,* and 15 (according to Maguire in Maguire et al., 1978: 54) in *H. ionasii.* The taxa of Territorio Federal Amazonas, *H. tatei* and *H. neblinae,* and their variations, possess 15–20 stamens.

The length of the anthers varies from 3–8.5 mm. Smaller anthers of 3–3.5 mm are found in *H. nutans* and *H. ionasii,* while larger anthers often 6–8 mm long are found in *H. heterodoxa* of Estado Bolívar and in the *H. tatei-H. neblinae* complex of Territorio Federal Amazonas. However, *H. heterodoxa* sometimes has anthers only 4.5–5 mm long, while anthers of only 5 mm long may be found in the *H. neblinae* group (*Steyermark 103775* [VEN]) and may vary in *H. minor* from 3–5 mm.

Length of the upper pubescent interior zone of the pitcher. In *H. nutans* and *H. minor* the upper zone of pubescence on the interior surface of the pitcher is relatively shorter in proportion to the length of the pitcher than in the other known taxa, occupying from ¼–⅜ the entire length, whereas in *H. heterodoxa* and the taxa of the Territorio Federal Amazonas the pubescent upper zone varies from ⅜–½ the entire length. In *H. heterodoxa, H. tatei,* and *H. neblinae* the pubescent zone varies in length from 7–18 cm, whereas in *H. nutans* and *H. minor* it is 2–8 cm long.

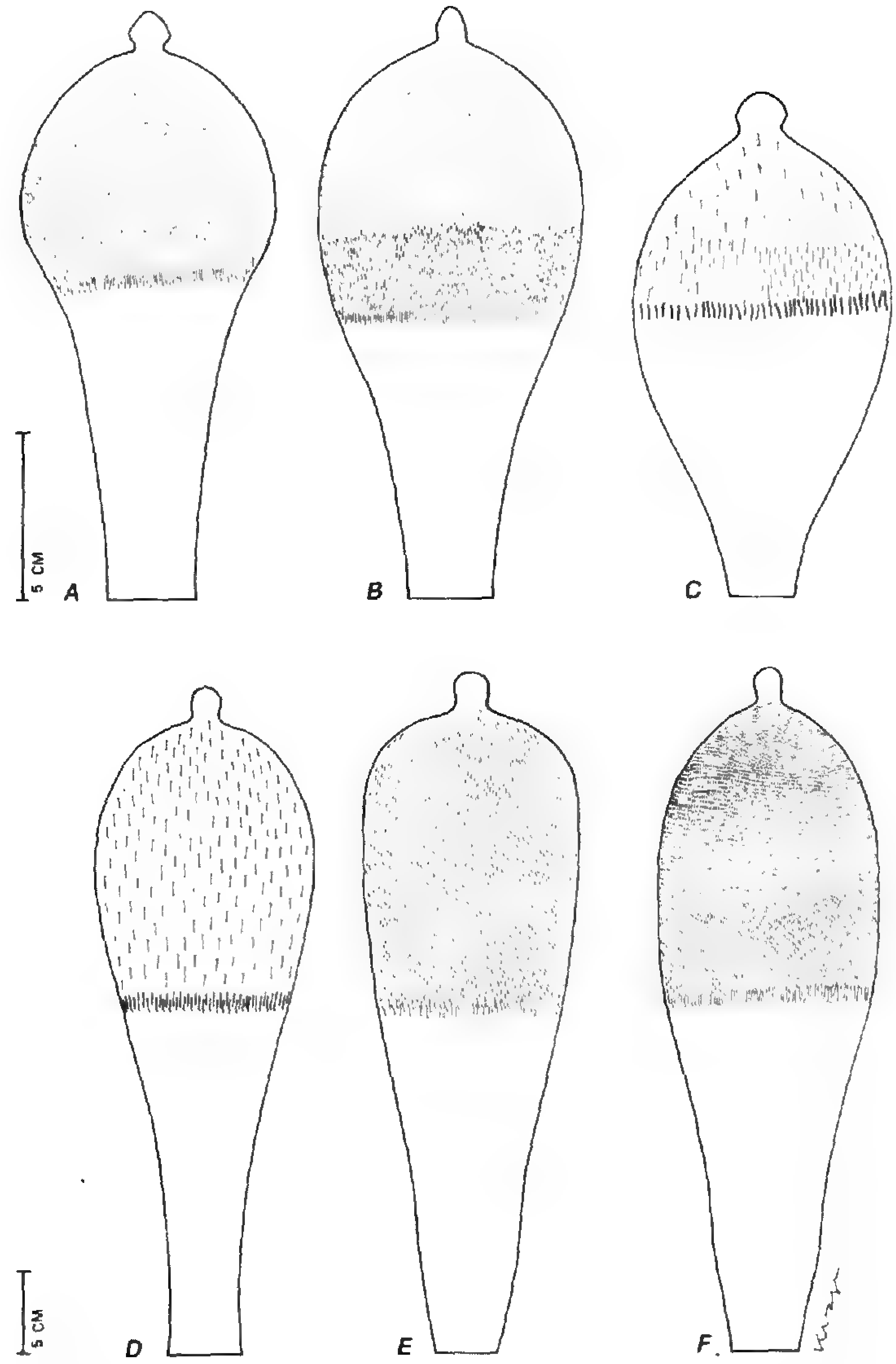

FIGURE 2. Interior leaf surface of species of *Heliamphora,* semi-diagrammatic.—A. *Heliamphora nutans.*—B. *H. heterodoxa*—C. *H. minor.*—D. *H. ionasii.*—E. *H. tatei* var. *tatei.*—F. *H. tatei* var. *neblinae.*

Trichomes of the upper pubescent zone. An examination of the trichomes of the upper pubescent zone of the pitcher reveals some differences which are mainly constant within a given taxon (Fig. 2). In *H. nutans, H. heterodoxa,* and in the taxa from Territorio Federal Amazonas, the upper pubescent zone consists of a velvety mat of minute, densely crowded, retrorse trichomes mainly 0.2–2 mm long. These minute hairs are shortest in the upper half of the zone, becoming longer toward the basal part, eventually merging with a basal zone of more elongated retrorse trichomes. A longer type of trichome 2–5 mm long, with the hairs more widely separated from one another, prevails in *H. ionasii* and *H. minor,* the former having the elongated hairs scattered over most of the surface, whereas in the latter, the longer hairs are dispersed more prominently in the lower portion of the zone, with a mixture of longer scattered hairs over a dense covering of minute trichomes 0.5 mm or shorter in the upper interior sector. Glabrous

TABLE 1. Summary of characters in the realignment of the genus *Heliamphora*.

	minor	*nutans*	*heterodoxa*	*tatei*	*tatei* var. *neblinae*	*ionasii*
Pitcher length (cm)	5–22(–30)	15–29	12–32(–42)	25–50	(12–)15–30	40–50
Pitcher length hairiness (cm)	2–8	6–8.5	7–18	9–14	10–15	14.5–19
Pitcher hairiness ratio	⅓–⅜	⅓–⅜	½ or less to ⅜	⅜ to nearly ½	⅜ to nearly ½	⅜ or more
Pedicel pubescent	densely pubescent			sparsely densely	more or less	
Pedicel glabrous	—	rarely pubescent	rarely pubescent			—
Tepals in anthesis (mm)	21–50 by 7–19	35–45 by 11–16	30–60 by (10–)12–25	3 by 7–30	35–60 by 13–35	30–35
Tepals in fructification (mm)	40–53 by 12–20	45–47 by 20	45–80 by 18–37	45–72 by 20–40	70 by 30	55–60 by 15
Anther length (mm)	3–5	3–3.5	4.5–6(–8.5)	6–7.5	5–8	3.5
Lowest bract exceeding lowest pedicel	variable			rarely only equalling	sometimes only slightly exceeds	
Lowest bract shorter than lowest pedicel	—	—	—			—
Pedicel length (cm)	1.5–10	2–7	2–11(–16)	2–10	1–7.5	8–12
Height of plant (m)	0.1–0.85	0.3–0.5	0.3–0.9	0.3–2	0.4–1.2	0.85
Number of flowers to scape	(1–)2–5	4	2–7	2–3	2–3(–4)	8–10
Floral bract rounded	—		—			—
Floral bract cuspidate	rarely		mainly	—	—	—
Length of lowest floral bract (cm)	2–6	3–3.5	2–10	6–17	(4.5–)9–21	4–5
Pitcher appendage (mm)	3–15(–20) by 2–15(–20) as broad as long or broader than long	2–7 by 5–12 broader than long	6–35 by 5–30 often longer than broad to as broad as long (var. *exappendiculata* 0.2 by 2–10)	10–40 by 5–20 longer than broad	25–40 by 20–42 (also 11 by 11 as broad as long, also longer than broad) (*neblinae* f. *parva* 6–28 by 6–20)	16–20 by 10–30 about as broad as long
Lowest floral bract bearing appendage				—	—	
Lowest floral bract lacking appendage	—	—	—	sometimes	sometimes	—
Number of anthers	10–14	10–14	(7–)8–14(–16)	15–20	15–20	15

forms are known in *H. heterodoxa, H. minor,* and *H. tatei* f. *macdonaldae.*

Pitcher shape and length. The ventricose shape of the pitcher has been employed by Maguire (in Maguire et al., 1978: 50–51) to distinguish the species occurring in the Estado Bolívar from those having an "essentially tubular" shape found among the taxa of the Territorio Federal Amazonas. Unfortunately, the character of the shape, while more or less uniform among the taxa from the Territorio Federal Amazonas, varies considerably in *H. heterodoxa, H. minor,* and *H. nutans,* changing from a ventricose to a tubular type. Steyermark (in Steyermark et al., 1951: 240) noted previously that under conditions of more abundant moisture and shade, *H. heterodoxa* had larger and more elongated pitchers (*Steyermark 59934*), and in subsequent collections (*Steyermark et al. 115698, 115742, Steyermark & Wurdack 374, 375, Steyermark 121104*) this was noted on collection labels.

In *H. minor* the pitchers, although usually ventricose, are more elongated and subtubular in *Steyermark, Huber & Carreño 128666. Heliamphora nutans* has ventricose as well as more elongated tubular pitchers, as shown by *Delascio & Brewer 4733* from Ilu-tepui and *Delascio & Brewer 4967* from Kukenan-tepui. In the Territorio Federal Amazonas the taxa usually have the pitchers elongated to as much as 50 cm in length, but may be smaller and reduced to 12 cm long when they are growing in more desiccated or more exposed situations, as exemplified by *Steyermark 103775* and *103844* from Neblina, by *Farinas, Velasquez & Medina 279* and *549* from Duida, and by the type collection (*Maguire, Wurdack & Bunting 37171*) of *H. neblinae* var. *parva* Maguire. In his key, Maguire (in Maguire et al., 1978: 51) partly differentiated *H. ionasii* from *H. heterodoxa* on the basis of pitcher length, indicating 40–50 cm long for *H. ionasii,* based upon the type collection only, and "30 cm or less long" for *H. heterodoxa.* However, the abundant material of *H. heterodoxa* represented in VEN shows a variation of pitcher length from 12 to 42 cm.

Elongation of the cauline axis. Some emphasis has been placed by Maguire (in Maguire et al., 1978: 50–53) upon the differentiation of the taxa from Estado Bolívar having rosette-forming pitchers on shortened axes from those with pitchers cauline on more elongated axes 2–5 dm long. In this manner, *H. nutans* and *H. minor* are separated from *H. heterodoxa* and *H. ionasii.* However, no reliability can be placed upon this character. Observations of living plants of *H. minor* on Chimantá Massif and Auyan-tepui furnish evidence of the effect of the environment on habit of growth with reference to the elongation of the caudex. Field observations and voucher herbarium material indicate that the plants growing in desiccated areas exposed to full sun, especially during the months of the dry season, form rosettes with a shortened axis, whereas those plants inhabiting the moister cliff faces, where water is dripping or where more shade occurs, develop more elongated axes with cauline pitchers, as exemplified by the specimen of *H. minor* (*Steyermark, Huber & Carreño 128666*) from Chimantá Massif. Some specimens of *H. nutans* (*Delascio & Brewer 4733*) from Kukenan-tepui have a pitcher attached 5 cm above the rosette clump, and in *Maguire 33379* (VEN) the caudex is elongated at least 5 cm below the leafy rosette.

Although the cauline axis is more commonly elongated in *H. heterodoxa,* the degree of elongation varies with the habitat. One can find rosette-forming plants with a shortened axis in *H. heterodoxa* var. *heterodoxa,* especially in open wet or exsiccated savanna-like habitats (*Maguire & Wurdack 33890* [VEN], *Steyermark & Dunsterville 104240* [VEN]), and in var. *exappendiculata* (*Steyermark 74888* [VEN] and *Steyermark & Wurdack 441* [VEN]).

Height of plant. The height of the plants in *Heliamphora* varies, of course, according to the elongation of the cauline axis. There is considerable variation in this respect among the several taxa. Dwarfed plants of *H. minor* may attain only 1 dm in height (including the inflorescence), 3 dm in *H. nutans,* and 3 dm in *H. heterodoxa,* but *H. nutans* may reach a height of 5 dm, *H. minor* may attain 8.5 dm, and *H. heterodoxa* as much as 9 dm.

The taxa (*H. tatei* and *H. neblinae*) in Territorio Federal Amazonas generally attain a relatively taller height, reaching an average of between 1–2 m in *H. tatei,* and, on occasion (according to Maguire in Maguire et al., 1978: 56–57) to 4 m. However, in the same colonies of *H. tatei,* smaller plants, only 3–6 dm tall, may occur, as exemplified by individual specimens from Cerro Duida (*Steyermark et al. 126392, Farinas, Velasquez & Medina 277*) and Cerro Marahuaca (*Steyermark et al. 126356*). In *Steyermark, Liesner & Brewer-Carías 124564* from Cerro Duida, plants of *H. tatei* are noted to vary from 0.5 to 1.5 m in height, and plants of *H. neblinae* from Cerro de la Neblina may vary from 0.5 to 1.5 m, smaller individuals (*Steyermark 103745*) having been referred by Maguire (in Maguire et al., 1978: 56–57) to *H. neblinae* var. *parva*.

So far as height and elongation of the caudex are concerned, there is intergradation between populations of plants of *H. tatei* from Cerro Duida, Cerro Huachamacari, and Cerro Marahuaca, and of *H. neblinae* from Cerro de la Neblina. These two taxa do not reveal any real differences in anther length, as stated by Maguire, but do exhibit a distinct character in their type of pubescence occurring on the upper interior surface of the pitcher.

Branching of axis. In his key to *Heliamphora* Maguire (in Maguire et al., 1978: 51) alludes to the stems of *H. tatei* as being "dendroid, much branched," as contrasted with "stems not dendroid, simple or little branched" in *H. neblinae.* The terminology "dendroid, much branched," as employed by Maguire, is in need of clarification and modification. If a "dendroid, much-branched" stem leads one to expect a much-branched, tree-like habit, certainly there is nothing evident from herbarium material or photographs to justify this description. Therefore, in order to verify, clarify, and re-examine this habital character, the present writer was given the opportunity during separate helicopter trips to the summits of Cerro Duida and Cerro Huachamacari in 1981, 1982, and 1983, where thousands of individual plants of *H. tatei* occur, to observe, record, collect, and make detailed photographs of the growth habit of this species.[2] As a result of an examination of numerous individuals, the following conclusions have been drawn:

The ramification noted by Maguire is subject to various interpretations. In many individuals there is no indication of branching (Fig. 3) and only a simple, solitary stem is seen, as exemplified by *Steyermark 129428-C* and *D* (VEN). In other individuals a shortened lateral axis is developed which bears an abbreviated rosette or leaf cluster. This lateral leaf cluster on a shortened axis may occur along the side of the stem (*Steyermark 129428-A* and *E* [VEN]), or near or at its apex (*Steyermark 129428-B* [VEN]), in the latter case producing a bifurcate aspect (Fig. 4). This short attachment, usually either one or sometimes two, developed part way up the main stem or producing a bifurcation when developed at or near the apex, provides the basis for Maguire's use of the term "branched." However, no individuals were found, among the numerous ones examined, which could be described as "much branched." Many specimens were seen with several leafy plants growing from the base of the stem, and these basal growths attained different lengths of leafy tufts (Fig. 5). Such individuals, however, cannot be considered as having a branched stem, but merely as having leafy offshoots arising from their base. Moreover, of the numerous individual specimens observed, a larger proportion exhibited only simple, unbranched stems which lack any attached leafy rosettes or leafy clusters.

Thus, the usual growth habit which was observed on the *Heliamphora tatei* plants from the summits of Cerro Duida and Cerro Huachamacari is that of a simple, monopodial stem which continues to elongate upward, the older dead pitchers, which occur along the longitudinal vertical axis of the stem, persisting and remaining attached to the axis for many years, while the new pitchers, which form the green leafy growth, appear in the uppermost and apical portion of the same axis. In some plants a shortened leafy rosette may be produced, but no elongated ligneous "dendroid" branches are present.

Ebracteate and bracteate scape. A character used by Maguire in his key (in Maguire et al., 1978: 50–51) to distinguish the taxa of Territorio Federal Amazonas from those in the Estado Bolívar is that of the presence of a bract which is commonly found below the middle of the inflorescence in the taxa from Territorio Federal Amazonas, while it is absent among the taxa from Estado Bolívar. Actually, each pedicel of the inflorescence in *H. neblinae* and *H. tatei* is subtended by a leafy bract, but the lowest bract is more elongated and more foliose than the others. However, in the majority of specimens examined, no other bract occurs below the lowest

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[2] I am deeply grateful to the Terramar Foundation for their generous support in supplying helicopter trips to the summit of Cerro Huachamacari, particularly to Armando and Fabian Michelangeli. Special thanks are here acknowledged to Walter Smitter who photographed the plants of *Heliamphora tatei* on Cerro Huachamacari. I am also greatly thankful to Dr. Charles Brewer-Carías, who supplied helicopter support to the summit of Cerro Duida.

FIGURE 3. Completely unbranched axis of *Heliamphora tatei*.

one subtending the lowest pedicel. In the majority of specimens examined, the lowest bract occurs above the middle of the scape. After an examination of ample material in VEN, I have had to conclude that this character has no taxonomic value. In fact, a bract may sometimes be present on the scape below the inflorescence on some of the taxa from Estado Bolívar, as exemplified in *H. minor* by *Steyermark et al. 116001* from Auyan-tepui, *Steyermark, Huber & Carreño 128269* and *128666* from Chimantá Massif, *H. heterodoxa* var. *heterodoxa* (*Steyermark & Nilsson 338* and *Steyermark 121104*) and *H. nutans* (*Delascio & Brewer 4967*) from Ilu-tepui, and may be absent, on the other hand, on many specimens from the Territorio Federal Amazonas.

Floral bract. The applicability of the relative

FIGURE 4. Lateral leaf cluster on stem of *Heliamphora tatei*.

length of the floral bracts as compared with the length of the pedicel, as used by Maguire (in Maguire et al., 1978: 50–51) is generally useful with reference to the lowest floral bract only, but an unreliable character for separating the taxa of Estado Bolívar from those of Territorio Federal Amazonas when applied to the bracts other than the lowest one. While the lowest floral bract is shorter than the lowest pedicel in *H. ionasii*, *H. heterodoxa*, and *H. nutans*, all originating from Estado Bolívar, it varies greatly in *H. minor*, also from Estado Bolívar. Thus, in *H. minor* the lowest bract is found to either exceed the lowest pedicel or it may be shorter. This variation may depend on the relative age of the plant, since longer pedicels are often correlated with the lowest flowers which are the first to appear in anthesis, whereas the flowers on the shorter upper pedicels come into anthesis at a later stage of flower succession. Moreover, in the taxa from the Territorio Federal Amazonas the floral bract, on some specimens, may only equal or slightly exceed the pedicel.

This floral bract varies in length from 2–6 cm in *H. nutans*, *H. minor*, and *H. ionasii*, and from 2–10 cm in *H. heterodoxa*, whereas in the taxa from Territorio Federal Amazonas, variation extends in length from (4.5–)6 to 21 cm. In the taxa originating from Territorio Federal Amazonas the floral bract is usually provided with an appendage similar to that of the pitcher, whereas this appendage is lacking in the taxa from the Estado Bolívar. However, some specimens of the taxa from Territorio Federal Amazonas may have only a cuspidate apex instead of a definite appendage. In *H. minor*, *H. ionasii*, and *H. heterodoxa* the apex of the floral bract is rounded or cuspidate, although mainly cuspidate in *H. heterodoxa* but rarely so in *H. minor*. So far as specimens examined are examined, it is cuspidate in *H. nutans*.

Pedicel length and indument. The presence or absence of pubescence on the pedicel was used by Maguire in his key (in Maguire et al., 1978: 50–51) to differentiate some of the taxa. Within certain limits this character appears to have value. It is found to be useful in the majority of specimens examined, although showing variability. The pedicels are glabrous in *H. ionasii*, *H. heterodoxa*, and *H. nutans*, but rarely pubescent in *H. heterodoxa* (*Steyermark & Wurdack 374, 375* [VEN] and *Steyermark 74888* [VEN]) and in *H. nutans* (*Delascio & Brewer 4967* [VEN]). They are nearly always pubescent in *H. minor*, and usually so in the taxa from the Territorio Federal Amazonas referred to *H. tatei* and *H. neblinae*, but in *H. tatei* may vary from pubescent to glabrate. In Maguire's key (in Maguire et al., 1978: 50) the difference in pedicel glabrity has been inadvertently transposed, and should actually read "pedicels glabrous" for *H. nutans* and "pedicels pubescent" for *H. minor*, instead of vice-versa as given in the key.

The length of the pedicel varies according to the maturity of the inflorescence, the lowest one maturing earlier than the others, which results in the lowest fruiting pedicel attaining the longest length. This length varies with the different taxa, the maximum of 16 cm recorded for *H. heterodoxa*, 12 cm for *H. ionasii*, 10 cm for *H. minor* and *H. tatei*, 7.5 cm for *H. neblinae*, and 7 cm for *H. nutans*, but minimum lengths of 1–2 cm are known in the flowering pedicels of all the taxa, except for *H. ionasii*, where 8 cm is recorded.

Number of flowers in an inflorescence. The greatest number of flowers on one scape has been recorded for *H. ionasii*, in which 8–10 occur. In

FIGURE 5. Several leafy shoots growing in clump at base of plant of *Heliamphora tatei.*

H. heterodoxa, 2–7 flowers may be present, in the taxa from Territorio Federal Amazonas, referred to *H. tatei* and *H. neblinae,* 2–4 flowers appear; in *H. nutans* we find 4, and in *H. minor* the number ranges from generally 2 to 5, rarely solitary.

Appendage of the pitcher. The shape and size of the pitcher appendage is extremely variable, and, except for *H. heterodoxa* var. *exappendiculata,* in which it is scarcely developed, is an unreliable taxonomic character to serve for the differentiation of taxa, although it was used originally by Gleason (1931: 367) in his key to separate the various taxa in size and shape. *Heliamphora nutans* and *H. minor* may have the appendages as short as 2–3 mm long, but vary in *H. nutans* from a minimum length of 3–7 mm to a maximum length of 10 mm and in *H. minor* to 20 mm. On the other hand, the taxa from the Territorio Federal Amazonas show relatively longer or broader appendages, varying from 10–40 mm by 5–20 mm in the taxon referred to *H. tatei* var. *macdonaldae*, and from 10–40 mm by 10–42 mm in the taxon referred to *H. neblinae* var. *neblinae*. However, in *H. neblinae* var. *parva* the appendage is much smaller, 6–28 mm by 6–20 mm, thus breaking down the difference between the taxa from the Territorio Federal Amazonas and *H. heterodoxa* var. *heterodoxa* with appendages 9–40 mm by 7–30 mm and *H. ionasii* with appendages 16–20 mm by 10–30 mm.

Perianth. While the usual number of perianth segments (tepals) is 4, specimens occur with 5 or 6. In *H. minor* and *H. heterodoxa* the tepals vary from 4 to 5, and in a glabrous variety of *H. heterodoxa* (*Cardona 2661* [VEN]) 6 tepals are present. In his key to *H. neblinae*, Maguire (in Maguire et al., 1978: 57) states that the perianth segments are "commonly 5–6" in *H. neblinae* var. *neblinae* and "commonly 4" in var. *viridis*. However, although the isotype of var. *neblinae* (*Maguire, Wurdack & Bunting 37151*) at VEN has 6 tepals, most of the other specimens examined (*Maguire, Wurdack & Bunting 37035* and *Steyermark 103956*) and cited by Maguire as var. *neblinae*, have only 4 segments, whereas *Steyermark 103775* and *Maguire, Wurdack & Maguire 42465* show both 4 and 5 segments. Since the number of tepals is a variable character within these varieties, and no other taxonomic differences are indicated, they may be considered only as variations of tepal number within the same taxonomic variety.

The inner perianth segments, usually 2, are shorter and narrower than the generally 2 outer ones. They are always smaller in anthesis than in fructification. The tepals of *H. minor* and *H. nutans*, when in flower, are generally smaller than any of the other taxa, with an average length of 25–35 mm, but attain 45–50 mm in fruit. The largest perianth segments are encountered in *H. heterodoxa* of Estado Bolívar, attaining a maximum length of 60 mm, and in the taxa from Territorio Federal Amazonas, attaining a maximum length varying from 55–60 mm. In fructification these same taxa (*H. heterodoxa, H. tatei*, and *H. neblinae*) attain greater lengths of 80, 72, and 70 respectively. Since the minimum and maximum lengths show a wide range and intergrade between the various taxa, this character has not been found applicable for purposes of differentiation.

The perianth segments in *H. minor* are lanceolate, broadest at the base, and acuminate to cuspidate in anthesis. Those of *H. nutans* are similar in shape but less acuminate or cuspidate, while in *H. heterodoxa* the segments have a slightly broader oblong-lanceolate or ovate-oblong shape, varying from broadest at or near the base to broadest toward the middle, and from an acute to cuspidate apex. The taxa from Territorio Federal Amazonas, because of their generally broader outer tepals, have an oblong-elliptic or lance-oblong form, obviously broadest around the middle and vary at the apex from acute to obtuse.

Other variations. Within the genus *Heliamphora*, the interior upper surface of the pitcher is generally covered by a zone of numerous, closely packed, minute trichomes or with longer trichomes placed more distantly between one another. In *H. heterodoxa* var. *glabra, H. heterodoxa* var. *exappendiculata* f. *glabella, H. minor* f. *laevis*, and *H. tatei* var. *macdonaldae* this ordinarily pubescent zone is replaced by one nearly or completely glabrous, excluding the basal aggregation of elongate, retrorse hairs located at the summit of the glabrous lower interior portion of the pitcher.

Observations of large colonies of *H. tatei* and var. *macdonaldae* on Cerro Duida in 1981 and 1982 reveal a great inconstancy in the occurrence of glabrity on the upper interior surface of the pitcher. As indicated on the label accompanying the specimens of *Steyermark, Guariglia, Holmgren, Luteyn & Mori 124564*, not only do internally glabrous pitchers occur within the same colony, but even on the same plant. In this author's opinion, the internally glabrous plants should be considered at most a form, rather than a variety, of *H. tatei*. The glabrous variation of *H. heterodoxa*, described as a variety by Maguire, likewise may be considered as merely a glabrous state of the species and recognized as only a form.

Results. A re-examination of herbarium and living material of *Heliamphora* collected on recent expeditions by the author have shown a high degree of variability and plasticity among the several taxa within the genus. The characters employed by Maguire (in Maguire et al., 1978: 50–51) in the most recent treatment of the genus fail to provide for this degree of variation. It is thus necessary to modify and realign the taxa based on less variable characters. As a result, the following key and changes in nomenclature are given:

Heliamphora tatei Gleason, Bull. Torrey Bot. Club 58: 368. 1931.

Heliamphora tatei Gleason var. **tatei** f. **tatei.**

Heliamphora tyleri Gleason, Bull. Torrey Bot. Club 58: 368. 1931.

Heliamphora tatei Gleason var. **tatei** f. **macdonaldae** (Gleason) Steyerm., stat. nov. *Heliamphora macdonaldae* Gleason, Bull. Torrey Bot. Club 58: 367. 1931.

Heliamphora tatei var. *macdonaldae* (Gleason) Maguire, Mem. New York Bot. Gard. 29: 57. 1978.

Heliamphora tatei Gleason var. **neblinae** (Maguire) Steyerm., stat. nov. *Heliamphora neblinae* Maguire, Mem. New York Bot. Gard. 29: 57. fig. 54. 1978.

Heliamphora neblinae Maguire var. *viridis* Maguire, Mem. New York Bot. Gard. 29: 59. 1978.

Heliamphora tatei Gleason var. **neblinae** f. **parva** (Maguire) Steyerm., stat. nov. *Heliamphora neblinae* var. *parva* Maguire, Mem. New York Bot. Gard. 29: 59. fig. 49: G–H, 50: A–C. 1978.

Heliamphora heterodoxa Steyerm. var. **heterodoxa** f. **glabra** (Maguire) Steyerm., stat. nov. *Heliamphora heterodoxa* var. *glabra* Maguire, Mem. New York Bot. Gard. 29: 54. 1978.

Heliamphora minor Gleason f. **laevis** Steyerm., f. nov. TYPE: Venezuela. Bolívar: crece en zonas pantanosas, Cerro Auyan, 2,100 m, Jan. 1949, *F. Cardona 2661* (holotype, VEN). PARATYPES: Venezuela. Bolívar: Piar, stream margin at edge of wet savanna, Macizo del Chimantá, cumbre del altiplanicie en la base meridional de los farallones superiores del Apacará-tepui, sector N del macizo, 5°20′N, 62°12′W, 2,200 m, *Steyermark, Huber & Carreño 128416* (VEN); lugares muy húmedos, sabana y bosque, Salto Angel, alrededores caida de agua, Auyantepui, 13 Aug. 1968, *Foldats 7008* (VEN); summit, Auyan-tepui, 2,100 m, 18 Feb. 1984, *Luteyn & Steyermark 9590* (NY, VEN).

A *H. minor* amphoris intus zona media barbata excepta glabris, tertia vel quarta supera ventricosa occupatis recedit.

This form differs from typical *H. minor* in the completely glabrous inner face of the upper expanded portion of the pitcher, except for the zone of elongate hairs at the constriction at the base of the upper expanded portion. In *Steyermark et al. 128416* this glabrous upper expanded portion occupies about a fourth of the length of the pitcher. In typical *H. minor,* the interior upper ventricose face of the pitcher is usually pubescent with a zone of scattered elongate hairs. In the newly described form these hairs are completely absent except for the zone of hairs at the base of the ventricose portion at its constriction. The *Steyermark, Huber & Carreño 128416* collection occurred in a shaded zone of shrubbery by the border of a savanna where another collection of *H. minor* (*Steyermark, Huber & Carreño 128417*) was growing. This last collection exhibits a diminished number of hairs, tending toward the f. *laevis.*

I have referred the *Cardona, Foldats, Luteyn & Steyermark,* and *Steyermark et al.* collections to *H. minor* rather than to *H. heterodoxa,* since the upper ventricose zone is limited to ¼–⅓ of the total length of the pitcher instead of having this upper portion ⅜–½ of the total length as a characteristic of *H. heterodoxa.*

Heliamphora heterodoxa var. **exappendiculata** f. **glabella** Steyerm., f. nov. TYPE: Venezuela. Bolívar: Auyan-tepui, cumbre de la parte norte de la sección sur (division occidental), suelo arenisco entre "Drizzly Camp" y "Second Wall," 1,600–1,800 m, 11 May 1964, *Steyermark 93712* (holotype, VEN).

A var. *exappendiculata* ascidiis interiis in dimidio superiore glaberrimis recedit.

This form differs from var. *exappendiculata* in having the interior of the pitcher glabrous, except for some hairs at the basal zone of the expanded portion, whereas in var. *exappendiculata* the expanded interior of the upper portion of the pitcher is densely covered with trichomes.

Concluding remarks. As an auctoctonous genus, isolated on the ancient Roraima formation of the Guayana Shield of South America, and evidently separated since remote geological time from its nearest North American relatives, *Heliamphora* would appear to be a genus of ancient

KEY TO THE SPECIES, VARIETIES, AND FORMS OF *HELIAMPHORA*

1. Anthers mainly 16–20; lowest floral bract usually equalling or much exceeding the lowest pedicel; plants of Territorio Federal Amazonas 2
2. Upper interior portion of pitcher glabrous above the pubescent ring .. *H. tatei* var. *tatei* f. *macdonaldae*
2. Upper interior portion of pitcher densely pubescent above the pubescent ring 3
3. Upper pubescent zone of hairs with a mainly uniform length of 0.8–2 mm .... *H. tatei* var. *tatei* f. *tatei*
3. Upper pubescent zone of hairs not uniform, the indument toward the apical half consisting of hairs 0.2–1 mm long, but the lower portion with more elongate hairs 1–1.5 mm long 4
4. Exterior surface of pitcher more or less pubescent .... *H. tatei* var. *neblinae* f. *neblinae*
4. Exterior surface of pitcher glabrous .... *H. tatei* var. *neblinae* f. *parva*
1. Anthers (4–)7–15(–16); lowest floral bract usually shorter than the lowest pedicel; plants of Estado Bolívar 5
5. Interior of the upper ventricose portion of pitcher glabrous or nearly so, except for the basal zone of hairs 6
6. Appendages of the pitchers absent or scarcely developed .... *H. heterodoxa* var. *exappendiculata* f. *glabella*
6. Appendages of the pitchers obviously developed, 3–40 mm long 7
7. Anthers 3–5 mm long; upper ventricose portion of pitcher occupying ¼–⅓ of the total length .... *H. minor* f. *laevis*
7. Anthers (4.5–)5–8 mm long; upper ventricose portion of pitcher occupying ⅜–½ of the total length .... *H. heterodoxa* var. *heterodoxa* f. *glabra*
5. Interior of the upper ventricose portion of pitcher usually pubescent 8
8. Pubescent upper interior face of the pitcher (excluding the basal ring of hairs) with some or all of the hairs elongated to 2–5 mm and scattered or relatively distant from each other, or deciduous over a glabrous surface 9
9. Pedicels glabrous; scapes 8–10-flowered; pitchers 40–50 cm long; upper pubescent zone of the interior of the pitcher 14.5–19 cm long, extending from ⅜ or more of the length of the pitcher .... *H. ionasii*
9. Pedicels more or less pubescent; scapes 1–5-flowered; pitchers 5–22(–30) cm long; upper pubescent zone of the interior of the pitcher 2–8 cm long, extending from ¼–⅜ the length of the pitcher .... *H. minor*
8. Pubescent upper face of the interior of the pitcher (excluding the basal ring of hairs) with a dense minute, more or less uniform velvety indument of hairs 0.5–1 mm long 10
10. Anthers 3–3.5 mm long; upper pubescent zone of the interior of the pitcher occupying ⅓–⅜ the length of the pitcher, 6–8.5 cm long; most of the indument of the upper pubescent zone consisting of more or less uniform hairs 0.7–1 mm long .... *H. nutans*
10. Anthers (4.5–)5–8 mm long; upper pubescent zone of the interior of the pitcher occupying ⅜–½ the length of the pitcher, 7–18 cm long; most of the upper indument of the upper pubescent zone consisting of hairs 0.5–0.7 mm long, the lower portion with longer hairs 0.7–1 mm long .... *H. heterodoxa*

geological origin. However, judging by the high degree of variation and plasticity shown by the known taxa of the genus, it would indicate that these taxa have become separated from one another in only relatively recent times, and that they are still in the process of evolutionary instability as shown by the similarity of their floral characters and high degree of vegetative variation. The degree to which the taxa have diverged during their evolutionary history has been relatively insufficient to have resulted in their sharp differentiation from one another.

LEGUMINOSAE

CAESALPINOIDEAE

Aldina berryi Cowan & Steyerm., sp. nov. TYPE: Venezuela. Bolívar: cumbre, Cerro Guaiquinima, sector suroeste central, bosque de galería y bosque alto, a lo largo del afluente suroccidental del Río Carapo, 5°45′N, 63°35′W, 950 m, 26 May 1978, common in the tall forest of trees 20–25 m tall, *Steyermark, Berry, Dunsterville & Dunsterville 117468* (holotype, VEN; isotype, US).

Arbor 20-metralis; ramis, petiolis, rhachibus et foliolis glabris; foliis 1–3-foliolatis; petiolis 2.5–6 cm longis; foliolis 7–9.5 cm longis 3–5 cm latis, inflorescentiis terminalibus racemosis 8–11-floris 7–11 cm longis; pedicellis 3–7 mm longis dense badio-tomentosis; calyce 1.2–1.5 cm longo dense fusco-tomentoso, in anthesi inaequaliter 4–5-lobato, petalis 5–7 oblanceolatis vel obovatis apice rotundatis 25 mm longis 12–13 mm latis glabris; ovario lineari-elliptico 4–5 mm longo 1.5–2 mm lato glabro vel basi pilis paucis minutis adpressis munito, stipite 5 mm longo glabro; stylo subulato 2–3 mm longo glabro.

Tree 20 m tall; branches, petioles, rachis of leaves and leaflets glabrous; leaves 1–3-foliolate or the uppermost sometimes simple, mainly alternate; petioles 2.5–6 cm long; lateral petiolules 7–11 mm long, terminal 22–30 mm long, thickened portion 11–13 mm long; leaflets chartaceous, gray green beneath, ovate or oblong-ovate, obtusely acuminate at apex, acumen 4–5 mm by 2–3 mm, 7–9.5 cm by 3–5 cm; lateral nerves inconspicuous to obsolete, 10–14 on each side, tertiary venation absent; inflorescence terminal, simply racemose, 8–11-flowered, 7–11 cm long; peduncle 1.5–2 cm long, densely brown-tomentose; flowers pedicellate, pedicels 3–7 mm long, articulate at apex, densely brown-tomentose; calyx (in bud) obovoid to ellipsoid, densely dark brown tomentose; unequally 4–5-lobed in anthesis with reflexed lobes, 1.2–1.5 cm long (tube olive green, 7–9 mm long, 10–11 mm wide at summit; 3 lobes broadly lanceolate, subacute, 9–10 mm by 4–5 mm, fourth lobe ovate to broadly ovate, subobtuse, 10 mm by 9 mm, all lobes glabrous and white within except for pilosulous margins above middle); petals white, 5–7, oblanceolate or obovate, rounded at apex, 25 mm by 12–13 mm, glabrous; stamens numerous, uniform, filaments white, fasciculate, 15–18 mm long, glabrous; anthers yellow, linear, rounded at upper end, asymmetrically bilobed at base, dorsifixed, 4.5–6 mm by 1 mm; ovary linear-elliptic, 4–5 mm by 1.5–2 mm, glabrous or with a few, minute appressed hairs basally, stipe glabrous, 5 mm long; stigma terminal; fruit not seen.

This taxon is named for Paul Berry, who accompanied the author on the present expedition, and who rendered great collecting assistance. *Aldina berryi* is very conspicuous when flowering with its masses of fragrant, white flowers at the summits of the tall forest on Cerro Guaiquinima. It is distinguished by the complete glabrity of the ovary and vegetative parts.

PAPILIONOIDEAE

Dipteryx phaeophylla Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Cerro Guaiguinima, cumbre, Salto de Río Szczerbanari, parte central del cerro, 5°44′4″N, 63°41′8″W, 750 m, 20–25 Jan. 1977, *Steyermark, Dunsterville & Dunsterville 113200* (holotype, VEN). PARATYPE: same locality and date, *Steyermark, Dunsterville & Dunsterville 113248* (VEN).

Arbor 4–20-metralis; foliis petiolatis 5-foliolatis paribus lateralibus oppositis, foliolis oblongo-vel lanceolato-ellipticis apice caudatis acumine tenui 1–2 cm longo basi obtusis 7–10.5 cm × 2–3.5 cm subtus minute adpresso-puberulis; petiolis rhachidique minute adpresso-puberulis; infructescentia pedunculata 12–21 cm longa minute denseque adpresso-puberulis; fructu fusiformi-elliptico extremitatibus subacutis 4–6 cm × 1.2–1.8 cm minute adpresso-puberulis.

Tree 4–20 m tall; leaves petiolate, 5-foliose, the two lateral pairs opposite; leaflets dark green above, brown below, oblong- to lance-elliptic; caudate at the apex with a slender acumen 1–2 cm long, obtuse at base, 7–10.5 cm by 2–3.5 cm, glabrous above, minutely appressed-puberulent below on surface and midrib; lateral nerves 8–10 each side, obsolete below, slightly evident above; midrib elevated below, depressed above; tertiary venation minutely and obsoletely reticulate below; petiole and leaf-rachis 3.5–5 cm long, minutely appressed-puberulent; petiolule 5–10 mm long, minutely appressed-puberulent; infructescence paniculate, 12–21 cm long, the fertile portion 7–15 cm long, densely appressed-puberulent, pedunculate; peduncle 4.5–8 cm long, densely and minutely appressed-puberulent; legume mustard brown, fusiform-elliptic, subacute at both ends, finely reticulate, 4–6 cm by 1.2–1.8 cm, minutely appressed-puberulent; flowers not seen.

This taxon is characterized by the minutely dense puberulence which occurs on the infructescence, lower leaf surface, rachis and petioles of the leaves, and the caudate-tipped leaflets.

LINACEAE

Ochthocosmus berryi Steyerm., sp. nov. TYPE: Venezuela. Amazonas: tall forest along stream, NE shoulder at base of bluff, Cerro Aratitiyope, 90 km SW of Ocamo, 1,000 m, 26 Feb. 1984, *Steyermark, Berry & Delascio 130228* (holotype, VEN).

Arbor 8-metralis; foliis obovatis apice rotundatis retusis basi cuneatim angustatis 3.5–6.5 cm × 2–4 cm, marginibus utroque latere obsolete 6–7-crenulatis; inflorescentiis multifloris folio brevioribus epedunculatis vel pedunculatis usque 5 mm longis; sepalis inaequalibus quattuor 0.8–1 mm × 0.5 mm glanduliferis, sepalo quinto longiore 1.2–2.5 × 0.5–0.6 mm eglandulifero; petalis late obovatis 3.5 mm × 1.8 mm; filamentis 2–3.5 mm longis.

Tree 8 m tall. Leaves obovate, subcoriaceous, pale green below, rounded at the retuse apex, cuneately narrowed at base, 3.5–6.5 cm by 2–4 cm, dull green above with inconspicuous nervation, faintly nerved below, obscurely 6–7-crenately toothed along each margin; petioles 3–5 mm long. Inflorescence paniculate, many-flowered, the flowering portion 2.5–3 cm long, 2–3 cm broad, shorter than the leaves, epedunculate or the peduncle to 5 mm long, flowers white. Pedicels 1.2–2.5 cm long. Sepals unequal, 4 of them ligulate-oblong, rounded at apex, 0.8–1 mm by 0.5 mm, prominently glandular on the thickened margins; fifth sepal longer, ligulate-oblong, 1.2–2.5 mm by 0.5–0.6 mm, eglandular. Petals broadly obovate, rounded at apex, 3.5 mm by 1.8 mm. Filaments 2–3.5 mm long. Style 1.4–1.8 mm long, usually longer than the ovary. Ovary 1.1 mm long.

This species is related to *O. floribundus* Gleason, from which it differs in the shorter inflorescence, shorter than the leaves, inflorescence epedunculate or at most to 5 mm in length, the eglandular, elongated fifth sepal contrasting with the other four shorter glandular sepals, which are more prominently thickened and more abundantly glandular than in *O. floribundus,* and the relatively smaller and more broadly obovate petals.

The other species known from Territorio Federal Amazonas of Venezuela, *O. multiflorus* Ducke, together with its variations, is a small ligneous plant of the savannas with entire or nearly entire leaf margins. *Ochthocosmus berryi* is a tree in a woodland habitat.

RUTACEAE

Rutaneblina Steyerm. & Luteyn, gen. nov. TYPE: *R. pusilla* Steyerm. & Luteyn.

Inflorescentia terminalis multiflora subsessilis subcapitata. Flores actinomorphi hermaphroditi. Sepala 5 imbricata libera dorsaliter carinata inaequalia, exterioribus majoribus, petala 5 libera imbricata dorsaliter oblique carinata. Stamina 5, antheris basifixis, filamentis basi intus glanduliferis. Discus obsoletus. Pistillum sessile, stigmate capitato obscure 5-lobato, stylo simplici. Ovarium subglobosum, carpellis 5 basi connatis supra medium liberis unilocularibus. Ovulum in quoque locule solitarium. Folliculi 4–5 divaricati glabri, folia simplicia 3-verticillata. Fruticulus. Folia ternata, integerrima vel obscure crenulata, nervis lateralibus nullis.

Rutaneblina pusilla Steyerm. & Luteyn, sp. nov. TYPE: Venezuela. Amazonas: altiplanicie en la cumbre del brazo noroccidental, Cerro de la Neblina, al norte del campamento base a lo largo del Río Mawarinuma, afluente del Río Baria, 0°52–53′N, 66°05′W, 1,880 m, 8 Feb. 1984, *Steyermark 129798* (holotype, VEN). PARATYPE: same locality and date, *Luteyn 9451* (NY, VEN). Figure 6.

Frutex pusillus 0.7–1 metralis; foliis 3-verticillatis breviter petiolatis, obovatis apice truncatis vel subtruncatis mucronulatis basi acutis vel subacutis 1–2.5 cm longis 1–1.5 cm latis glabris; petiolis 1–2 mm longis; inflorescentia terminali 1.1 cm longa 1.3–1.5 cm diam. bracteata; bracteis lanceolatis 4–5 mm longis 1.2–1.5 mm latis; pedicellis 2 mm longis; bracteolis ovato-deltoideis acutis 1 mm longis; sepalis in fructu persistentibus non auctis, exterioribus ovato-triangularibus subobtuse acutis 2.1 mm × 1–1.5 mm, interioribus lanceolatis 2 mm × 1 mm, marginibus subscariosis; petalis elliptico-oblanceolatis subacutis 3–3.5 mm longis 1.1–1.5 mm latis intus utroque latere 4–6 nervis instructis; staminibus 2 mm longis, filamentis 1.4–1.5 mm longis glabris, antheris deltoideo-ovoideis apice obtuse apiculatis 0.7 mm longis; pistillo 1.5 mm longo, stylo 0.3 mm longo, ovario 1 mm longo 1.2 mm lato; folliculis rugulosis punctatis oblongis 7 mm longis 5 mm latis.

Low shrub 0.7–1 m tall with irregularly curving branches. Leaves 3-verticillate, with fragrance of bitter orange, coriaceous, rich green both sides with pale yellow-green midrib above, obovate, truncate or subtruncate at apex with mucro 0.5 mm long, narrowed to an acute or subacute base, 1–2.5 cm by 1–1.5 cm, glabrous, entire or obscurely crenulate, midrib sulcate above, elevated below, lateral nerves absent, tertiary venation minutely reticulate on both surfaces; petiole 1–2 mm long; inflorescence 1.1 cm long, 1.3–1.5 cm diam., subtended at base by a few bracts; bracts coriaceous, lanceolate, acute, carinate, 4–5 mm long, 1.2–1.5 mm wide; flowers subtended by bracteoles ovate-deltoid, acute, 1 mm long; pedicels 2 mm long, 1.5 mm wide; sepals dull lavender, unequal, the outer ovate-triangular, 2.1 mm by 1.4–1.5 mm, the inner lanceolate, 2 mm by 1 mm, subobtusely acute, dorsally carinate, margins slightly paler subscarious, persistent and not enlarged in fruit; petals creamy white, elliptic-oblanceolate, subacute, dorsally carinate, 3–3.5 mm long, 1.1–1.5 mm wide, the inner surface with a broad median portion and 4–6 lateral branches; stamens 2 mm long, anthers deltoid-ovoid, bluntly apiculate at apex, bilobed basally, filaments 1.4–1.5 mm long, 0.4 mm wide, glabrous with glandular patches at

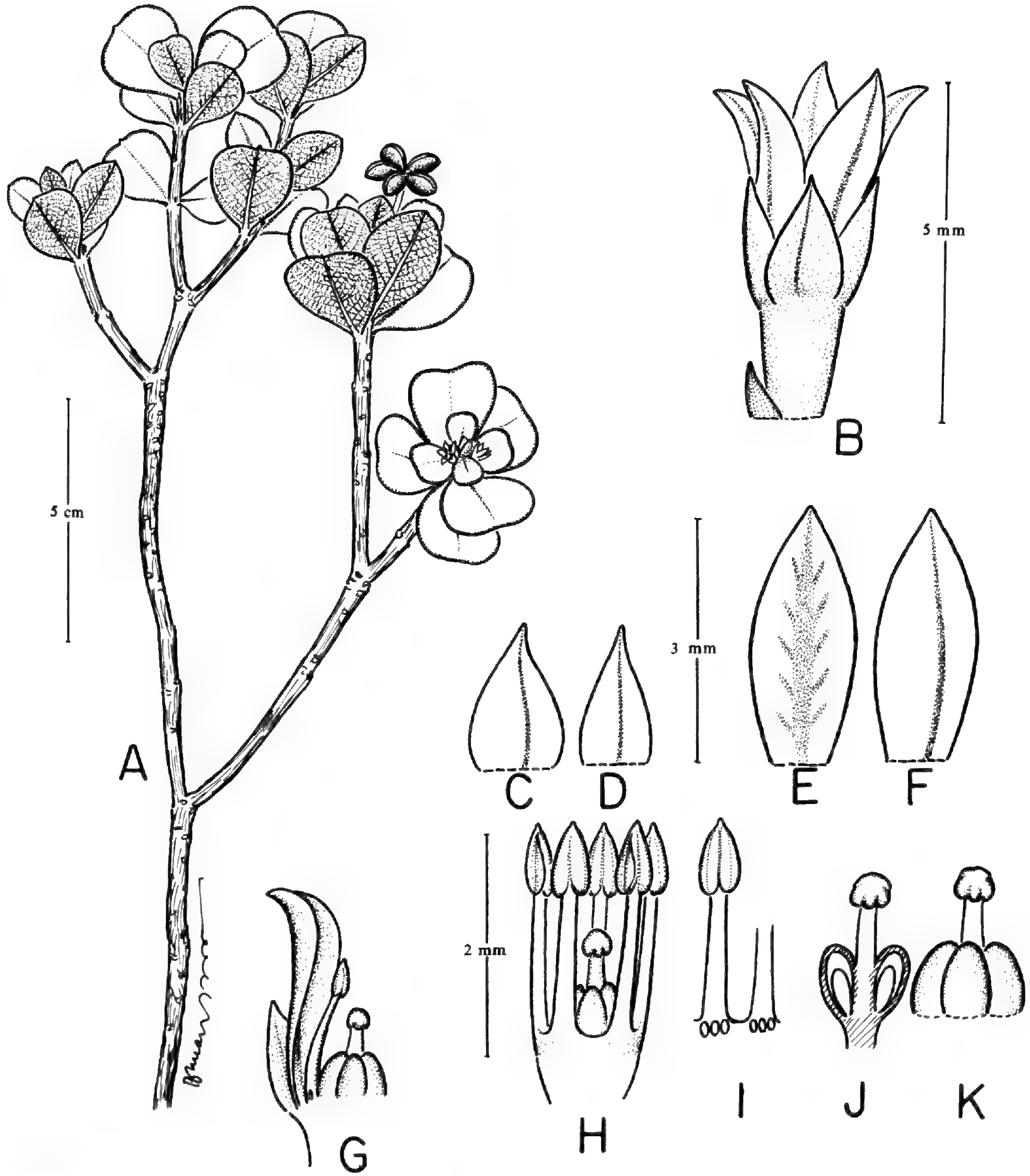

FIGURE 6. *Rutaneblina pusilla.*—A. Habit.—B. Flower, natural position.—C. Outer sepal, dorsal view.—D. Inner sepal, dorsal view.—E. Petal, ventral view.—F. Petal, dorsal view.—G. Portion of flower, showing relation of parts.—H. Stamens and pistil, with petals and sepals removed.—I. Portion of androecium, with glandular dark patches at base of filaments within.—J. Vertical section through gynoecium.—K. Gynoecium, natural position.

base within; gynoecium sessile, 1.5 mm long; stigma capitate, obscurely 5-lobulate, rounded, 0.3 mm long; style simple, 0.3 mm long; ovary subglobose, 1 mm high, 1.2 mm wide; fruit brown, the 4–5 divaricate follicles 7 mm long, 5 mm wide, glabrous, rugulose within.

This low shrub is common on the drier rocky elevation near the periphery of the summit, but also occurs in the slightly depressed and wetter valley portion. The inner portion of the cortex is orange and the leaves have a fragrance reminiscent of bitter orange.

The new genus cannot be placed generically in the treatment by Cowan (1967) of the Rutaceae of the Guayana Highland. Nor does it fit into any of the genera treated by Bentham and Hooker (1862) and by Engler (in Engler & Prantl, 1896). The genus is characterized by its combination of simple 3-verticillate leaves, 5 stamens equal in number to the imbricate sepals and petals, the free sepals and petals, the slightly unequal obliquely carinate sepals, the uniovulate 4–5 carpels connate below and free above, the follicular dehiscent spreading fruits, and the apparent absence of a disk which is represented apparently by only gland-like dark areas at the base of the filaments. The relationship of the genus is obscure and at this time not apparent.

Raveniopsis cowaniana Steyerm. & Luteyn, sp. nov. TYPE: Venezuela. Río Negro: Cerro de la Neblina, altiplanicie en la cumbre del brazo noroccidental, al norte del campamento base a lo largo del Río Mawarinuma, afluente del Río Baria, 0°52–53′N, 66°5′W, 1,880 m, 7–8 Feb. 1984, *Luteyn 9413* (holotype, VEN; isotype, NY). PARATYPE: same locality and date, *Steyermark 129814* (VEN).

Planta sublignea, caule simplici 0.3 m alto apicem versus dense pubescenti; foliis digitate trifoliatis, foliolis oblanceolatis 1.5–3.8 cm × 0.5–1.1 cm supra glabris valde sulcatinervis subtus dense lanuginosis pilis simplicibus munitis; inflorescentia coarctata subsessili 1–2 cm longa, pedunculo 1–5 mm longo dense pubescenti; corolla rubra 15 mm longa (tubo 7 mm × 2–3 mm sparse pilosa pilis simplicibus reflexis munito; lobis duobus anguste lanceolatis 4 mm × 1–1.5 mm; lobis tribus oblongo-vel obovato-ellipticis 5 mm × 3–3.5 mm extus sparse pubescentibus pilis simplicibus reflexis munitis).

Subligneous, simple-stemmed plant, 0.3 m tall; leaves revolute, dark green above with sulcate nerves, buff-woolly below, digitately trifoliate, shortly petiolate to subsessile; leaflets oblanceolate, subacute to obtusely acute or mucronate at apex, sensibly narrowed to the base, 1.5–3.8 cm by 0.5–1.1 cm, glabrous, strongly sulcate-nerved and strongly punctate above, densely buff woolly below; petiole well-developed; inflorescence terminal, subterminal, or axillary, subsessile or shortly pedunculate, congested, cincinnate, unilaterally racemose, 1–2 cm long; peduncle 1–5 mm long, densely woolly pubescent; flowers sessile or pedicellate to 2 mm long; calyx lobes 5 unequal, imbricate, densely buff-olive pubescent, the outer two lobes broadly lanceolate, 9–11 mm by 3–4 mm, the interior 3 lobes narrowly lanceolate, subacute, 5 mm by 1.5–2 mm; calyx tube 1–2 m long; corolla red, 15 mm long, zygomorphic with 2 narrower and 3 broader lobes, tube cylindric, 7 mm by 3 mm except 2 mm wide at base, sparsely pilose with simple reflexed hairs, the 2 narrower lobes narrowly lanceolate, 4 mm by 1–1.5 mm, the 3 broader lobes oblong- or obovate-elliptic, subacute, 5 mm by 3–3.5 mm, pubescent without, exterior pubescent with simple, sparse, reflexed hairs, interior of corolla tube 5-ridged with thickened pubescent ridges; fertile anthers lanceolate, narrowed to apex, 2 mm by 0.6 mm, filaments 0.6 m long; ovary depressed-subglobose, 1.5 mm long; style 10 mm long; stigma capitate.

The only other known trifoliate species of *Raveniopsis* are *R. trifoliolata* Cowan of Cerro de la Neblina and *R. stelligera* Cowan of Cerro Yutaje. The new taxon here described from Cerro de la Neblina differs from *R. stelligera* in the simple pubescence with much longer corollas and petioles, and from *R. trifoliolata* in the congested, short, densely pubescent inflorescence, smaller, narrower leaves with very short or even subsessile petioles, deeply sulcate upper leaf surface, and densely pubescent lower leaf surfaces and upper portion of the stems.

The species commemorates the name of Dr. Richard S. Cowan, for his excellent work on the genus *Raveniopsis* and other genera of Rutaceae of the Guayana Highland.

NOTE ON *RAVENIOPSIS FRATERNA* AND *R. SERICEA*

Raveniopsis fraterna Cowan is distinguished from *R. sericea* Cowan on the basis of its longer corolla tube (9 mm), larger calyx (5.5 mm by 3 mm), together with its tomentose branchlets and lower leaf surface, as contrasted with the smaller corolla tube (5.5 mm), smaller calyx (3–3.5 mm by 2–3 mm), together with the sericeous pubescence of stems and lower leaf surface of *R. sericea.* Cowan (in Maguire et al., 1960: 32) states that paratypes of *R. sericea* (*Steyermark & Wurdack 811* and *Steyermark 75905*) do not conform to the uniform type of tomentum shown by the type collection (*Steyermark & Wurdack 646*) from Chimantá. The collections of *Steyermark et al. 128764* and *128902* from Chimantá Massif have the smaller measurements of *R. sericea,* but it is doubtful if the two taxa can be maintained separately as species. It is probable that only one taxon can be recognized which varies in size of calyx and corolla and type of tomentum.

EUPHORBIACEAE

Phyllanthus jablonskianus Steyerm. & Luteyn, sp. nov. TYPE: Venezuela. Amazonas: Río Negro, Cerro de la Neblina, altiplanicie en la cumbre del brazo noroccidental, al N del campamento base a lo largo del Río Mawarinuma, afluente del Río Baria, 0°52–53'N, 66°5'W, 1,880 m, 8 Feb. 1984, *Steyermark 129816* (holotype, VEN; isotype, NY). PARATYPE: same locality and data, *Luteyn* (VEN, NY). Figure 7A–E.

Suffrutex 0.2–0.4-metralis; ramificatione phyllanthoidea; foliolis ellipticis, obovati-ellipticis vel anguste oblanceolatis apice rotundatis basi acutis vel obtusis glandulis hypophyllis destitutis 10–25 mm × (3–)6–9 mm supra nitidis; *floribus masculinis*: laciniis calycinis ligulato-oblongis 1.5 mm × 0.8 mm, disco 6 glanduloso, glandulis distinctis, quadrato-oblongis; staminibus 3, antheris 0.2 mm longis thecis globosis, filamentis liberis laciniis calycinis brevioribus; *floribus foemineis*: disco annulari undulato subcarnoso, laciniis calycinis 6 suborbicularibus apice rotundatis 1.8–2 mm × 1.2–1.5 mm; stylis 3 ad basin profunde bifidis 1.2 mm longis; capsulis 5–6.5 mm diam.

Wiry-stemmed shrub 0.2–0.4 m tall; leaflets elliptic to obovate-elliptic or narrowly oblanceolate, rounded at apex, narrowed to an acute or obtuse base, 10–25 mm by (3–)6–9 mm, 2–3.5 (rarely 5) times longer than broad, lustrous and prominently impressed-nerved above, less impressed-nerved below, lateral nerves 4–5 each side, sublaminal gland absent; petioles 1–2 mm long; *staminate flowers*: solitary or 2–3-fasciculate, 3.5–3.8 mm diam., 6 segments spreading, ligulate-oblong, 1.5 mm by 0.8 mm; disk with 6 distinct quadrate-oblong glands rounded-truncate at distal end, 0.4 mm by 0.3 mm; 3 anthers 0.2 mm long with globose anther sacs 0.4 mm wide; filaments free, stout, 0.8 mm long, shorter than the perianth segments; pedicels filiform, 2–5 mm long; *pistillate flowers*: 3 mm high, 4 mm across, 6 perianth segments ascending, suborbicular, rounded at apex, 1.8–2 mm by 1.2–1.5 mm; pedicel 8–10 mm long in anthesis, 10–15 mm long in fruit; 3 styles deeply bifid to the base, each style subulate, spreading, 1.2 mm long; ovary subglobose 1.3 mm diam., disk annular, 6-undulate-lobulato, 2 mm across at base of ovary; capsule subglobose, 6 mm high, 5–6.5 mm diam., the style and columella persistent; mature seeds 3-sided, dorsally convex, lateral sides flat, 2.1–2.5 mm long, 1.5–2 mm broad, smooth.

From *P. maguirei* Jabl. of Neblina the new taxon differs in the broader leaflets mainly 2–3.5 times longer than broad which are mainly obovate-elliptic to elliptic, and in the well-developed pistillate disk. From *P. neblinae* Jabl., also of Neblina, this new taxon differs in the much narrower, non-emarginate leaflets which are usually elliptic to obovate-elliptic and lustrous above. In leaflet shape, conspicuous nervation and lustrosity above, it resembles *P. longistylus* Jabl., but lacks the long style and sublaminal gland of that species. Additionally, it differs from *P. strobilaceus* Jabl. in the short anthers with globular anther sacs and free styles bifid to the base.

The species commemorates the name of the dedicated worker on the Euphorbiaceae of the Guayana Highland, Dr. Eugene Jablonski.

Phyllanthus vacciniifolius (Müll.-Arg.) Müll.-Arg. subsp. **vinillaensis** Steyerm., subsp. nov. TYPE: Venezuela. Amazonas: Serrania Vinilla, N of Cerro Aratitiyope, on sandstone scrub-covered slopes, 440 m, 1 Mar. 1984, *Steyermark, Berry & Delascio 130328* (holotype, VEN). Figure 7F–I.

A *P. vacciniifolius* ramulis deciduis usque 13 cm longis, foliolis 15–30 gerentibus recedit.

Shrub or treelet 2–2.5 m tall, branchlets with 15–30 leaflets, to 13 cm long; leaves broadly obovate, rounded at apex, acutely narrowed to base, 7–12 mm by 5–9 mm, laminal gland on lower side 1.5 mm below apex, lateral nerves 7–10 each side; petiole 1.5 mm long; *staminate flower*: pedicel 1.5 mm long, outer perianth segments 2.1 mm by 1.8 mm, inner ones 2.1 mm by 1 mm; 3 anthers narrowly oblong, long-apiculate, nearly 3 times longer than wide, filaments scarcely developed, disk glands 3 separate, subreniform; *pistillate flower*: pedicel 4.5–5 mm long; outer perianth segments 2.2 mm by 0.8 mm, inner ones 2.5–1.1 mm; ovary continuing into a conic style, 1.5 mm long, style 1 mm long, 6 disk glands 0.4 mm long, separated, shallowly crenulate on summit; capsule subglobose, 3 mm high, 4 mm diam.

This new subspecies is disjunct in its distribution, where it is isolated in the Territorio Federal Amazonas. Typical *P. vacciniifolius* is otherwise known only from the sandstone table mountains and the Gran Sabana of Estado Bolívar in eastern Venezuelan Guayana. The subspecies *vinillaensis* has the same elongate extension of the anthers, the erect short conical style,

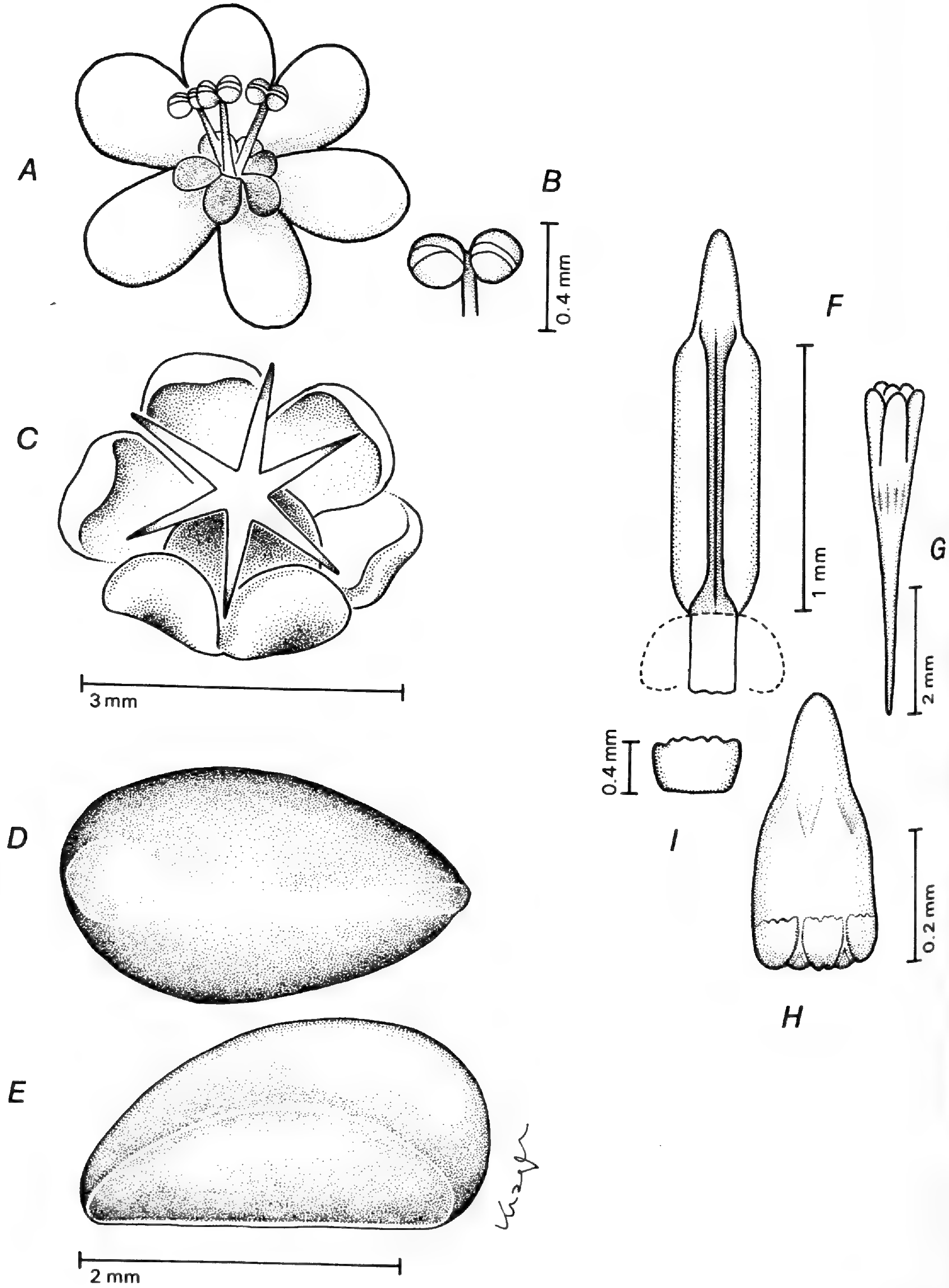

FIGURE 7. *Phyllanthus.* A–E. *P. jablonskianus.*—A. Staminate flower.—B. Stamen.—C. Pistillate flower.—D. Seed, ventral view.—E. Seed, dorsal view. F–I. *P. vacciniifolius* subsp. *vinillaensis.*—F. Stamen with disk gland indicated by dashed lines.—G. Pistillate flower with pedicel.—H. Pistil, showing disk glands in place.—I. One of disk glands.

and the same size and shape of the leaflets of typical *P. vacciniifolius.* It differs in the number of leaflets on the deciduous branchlets, these varying from 15–30, whereas in typical *P. vacciniifolius* the leaflets vary from 5–15(–20), although Jablonski (in Maguire et al., 1967: 89) placed that species in the part of the key having "deciduous branchlets with 5–12 leaflets." *Phyllanthus strobilaceus* Jabl. has 20–30 leaflets on the deciduous branchlets, thus simulating subsp. *vinillaensis,* but the anthers are rounded at the summit and the style is depressed and 3-lobed instead of erect and conical.

OCHNACEAE

Perissocarpa Steyerm. & Maguire, gen. nov. TYPE: *P. steyermarkii* (Maguire) Steyerm. & Maguire.

Flores sessiles vel fere sessiles. Sepala 3 plus minusve persistentia. Petala 5 valde imbricata alba. Stamina 5. Stylus brevis simplex conicus basi latus. Fructus indehiscens lignescens non lobatus 2–3-locularis. Arbor vel frutex.

The name is derived from *perissos* = odd, in the sense of different or extraordinary, and *karpos* = fruit.

The new genus is related to *Elvasia,* but that genus has the flowers distinctly pedicellate, sepals quickly deciduous in anthesis, yellow petals, more numerous stamens (7–25), an elongated filiform or subulate style, and a distinctly 5-lobed fruit.

Elvasia steyermarkii Maguire (1968: 297, fig. 6) was described from flowering material collected from the Peninsula of Paria, Estado Sucre, Venezuela, by Steyermark and Rabe in 1966. Because of its reduced number of stamens, Sastre (pers. comm.) doubted its placement in the genus *Elvasia.* Subsequently, fruiting specimens from the summit of Cerro Sarisarinama and Jaua in the Venezuelan Guayana and from the state of Táchira, Venezuela, were collected between 1974 and 1981, but remained unrecognized as to either family or genus until 1982 and 1983, when newly collected flowering material provided evidence of the conspecificity between the flowering and fruiting specimens.

A study of the specimens known at the present time reveals the existence of at least two species and one subspecies. One of the undescribed species occurs on the summits of some of the sandstone table mountains of the Guayana while a new subspecies, related to the taxon of the northeastern portion of Venezuela, occurs in the sandstone hills of the state of Táchira in the western Venezuelan Andes.

KEY TO THE SPECIES OF *PERISSOCARPA*

1. Inflorescence umbellately or subumbellately branched, epedunculate; apex of the petals subtruncate, broadly rounded, or very slightly emarginate; petiole 1–8 mm long .... *P. umbellifera*
1. Inflorescence paniculately branched, pedunculate; apex of petals deeply emarginate; petiole 5–25 mm long 2
   2. Petals with a narrow sinus at apex, 2 mm wide above the middle, 3.5–4 mm long; plants of northeastern Venezuela .... *P. steyermarkii* subsp. *steyermarkii*
   2. Petals with a broad sinus at apex, 4–5 mm wide above the middle, 3 mm long; plants of the western portion of the Andes of Venezuela .... *P. steyermarkii* subsp. *tachirensis*

Perissocarpa steyermarkii (Maguire) Steyerm. & Maguire, comb. nov. *Elvasia steyermarkii* Maguire, Acta Bot. Venez. 3: 297. fig. 6. 1968.

Tree 8–15 m. Leaf-blades oblong-obovate to broadly elliptic, rounded to acuminate at apex, cuneately narrowed at base, 9–18 cm long, 4–10 cm wide; petioles 1–2.5 cm long. Inflorescence paniculate, in anthesis to 15 cm long, in fructification 15–23 cm long with 6–12 ascending axes 3–8 cm long; peduncle stout in fructification, 3.5–10 cm long, 3–6 mm diam. Flowering axes subspicate, densely flowered, pedicels very short, ca. 1 mm long. Sepals ovate-oblong, suborbicular, or oblong-subpandurate, apex incurved with a bilobate scarious appendage, 3–4 mm long, 1.5–2 mm wide, at first erect, at length reflexed. Petals white, suborbicular- to rhomboid-obovate, broadest above the middle, narrowed to base, emarginate or bilobate at apex with a narrow to broad sinus, strongly incurved-imbricate, convolutely adherent, 3–4 mm long, 2–5 mm wide above the middle. Stamens with filaments 0.3–0.5 mm long, anthers 1.2–2 mm long. Style 0.5–0.8 mm long. Fruit ferruginous-brown, subglobose-pyriform, when mature 1.5–1.6 cm long (high), 1.5–2 cm broad. Seeds 3, trigonous, 1.5 cm long, 1.5 cm broad.

KEY TO THE SUBSPECIES OF *PERISSOCARPA STEYERMARKII*

Petals narrowly emarginate at apex, 2 mm wide above the middle, 3.5–4 mm long, plants of northeastern Venezuela .... *P. steyermarkii* subsp. *steyermarkii*

Petals broadly emarginate at apex, 4–5 mm wide above the middle, 3 mm long; plants of the western portion of the Andes of Venezuela .... *P. steyermarkii* subsp. *tachirensis*

Perissocarpa steyermarkii (Maguire) Steyerm. & Maguire subsp. **steyermarkii**, *Elvasia steyermarkii* Maguire, Acta Bot. Venez. 3: 297. fig. 6. 1968. TYPE: Venezuela. Sucre: Cerro de Humo between Los Pocitos and La Roma, Peninsula de Paria, 700–800 m, 11 Aug. 1966, *Steyermark & Rabe 96342* (holotype, NY; isotype, VEN).

Distribution: evergreen forests of the Peninsula de Paria, Estado Sucre, and Cerro Turumiquire, Estado Monagas, northeastern Venezuela.

Specimens examined. VENEZUELA. SUCRE: Cerro de Humo between Los Pocitos and La Roma, Peninsula de Paria, 700–800 m, 11 Aug. 1966, *Steyermark & Rabe 96342* (holotype, NY; isotype, VEN). MONAGAS: Acosta, Serrania del Turumiquire, altiplanicie en la Fila de Montana, cabeceras del Río Negro (afluente del Río Colorado) en el borde sur de la meseta, 10°02'N, 63°52'W, 1,600 m, 12 May 1982, *Huber, Canales & Vasquez 6317* (VEN).

Perissocarpa steyermarkii subsp. **tachirensis** Steyerm. & Maguire, subsp. nov. TYPE: Venezuela. Táchira: between dam site and narrow ridge, along Río San Buena, wooded sandstone hills, area of Presa Las Cuevas (Desarrollo Dorados Camburito y Complimentario Agua Linda), ca. 10 km E of La Fundación, 7°47–48'N, 71°46–47'W, 550–600 m, 21 June 1981, *Steyermark & Manara 125174* (holotype, VEN). Figure 8.

A subsp. *steyermarkii* petalis supra medium 4–5 mm latis apice bilobato sinu lato recedit.

Distribution: sandstone slopes in evergreen forest, foothills of the southwestern-facing slopes of the Andes, 450–1,000 m, Estado Táchira, western Venezuela.

Specimens examined. VENEZUELA. TACHIRA: Uribante, forest along road from La Siberia to entrance to Las Cuevas Represa, 10 July 1983, *van der Werff & Gonzalez 5282* (MO, VEN); on Río San Buena, 10 km W of La Fundación around Represa Dorada, 700–1,000 m, 7°47–48'N, 71°46–47'W, 13–15 Mar. 1980, *Liesner, Gonzalez & Smith 9655* (MO, VEN); 10 (airline) km ESE of La Fundación, 23 km by road, around Represa Dorada, 0–3 km below dam, 459–650 m, 7°47'N, 71°46–47'W, 29 Apr. 1981, *Liesner & Guariglia 11577* (MO, VEN), 600–900 m, 30 Apr. 1981, *Liesner & Guariglia 11593* (MO, VEN), 600–1,000 m, 10–13 Mar. 1981, *Liesner & Gonzalez 10249* (MO, VEN); between dam site and narrow ridge, along Río San Buena, area of Presa Las Cuevas, ca. 10 km E of La Fundación, 7°47–48'N, 71°46–47'W, 550–600 m, 21 June 1981, *Steyermark & Manara 125174* (holotype, VEN).

Perissocarpa umbellifera Steyerm. & Maguire, sp. nov. TYPE: Venezuela. Amazonas: Cerro Duida, between rim and camp, occasional along ridge trail from Culebra, Río Cunucunuma, 1,400 m, 18 Nov. 1950, *Maguire, Cowan & Wurdack 29529* (holotype, VEN; isotype, NY).

Frutex 1.5–3-metralis; foliis obovato-ellipticis, elliptico-oblongis vel late oblongis apice rotundatis truncatis vel obtusis mucronulatis basi cuneatim acutis vel obtusis 2.5–11 cm longis 1.8–6 cm latis; petiolis 1–8 mm longis; inflorescentia sessili subumbellatim ramosa expedunculata 2–6.5 cm longa, axibus 3–9 valde adscendentibus 2–6 cm longis; floribus brevipedicellatis, pedicellis 0.5 mm longis; sepalis suborbiculari-ovatis 2 mm longis; petalis flabellatis apice nihil vel leviter emarginatis 2.5 mm longis apice 2.5–3 mm latis; fructu subgloboso-pyriformi 6–11 mm longo 8–11 mm lato (immaturo).

Shrub 1.5–3 m tall. Leaves alternate, opposite, or pseudo-verticillate, elliptic-oblong, broadly elliptic to subovate-oblong, rounded, truncate, or obtuse at the mucronulate apex, cuneately acute to obtuse at base, 2.5–11 cm long, 1.8–6 cm wide, midrib subelevated below, finely impressed above; petioles 1–8 mm long. Inflorescence terminal, sessile, epedunculate, subumbellately branched with 3–9 strongly ascending, candelabra-like axes 2–6 cm long, 2–5 mm thick, the rachis 1–2 mm thick, closely flowered from base to apex. Floral bracts triangular-lanceolate to triangular-ovate, acute to long acuminate, 1.5–2 mm long, 0.5–1.2 mm wide. Pedicels 0.5 mm long. Sepals suborbicular, rounded, incurved, eventually reflexed, 1.5 mm long, 1.3–1.5 mm wide. Petals white, flabellate, scarcely or not at all emarginate at apex, 2.5 mm long, 2.5 mm wide at apex. Fruit brown, rugulose, immature, subglobose-pyriform, 6–11 mm long, 6–11 mm broad.

Distribution: dwarf forest and rocky openings on sandstone mesetas of the Venezuelan Guayana in Territorio Federal Amazonas (Sipapo, Duida) and Estado Bolívar (Sarisarinama) at altitudes of 1,250–1,400 m.

Specimens examined. VENEZUELA. BOLÍVAR: Cerro Sarisariñama, cumbre, porción noreste, 4°41'40"N, 64°13'20"W, 1,410 m, 10 Feb. 1974, *Steyermark, Carreño & Brewer-Carías 108902* (VEN), 14 Feb. 1981,

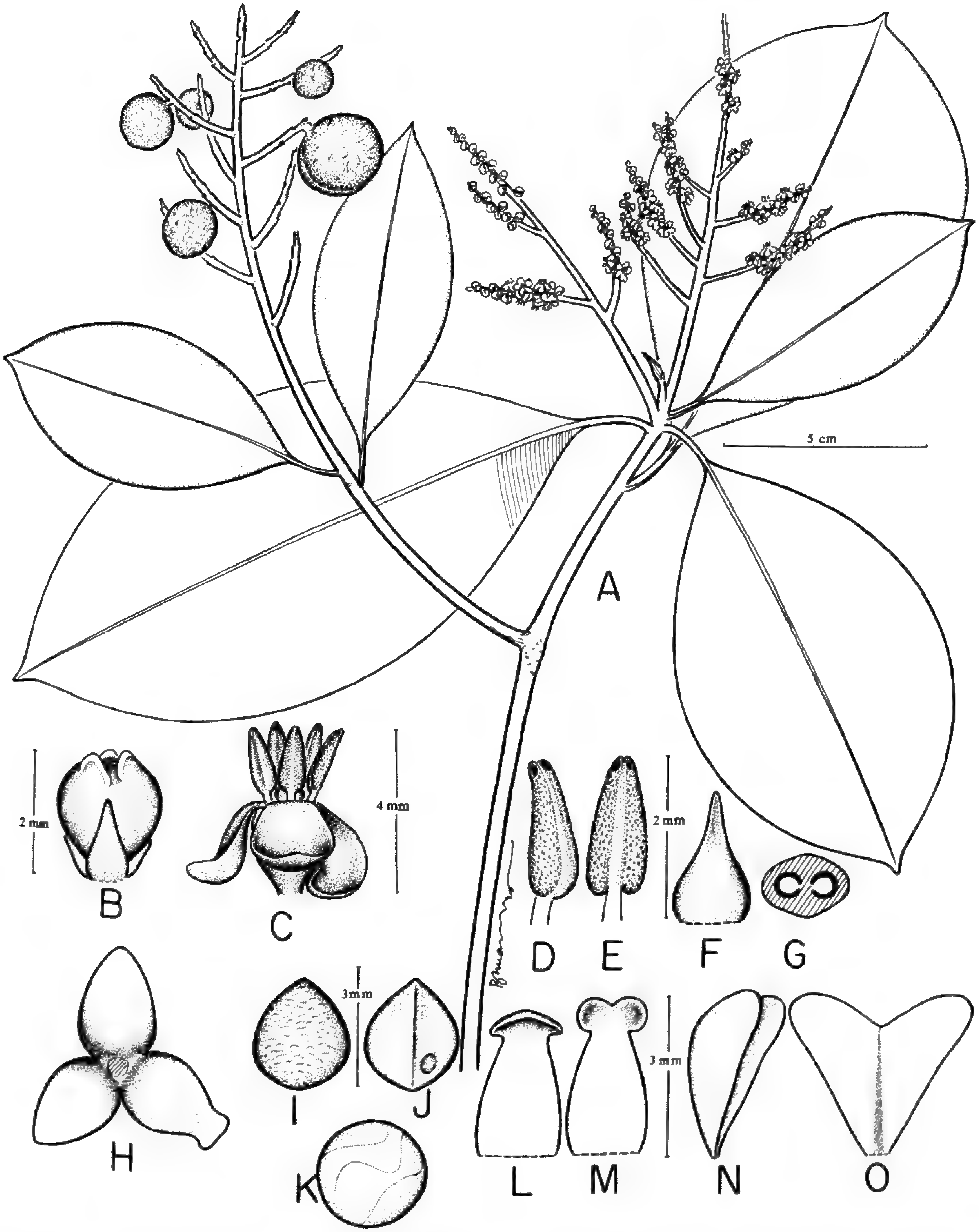

FIGURE 8. *Perissocarpa steyermarkii* subsp. *tachirensis.*—A. Habit of branch with inflorescence and infructescence.—B. Flower in late bud.—C. Flower, late anthesis, natural position.—D, E. Stamen.—F. Pistil.—G. Cross-section of ovary.—H. Calyx, dorsal view.—I. Seed, dorsal view.—J. Seed, ventral view.—K. Corolla in bud.—L. Calyx lobe, interior view showing involute appendage.—M. Calyx lobe, exterior view.—N. Petal, lateral view.—O. Petal, ventral view.

Steyermark, Liesner & Brewer-Carias 124300 (VEN). AMAZONAS: Cerro Sipapo (Paraque), lower Caño Negro, 1,400 m, 11 Jan. 1949, *Maguire & Politi 28091-A* (NY, VEN); Cerro Duida, between rim and camp, occasional along ridge trail from Culebra, Río Cunucunuma, 1,400 m, 18 Nov. 1950, *Maguire, Cowan & Wurdack 29529* (holotype, VEN; isotype, NY); arriba de la Culebra, 1,250 m, Oct. 1983, *Colonnello 738* (VEN).

Tyleria breweriana Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Sucre, Meseta de Jaua, cumbre, sección oriental-central, afloramientos de piedra arenisca en sitios expuestos con vegetación herbacea y arbustos achaparrados, 4°35′N, 64°15′W, 2,020 m, 14 Feb. 1981, *Steyermark, Brewer-Carías & Liesner 124326* (holotype, VEN). Figure 9.

Frutex 1–1.5 m altus glaberrimus, ramis negris 3–3.5 mm diam.; foliis petiolatis, petiolis 1.5–2 cm longis 1 mm latis; stipulis membranaceis lineari-lanceolatis aristatis 2.5 cm longis 4 mm latis integris valde convolutis caducis; laminis late ellipticis longiaristatis, arista 4–8 mm longa, basi cuneatim decurrentibus 4–5 cm longis 1.7–2.2 cm latis, marginibus minute confertimque adpresso-serrulatis glabris; inflorescentia erecta, 5-flora 3 cm longa; calyce quincunciali, sepalis 5, ovato-oblongis apice obtusis vel rotundatis 7 mm longis 3–4 mm latis; petalis albis ad centrum flavis 5 obovato-oblongis 15 mm longis 10 mm latis.

Tyleria breweriana belongs to the aristate-leaved group of species represented by *T. aristata, T. pendula,* and *T. tremuloidea* of Cerro de la Neblina of Venezuela and *T. silvana* of adjacent Brazilian Serra Pirapucú. It appears most closely related to *T. pendula* Maguire & Wurd., from which it differs in its erect, few-flowered, shorter inflorescence, shorter, broadly elliptic leaf blades, and shorter petioles.

This is the second species of *Tyleria* to be recorded from the Meseta de Jaua, the first being *T. phelpsiana* Maguire & Steyerm. (in Steyermark et al., 1972: 868. fig. 9), a species of quite different leaf morphology of the group related to *T. floribunda* and *T. spathulata* of Cerro Duida.

The following key is presented to indicate the position of *T. breweriana* with respect to the other known members of the aristate-leaved group.

KEY TO THE SPECIES OF *TYLERIA*

1\. Leaves sessile; petals 15–20 cm long, rose or pink .... *T. spectabilis*
1\. Leaves petiolate; petals 4 cm or less long, white or white with yellow at base 2
  2. Sepals acute to subacute at apex 3
    3. Sepals glandular-scarious at apex; arista of leaf blade 16–22 mm long .... *T. silvana*
    3. Sepals non-glandular at apex; arista of leaf-blade 5–8 mm long 4
      4. Flowers solitary; petals 1.6–1.8 cm long, 0.8–1 cm wide; petiole 3–5 mm long; pedicels 7–9 mm long .... *T. aristata*
      4. Flowers 2–4, racemose; petals 2.5–4 cm long, 1.8–3 cm wide; petiole 1.2–1.8 cm long; pedicels 12–15 mm long .... *T. tremuloidea*
  2. Sepals obtuse to rounded at apex 5
    5. Inflorescence pendulous, many-flowered, 10–15 cm long; leaf blades 7–11 cm long, oblanceolate; petiole 2–4 cm long .... *T. pendula*
    5. Inflorescence erect, 5-flowered, 3 cm long; leaf blades 4–5 cm long, broadly elliptic; petiole 1.5–2 cm long .... *T. breweriana*

NOTES ON *ADENANTHE BICARPELLATA*

This monotypic genus, endemic to the summit of the Chimantá Massif, Estado Bolívar, of the Venezuelan Guayana, shows quantitative variation in both vegetative and floral characters. A recent collection from the summit of the Macizo de Chimantá (*Steyermark, Huber & Carreño 128637*) manifests maximum extremes of measurements. The plants noted here grew in dense thickets of moist forest along a small stream on Amuri-tepui, one of the sectors of Chimantá Massif. In such forested habitats plants of *Adenanthe* attain a height of 5 m as contrasted with a usual height of 1–2 m. Correlated with the greater size of the plants are larger leaves, stipules, and fruits, as well as an increase in the relative number of flowers with a greater degree of branching of the inflorescence and with the lateral axes branched from the base; normally the inflorescence is unbranched.

These quantitative differences may be appreciated when one compares the measurements taken from collections originating from the usual open or savanna-like habitats of the species on Chimantá Massif with those from the wet forests.

Open or savanna-like habitats	*Collection of Steyermark, Huber & Carreño 128637 from wet forest*
Petals 1.5 cm by 0.8–1 cm	2.3 cm by 1.3 cm
Sepals 5–8 mm long	8–12 mm long
Anthers 3.5–4 mm long	4–6 mm long
Stipules 8–10 mm by 7 mm	20–27 mm by 8–15 mm
Leaves 2.5–4.5 cm by 1–2 cm	10–13 cm by 3–4 cm
Inflorescence 5–15 cm by 5–6 cm	15–22.5 cm by 7 cm
Inflorescence bears 7–10 lateral axes	Inflorescence bears 10–12 lateral axes
Lateral axes usually unbranched	Lateral axes branched
Inflorescence 17–22-flowered	Inflorescence up to 50-flowered
Capsule 8–14 mm	Capsule 16–18 mm long

Such differences, at first glance, might indicate that the collection of *Steyermark, Huber & Carreno 128637* merits some taxonomic recognition. However, most of these apparent differences break down when other specimens originally included in the type description of this taxon (Maguire et al., 1961, fig. 27: A, B) are examined. In only two characters, i.e., the much larger stipules and the larger capsules, does the *Steyermark et al. 128637* collection manifest any noteworthy contrast. Such contrasts may be the result of development in the more shaded and moister forest habitat instead of the more exposed, often drier ambience under which *A. bicarpellata* usually occurs. Pending future observations and a more intensive study of the different habitats in which this species occurs, no separate taxonomic category is being established at present for this unusually robust collection of *Adenanthe.*

THEACEAE (BONNETIACEAE)

Acopanea Steyerm., gen. nov. TYPE: *A. ahogadoi* Steyerm.

Fruticulus demissus. Folia basalia rosulata ut videtur enervata in sicco multi parallelo-pinnato-nervia. Caulis florifer simplex reptans radicans horizontalis vel leviter decumbens bracteatus. Bracteae foliosae subsecundae 1–2 flores gerentes. Flores pedicellati, quoque pedicello terete unibracteato et 3-bracteolis subtendenti. Sepala inaequalia. Stamina numerosa uniseriata, filamentis monadelphis basaliter ad membranam affixis. Ovarium 3-loculare, placentatione axillari gemina, stylo 3-partito. Capsula septicidalis. Semina lineari-oblonga 1–3 anguste alata.

Restricted to Acopán-tepui of the Chimantá Massif of southeastern Venezuelan Guayana.

Acopanea ahogadoi Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Piar, Macizo del Chimantá, sector SEE, altiplanicie suroriental del Acopán-tepui, cabeceras del Río Arauac, praderas humedas sobre turberas, 5°11′N, 62°00′W, 1,920 m, 14–16 Feb. 1984, *Steyermark, Luteyn & Huber 129924* (holotype, VEN; isotype, NY). PARATYPE: same locality and date, *Huber, Steyermark & Luteyn 9023* (VEN, NY). Figure 10.

Planta pusilla, caule brevi ligneo 2–11 cm longo 1–2 cm crasso apice foliis rosulatis coronato; foliis adscendentibus supra sordido-viridibus subtus glaucifarinosis marginibus pallido-purpureis naviculatis subinvolutis elliptico-lanceolatis vel elliptico-oblanceolatis apice subobtusis vel obtuse acutis basi paullo angustatis, 4.5–8.5 cm longis 0.8–2 cm latis, subtiliter paralleloneuris infra medium pinnatinervatis, praecipue marginibus superioribus minute ciliolato-serrulatis glanduliferis, ciliis caducis; inflorescentia basi vel infra rosulam foliorum exorienti, caule elongato reptanti radicanti simplici vel semel ramoso 55–70 cm longo 2 mm lato supra medium vel parte superiore 3–13 bracteis foliosis instructa; bracteis alternis oblanceolatis vel lanceolatis acutis vel subacutis coriaceis 1.5–7 cm distantibus 1–2(–3) cm longis 3–6(–9) mm latis, marginibus minute serrulatis; pedicellis 2–5 mm longis 1.5–2 mm latis; bracteolis 3 naviculatis vel dorsaliter obtuse carinatis ligulatis vel lineari-lanceolatis apice abrupte breviter cuspidatis 4.5–5 mm longis 1.2–1.3 mm latis dentibus 1–2-setulosis adscendentibus instructis; sepalis vinaceo-rubris vel marronionis exterioribus duobus ovatis acuminatis 7 mm × 3 mm, ceteris late oblongo-ellipticis 7.5 mm × 3.5–4 mm, fructiferis 20–25 mm × 6–7 mm; petalis albidis roseolisque late flabelliformibus apice late rotundatis vel subtruncatis basin versus angustatis 10–13 mm longis supra medium 11–16 mm latis basi 2 mm latis; staminibus numerosis, filamentis albidis 1.5–2.5 mm longis basaliter ad membranam 1.5 mm longam affixis; antheris aureis suborbicularibus 0.7–0.8 mm longis 0.8 mm latis; ovario anguste ovoideo 3–3.5 mm × 1.5–2 mm glabro; styli ramis albidis divaricate adscendentibus 1.8–2 mm longis; stigmatibus truncatis apice breviter fimbrillatis; capsula sublignea subcoriacea ovidea 2–2.2 cm × 1–1.2 cm, mesocarpio subligneo 2–3 mm crasso; seminibus anguste oblongis una extremitate truncata cetera extremitate acutate obtusa 1.5

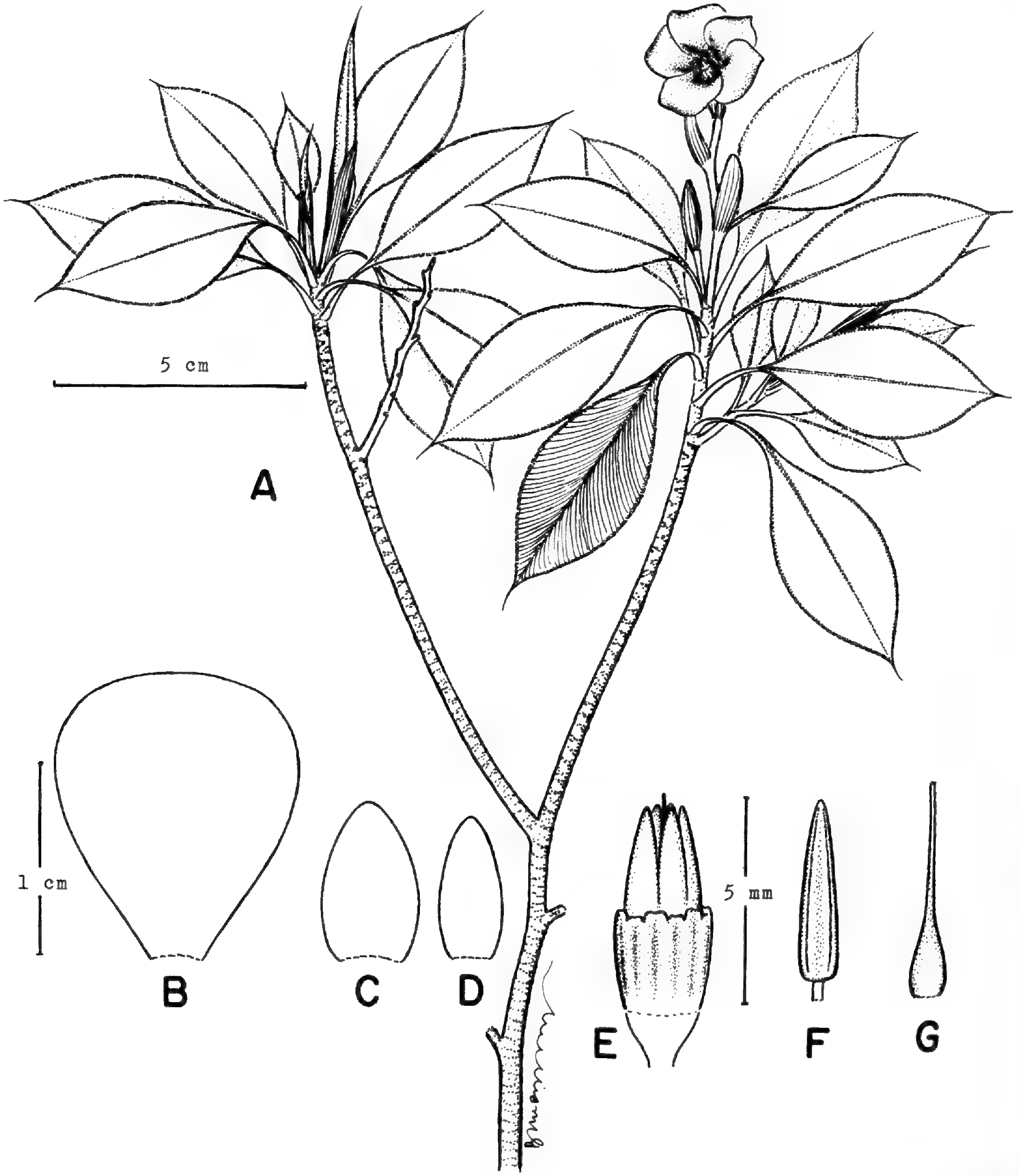

FIGURE 9. *Tyleria breweriana.*—A. Habit of flowering branch.—B. Petal.—C. Outer sepal.—D. Inner sepal.—E. Upper half showing natural position of stamens, lower half showing staminodia united, 5 larger ones alternating with 5 smaller.—F. Stamen.—G. Pistil.

mm × 0.5 mm 1–3 anguste porcatis vel alatis, pagina minute punctata.

This unusual species is dedicated to Antonio Ahogado, who is chief of the planning program for the Electrification of the Caroni river basin of the state of Bolívar in Venezuela, the administration known as EDELCA. Through the efforts of Mr. Ahogado, the expedition to Acopán-tepui was made possible.

This genus is characterized by the trailing and rooting, unbranched inflorescence on an elongated axis and the 1-seriate monadelphous fila-

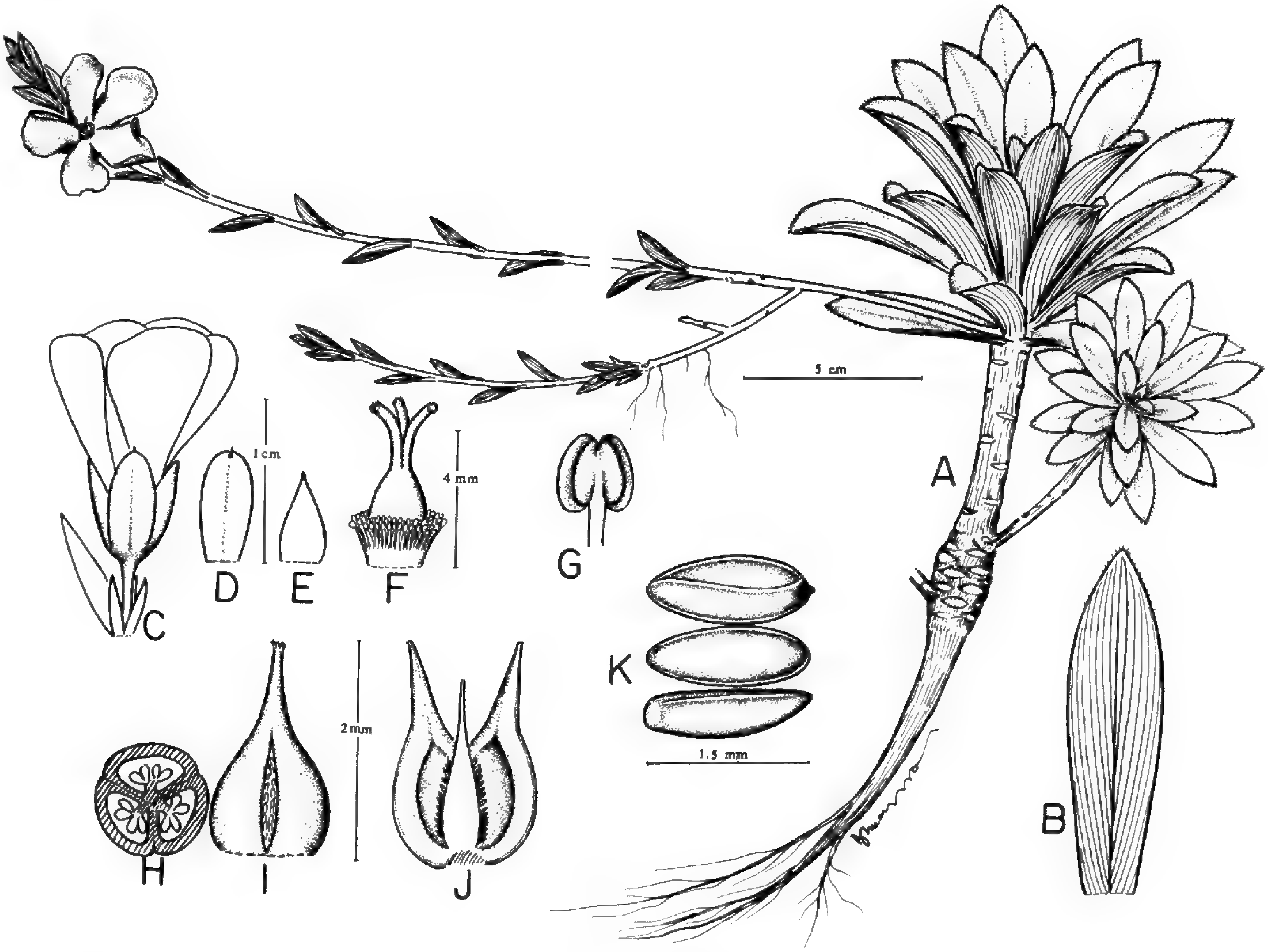

FIGURE 10. *Acopanea ahogadoi.*—A. Habit.—B. Leaf showing parallel and pinnate venation.—C. Flower in natural position, with single bract subtending 3 bracteoles.—D. Inner sepal, dorsally cuspidate.—E. Outer sepal, dorsal view.—F. Androecium and gynoecium.—G. Anther with upper portion of filament.—H. Cross section of ovary.—I. Septicidal capsule at beginning of dehiscence.—J. Showing two valves of the dehiscent capsule with persistent columella and adherent seeds.—K. Seeds, various positions.

ments attached to a basal membrane. The trailing, rooting, unbranched inflorescence is unknown elsewhere in the family and immediately distinguishes the genus from any of its congeners of *Neotatea, Neogleasonia, Neblinaria, Bonnetia,* and *Archytaea.* It is at present known only from the summit of Acopán-tepui, one of the subdivisions of the large Chimantá Massif.

Characters which the new genus shares with its congeners are noted as follows:

Whorled bracteoles. These are found in *Neblinaria* and some species of *Bonnetia.*

Terete peduncle or pedicel. Present in both *Neogleasonia* and *Neotatea,* and some species of *Bonnetia.*

Leaf venation. *Neogleasonia* and *Neblinaria* have a similar type of venation both multiparallel and finely pinnate below the middle.

Ciliolate upper margins of the leaves. These are to be noted in some specimens of *Neogleasonia.*

Leaf scars. Located on the thickened stem below the leaf rosette of the new genus, they likewise appear on some specimens of *Neogleasonia.*

The elongate, bracteate, simple, trailing and rooting axis of the inflorescence bearing alternately arranged, 3–13 foliose bracts with 1–2 flowers in each bract is not duplicated elsewhere in the family. The attachment of the 1-seriate monadelphous filaments to a basal membrane may be considered as approaching the pentadelphous stamens of *Archytaea* and sets it apart from *Bonnetia, Neblinaria, Neotatea,* and *Neogleasonia.* On the other hand, the 3-celled ovary with axile geminate placentation, septicidal capsule with persistent columella, the narrowly winged seeds, numerous stamens and sessile or subsessile, alternate, densely crowded, rosulate leaves are common to its closest congeners of *Neblinaria, Neogleasonia, Neotatea,* and *Archytaea.*

NOTES ON *BONNETIA*

In his treatment of *Bonnetia* for the flora of the Guayana Highland Maguire (in Maguire et al., 1972: 139–154) has identified certain collections with *B. wurdackii* Maguire and *B. tepuiensis* Kobuski & Steyerm., which upon further study, supplemented by newly made field observations and collections, reveal the existence of three new species and one variety. They are described below.

Bonnetia chimantensis Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Chimantá Massif, Torono-tepui, savanna below summit of W escarpment, 2,090 m, 9 Feb. 1955, *Steyermark & Wurdack 680* (holotype, VEN; isotypes, F, NY).

Frutex 1-metralis; foliis dense rosulatis sessilibus ellipticis vel oblongo-ellipticis apice acutis basi obtusis 12–27 mm × 5–8 mm; stylis 3-partitis.

Leaves rigidly coriaceous, elliptic or oblong-elliptic, acute at apex, slightly narrowed to an obtuse base, sessile, 12–27 mm by 5–8 mm, pinnately nerved below, enervate above; flowers 3 at the apex, pedicellate; pedicels 4 mm by 1.5 mm; sepals ovate, obtusely acute, 7–8 mm by 4–4.5 mm, dorsally convex; petals white with pink, oblong-obovate, rounded at apex, narrowed to the base, 9–9.5 mm by 4–6 mm; stamens numerous, filaments fascicled, free, 1.5–2 mm long; pistil 5.5 mm long, ovary 3.5 mm by 2.5 mm, styles 3, distinct, 2 mm long.

This species differs from *B. tepuiensis* Kobuski & Steyerm., with which it was identified by Maguire in having the style 3-parted, leaves narrowed to an acute, non-retuse apex, obtuse and not rounded base, leaves smaller, elliptic or oblong-elliptic instead of broadly ovate or oblong, leaves clustered into a conspicuous rosette at apex, and shorter filaments.

Bonnetia huberiana Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Chimantá Massif, Torono-tepui, summit at edge of escarpment in and among zanjones, 2,165–2,180 m, 9 Feb. 1955, *Steyermark & Wurdack 633* (holotype, VEN; isotypes, F, NY, US). PARATYPES: Venezuela. Bolívar: Chimantá Massif, E section of Chimantá-tepui, 5°18′N, 62°03′W, 2,450–2,500 m, 9 Feb. 1983, *Steyermark, Huber & Carreño 128973* (VEN); Amurí-tepui, 5°10′N, 62°07′W, 3 Feb. 1983, *Steyermark, Huber & Carreño 128559* (VEN); Acopán-tepui, NW portion, highly eroded sandstone strata around zanjones, 1,960 m, 16 Feb. 1984, *Steyermark, Luteyn & Huber 129991* (VEN).

Frutex 1.5–2.5-metralis; foliis concoloribus lineari-oblanceolatis apice subacutis 10–26 mm × 2.5–7 mm, marginibus superioribus crenulato-subspinulosis dentibus duobus minutis adpressis in quoque 1 mm munitis; floribus solitariis; petalis luteis flabelliformibus 8 mm longis supra medium 7 mm latis basi 2 mm; stylis tribus 1.8–2.5 mm longis usque ad basem divisis.

Leaves sessile to subpetiolate 1 mm long, ascending to spreading, coriaceous or subcoriaceous with the margins thinner, concolorous or slightly paler green below, linear-oblanceolate, subacute at apex, gradually narrowed to the base, 10–26 mm long, 2.5–7 mm wide, upper margins subspinulose-crenulate with 2 minute appressed teeth to every 1 mm; flowers solitary, fruiting pedicels terete, 8–16 mm long; bracts sepaloid, closely subtending calyx, oblanceolate; petals yellow, flabelliform, rounded at apex, 7 mm wide above middle, 2 mm wide at base; stamens numerous, multiseriate, filaments free, 0.5–1.5 m long, anthers subreniform 0.6 mm by 0.2–0.3 mm; styles 3, subulate 1.8–2.5 mm long, divided to the base; capsule 8.5 mm long.

This species was originally identified by Maguire (in Maguire et al., 1972: 148) as *B. wurdackii.* It differs from that species in the smaller petals, narrowly linear-oblanceolate, subacute leaves with subspinulose appressed teeth on the leaf margins. It is related to *B. roraimae* Oliver from which it is distinguished by the yellow petals and concolorous yellow-green leaves. Maguire employed the character of the leaf-margin as one of his criteria in differentiating *B. roraimae* from *B. wurdackii,* those of *B. roraimae* being described as "scario-spinulose" and of *B. wurdackii* as "narrowly scarious, feebly or not at all spinulose." The leaf margins of *B. roraimae* are more numerously subspinulose-crenulate than those of *B. wurdackii,* the new taxon resembling more those of *B. wurdackii.*

Bonnetia tepuiensis Kobuski & Steyerm. subsp. **minor** Steyerm., subsp. nov. TYPE: Venezuela. Bolívar: Chimantá Massif, *Bonnetia* thicket along upper part of branch tributary to Caño Mojado, E of N escarpment of Torono-tepui, 1,975 m, 20 Feb. 1955, *Steyermark & Wurdack 990* (holotype, VEN; isotypes, F, NY, US). PARATYPES: Venezuela. Bolívar: Chimantá Massif, Río Tirica above middle falls below summit camp, central section, summit, 1,863 m, 5 Feb. 1955, *Steyermark & Wurdack 481* (F, NY, VEN).

A *B. tepuiensis* foliis minoribus 1–2 cm longis 0.8–1.4 cm latis nervis subtus desunt supra inconspicuis vel desunt; sepalis dorsaliter carinatis recedit.

Shrub to small tree 1–4 m; leaves spreading, ovate, obtuse, obtusish or retuse at apex, narrowed to a rounded or obtuse base, 1–2 cm long, 0.8–1.4 cm wide, nerves below not evident, faintly impressed above, margins thin-scarious with deciduous dark cilia, the bases of which often persist; flowers solitary, sessile; flowers sessile, solitary; sepals dorsally keeled, the outer broadly ovate, acute, or cucullately incurved, subobtuse ventrally (when viewed dorsally), 8–10 mm by 4–5 mm, the inner sepals suborbicular, abruptly acute, 6 mm by 5 mm; petals white with pink margins, obovate, abruptly mucronate at apex, 10 mm by 4.5–5 mm; stamens fasciculate in separate phalanges, filaments 2–2.5 mm long; pistil 5 mm long, style undivided, 2 mm long.

Bonnetia tepuiensis was described (Kobuski, 1948: 399) from specimens collected by Steyermark from the slopes of Carrao-tepui of Estado Bolívar. The leaves on the type (*Steyermark 60871*) and paratype (*60902*) are 2–2.8 cm by 1.5–1.8 cm and the sepals are dorsally convex and not keeled. Subsequent collections show leaves up to 6.5 cm by 3 cm. The lateral nerves and veins of subsp. *tepuiensis* are impressed on both surfaces being inconspicuous to scarcely manifest on the lower surface and more conspicuous on the upper surface.

In the subsp. *minor* the leaves are smaller, and enervate or with nerves scarcely evident on the upper surface and absent or essentially so on the lower surface, while the sepals are dorsally carinate. The known specimens of the subsp. *minor* are restricted to the summit of the Chimantá Massif, whereas subsp. *tepuiensis* occurs farther to the east in the Venezuelan Guayana in Cerro Venamo, Ilu-tepui and Ptari-tepui.

Bonnetia toronoensis Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Chimantá Massif, Torono-tepui: dryish open savanna, N-facing slopes, summit above valley of Caño Mojado, 2,030–2,150 m, 21 Feb. 1955, *Steyermark & Wurdack 1047* (holotype, VEN; isotypes, F, NY, US).

Frutex 1.5–2-metralis; foliis conferte imbricatis oblongo-lanceolatis apice subacutis vel acutis basi leviter angustatis obtuse 1.7–3.1 cm by 0.7–1.3 cm subtus valde pinnatinervatis nervis elevatis supra impressinervis, marginibus minute conferteque denticulatis; sepalis ovato-oblongis obtusis vel rotundatis 8–9 mm × 4–5 mm; petalis rosaceis subdeltoideo-obovatis 11–12 longis apicem versus 9–10 mm latis; stylo partim 3-partilo.

Leaves deep green above, pale yellow-green below with wine-red margins, sessile, closely imbricate, spreading to ascending, coriaceous, oblong-lanceolate, subacute to acute at apex, slightly narrowed to an obtuse base, 1.7–3.1 cm by 0.7–1.3 cm, strongly nerved below with fine elevated nerves, less prominently impressed nerved above, lateral nerves 9–12 each side, anastomosing with less prominent tertiary veins, margins finely and closely denticulate with slender setulose teeth ca. 10 to each 5 mm of margin; sepals unequal, ovate-oblong, obtuse or rounded at apex, minutely denticulate around apex, convex dorsally, 8–9 mm by 4–5 mm; petals pink, subdeltoid-obovate, subtruncate at apex, narrowed to base, 11–12 mm long, 9–10 mm wide near apex, 2.5 mm wide at base; style 3-parted one-third distance from the top.

In the size and close imbrication of the leaves, this species resembles *B. tepuiensis* subsp. *minor* but is distinguished from that subspecies by the 3-parted instead of entire style. The prominently nerved lower leaf surface is also in marked contrast to the enervate lower surface of the leaves of *B. tepuiensis* subsp. *minor*. Additionally, the sepals of *B. toronoensis* are obtuse to rounded at the apex and the leaf apex is subacute to acute.

NOTES ON SOME GENERA OF THE THEACEAE (BONNETIACEAE)

In his key to the genera of the Bonnetiaceae, a family which Maguire (in Maguire et al., 1972: 131–165) recognized as distinct from the Theaceae, the distinction is drawn between *Bonnetia* on the one hand, and *Neblinaria, Neogleasonia,* and *Neotatea* on the other, primarily on the basis of the leaf venation and secondarily on whether the flowers are solitary and axillary or "solitary or the inflorescence variously compound." As regards the character of the venation, the leaves are stated to be "pinnately veined" in the case of *Bonnetia* and "closely parallel-nerved (veined)" for *Neblinaria, Neogleasonia,* and *Neotatea.*

In an attempt to apply this distinction to the various taxa within the genera above treated, one encounters difficulties in separating one group from another. For example, *Neotatea* obviously has closely parallel nerves but at the same time they are pinnately arranged. *Bonnetia lanceifolia* has leaves scarcely or inconspicuously nerved, difficult to classify. *Neogleasonia duidae* has finely nerved leaves both pinnately nerved as well as closely parallel and strongly simulate those of *Neotatea longifolia,* the major difference in venation being that the angle of the nerves with respect to the midnerve is greater in *Neogleasonia duidae.* In their original diagnosis Kobuski and Steyermark (in Kobuski, 1948: 411) described the leaves of *Bonnetia duidae* (basionym of *Neogleasonia duidae*) as having the "veins lateralibus numerosis, proximis (ca. 20 per cm), parallelibus, subangulo acutissimo adscendentibus." This character influenced Maguire to transfer this species to the genus *Neogleasonia,* although its placement in that genus he considered at the time to be tentative (Fig. 11).

With respect to the genera *Neblinaria* and *Neogleasonia* having "closely parallel-nerved (veined)" leaves, it should be stressed that although the nerves are closely parallel, yet they emerge at various higher levels from the central zone of the leaf in *Neogleasonia* than in *Neblinaria,* those of the latter genus having nearly all of the parallel nerves arising at or close to the leaf base, whereas in *Neogleasonia* the uppermost nerves, although parallel to the others, arise pinnately and ascend strongly from 1.5–3 cm above the base of the leaf. In *Neogleasonia* a midnerve is more evident on the lower leaf surface, whereas in *Neblinaria* scarcely any midnerve is developed (Fig. 11).

So far as the parallel leaf venation is concerned, there is little to separate *Neblinaria* from *Neogleasonia.* So far as characters used to separate *Neblinaria* from *Neogleasonia* and *Neotatea,* we are informed (Maguire et al., 1972) that in *Neblinaria* the "peduncles" are "strongly ancipitous and exceeding the leaves; bracts conspicuous, whorled, surmounting the peduncle and subtending a short pedicel; pachycaulous treelet," whereas *Neogleasonia* and *Neotatea* differ by having "Peduncles terete, shorter than the subtending leaves; bracts inconspicuous or lacking; nonpachycaulous shrubs or small trees."

The importance attached to the character of the peduncle as terete or ancipital in differentiating the above three genera would appear to be weak and inconsistent in view of the fact that in his key to the species of *Bonnetia* Maguire (in Maguire et al., 1972: 139) divides the various taxa into those with ancipital peduncles as contrasted with ones having terete peduncles. Also, among the species of *Bonnetia,* are some, such as *B. stricta* and *B. cubensis,* with whorled conspicuous bracts as in *Neblinaria,* and others, such as *B. paniculata, B. celiae,* and *B. kathleenae,* with inconspicuous bracts as in *Neogleasonia* and *Neotatea.*

Finally, the importance of the pachycaulous character of *Neblinaria* versus the nonpachycaulous *Neogleasonia* and *Neotatea* may be judged as relatively very weak in distinguishing these genera. The thick, corky epidermis, present in a striking degree of development in *Neblinaria,* may be viewed as having evolved as a response to particular environmental conditions. Instances of corky pachycaulous stems are found in many species of plants, such as in the cork oak, *Quercus suber, Gnetum schwackeanum,* species of *Cissus,* and many others, but such species are not considered generically distinct because of such a development. In *Neogleasonia wurdackii* a relatively thick or pachycaulous stem is developed, but does not possess the corky nature seen in *Neblinaria.* Actually, the pachycaulous stems of *Neblinaria* do not possess a woody resistance as in a true shrub or tree, but quickly snap off or break when knocked or brushed against. Moreover, those who have collected *Neogleasonia wurdackii* and *Neotatea* testify that their stems may be termed pachycaulous as in *Neblinaria.*

In view of the fact that the various criteria used by Maguire to differentiate *Bonnetia* from *Neblinaria, Neogleasonia,* and *Neotatea* intergrade in such characters as leaf venation, ancipital versus terete peduncles, whorled conspicuous bracts contrasted with inconspicuous bracts, and the degree of pachycauly, it is concluded that such criteria cannot be maintained. Moreover, all the above genera share the same basic floral morphology, such as a 3- rarely 4-celled ovary, axile placentation with numerous exalbuminous ovules, geminate placentae, mainly 4-celled anthers, tricolpate pollen, and septicidally dehiscent capsules with a persistent columella. Moreover, vegetatively they all have alternate, exstipulate leaves. Only the lactiferous nature of *Neotatea* may be considered as a strong generic

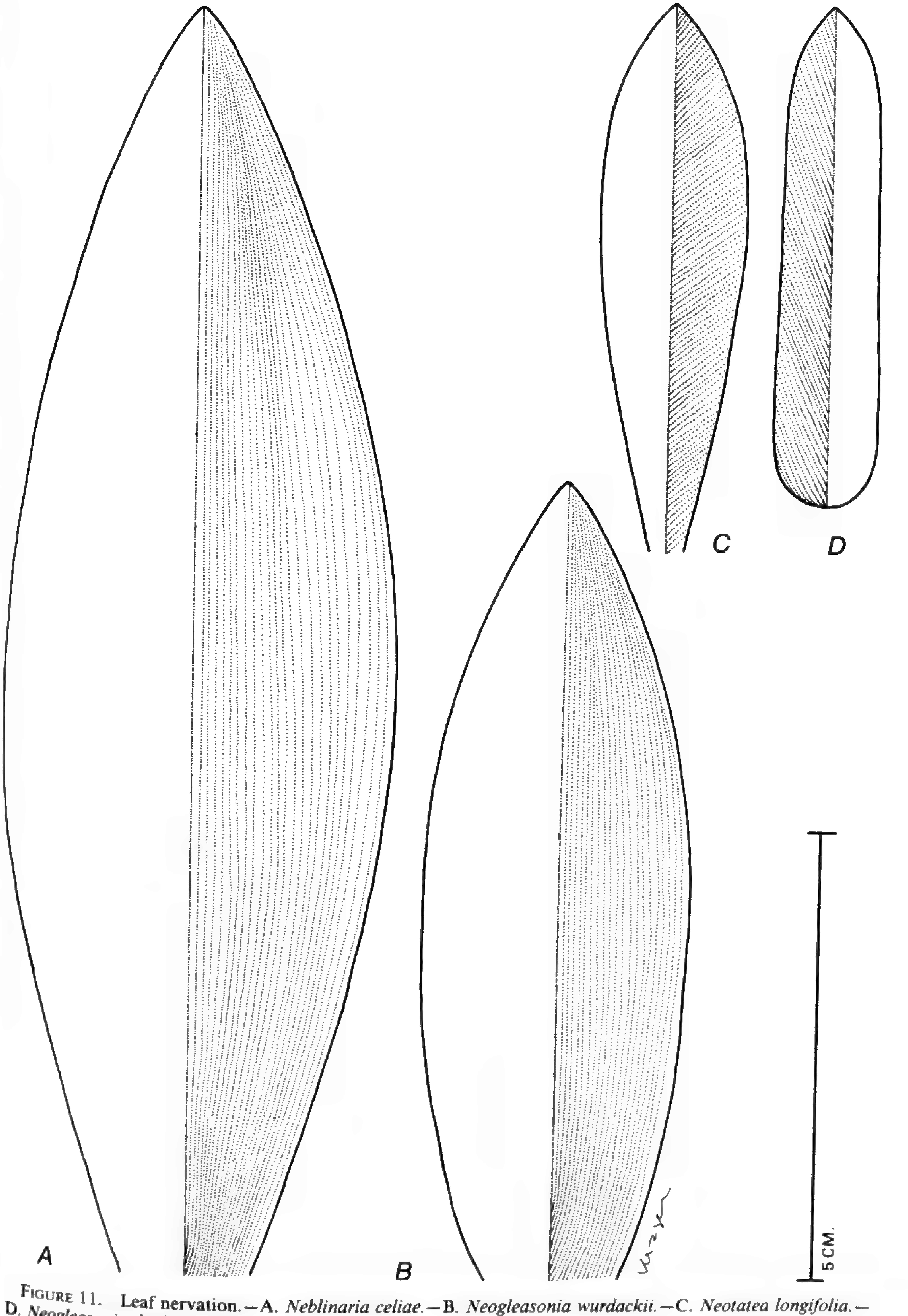

FIGURE 11. Leaf nervation.—A. *Neblinaria celiae.*—B. *Neogleasonia wurdackii.*—C. *Neotatea longifolia.*—D. *Neogleasonia duidae.*

character of sufficient significance to warrant its separation from *Neblinaria, Neogleasonia,* and *Bonnetia.* Historically, we may note that many specimens earlier determined by Maguire as pertaining to the genus *Bonnetia* were later transferred by him to *Neogleasonia* and *Neotatea.*

The following nomenclatural changes are necessary as a result of the above conclusions:

Bonnetia maguireorum Steyerm., nom. nov. *Neblinaria celiae* Maguire, Mem. New York Bot. Gard. 23: 157. 1972 non *Bonnetia celiae* Maguire, Mem. New York Bot. Gard. 23: 143. 1972.

Bonnetia multinervia (Maguire) Steyerm., comb. nov. *Neogleasonia multinervia* Maguire, Mem. New York Bot. Gard. 23: 158. 1972. *Neogleasonia wurdackii* Maguire, Mem. New York Bot. Gard. 23: 160. 1972 non *Bonnetia wurdackii* Maguire, Mem. New York Bot. Gard. 23: 147. 1972.

It is not possible to retain *Neogleasonia multinervia* and *Neogleasonia wurdackii* as distinct taxa. Both species show ciliation of the leaves, one of the characters used in the separation of the two taxa, the youngest upper ones of a rosette often having ciliation in the upper half or near the apex, whereas the lower margins or older leaves are eciliate. Maguire's description of the leaves of *Neogleasonia multinervia* as "lanceolate" was based on a single collection, as opposed to "ovate, sublanceolate, oblanceolate" for *N. wurdackii* based on many collections. However, comparison of many collections of *N. wurdackii* with the isotype of *N. multinervia* (*Maguire 33329*) show little, if any, difference in leaf shape; those of *N. wurdackii* have leaves on the older lower portion of the rosette becoming sublanceolate, while the young new leaves of the rosette tend to be more ovate. Another character employed by Maguire for differentiating the two taxa was that of petal length "petals 3 cm long, showy" in *N. wurdackii.* This character is found to intergrade as additional collections from Chimantá Massif have become available.

Bonnetia neblinensis Steyerm., nom. nov. *Neotatea neblinae* Maguire, Mem. New York Bot. Gard. 23: 163. 1972 non *Bonnetia neblinae* Maguire, Mem. New York Bot. Gard. 23: 148. fig. 23. 1972.

Bonnetia colombiana (Maguire) Steyerm., comb. nov. *Neotatea colombiana* Maguire, Mem. New York Bot. Gard. 23: 164. 1972.

MYRTACEAE

Calycolpus calophyllus (H.B.K.) Berg var. **angustifolius** Steyerm., var. nov. TYPE: Venezuela. Amazonas: Atabapo, Salto Matushi, Río Cunucunuma, vía la comunidad de Huachamacari, río arriba de la comunidad de Culebra, 3°43′N, 65°40′W, 220 m, 5 Apr. 1983, *Steyermark & Delascio 129391* (holotype, VEN).

A *C. calophyllus* foliis anguste lanceolato-ellipticis apice attenuato-acuminatis basi cuneatis 5–9 cm longis 1–2.1 cm latis 4–5-plo longioribus quam latioribus recedit.

Calycolpus calophyllus is a shrub or small tree of the Territorio Federal Amazonas of Venezuela with leaves ovate to elliptic-ovate, abruptly short-acuminate or obtusely acute at apex, 2–4 cm wide, and generally 1.5–2.5 times longer than broad.

Myrcia bonnetiasylvestris (Steyerm.) Steyerm., comb. nov. *Gomidesia bonnetiasylvestris* Steyerm., Fieldiana, Bot. 28(3): 1016. 1957.

Recent collections from Chimantá Massif indicate that this taxon should be placed more logically in the genus *Myrcia.* A more detailed examination of the anthers indicates a 2-locular instead of 4-locular condition. The calyx lobes were described in the original publication as suborbicular and rounded but a re-examination of the type collection as well as newly collected, more mature specimens, reveals that the calyx lobes are ovate-lanceolate and acute. I am indebted to Dr. Landrum for his observations and kind suggestions.

Specimens examined. VENEZUELA. BOLÍVAR: Chimantá Massif, Chimantá-tepui, sector central-noreste, headwaters of Río Chimantá, 5°18′N, 62°09′W, 2,100 m, 27 Jan. 1983, *Steyermark, Huber & Carreño 128117*; Amuri-tepui, 5°10′N, 62°07′W, 1,850 m, 2 Feb. 1983, *Steyermark, Huber & Carreño 128472*; 5°09′N, 62°07′W, 2,170 m, 6 Feb. 1983, *Steyermark, Huber & Carreño 128756*; Chimantá-tepui, E sector, 5°18′N, 62°03′W, 2,450 m, 7 Feb. 1983, *Steyermark, Huber & Carreño 128885.*

RUBIACEAE

Aphanocarpus steyermarkii (Standley) Steyerm. f. **glabrior** Steyerm., f. nov. TYPE: Venezuela. Bolívar: cumbre de Aprada-tepui, 5°22′N, 62°20′W, 2,460–2,500 m, 25 Feb. 1978, *Steyermark, Carreño, McDiarmid & Brewer-Carías 115968* (holotype, VEN).

A *A. steyermarkii* foliis subtus glabris vel glabrescentibus recedit.

Aphanocarpus steyermarkii, known from the Gran Sabana and sandstone slopes and summits of a few of the eastern tepuis (Auyan-tepui, Chimantá-tepui, Ptari-tepui) of Estado Bolívar, has leaves densely gray-silvery sericeous pubescent on both upper and lower surfaces. The present collection of the species, newly recorded for Aprada-tepui, has the lower leaf surface glabrous or nearly so. Some of the youngest leaves may exhibit traces of pubescence on the midrib or surface, but are generally glabrescent or glabrous. A collection from Auyan-tepui (*Steyermark et al. 116000*) has the lower leaf surface only sparsely to moderately sericeous-pubescent, but not glabrous throughout as in the case of *A. glabrior.*

Aphanocarpus steyermarkii f. **elongatus** Steyerm., f. nov. TYPE: Venezuela. Bolívar: Piar, Macizo de Chimantá, sector centro-noreste del Chimantá-tepui, cabeceras orientales del Cano Chimantá, 5°18′N, 62°09′N, 2,000 m, 26–29 Jan. 1983, *Huber & Steyermark 6945* (holotype, VEN). PARATYPE: same locality and date, *Steyermark, Huber & Carreño 128188* (VEN).

A *A. steyermarkii* pedunculis 9–13 cm longis prolongatis duos capitulos discretos gerentibus recedit; involucri bracteis foliosis usque 10–17 mm longis.

Collections of this endemic species of the Venezuelan Guayana generally have simple monocephalous peduncles 1.3–5(–7) cm long. On a recent expedition to the summit of the Chimantá Massif, specimens were obtained with very elongated peduncles measuring 9–13 cm long which exceeded the leaves. Moreover, the specimens with the unusually longer peduncles bear more than one head of flowers with an elongated proliferation or axis which terminates in an additional inflorescence. Two of the involucral bracts, which subtend the inflorescences of these specimens with elongated peduncles, are foliose and attain a length of 10–17 mm, whereas generally the involucral bracts of *A. steyermarkii* are shorter and only 3–10 mm.

NOTES ON *PSYCHOTRIA CRASSA* BENTH.

Psychotria crassa Benth. is a characteristic sprangling to subscandent shrub of wet forests on the summits and upper slope forests of the sandstone table mountains throughout the Venezuelan Guayana and adjacent northern Brazil. Throughout this range it exhibits some variation in leaf size and shape. Generally the leaf blades vary from ovate or elliptic-obovate to broadly oblong-elliptic and from 1.5–5 cm wide. Moreover, the peduncle, axes of the inflorescence, and pedicels are red, the calyx and hypanthium often roseate or reddish, and the fruit dark red.

Among the extensive collections of this species in the Herbario Nacional de Venezuela (VEN) are two variations of noteworthy comment. One is a narrow-leaved variation with leaf blades narrowly lanceolate or elliptic-lanceolate and 0.5–1.2 cm wide. The other variation departs from the usual coloration in having the peduncle, axes of the inflorescence, pedicels, calyx and hypanthium, and fruit completely white. The variations may be considered merely as taxonomic forms as follows:

Psychotria crassa Benth. f. **angustior** Steyerm., f. nov. TYPE: Venezuela. Bolívar: Piar, Macizo de Chimantá, sección oriental del Chimantá-tepui, cabeceras del afluente derecho superior del Río Tirica ("Cano del Grillo"), 5°18′N, 62°03′W, 2,450 m, 7–9 Feb. 1983. *Steyermark, Huber & Carreño 128992* (holotype, VEN). PARATYPES: Venezuela. Bolívar: cumbre del Macizo de Chimantá, sector nororiental, Tirepón (Torono)-tepui, 5°22′N, 61°58′W, 2,540 m, 24 Feb. 1978, *Steyermark, Carreño, McDiarmid & Brewer-Carías 115867* (VEN); altiplanicie en la base meridional de los farallones superiores del Apacará-tepui, sector norte del macizo, 5°20′N, 62°12′W, 2,200 m, 30 Jan.–1 Feb. 1983, *Huber & Steyermark 7006* (VEN).

A *P. crassa* foliorum laminis anguste lanceolatis vel elliptico-lanceolatis 0.5–1.2 cm latis recedit.

Other collections which approach this form are from Chimantá Massif (*Steyermark, Huber & Carreño 127983, Huber & Steyermark 7128, Steyermark et al. 115768*), from Ilú-tepui (*Delascio & Brewer-Carías 4954*), from Kukenan-tepui (*Delascio & Brewer-Carías 4910*), from Roraima (*Delascio & Brewer-Carías 4853, Steyermark, Brewer-Carías & Dunsterville 112450*), and Ptari-tepui (*Steyermark et al. 115704*).

Psychotria crassa f. **alba** Steyerm., f. nov. TYPE: Venezuela. Bolívar: Piar, Macizo de Chimantá, sector centro-noreste del Chimantá-tepui, cabeceras orientales del Caño Chimantá, 5°18′N, 62°09′W, 2,000 m, 26–29 Jan. 1983, *Steyermark, Huber & Carreño 128062* (holotype, VEN).

A *P. crassa* inflorescentiae pedunculis axibusque, pedicellis calyce hypanthioque frutos albidis recedit.

Remijia berryi Steyerm., sp. nov. TYPE: Venezuela. Amazonas: Estación Experimental de Santa Barbara del Orinoco, a 1–2 km al sur de Trapichote, 130 m, 26 Feb.–2 Mar. 1976, *Berry & Chesney 2116* (holotype, VEN).

Arbor 10-metralis, ramulis junioribus adpresso-pubescentibus; foliis ovatis, elliptico-ovatis vel lanceolato-ellipticis apice subacutis basi cuneatim angustatis 8–14 cm × (2.5–)6.5–8.5 cm praeter costam medium inferioram axillasque foliorum utrinque glabris; nervis lateralibus utroque latere 11–12; infructescentia trichotome ramosa longipedunculata, pedunculo 9–10 cm longo sparsim pilosulo; capsulis 10–15 mm × 5–7 mm tenuiter pubescentibus.

Tree 10 m, younger branches appressed-pubescent; leaves broadly ovate or elliptic-ovate to lanceolate or lance-elliptic, subacute at apex, cuneately narrowed at base, 8–14 cm long, (2.5–) 6.5–8.5 cm wide, glabrous on both sides except sparsely pilose along midrib and leaf axils below, lateral nerves 11–12 each side, divaricately ascending at an angle of 30°; infructescence axillary, trichotomously branched, long pedunculate, to 12 cm long (including peduncle), broader than long, 3.5–4 cm high, 4–7 cm broad, the 3 main axes slender, 1.5–2.5 cm long, sparsely pilose; peduncle slender, 9–10 cm long, 2 mm wide, sparsely pilosulous; bract subtending base of infructescence lance-triangular, 1.5 mm long, pilosulous; fruiting pedicels appressed-pilosulous; fruiting calyx and hypanthium 1.5–3 mm long, appressed-pilosulous without; fruiting calyx lobes ovate-lanceolate, subacute, 1.2–1.7 mm long, 0.5 mm wide, appressed pilosulous without, glabrous within; capsule oblong-elliptic, 10–15 mm by 5–7 mm, finely pubescent, dehiscent downward from apex; seeds fusiform, 6–8 mm by 1.5–2 mm.

This taxon is characterized by the relatively small leaves acute or subacute at both ends, their glabrity except for the sparsely pilose lower midrib and leaf-axils, the sparsely and finely pubescent upper branches, peduncles, and capsules, the slender elongated peduncles, and the relatively short infructescence.

Remijia delascioi Steyerm., sp. nov. TYPE: Venezuela. Amazonas: Cerro Vinilla, sandstone outcrops along small stream in gallery forest, N of Cerro Aratitiyope and SW of Ocamo, 440 m, 1 Mar. 1984, *Steyermark, Berry & Delascio 130339* (holotype, VEN).

Planta lignea 1–1.5-metralis, caule simplici; foliorum laminis lineari-ellipticis vel anguste lanceolato-ellipticis apice subobtusis basi acutis 11–21 cm × 1–2.5 cm 10-plo longioribus quam latioribus, maturis supra glabris subtus praeter costam medium inferiorem strigosam glabris, nervis lateralibus utroque latere 11–15, petiolis 6–15 mm longis, pedunculo dense strigoso 6.5–9.5 cm; calyce hypanthioque dense sericeo 6 mm × 1.5 mm, calycis tubo cylindrico spathaceo obscure leviterque dentato 4 mm longo; capsulis oblongo-cylindricis 12 mm × 5 mm strigillosis.

Single-stemmed ligneous plant 1–1.5 mm tall; leaves petiolate, petioles tawny, 6–15 mm by 1 mm, tomentose to glabrous above; leaf blades erect, pale yellow-green below with buff midrib, linear-elliptic to narrowly lance-elliptic, narrowed to a subobtuse apex, narrowed to an acute base, 11–21 cm by 1–2.5 cm, averaging 10 times longer than broad, glabrous above at maturity, glabrous below except for the subelevated strigose midrib, the youngest leaves sparsely strigose above on surface, densely strigose on midrib, moderately to densely strigose below on surface and midrib; lateral nerves 11–15 each side, ascending at an angle of 60°; tertiary venation finely reticulate beneath; inflorescence axillary, immature; peduncle densely strigose 6.5–9.5 cm long in fruiting stage; bracts brown-maroon, in preanthesis broadly lanceolate, obtusish, 6 mm by 2 mm, sericeous without; 2 bracteoles subtending flowers lanceolate, obtusish, 3.5 mm by 1 mm, densely sericeous without; calyx and hypanthium brown-maroon, densely sericeous, 6 mm by 1.5 mm; calyx tube cylindrical, spathaceous, unequally and shallowly obscurely dentate, glabrous within, 4 mm long, with scattered linear-oblong glands at base of calyx tube within; fertile portion of inflorescence in bud 4 cm long, in fruit 4.5–9 cm long; capsules oblong-cylindric, 2 mm by 5 mm, strigillose.

This taxon differs from other known species of the genus in the extremely narrow, linear-elliptic to narrowly lance-elliptic leaves which are narrowed at both ends and only 1–2.5 cm wide, averaging 10 times longer than broad. The mature leaves are glabrous on both surfaces with only the midrib beneath strigose. The spathaceous calyx-tube is well developed with shallow, scarcely evident teeth at the summit.

Sipanea carrenoi Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Gran Sabana, open densely covered slopes, al pie del Salto del Aponguao, 42.5 km al NE de la Misión de Santa Teresita de Kavanayén, 1,130 m, 22 Feb. 1978, *Steyermark, Carreño, Dunsterville & Dunsterville 115598* (holotype, VEN).

Planta herbacea, caulibus prostratis vel decumbentibus effusis elongatis repentibus ad nodos radicantibus pubescentibus; laminis elliptico-oblongis apice obtusis vel subacutis 1–2 cm × 0.6–0.9 cm omnino glabris; nervis lateralibus utroque latere 2–3; inflorescentia plerumque 3–7-flora, raro 1-flora; corolla 15–21 mm longa, tubo 1–13 mm longo extus superne sparsim pilosa intus orificio barbato; capsulis 9 mm × 2.5 mm dense hirsutulo pilis adscendentibus instructis.

Herbaceous 0.2 m; stems sprawling or trailing, densely or moderately pilose with subspreading-ascending hairs; stipules triangular-lanceolate, 2–3 mm by 0.5 mm, densely strigose without; leaves short-petiolate, petioles 0.5–1.5 mm long, margins pilose-ciliate; leaf blade elliptic-oblong, obtuse to subacute at apex, acutely narrowed to the base, 1–2 mm by 0.6–0.9 mm, glabrous both sides, revolute on margins; lateral nerves 2–3 each side, lightly impressed on lower surface, not evident on upper surface; inflorescence terminal, rarely axillary, cymosely 3–7-flowered, rarely 1-flowered, sessile or with short lateral branches; bract subtending inflorescence narrowly elliptic-oblanceolate, acute, 0.4 mm by 0.9 mm, ciliate; calyx 7–7.5 mm long, lobes 4.5 mm by 0.7–0.8 mm, linear-lanceolate, acuminate, glabrous except for ciliate margins; corolla hypocrateriform-infundibuliform, 15–21 mm long, tube 10–13 mm long, sparsely pilose without in upper portion, glabrous within except at orifice; orifice within furnished with a dense brush of hairs which are not exserted; lobes suborbicular, rounded or obtuse, 6–6.5 mm by 5–7 mm, glabrous without; anthers linear, 3–3.5 mm; style 10 mm long, glabrous in lower half, papillate above; squamellae solitary, inserted in the sinus between each calyx lobe, lanceolate, obtuse; capsule cylindric, 9 mm by 2.5 mm, densely hirsutulous with ascending hairs.

This taxon is related to the common *S. pratensis* Aubl., from which it differs in the creeping rooting habit of the stems and the densely crowded, smaller, glabrous, obtuse to subacute, fewer-nerved leaves. The species is named in commemoration of my valued field assistant, Victor Carreño Espinosa.

COMPOSITAE

A re-examination of *Achnopogon quelchioides* Aristeg., based on *Steyermark 93497* from Auyan-tepui, shows that it cannot be separated from *A. steyermarkii* Aristeg., also from Auyan-tepui. Steyermark noted in his collection of *A. quelchioides* that the flowers are "clustered as in *93496* (*Quelchia bracteata*) but with larger size of flowers and leaf pubescence as in *93512* (*A. steyermarkii*)," leading to the supposition that it was a putative hybrid between these two collections.

However, there appears to be no differences in separating *A. quelchioides* from *A. steyermarkii,* both having sessile, 2–3-flowered heads, white corollas, glabrate bracts in several series, subsessile to shortly petiolate, broadly oblong to oblong-obovate leaf blades, rounded at the apex with a minute mucro, and densely lanulose, brown stems and leaf bases.

Some collections of *Achnopogon steyermarkii* (*Steyermark et al. 116088, 116139,* and *Foldats 7117*), all from the summit of Auyan-tepui, have been misidentified as *Quelchia* × *grandifolia* Maguire, Steyerm. & Wurd., considered by their authors to be a putative hybrid between *Quelchia bracteata* and *Q. eriocaulis.* The latter species has sessile inflorescences with red or pink corollas, densely ferruginous lanate stems, and a tawny-brown lanulose lower leaf surface, whereas *Q. bracteata* has pedunculate inflorescences with white corollas, closely or densely sericeous stems with malpighioid hairs, and the lower surface of the leaves pubescent to glabrous, but not densely lanate.

In habit, *Achnopogon steyermarkii, A. quelchioides, Quelchia eriocaulis,* and *Q. bracteata* simulate one another in their simple, ligneous stems enveloped in their upper portion by densely crowded, ascending, subsessile to shortly petiolate leaves, which conceal the inflorescences present at their base. However, the corollas immediately distinguish these four taxa, *Quelchia* having the inflorescence 1-flowered with regular 5-lobed corollas, whereas *Achnopogon* has 2–5-flowered inflorescences with bilabiate corollas.

The synonymy of *Achnopogon steyermarkii* follows:

Achnopogon steyermarkii Aristeg., Acta Bot. Venez. 2(5–8): 350. fig. 30. 1967.

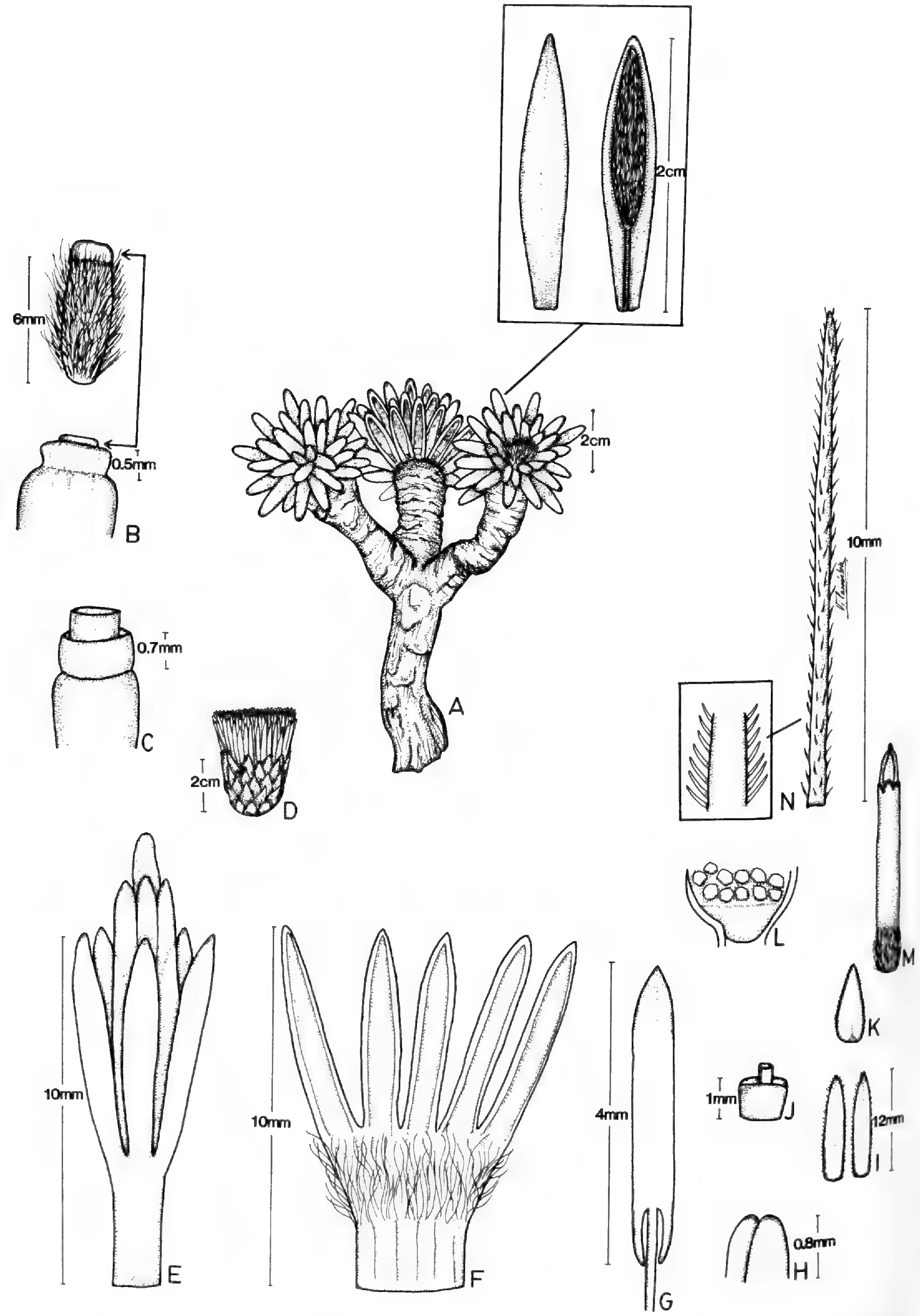

FIGURE 12. *Chimantaea huberi.*—A. Habit.—B. Upper half, mature achene; lower half with crown of achene and stylar base.—C. Upper part of achene in late bud stage, showing corona and stylar base.—D. Capitulum of

Achnopogon quelchioides Aristeg., Acta Bot. Venez. 2(5–8): 348. fig. 29. 1967.

Chimantaea acopanensis Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Piar, Macizo de Chimantá, sector SSE, altiplanicie, sur-oriental del Acopán-tepui, cabeceras del Río Arauac, praderas humedas y arbustales enanos sobre turberas, bosquecillos ribereños y vegetación sobre rocas abiertas, 5°11′N, 62°00′W, 1,920 m, 14–16 Feb. 1984, *Steyermark, Luteyn & Huber 129932* (holotype, VEN).

Planta pusilla rosulata caespitosa usque ad 10 cm alta; foliis linearibus apice rotundatis vel obtusis 35–40 mm × 3.5–6 mm valde revolutis supra non-sulcatis glabris subtus brunneo-lanuginosis; capitulis terminalibus sessilibus solitariis 28-floris 2 cm altis 2.5 cm latis; involucro 5-seriato, bracteis lineari-lanceolatis acuminatis intimis 14 mm × 2.5 mm extimis 10 mm × 2 mm tertia parte superiore dense lanulosis; receptaculo plano alveolato; paleis tribus inter flores exteriores subulatis 19 mm × 0.5–1.5 mm in dimidio superiore pilosulis marginibus omnino ciliolatis; corolis 14 mm longis, lobis lineari-ligulatis subobtusis 10 mm × 1 mm; antheris 5 mm longis basi bicaudatis; stylo 16 mm longo; achaeniis fusiformi-cylindricis 4–4.5 mm × 1 mm laxe pilosis; pappi setis 12–14 mm longis.

Perennial dwarf caespitose plant with long taproot, acaulescent, to 10 cm tall; leaves olive green and non-sulcate above, buff-brown lanulose below, coriaceous, strongly revolute, linear, rounded or obtuse at apex, slightly contracted into a subsessile densely lanate base, 35–40 mm by 3.5–6 mm; heads sessile, solitary, terminating the leaf rosette, campanulate, 28-flowered, 2 cm high, 2.5 cm wide; involucre 5-seriate, bracts linear-lanceolate, attenuate to an acuminate dark magenta apex, densely buff tomentose in the upper third, glabrous in lower third, innermost 14 mm by 2.5 mm, outermost 10 mm by 2 mm; receptacle flat, shallowly alveolate; heads homogamous; paleae 3, inserted between the outer florets, subulate, 19 mm by 0.5–1.5 mm, pubescent in upper half; corollas 14 mm long, the tube 4 mm long, 1.8 mm wide at summit, 1.2 mm wide at base, lobes equal, linear-ligulate, subobtuse, 10 mm by 1 mm; anthers dark magenta-wine red, 5 mm long; style lavender, 16 mm long, stigmas ligulate-oblong, obtuse; achene slenderly fusiform-cylindric, 4–4.5 mm by 1 mm, loosely pilose; pappus tawny, the numerous bristles 12–14 mm long, minutely serrulate.

This taxon may possibly prove to be a putative hybrid between *C. huberi* Steyerm. and *C. humilis* Maguire, Steyerm. & Wurd., both species occurring in the immediate area. The non-sulcate upper leaf surface and densely buff tomentose involucral bracts together with the deep brown lanulose pubescence are shared with *C. humilis,* whereas the dwarf caespitose, rosulate habit and non-sulcate upper leaf surface are shared with *C. huberi.*

Chimantaea huberi Steyerm., sp. nov. TYPE: Venezuela. Bolívar: Piar, Macizo del Chimantá; pequenas altiplanicies on la base septentrional de los farillones superiores del Amuri-tepui (sector occidental del Acopán-tepui), 5°10′N, 62°07′W, rocky exposed outcrops of savanna on heliport just W of campsite, 1,850 m, 2–5 Feb. 1983, *Steyermark, Huber & Carreño 128815* (holotype, VEN; isotypes, K, MO, NY, U, US). PARATYPES: same locality, 2–5 Feb. 1983, *Huber & Steyermark 7118* (K, MO, NY, U, US, VEN); altiplanicie suroriental del Acopán-tepui, cabeceras del Río Arauac, praderas húmedas sobre turberas, 5°11′N, 62°00′W, 1,920 m, 14–16 Feb. 1984, *Steyermark, Luteyn & Huber 129924* (VEN); Apacará-tepui, 5°20′N, 62°12′W, 2,300 m, 1 Feb. 1983, *Steyermark, Huber & Carreño 128419* (VEN).

Planta pusilla rosulata caespitosa 1–3 cm alta; foliis linearibus vel lineari-oblanceolatis apice subobtusis cum apiculo diminuto obtusiusculo acuto 10–20 mm × 2–4 mm supra glabris subtus albo-pannosis valde revolutis; capitulis sessilibus 2 cm × 0.7–0.8 cm; involucro campanulato 6–7-seriato in base tomentosa albida insidenti; phyllariis ca. 30 praeter margenes ciliatos glabris, exterioribus late triangulari-lanceolatis acuminatis 7 mm × 4 mm intimis anguste ligulato-subspathulatis 14 mm × 2 mm; receptaculo plano alveolato glabro; paleis non visi; floribus 7–15 actinomorphicis, corolla albida 10 mm longa trans medium fissa 5-nervata, tubo 3 mm × 2 mm, limbo 1 mm × 2 mm, lobis erectis ligulato-lanceolatis subobtusis 6.5 mm × 0.9–1 mm, tubo lobisque extus glabris, tubo intus fauce dense lanuginoso-barbata ceterum gla-

←

flowers with involucre.—E. Floret, exterior view.—F. Interior of floret.—G. Stamen.—H. Stigmas.—I. Middle involucral bracts.—J. Stylar base surrounded by coronal disk.—K. Outermost involucral bract.—L. Alveolate portion of receptacle.—M. Corolla in bud with lanulose tomentum of involucral base.—N. Pappus seta and portion enlarged.

bro; achaeniis 6 mm × 2 mm densissime albo-sericeis; pappo ochroleuco pluriseriato, setis 8–10 mm longis.

Dwarf perennial, caespitose rosulate plant 1–3 cm tall, forming large mats; stems greatly reduced, subligneous, or not evident, simple or branched, 0.5–1.5 cm diam.; leaves numerous, stiff-coriaceous, erect, strongly revolute, crowded, sessile, linear, linear-sublanceolate or linear-oblanceolate, subobtuse at apex with a minute obtusely acute thick apiculum, slightly narrower and subunguiculate toward the base, 10–20 mm by 2–4 mm, shining and rich green above, white pannose tomentose below for 7–16 mm but the narrower, sulcate, basal 2–5 mm portion below glabrous; flower heads homogamous, sessile, terminal, 2 cm by 0.7–0.8 cm; mature involucre shortly campanulate, 6–7-seriate, on a white tomentose base; involucral bracts maroon-purple, rigidly chartaceous, ca. 30, glabrous except for the ciliate margins, the outer broadly triangular-lanceolate, acuminate, convex, 7 mm by 4 mm, intermediate ligulate-lanceolate, acute or obtuse, 12 mm by 2.5 mm, interior narrowly ligulate-subspathulate, 14 mm by 2 mm; receptacle flat, alveolate, glabrous; pales not seen; flowers 7–15; corolla white, 10 mm long, cleft more than halfway down, 5-nerved, tube salverform, 3 mm by 1.5–2 mm, throat 1 mm by 2 mm, lobes erect, ligulate-lanceolate, subobtuse, the apex and margins somewhat thickened, 2-nerved, 6–6.5 mm by 0.9–1 mm, tube and lobes glabrous without, lobes glabrous within, tube densely barbate-lanuginose within at the throat, elsewhere glabrous; anthers lavender-brown, linear, 4 mm by 0.6 mm, acute at apex, sagittate at base, basal appendages free, somewhat incurved at the apex, 1 mm long, glabrous; pollen grains tricolpate, not spinose; style pale green at apex, surrounded by an entire fleshy collar 0.7 mm high and 1 mm wide at base; achenes cylindric 6 mm by 2 mm at apex with a short slightly undulate to entire crown 1 mm high, densely white-sericeous; pappus buff, multiseriate, the awns subequal, 8–10 mm long, barbellate, slightly coherent at base.

It is a great pleasure to name this unusual taxon for Dr. Otto Huber, dedicated student of the Guayana flora, under whose successful management the expeditions to Chimantá were completed.

This taxon may be considered a very reduced member of the genus *Chimantaea* and derived from a still further reduction of an evolutionary branch of *Chimantaea rupicola* Maguire, Steyerm. & Wurd. From the other known species of the genus, all of whose taxa but one (*C. cinerea* (Gl. & Blake) Maguire, Steyerm. & Wurd. of Auyan-tepui) are known from the Chimantá Massif, *C. huberi* differs in the very dwarfed, rosulate, caespitose plants growing in dense mats less than 3 cm high, the short corolla and corolla lobes, the absence of paleae, and the much shorter, narrower leaves. Anatomical studies of the leaves and palynological examination agree with the placement of this species in *Chimantaea.*

In their original description of the genus *Chimantaea,* Maguire, Steyermark & Wurdack (in Maguire et al., 1957: 428) described the receptacle as pubescent with few (2–5) marginal pales, tips of the corolla lobes more or less barbellate, and pollen grains spinulose. Later, Aristeguieta (1964: 831, 879) correctly described the generic characters in broader terms and allowed for an absence or presence of pales on the pubescent or non-pubescent receptacle, as well as for a glabrous or pilose apex of the corolla-lobes. Moreover, the pollen, stated in the original description of the genus to be spinose (in Maguire et al., 1957b: 428), may be nearly psilate in some species, such as *C. similis,* as shown by Carlquist (1957: 446–447. fig. 93c). Senora Maria Léa Labouriau of IVIC (Instituto Venezolano de Investigaciones Cientificas) of Caracas, Venezuela, an authority on pollen, has kindly supplied me with a description of the pollen of *C. huberi* as follows: subprolate, non-spinose lobate grains with salient poles. Fossa perturate. Grains very dark colored. Apertures: 3 colporate. Colpi long, conspicuous large lalongate pores with sharp ends. Exine non-espinose with vestigial spinules, very thick at the polar region. Sexine very thick with two layers: tegilum and infrategillar bacula layer; bacula visible from ×400 up. She concludes that the grains are very similar to those of Carlquist's description of *C. similis.*

The anatomical study of the leaves was made by Senorita Luisa Lopez of the Direccion de Investigaciones Biólógicas of the Jardin Botánico in Caracas, Venezuela, whose description is as follows:

> Epidermis adaxial sclerified with one layer of cells, with prominent cuticular membrane, hypodermis adaxial with 3–4 cells in thickness, thickened walls, constituting a band along the length of the leaves: mesophyll undifferentiated

with a spongy parenchyma and palisade cells of tubular form sometimes present. Subhydermal sclereids are scattered in small groups in the mesophyll. Epidermis abaxial monostratified with the stomata sunk below a tomentum of simple hairs with slender walls. Toward the leaf margin an exceptional development of sclerenchyma occurs which facilitates the revolute portion of the leaf to function. She notes that the marked sclerophyll type of leaf enables the plant to adapt to loss of water, high evaporation, and unfavorable edaphic conditions. The scleromorphic leaves of the species are small and coriaceous and are provided with cutinized cell walls. She notes that there is evidence to show that a lack of nitrogen is responsible for the appearance of scleromorphous characters, and that nitrogen deficiency is associated with sclerophylly.

Chimantaea huberi possesses characters common to both of the genera *Chimantaea* and *Stomatochaeta*. In common with *Stomatochaeta* it possesses small flower heads, glabrous corolla lobes, and an entire stylar base 1 mm or less high, but differs from *Stomatochaeta* in having a 5-nerved corolla tube, non-malpighioid pubescence, and densely pubescent achenes. While sharing with *Chimantaea* a 5-nerved corolla tube, free anther tails, and similar tomentum on the lower side of the strongly revolute leaves, it differs from the other species of *Chimantaea* in the smaller, fewer-flowered heads and an entire, instead of 5-lobed basal corona of the style. However, it shares the glabrous receptacle with both *C. eriocephala* and *C. similis* and the glabrous apices of the corolla lobes with *C. cinerea* and *C. similis*. The epaleaceous receptacle of *C. huberi* manifests its still further reduction from its most closely derived taxon, i.e., *C. rupicola* which possesses 1–2 deciduous marginal paleae. *Chimantaea huberi* represents the extreme reduction in a series from a tall arborescent "espeletioid" type to 3 m tall, as shown by *C. mirabilis* and *C. lanocaulis*, to a nearly herbaceous rosulate chabit, a tendency suggested by Maguire, Steyermark and Wurdack (in Maguire et al., 1957a: 377).

Chimantaea huberi occurs in open exposed situations, on bare open, exsiccated, flat sandstone outcrops (as noted in *Steyermark et al. 128419* and *128815*) or in open swampy ground of savanna-like habitats where the soil is more saturated with water (as in *Steyermark et al. 129924*). It is frequently associated with a species of Eriocaulaceae, *Syngonanthus obtusifolius*, which it resembles strikingly in such characters as erect, olive green, stiff-coriaceous leaves, and white tufts of tomentum at the base of the leaf rosette. In such instances, the convergence of morphological characters is so close that one must observe the two with especial perception in order not to confuse the two families. Where *Chimantaea huberi* grew on the dry sandstone ledges, it was also associated with *Brocchinia reducta, Stegolepis ligulata, Ledothamnus decumbens, Achnopogon virgatus*, and other xeromorphic species. On the wet swampy savanna-like habitat it was associated with such species as *Epidendrum alsum, Tepuia venusta, Myrtus alternifolia, Stegolepis ligulata, Tillandsia stenoglossa, Stomatochaeta cymbifolia*, and others.

Chimantaea cinerea (Gl. & Blake) Maguire, Steyerm. & Wurd. f. **glabra** Steyerm., f. nov. TYPE: Venezuela. Bolívar: Auyan-tepui, lado derecho del Salto Angel, 15 Aug. 1968, *Ernesto Foldats 7100* (holotype, VEN).

A *C. cinerea* corollae lobis secus margines pilosulis; achaeniis glabris recedit. Folia obovata apice rotundata basi angustata petiolata, 5–7 cm × 2.5–3.5 cm supra glabra subtus dense cinerea, nervis lateralibus obscuris utroque latere 8–10; petiolis 5–7 mm × 3–3.5 mm cinereo-tomentosis; corollis 19–20 mm longis, tubo 5 mm longo intus basi loborum dense piloso aliter glabro; achaeniis 6–7 mm longis glabris; pappi setis 18–20 mm longis.

This form has the glabrous achenes of *C. similis* Maguire, Steyerm. & Wurd. but the margins of the corolla lobes are pilosulous, as in *C. cinerea*. The differences separating *C. cinerea* and *C. similis* are perhaps not sufficient for specific recognition. The achenes of *C. cinerea* vary from densely or moderately sericeous to only sparsely so, while the corolla lobes may vary from usually pilose to glabrous, as in the collection of *Pannier & Schwabe 1927-A* from Auyan-tepui. The corolla lobes of *C. similis*, on the other hand, while ordinarily glabrous, may also show some pilosity. The two taxa are isolated on separate tepuis, *C. cinerea* occurring on Auyan-tepui and *C. similis* on the Chimantá Massif.

NOTES ON HYBRIDIZATION IN *CHIMANTAEA* AND *QUELCHIA*

On the extensive series of plateaus which comprise the Chimantá Massif (Macizo de Chimantá) there have evolved many genera and species known nowhere else in the Venezuelan Guayana. Of these, one of the most remarkable genera is the mutisioid composite, *Chimantaea.* Except for the occurrence of two species, one found on the nearby (but distant) Auyan-tepui, the other on Aprada-tepui, both in the state of Bolívar, the remainder of the taxa are known only from Chimantá Massif of Bolívar state. It is on the Chimantá Massif where the main evolutionary process has developed in the genus.

Although eight species have been described as the result of two major expeditions there in 1953 and 1955, recent explorations during 1983 and 1984 have provided further opportunities for additional collections and observations of the genus. These have resulted in the discovery of at least two new taxa pertaining to the genus, one with a remarkable dwarf rosette, *C. huberi,* which resembles an eriocaulaceous taxon (*Syngonanthus obtusifolius*), with which it is often associated, and the second one, similarly dwarfed, but suspected to be of hybrid origin, namely *C. acopanensis.*

Actually, the more abundant collections of many more individual plants of the genus on Chimantá Massif have furnished increasing evidence to substantiate grounds which support the belief in 1) the occurrence of some hybridization taking place between the various taxa and 2) variation in vegetative characters which show degrees of intergradation, making it difficult to assign individual specimens to a definite category. Although it is true that the eight previously described taxa may be readily recognized as distinct entities as such, nevertheless some specimens appear as more or less intermediate in character or combine characters common to different taxa. This is apparent in such collections as *Steyermark, Huber & Carreño 128518* which appears intermediate between *C. eriocephala* Maguire, Steyerm. & Wurd. and *C. humilis* Maguire, Steyerm. & Wurd. The leaves of *C. humilis* vary in width, some having the greater width of *C. eriocephala* or *C. humilis,* others having the narrower width of *C. mirabilis.* This latter type is exemplified by the collection of *Steyermark, Huber & Carreño 128511* which shows an intermediate stage between *C. humilis* and *C. mirabilis.* Another collection, *Steyermark et al. 128332-A,* has leaves too narrow for *C. similis* but resembles that taxon in other characters.

The newly described taxon, *C. acopanensis,* was found growing near the newly described *C. huberi,* and in the near vicinity *C. humilis* occurred. The dwarf habit of *C. acopanensis* suggests *C. huberi,* but the larger leaves and flower-heads, as well as the densely tomentose involucral bracts, indicate characters shared with *C. humilis.* Nevertheless, *C. acopanensis* may be readily recognized from other taxa of the genus by its combination of a dwarf rosette habit, tomentose involucral bracts, and shape and size of leaves and heads.

Likewise in the genus *Quelchia* a putative hybrid has been recorded as *Quelchia* × *grandifolia* (Maguire et al., 1957b: 436). This manifests characters of both *Q. eriocaulis* Maguire, Steyerm. & Wurd. and *Q. bracteata* Maguire, Steyerm. & Wurd., both of which taxa occur in the immediate vicinity.

NOTE ON *GONGYLOLEPIS BENTHAMIANA* VS. *G. PANICULATA*

Aristeguieta (1964: 895) separated *G. paniculata* Maguire & Phelps from *G. benthamiana* Schomb. on the basis of leaf length and width, length of involucre, and number of seriate bracts. In an examination of material in VEN, the size of leaves for *G. benthamiana* varies from 7.5–16.5 cm by 2–5.5 cm (Aristeguieta, 1964: 900 gives 7.5–16.5 cm by 2–5.5 cm) and for *G. paniculata* varies from 12–27 cm by (2.5–)5–8(–9) cm.

In the key to *Gongylolepis,* Maguire (in Maguire et al., 1953: 155), in addition to separating these taxa by leaf dimensions, employs an additional character not used by Aristeguieta, namely, leaf venation. Thus, for *G. paniculata* the primary veins are stated as "extending little beyond the middle, then anastomosing and with the secondary veins reticulate, veins on upper surface merely prominulous," whereas for *G. benthamiana* the primary veins are stated as "extending nearly to the margins before anastomosing, veins on upper surface prominent, strongly reticulate." An examination of material in VEN verifies this difference in venation given by Maguire. The differences mentioned for size of involucre and number of seriate bracts likewise is borne out by an examination of material at VEN.

Previously, all material of *G. benthamiana* has been known to occur only in Estado Bolívar of eastern Guayana of Venezuela, from the Gran Sabana west to Cerro Guaiquinima, Cerro Marutani (on the Brazilian-Venezuelan frontier at the headwaters of Río Paramichi, an affluent of the Río Paragua), and Cerro Marajanu of the Meseta de Jaua in the Upper Caura. In contrast, *G. paniculata* is known only from the sandstone table mountains of the Territorio Federal Amazonas. It was, therefore, a great surprise while collecting on the savanna-covered sandstone substrata of the Serrania Vinilla in Territorio Federal Amazonas to find *G. benthamiana* as one of the common species and far removed from its occurrence in eastern Guayana. These collections, represented by *Steyermark, Berry & Delascio 130329,* have the leaves with the size and venation typical of *G. benthamiana,* and, additionally, the smaller involucres with 6-seriate bracts of that species. Two other collections from the Serrania Vinilla (*Huber 6044* and *6175*) also are typical *G. benthamiana,* although they were originally misidentified as *G. paniculata,* probably because *G. paniculata* is a widespread species in Territorio Federal Amazonas.

An additional observation made in connection with a study of these two taxa is that the heads of *G. paniculata* are narrowed at the base, whereas those of *G. benthamiana* are more rounded basally, producing a shallowly campanulate shape to the involucre.

This disjunct distribution separates *G. benthamiana* about 300 km southwest of its nearest outpost in Estado Bolívar.

Mikania michelangeliana Steyerm., sp. nov. TYPE: Venezuela. Amazonas: Cerro Marahuaca, summit, borde noroeste, meseta sureste, valle Yekuana, bordering small stream, 2,560 m, 10 Oct. 1983, *Steyermark 129456* (holotype, VEN).

Planta scandens, caulibus saltem juvenilibus papillatis tomentellisque; foliis elliptico-ovatis apice acutis vel acuminatis basi cuneatis 3–5-plinervatis 2–3.2 cm × 1.3–2 cm utrinque glabris subtus negro-punctatis, marginibus minute denticulatis; inflorescentiis cymosis 4–4.5 cm × 4–4.5 cm, axibus pedicellisque dense breviter tomentellis papillatisque; capitulis 4–5-floris 7–9 mm × 3 mm; corollis 4.5 mm longis; achaeniis 4–4.5 mm longis sparsim vel dense papillato-puberulis.

Stems, especially the young ones papillate-tomentellose; leaves elliptic-ovate, acute to acuminate at apex, cuneate at base, 3–5-plinerved, 2–3.2 cm by 1.3–2 cm, glabrous both sides, black-punctate below, margins minutely denticulate with 4–5 teeth on each side, tertiary venation absent or obscure; petioles 4–6 mm long, glabrous or sparingly puberulent; inflorescence terminal and axillary, cymose, 4–4.5 cm by 4–4.5 cm, axes short-tomentose mixed with papillate hairs; pedicels 2–4 mm long, densely tomentellose, heads 4–5-flowered, 7–9 mm by 3 mm; involucral bracts ligulate, subacute at apex, slightly unequal, 4–5 mm by 0.8–1 mm, longitudinally 3-nerved, densely minutely puberulent without; corollas infundibuliform, 4.5 mm long, tube in upper portion glabrous without, lower constricted portion sparsely glandular, lobes broadly lanceolate, acute, 1 mm long; achenes linear, quadrangular, 4–4.5 mm long, sparsely to densely papillate-puberulous; pappus cream-colored, bristles numerous, 4–5.5 mm long, serrulate.

In leaf size and shape this taxon approaches *M. lucida* Blake, and in stem pubescence is similar to that of *M. lucida* f. *hirticaulis* Steyerm. From both of these taxa *M. michelangeliana* differs in the more sharply acute leaf apex, the minutely denticulate leaf margins, the conspicuously black-dotted lower leaf surface, and the short tomentum intermixed with a papillate indument on most of the stem and axes of the inflorescence.

I take pleasure in associating the name of Armando Michelangeli with the new species. Through his efforts as administrator of the Terramar Foundation, exploration of the summit areas of Cerro Marahuaca has been made possible.

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NOTES

A NEW COMBINATION IN *DALECHAMPIA* (EUPHORBIACEAE)

Fifteen species of *Dalechampia* are known from Central America. One of these was mistakenly described as a *Tragia* and has not yet been transferred to *Dalechampia.* While preparing the treatment of *Tragia* for a revised synopsis of Panamanian Euphorbiaceae (Webster & Huft, in prep.), I discovered that *Tragia shankii* was the same as an otherwise undescribed *Dalechampia* that is represented by several collections from the Caribbean slope of Costa Rica and Panama and from the Province of Chocó in Colombia. In order to make the proper name available for taxonomic and pollination studies being carried out by Dr. Scott Armbruster, I am making the combination here, rather than waiting for the appearance of the Panama paper. This is the "undescribed species" that is referred to in Armbruster (1982) as "La Osa" (Armbruster, pers. comm.).

Dalechampia shankii (A. Molina) Huft, comb. nov. *Tragia shankii* A. Molina, Ceiba 11: 68. 1965. TYPE: Costa Rica. Limón: drainage of Río Reventazón, 15 m, 23 Oct. 1951, *Shank & Molina 4427* (holotype, F-1563051; isotype, EAP, not seen).

Dalechampia shankii may be readily identified by its large, trilobed (or sometimes unlobed), deeply cordate leaves, densely hirsute orange indument, orange sericeous involucral bracts and capsules, and narrow, fimbriate, orange sericeous pistillate sepals.

Molina considered this species to be a close relative of *Tragia bailloniana* Muell. Arg., which constitutes the monotypic sect. *Zuckertia* (Baill.) Muell. Arg. and seems to be quite isolated within *Tragia.* In fact, the collection of Standley and Valerio cited below is apparently the basis for the erroneous report of *T. bailloniana* in Standley's "Flora of Costa Rica" (1937: 622). However, that species, which had previously been known only from southern Mexico and northern Central America as far south as Honduras, has only recently been collected in Costa Rica (Alajuela: along Upper Río Sarapiquí, near Cariblanco and along road to Colonia Virgen del Socorro, 19 Feb. 1982, *Burger et al. 11850,* F) and Panama (Chiriquí: Fortuna Dam site, 15 Sept. 1977, *Folsom et al. 5612,* MO).

The specimens cited below have been variously distributed as *Tragia bailloniana, T. shankii, Dalechampia tiliifolia,* or as undetermined *Dalechampia.* The two collections from Panama are not currently available to me and are included here on the authority of Armbruster (pers. comm.).

Additional collections. COSTA RICA. LIMON: Hacienda Tapezco-Hda. La Suerta, 29 air km W of Tortuguero, 10°30'N, 83°47'W, 40 m, 10 Mar. 1978, *Davidson et al. 6828* (F); Montaña de Andromeda, drainage of Río Estrella, 300 m, 26–28 Oct. 1951, *Shank & Molina 4475* (F); Finca Montecristo, below Cairo, 25 m, Feb. 1926, *Standley & Valerio 48568* (F).

PANAMA. COCLE: 16.5 km N of Llano Grande, in forest near saw mill, 29 Jan. 1980, *Armbruster & Herzig 79-213* (ALA); near saw mill, 16.7 km N of turnoff to Coclesito from Llano Grande, 700 ft., 6 Mar. 1978, *Hammel 1813* (MO).

COLOMBIA. CHOCO: Río San Juan, vic. of Palestina, 0–30 m, 28 May–4 June 1946, *Cuatrecasas 21512* (F, 2 sheets).

I am indebted to Dr. Scott Armbruster of the University of Alaska for valuable correspondence during the preparation of this paper.

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—*Michael J. Huft, Missouri Botanical Garden. Mailing address: Department of Botany, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605.*

ANN. MISSOURI BOT. GARD. 71: 341. 1984.

A NEW COMBINATION FOR A NORTH AMERICAN *EPILOBIUM*

In order to make the name available for several pending floristic works, we make the following new combination in advance of a complete revision of *Epilobium* in North America:

Epilobium glaberrimum Barbey subsp. **fastigiatum** (Nutt.) Hoch & Raven, comb. nov. *Epilobium affine* Bong. *β.? fastigiatum* Nutt. in Torrey & A. Gray, Fl. N. Amer. 1: 489. 1840. TYPE: "Plains of the Columbia River" (probably near Walla Walla, Washington), 1834–36, *T. Nuttall s.n.* (holotype, BM; isotype, NY). *Epilobium fastigiatum* (Nutt.) Piper, Contr. U.S. Natl. Herb. 11: 404. 1906. *Epilobium glaberrimum* Barbey var. *fastigiatum* (Nutt.) Trel. ex Peck, Man. Fl. Pl. Oregon 494. 1941.

This includes only partial synonymy. Full explanation of the rationale for recognizing this taxon as a distinct subspecies is given in Hoch (1978), and will be included in the revision now in progress.

We gratefully acknowledge support from the National Science Foundation through grants to both investigators.

LITERATURE CITED

HOCH, P. C. 1978. Systematics and evolution of the *Epilobium ciliatum* complex in North America (Onagraceae). Ph.D. dissertation. Washington University, St. Louis.

—*Peter C. Hoch and Peter H. Raven, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166–0299.*

ANN. MISSOURI BOT. GARD. 71: 342. 1984.

UPCOMING MEETINGS

AETFAT—Association pour l'Etude Taxonomique de la Flora d'Afrique Tropicale—Association for the Taxonomic Study of the Flora of Tropical Africa.

The Eleventh Congress of the Association will be held at the Missouri Botanical Garden, St. Louis, Missouri, from 11 to 14 June 1985. The central theme will be Modern Systematic Studies in African Botany, and several invited papers will be presented on this subject. Several special interest symposia are being organized, including Systematics and Floristics of African Bryophytes; African Lichens; Biology of Madagascar; and African Ethnobotany and Ethnomedicine. Contributed papers on African plant systematics, floristics, ecology, and related fields are welcomed. For registration and further information, write to: Dr. Peter Goldblatt, AETFAT General Secretary, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

Second International Legume Conference.

The Conference, entitled "*Biology of the Leguminosae,*" will be held on 23–27 June 1986 at the Missouri Botanical Garden, St. Louis, Missouri. The aim of the meeting is to discuss recent advances in our understanding of the biology of legumes, gained from both field and experimental research, and covering both pure and applied points of view. The multidisciplinary approach of the conference is designed to address a wide variety of research interests and to stimulate discussion among specialists. Scheduled topics include: life history studies; tree architecture; evolution and biology of inflorescences and pollen; floral organogenesis; ecology; ecological biogeography; pollen-stigma-style interactions; structure and function of legume fruits and seeds; mycorrhizal relationships; cyanogenesis; evolution of symbiotic genes; biological implications of genome evolution; ant-domatia, aphid-legume, tick-legume, and bruchid-legume co-evolution; biological changes induced by domestication; computerized data bases and biological research; international legume data bases. For further information write to: Dr. James L. Zarucchi, Legume Conference Coordinator, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

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The ANNALS publishes original manuscripts in systematic botany and related fields. Authors are asked to follow the suggestions below in order to expedite editing and publication. Manuscripts not prepared properly may be returned for revision prior to review. If an author feels that his manuscript presents special problems, he should write the editor concerning the best way to handle these before submitting the manuscript. Page costs are $55.00 per page; charges may be reduced under special circumstances, and the editor will help authors to seek additional funding if necessary.

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Use one paragraph per basionym as follows: taxon, author, literature citation, type citation, e.g., *Bauhinia dipetala* Hemsl., Diag. Pl. Nov. 1880. *Casparia dipetala* (Hemsl.) Britt. & Rose, N. Amer. Fl. 23: 216. 1930. Type: Mexico. Veracruz: Valle de Cordoba, *Bourgeau 1713* (holotype, K; isotypes, F, GH, P, US). (See also Regnum Veg. 58: 39–40. 1968 for examples of synonym citations.) Descriptions should follow style found in other ANNALS issues, e.g., in Wunderlin, 1983 (70: 95–127). Keys should be dichotomous, indented, with numbered couplets. Cite representative specimens as follows: Mexico. Oaxaca: Sierra San Pedro Nolesco, Talea, *Jurgensen 865* (BM, G, K, US). Use herbarium acronyms as listed in *Index Herbariorum* (Regnum Veg. 106). Use authority abbreviations as listed in *Draft Index of Author Abbreviations compiled at the Herbarium, Royal Botanic Gardens, Kew* (1980).

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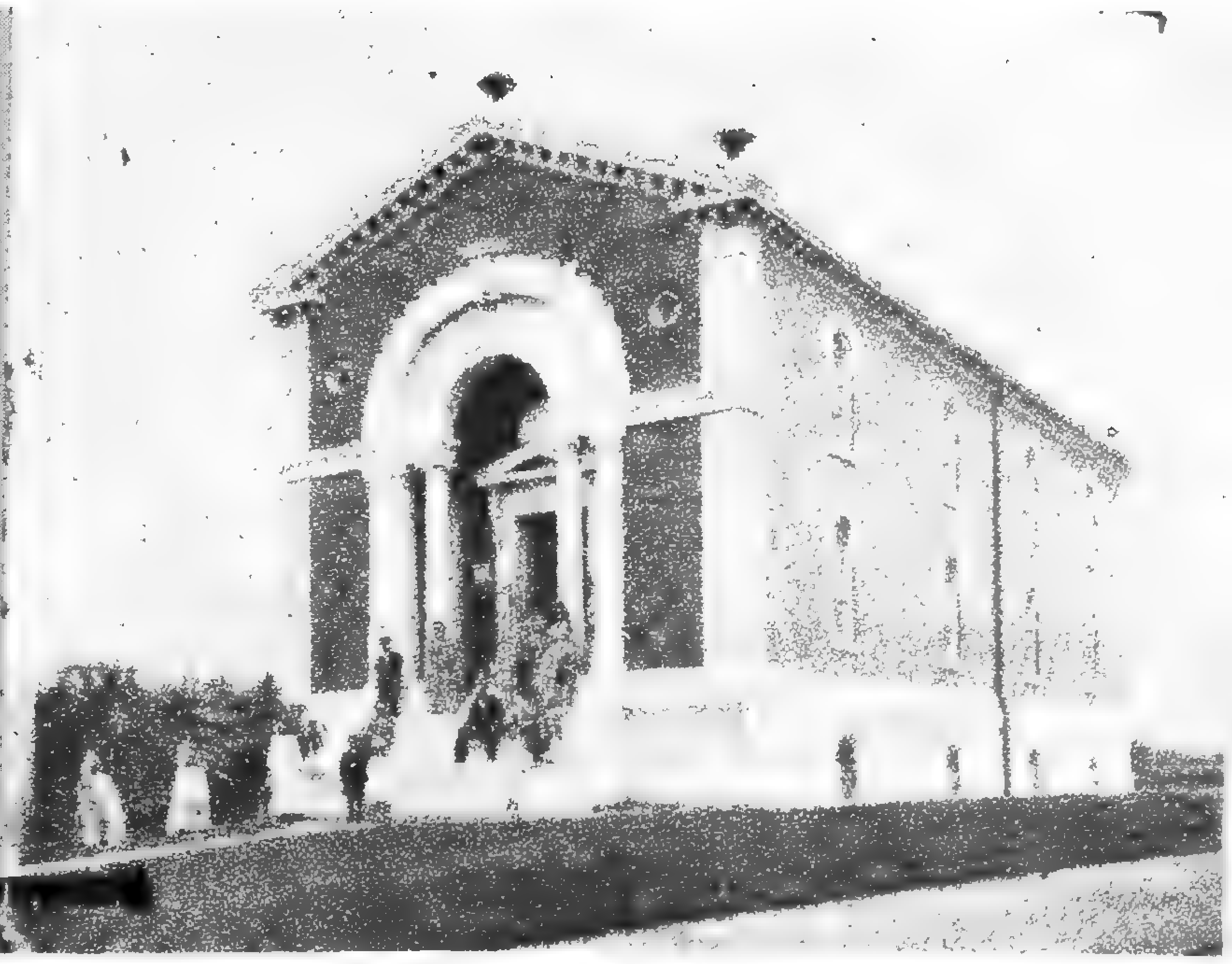

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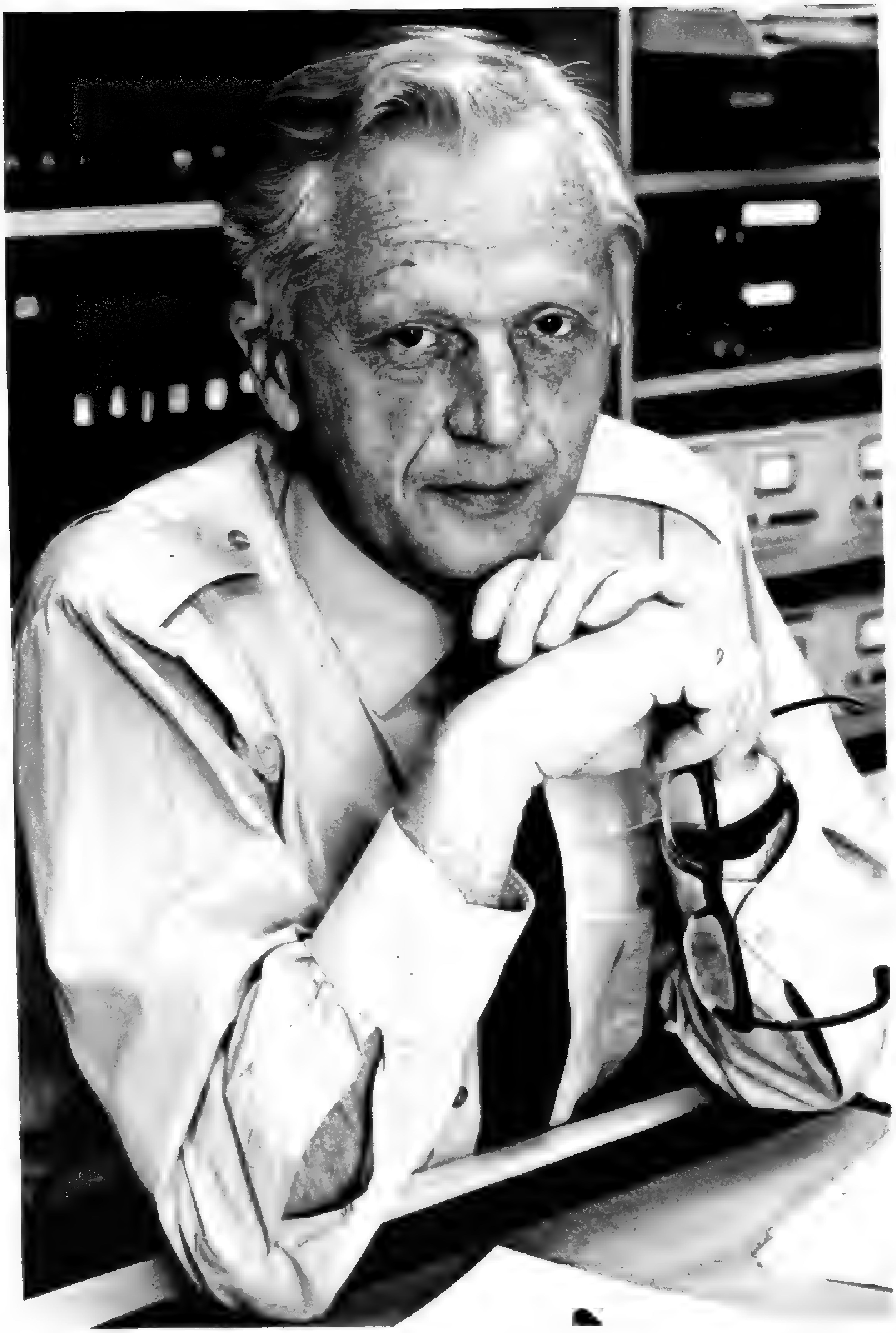

Dr. Jan Muller 1921–1983

ANNALS
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VOLUME 71 1984 NUMBER 2

Dedication

This symposium issue is dedicated to Dr. Jan Muller in recognition of his work on the systematics and fossil history of angiosperm pollen. His careful and analytical studies resulted in many pioneering and landmark papers. Jan Muller's careful observations and critical evaluations of fossil pollen records had an important impact upon the way in which his colleagues presently apply angiosperm pollen records to the history of this group. His leadership in assessing the fossil pollen records of extant angiosperms is recognized by research scholars around the world. Jan Muller's enthusiasm for searching out the truth of angiosperm lineages and his honest appraisal of the relationships of fossil angiosperm pollen to extant taxa will always be appreciated by his colleagues.

HISTORICAL PERSPECTIVES OF ANGIOSPERM EVOLUTION

Symposium volumes represent temporal nodes that lend themselves to taking stock of various disciplines. In the case of angiosperm paleobotany, the last major symposium volume, "Origin and Early Evolution in Angiosperms," C. B. Beck (editor), appeared eight years ago. Although that particular volume (Beck, 1976) stressed origin and early evolution only, some appreciation of changes in emphasis and approach in angiosperm paleobotany since that time may be gained by considering this volume in the perspective of its predecessor.

Historically, angiosperm paleobotany turned a corner 15–20 years ago. And in some ways, several papers published since that time represent a quantum change in the character of the field that brought angiosperm paleobotany in line with modern paleontological investigations. Previously, floristic investigations were emphasized and attention to individual fossils, their morphological characters and critical assessments of their affinities were secondary. As a result, generally, studies of relatively Recent (Neogene) floras had much validity while the identifications based on superficial features made many conclusions based on studies of older fossils erroneous (Dilcher, 1974). In addition, little was contributed to our understanding of evolution within the angiosperms. The confusion resulting from such approaches is well known.

As problems became evident in older paleobotanical research, the direction in angiosperm studies shifted to a more careful approach emphasizing the evaluation of the fossils themselves and the establishment of their affinities. This largely empirical direction was an important element in angiosperm paleobotany for a long time. Perhaps the excesses of previous researchers induced the response of willful myopia in many scientists during this conservative phase of angiosperm paleobotany. Whatever the motivating factors, it is only 15 to 20 years since the beginning of the trend in angiosperm paleobotany in which the investigation of evolution has been based upon newly devised systematic techniques and the recognition of extinct angiosperm forms, as well as patterns in the fossil record.

The present collection of papers provides an opportunity to gain some overview of the contemporary field of angiosperm paleobotany and, thus, to see how emphases have changed. While these manuscripts do not illustrate all that has been done recently in angiosperm paleobotany, they provide a representation of current work in this field. It is now possible to observe that certain areas of emphasis that were gathering momentum ten years ago have continued to become increasingly important, while other entirely new areas of concentration have become significant.

These following papers, as contributions to an international symposium on angiosperm paleobotany, represent a broad spectrum of research in both subject and philosophy. It would certainly serve our immediate purposes if all of them could be nested neatly under the rubric of modern angiosperm paleobotany and if each illustrated some extension of a commonly held philosophy. Yet the fact that this cannot be easily done is quite informative. There remain differences in approach in the modern scientific community studying angiosperm paleobotany, and there remain significant differences in attitude. These extend at times even to varying interpretations of particular fossil organs. Certainly, with respect to modern angiosperm paleobotany, V. Krassilov is an iconoclast whose contribution to this volume reveals more than his attitude. Krassilov's paper makes it clear that there are certain enigmatic early angiosperm fossils that need further investigation and that there is still disagreement as to the interpretation of angiosperm ancestry within the paleobotanical community. The contribution by Hughes also stands somewhat apart because he takes an overview pointing to some of the nagging problems in Mesozoic angiosperm paleobotany and makes some innovative proposals to deal with them.

The other papers are easier to group and illustrate where the field has been going during the past few years. Perhaps most obvious is the continuity in studies of angiosperm pollen. Doyle (1969), Muller (1970), and Brenner (1963, 1967) had (and continue to have) important impact during the late 1960s and early 1970s. Doyle's contribution was noteworthy because it stressed pattern in the context of evolution while Brenner stressed evolutionary history in the context of paleobiogeography, and Muller emphasized the importance of the critical evaluation in palynology to reveal past record of extant flowering plants.

Studies of palynology continue to stress pattern and history, but, in this volume, micromorphology and ultrastructural analysis are also important. Walker and Walker illustrate how careful analysis of single Lower Cretaceous palynomorphs can contribute to our understanding of variation in early angiosperm pollen, variation that might be misleading or go unnoticed without the application of modern techniques, and point out similarities between certain well-known Cretaceous palynomorphs and pollen of modern taxa. Zavada concentrates on morphological analysis of monosulcate pollen by proposing evolutionary trends based on modern taxa and carefully evaluating taxonomic characters used to distinguish angiosperm pollen from gymnosperm pollen. He then examines certain fossil palynomorphs, often pre-Cretaceous, in the context of their possible significance to angiosperm origins. Muller summarizes angiosperm history based on the palynological record and notes significant events in angiosperm evolution and evolutionary patterns. Muller's selective approach to the palynological literature, based on careful morphological analysis, gives credibility to the utility of the dispersed pollen record in documenting angiosperm history.

A relatively new area of angiosperm research involving the study of flowers and inflorescences has become a significant part of angiosperm paleobotany. Since serious investigations of fossil flowers and inflorescences have begun (e.g., Crepet et al., 1974, 1975; Tiffney, 1977), such investigations have become more common and have been conducted at various levels. Further evidence of their continuing importance are four papers reporting new floral finds by Dilcher and Crane, Crane and Dilcher, and Schaarschmidt and Friis. Fossil floral remains have also been used in the paper by Crepet to assess the importance and success of faithful pollinators in flowering plant history.

Another important and interesting aspect of angiosperm paleobotany involves emphasis on fruits. Bruce Tiffney's contribution to this symposium volume incorporates fruit and seed data in an analysis of the history and significance of animal dispersal of angiosperm fruits. Crepet and Tiffney's contributions both emphasize plant-animal interactions in an effort to assess the significance of animal involvement in angiosperm radiation and speciation from fossil data. Dilcher and Crane and Crane and Dilcher combine analyses of both fruiting material and flower forms, demonstrating that some early angiosperms shared the characteristic features and apparent reproductive biology of the Magnoliidae. Several associated plant organs are assumed to represent a single taxon based upon stratigraphy and anatomy in an effort to reconstruct a whole flowering and fruiting shoot of an ancient angiosperm. The flowering shoot has features which indicate that the co-adaptive evolution between floral morphology and pollinators was important by the mid-Cretaceous.

Leaf studies have been extremely important and recent emphases on fine venation analysis and cuticular features of fossil leaves have proven essential in interpreting their affinities (Hickey, 1973; Dilcher, 1974). The significance of pollen and leaf remains from the Atlantic Coastal Plain are well known (Hickey & Doyle, 1977), and Upchurch has analyzed patterns in the evolution of the cuticular features of angiosperm leaves from these deposits.

Emphasis on pattern with an eye on evolution in an ecological context continues to be important in angiosperm paleobotany. Such emphasis transcends the analysis of any one particular type of organ. However, sources of data once thought beyond the scope of angiosperm paleobotany (e.g., leaf cuticles, pollen ultrastructure, and floral structure) are proving valuable sources of insight into different aspects of angiosperm history that will prove important in understanding their evolution. In addition, it is obvious that morphological analysis has become extremely important in angiosperm paleobotany giving credibility to the assessment of relationships between fossil and modern taxa, providing a better idea of past variation, and potentially allowing a better assessment of homologies.

From the paleobotanical work represented here it is possible to speculate on the areas of important directions in angiosperm paleobotany. First, pattern analysis has the potential for contributing to our understanding of the process of evolution and to the understanding of certain evolutionary events in the context of ecology. Second, increasingly sophisticated morphological analysis, character state analysis, and knowledge of variability in extant as well as related extinct taxa combined with increasingly sophisticated systematic methods have great potential for having fossil angiosperm data make an important contribution to the classification of the flowering plants. Finally, it should be evident that empirical contributions (i.e., studies of fossils, their affinities, analysis of their characters in the context of related modern taxa including the establishment of homologies) will continue to be an important aspect of angiosperm paleobotany.

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ARCHAEANTHUS: AN EARLY ANGIOSPERM FROM THE CENOMANIAN OF THE WESTERN INTERIOR OF NORTH AMERICA[1]

David L. Dilcher[2] and Peter R. Crane[3]

Abstract

Archaeanthus linnenbergeri Dilcher & Crane, gen. et sp. nov., a multifollicular angiosperm fruit, is described from the mid-Cretaceous (uppermost Albian–mid-Cenomanian) Dakota Formation of central Kansas. Clusters of follicles were borne terminally at the apex of a stout branch with helically arranged leaves. Each cluster comprised 100–130 helically arranged follicles on an elongated receptacle. The follicles were stalked with a short, rounded tip and dehisced along a single adaxial suture. Ovules were numerous and borne along either side of the suture; 10–18 seeds matured in each follicle. The receptacle below the gynoecium shows three groups of scars, an upper group of numerous small scars interpreted as those of stamens with six to nine larger scars immediately below, interpreted as those of inner perianth parts. The flower is delimited at the base by three large, narrowly elliptical scars interpreted as those of outer perianth parts. A prominent scar below the base of the flower is thought to mark the position of floral bud-scales. *Archaeanthus* is linked with perianth parts (*Archaepetala beekeri* Dilcher & Crane, gen. et sp. nov. and *Archaepetala obscura* Dilcher & Crane, sp. nov.), bud scales (*Kalymmanthus walkeri* Dilcher & Crane, gen. et sp. nov.), and leaves (*Liriophyllum kansense* Dilcher & Crane, sp. nov.) on the basis of association evidence and structural agreement in the presence of distinctive resin-bodies. *Liriophyllum populoides* Lesq. is shown to be a separate species. The reconstructed *Archaeanthus* plant is most closely related to Recent Magnoliidae and in some features comes close to the hypothetical angiosperm archetype predicted by magnoliid floral theory; it demonstrates that many of the characters interpreted as primitive from neontological evidence are also ancient. *Archaeanthus* does not predate other kinds of angiosperm reproductive structure in the fossil record but conclusively demonstrates the existence of magnoliid-like plants and flowers early in angiosperm evolution.

Hypotheses of flowering plant phylogeny are inextricably linked to the evolutionary interpretation of angiosperm reproductive organs and thus to concepts of the primitive angiosperm flower. Traditionally such ideas have been based on comparative studies of living plants, and the fossil record has made little contribution. In recent years, however, knowledge of early angiosperm reproductive diversity has increased, and paleobotanical data relevant to these problems have begun to accumulate. In this paper we describe a new species of mid-Cretaceous angiosperm known from multifollicular fruits, perianth parts, bud-scales, and leaves, and discuss its relevance to concepts of floral evolution in flowering plants.

The earliest speculations on the nature of the primitive angiosperm flower developed from the pre-Darwinian classifications of the eighteenth and nineteenth centuries and polarized into two principal hypotheses: either the simple, unisexual and predominantly wind-pollinated flowers of the Amentiferae were primitive (Engler, 1897; Strasburger et al., 1898; Rendle, 1925, 1930; Wettstein, 1935) or the bisexual and predominantly insect-pollinated flowers of the magnoliid (Ranalean) angiosperms most closely approximate to the 'ancestral' flower (Bessey, 1897, 1915;

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Arber & Parkin, 1907). Subsequent investigations and interpretations, particularly of anatomical (Bailey, 1944; Eames, 1961; Dickison, 1975) and palynological evidence (Wodehouse, 1935, 1936; Walker 1974a, 1974b, 1976), led to the widespread acceptance of the second hypothesis, that the Magnoliidae are the most primitive living group of flowering plants and exhibit the most primitive floral morphology. This hypothesis is central in most of the putatively 'phylogenetic' classifications of flowering plants that have been proposed in the last 50 years (Hutchinson, 1959; Cronquist, 1968, 1981; Takhtajan, 1969; Stebbins, 1974; Thorne, 1976; Dahlgren, 1980), and although alternative viewpoints have been suggested (Corner, 1949; Melville, 1962, 1963; Meeuse, 1966), none have been widely accepted. Along with the development of the magnoliid hypothesis has come the recognition of 'evolutionary trends' for a wide range of characters. The primitive states in these trends have been combined into a concept of a hypothetical angiosperm morphotype (Takhtajan, 1969).

Until recently, direct paleobotanical evidence relevant to these evolutionary hypotheses has been conspicuously absent. The last two decades, however, have seen considerable advances in angiosperm paleobotany and an increasing awareness of the relevance of fossil material to concepts of flowering plant evolution (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Hughes, 1976; Doyle, 1978; Dilcher, 1979). A major radiation is regarded as having occurred during the Barremian to Cenomanian stages of the mid-Cretaceous, followed by further diversification throughout the Upper Cretaceous and Tertiary. No unequivocal angiosperms have so far been reported from pre-Barremian rocks, although there are many earlier, potentially relevant fossil plants about which we know too little (Doyle, 1978; Hill & Crane, 1982; R. A. Scott et al., 1960). Despite some insight into the timing of angiosperm evolution, the systematic origin of the group remains a mystery that continues to stimulate a variety of speculations (Melville, 1962, 1963; Meeuse, 1966; Retallack & Dilcher, 1981a). Such conjectures inevitably reduce to discussions of homology, particularly of reproductive structures, and have been severely limited by inadequate knowledge of early flowering plants. Few of the mid-Cretaceous angiosperms are known in detail from flowering or fruiting specimens, and even fewer are known from both vegetative and reproductive material. The species described in this paper is currently one of the more completely understood of all early angiosperms. We propose the name *Archaeanthus linnenbergeri* for multifollicular fruits and the vegetative branches on which they are borne. This species is linked with two kinds of perianth parts (*Archaepetala beekeri* Dilcher & Crane, gen. et sp. nov. and *Archaepetala obscura* Dilcher & Crane, sp. nov.), bud-scales (*Kalymmanthus walkeri* Dilcher & Crane, gen. et sp. nov), and leaves (*Liriophyllum kansense* Dilcher & Crane, sp. nov.) as parts of a single fossil plant on the basis of association and the anatomical similarity that all these organs contain the same distinctive resin-bodies. *Liriophyllum populoides* Lesq. is shown to represent a different species. The reconstructed *Archaeanthus* plant is closely allied to the Magnoliidae sensu lato, and in some features comes close to the hypothetical angiosperm morphotype predicted by magnoliid floral theory.

MATERIAL

With the exception of the specimens of *Liriophyllum populoides,* and one possible specimen of *Archaeanthus linnenbergeri,* from Morrison, Colorado, all of the material described in this paper is from the Dakota Formation at Linnenberger's Ranch near Bunker Hill, Russell County, central Kansas (see Retallack & Dilcher, 1981b, 1981c, for details of this locality). The plant material is preserved as compressions in a brown-gray clay with variable amounts of sand and silt. The specimens typically have good organic preservation. The associated macroflora is dominated by about 15 to 20 kinds of angiosperm leaves, but although the microflora is well preserved, angiosperm pollen accounts for only about 25% of the total palynomorphs. Most of the Linnenberger Ranch material described in this paper comes from a narrow sandy bed, low in the section at the locality; some of this material has been previously described by Dilcher et al. (1976, 1978) and Dilcher (1979). The Linnenberger plant assemblage is interpreted as a flora of local origin, deposited in a fluvial swale on the distal flanks of a levee system (Retallack & Dilcher, 1981b, 1981c).

In central Kansas, the Dakota Formation exhibits considerable lateral sedimentological variation but has been divided into two Members: the Terra Cotta Clay Member below, and the Janssen Clay Member above (Plummer & Romary, 1942). These are not mappable units and are clearly facies-related (Franks, 1975), but the Terra Cotta Clay Member typically consists of gray to greenish gray clays and shales with abundant lenticular, fine- to coarse-grained sandstone units, whereas the Janssen Clay Member consists of gray to dark gray claystones, siltstones, and shales with lenticular sandstones. Lignites are particularly abundant in the upper parts of the Janssen Clay Member (Schoewe, 1952). The Terra Cotta Clay Member is interpreted as predominantly fluvial and overbank, alluvial plain sediments deposited by streams flowing from the north and east, whereas the Janssen Clay Member represents a greater range of paleoenvironments, some of which, particularly in the higher parts of the section, were associated with the transgressing mid-Cretaceous Graneros Sea (Siemers, 1971; Franks, 1975). The sedimentology, paleontology, and other aspects of Dakota Formation geology are considered more fully by Plummer and Romary (1942, 1947), Siemers (1971), Hattin and Siemers (1978), Bayne et al. (1971), and Retallack and Dilcher (1981b, 1981c). The Linnenberger Ranch material comes from the Janssen Clay Member, relatively high in the Dakota Formation. The classic Dakota Sandstone Flora described by Lesquereux (1868, 1874, 1878, 1883, 1892), Gress (1922), and Newberry (1868) is probably predominantly from the sandstone facies of the same Member.

Toward the south and west, the Dakota Formation overlies the Kiowa Shale (Franks, 1975), which is dated on evidence of marine fauna and palynomorphs as late Albian (R. W. Scott, 1970a, 1970b; Ward, 1981), and in the north and east oversteps onto older Paleozoic rocks. In the south and west it interdigitates with, and is overlain by, the Graneros Shale, a shallow-water marine deposit representing the initial transgressive phase of the Greenhorn cyclothem. Sediments from the transitional zone represent a considerable diversity of marginal marine environments. Marine invertebrates securely date the Graneros as Cenomanian (Hattin, 1965; Eicher, 1975) and radiometric determinations of the 'X bentonite' in the upper part of the Graneros (Hattin, 1965, 1967) give an age of about 94.5 Ma (Kauffman, pers. comm.). Palynological investigations (Doyle, pers. comm.; Ravn, 1981) similarly indicate a Cenomanian age probably equivalent to zone III of the palynological zonation established by Brenner (1963), Doyle (1969), Doyle and Robbins (1977), and others for the mid-Cretaceous of the Atlantic Coastal Plain. Zavada (pers. comm.) has shown that the palynofloras from the upper Dakota Formation and Graneros are similar and contain about 20–35% angiosperm pollen, whereas the upper Kiowa Shale contains less than 5%. On the basis of all the evidence available, it seems likely that the Dakota Formation of central Kansas extends across the Upper and Lower Cretaceous boundary (Zeller, 1968; Kauffman et al., 1976). The fossil plants discussed in this paper from the Janssen Clay Member, therefore, date approximately from the Upper and Lower Cretaceous boundary and are of uppermost Albian or lowermost Cenomanian age.

The specimens of *Liriophyllum populoides* originally described by Lesquereux (1883) and discussed in this paper are from the Dakota Group of Morrison, Colorado, which, on the western edge of the Denver Basin, comprises the Lytle Formation below and the South Platte Formation above (Waage, 1955). The South Platte Formation consists of dark gray to black shales and brown weathering sandstones deposited in a range of marine-influenced estuarine, littoral, and alluvial plain environments (Waage, 1955; Weimer & Land, 1972). The majority of the 'Dakota Sandstone' plants from Morrison described by Lesquereux (1883) and Knowlton (1896, 1920) come from the Kassler Sandstone Member in the upper part of the South Platte Formation (Lee, 1920; Waage, 1955), equivalent to part of the 'J' sandstone (Weimer & Land, 1972) or the lower part of 'genetic unit C' (Weimer, 1970). They are preserved as impressions in a hard, pale gray sandstone. The Kassler Sandstone Member grades laterally into the marine Skull Creek Shales (R. G. Young, 1970) with *Inoceramus comancheanus* (Waage, 1955) and is generally accepted as upper Albian in age (Waage, 1955; McGookey et al., 1970; Kauffman et al., 1976; Berman et al., 1980).

Specific acronyms are used to designate the source of the fossil material studied. IU stands for Indiana University, HU stands for Harvard University, and USNM stands for United States National Museum, which is housed at the Smithsonian Institution.

SYSTEMATICS

In this section we describe six species representing four kinds of organs: multifollicular fruits (*Archaeanthus linnenbergeri*), leaves (*Liriophyllum populoides, L. kansense*), putative perianth parts (*Archaepetala beekeri, A. obscura*), and probable bud-scales (*Kalymmanthus walkeri*).

The measurements in the descriptions are based on all the material cited. Ranges and common dimensions are given in parentheses where available.

Archaeanthus Dilcher & Crane, gen. nov. TYPE: *Archaeanthus linnenbergeri* Dilcher & Crane, sp. nov.

DIAGNOSIS: Reproductive axis a cluster of follicles (a multifollicular fruit) with evidence of having been subtended by other floral organs. Receptacle stout, elongated, consisting of a distal tapering gynoecial zone bearing helically arranged follicles, with a shorter, more or less cylindrical zone below, showing circular and elliptical scars. Base of the flower delimited by three transverse, narrowly elliptic, slit-shaped scars. Follicles ellipsoidal, stalked, with a short, rounded tip and a distinct adaxial suture; containing numerous seeds.

DERIVATION: From *archae*—Greek, meaning beginning or first; *anthos*—Greek, meaning flower.

Archaeanthus linnenbergeri Dilcher & Crane, sp. nov. HOLOTYPE: IU 15703-4152.

DIAGNOSIS: As for the genus.

REFERENCES: '*Magnolia* species,' Lesquereux (1883: 73, pl. 11, fig. 6, brief description and drawing).

'Reproductive axes of *Liriophyllum*,' Dilcher et al. (1976: 854, fig. 1a, b, d, brief description and discussion with photographs and a line drawing).

'Reproductive axis' (*Carpites liriophylli* Lesquereux, 1883), Dilcher (1979: 311, figs. 40, 50, 51, brief discussion with photographs and line drawings. *Carpites liriophylli* is too poorly preserved to evaluate its similarity with our species).

OTHER MATERIAL: IU 15703; 2300, 2317, 2318, 2590, 3022, 3837, 3907, 4105, 4112, 4134–4150, 4152, 4153, 4155–4158, 4163, 4164, 4166–4170, 4198, 4532–4534.

NUMBER OF SPECIMENS EXAMINED: 44.

FIGURES: 1–37, 60a, f–h.

DERIVATION: After Albert and Edward Linnenberger, owners of the central Kansas locality from which this material was collected.

DESCRIPTION: Clusters of follicles (multifollicles) borne terminally and singly at the apex of a substantial vegetative branch 11–16 mm diam. Branch bearing helically arranged leaf scars at intervals of 28–35 mm. Leaf scars broadly elliptic, 1.5–3.3 mm long, 2.5 mm wide, pointed on either side. Surface of axis with occasional short, irregular, longitudinal, and transverse striations. Maximum length of branch preserved, 145 mm. Total length of the longest specimens seen, including branch and receptacle, 215 mm.

Receptacle elongated to 137 mm long (longest specimen incomplete). Gynoecial zone distal with irregular longitudinal ribs, elongating during development; most complete immature specimen 47 mm long, 7 mm wide at the base; longest mature specimen 137 mm long (incomplete), 8–12 mm wide at the base. Gynoecial zone gradually tapering distally and bearing 100–130 follicles. Immature carpels packed into a loose fascicle forming an ellipsoidal head ca. 22 mm diam., 50 mm high. Mature follicles loosely aggregated into an elongated conical head, ca. 70 mm diam. and to 152 mm high. Follicles borne helically leaving elongated, diamond-shaped scars, 1.5–4 mm long, 0.75–1 mm wide on the mature receptacle. Upper part of scars deeply impressed into the axis, becoming shallower in the lower half. Receptacle below the gynoecium short, more or less cylindrical, 7–9 mm long, tapering from 11–15 mm wide proximally to 8–12 mm distally in mature specimens. Receptacle immediately below the gynoecial zone bearing ca. 50–60 transversely elongated, elliptical scars ca. 1 mm broad (interpreted as those of stamens), followed below by 6–9 larger, more or less circular scars ca. 2 mm diam., apparently arranged in pairs (interpreted as those of inner perianth parts). Base of receptacle delimited by three prominent, narrowly elliptical, slit-shaped transverse scars pointed at either end, 2–3 mm high, 11–13 mm wide (interpreted as those of outer perianth parts). Pedicel with a distinct transverse ridge ca. 20–25 mm below the most proximal floral scars. Pedicel gradually broadening toward the ridge.

FIGURES 1–2. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov., IU 15703-4152.—1. Branch bearing the lower part of a receptacle with a cluster of follicles at the apex. Follicles on the extreme left not attached to the receptacle, × 1.—2. Detail of specimen in Figure 1 showing two scars at the base of the receptacle,

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interpreted as part of a whorl of three. Note the zone of the receptacle between these large scars and the base of the gynoecial zone. Compare with Figures 4 and 66, ×2.5. a. Base of gynoecial zone. b, c. Undifferentiated middle zone of the receptacle. d. Scars of outer perianth whorl. e. Pair of scars on pedicel attributed to a calyptra. f. Leaf scar.

Ridge bearing at least 2 narrow, transverse scars about 1 mm high (interpreted as those of bud-scales).

Immature carpels slightly reflexed, ca. 16 mm long, 1 mm wide, with rounded tips. Mature follicles ellipsoidal, more or less straight, occasionally slightly reflexed. Individual follicles 25–35 (–38) mm long, (1–)4–7(–11) mm wide; length of locule (10–)20–29(–31) mm. Follicles contracted proximally into a stalk, 4.5–8 mm long, and distally into a short, rounded apex. Apex sometimes shortly two-lobed; lobes formed by the two adaxial crests at the apex of the follicles. Stalk 1–2 mm wide at its midpoint, broadening proximally to 1.5–4 mm at the point of attachment to the receptacle. Angle of attachment typically 50–80°. Follicles, when shed, breaking away at the base of the stalk.

Mature follicles with a median, longitudinal, adaxial suture along the entire length, flanked on either side by a ridge 1 mm high, forming an adaxial crest. Cuticle of adaxial crest bearing long, simple, unicellular trichomes. Follicles with a single weak abaxial rib extending along the entire length. Locule uninterrupted, but in a few specimens transversely constricted by regular or irregular, ridges and surface undulations into 10–18 weakly delimited oval units (interpreted as indicating positions of seeds), 2–3 mm high, 1–2 mm wide. These units more or less confined to the upper two-thirds of laterally compressed follicles, each unit frequently with a central area of dark organic matter.

Mature follicle wall of at least two distinct layers. Endocarp striated, comprised of transverse, tightly packed fibers, 10–20 μm wide. Fibers frequently separated to form prominent transverse cracks in compressed follicles. Exocarp with no visible cellular detail.

Immature follicles containing numerous (about 100) ovules borne (presumably along either side of the adaxial suture) 1–2 mm below the outer surface of the adaxial crest. Ovules arranged close together and overlapping, elliptical, ca. 2 mm long, ca. 0.75 mm wide; one end pointed and oriented adaxially, the other rounded. Ovules

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FIGURES 3–6. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov.—3. IU 15703-2300. Composite photograph showing the upper gynoecial zone of a long receptacle bearing numerous helically arranged follicles. Branch on the right of the specimen showing scars of floral organs (see Fig. 4), ×1.—4. Composite photograph showing detail of branch in Figure 3. a. Base of gynoecial zone. b. Upper part of the middle receptacle zone showing small scars interpreted as staminal. c. Lower part of the middle receptacle zone showing larger scars interpreted as those of inner perianth parts. d. Scars of outer perianth whorl. e. Pair of scars on pedicel attributed to a calyptra. Compare Figures 1, 12, and 66, ×2.25.—5. IU 15703-4136. Fragment of a small, presumably aborted receptacle showing closely spaced, linear, helically arranged carpels, ×1.—6. IU 15703-2300. Detail showing several mature follicles attached to the receptacle. Note the ridged receptacle with helically arranged diamond-shaped scars left by the follicle bases, ×2.

FIGURES 7–12. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov.—7. IU 15703-4145′. Showing several follicles attached to a long receptacular gynoecial zone, ×1.—8. IU 15703-3022. Showing a mass of compressed follicles associated with a broad, ridged receptacle, ×1.—9. IU 15703-4150. Branch showing the base of a receptacle with attached follicles. Note the clearly defined base (a) of the gynoecial zone, ×1.—10. IU 15703-4532. Gynoecial zone of a small, presumably aborted receptacle showing numerous linear, blunt-tipped carpels (compare Lesquereux, 1883: 73, pl. 11, fig. 6), ×1.—11. Detail of specimen in Figure 10 showing linear, blunt-tipped carpels, ×4.—12. Detail of specimen in Figure 9 showing: a. Base of gynoecial zone. b, c. Undifferentiated middle zone of receptacle. d. Large scar of outer perianth whorl delimiting the base of the flower, ×2.

FIGURES 13–21. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov.—13. IU 15703-2317. Isolated follicle showing penetration of sediment through the adaxial suture, which has preserved a three-dimensional cast of the locule, ×2.—14. Same specimen as Figure 13 with the locule cast removed to show the abaxial ridge on the follicle surface, ×2.—15. Locule cast of the same specimen as Figure 13 removed from the rock and showing penetration of sediment through the adaxial suture into the follicle, ×2.—16. Locule cast of the same specimen as Figure 13, abaxial view showing longitudinal ridge, ×2.—17. IU 15703-2318. Several follicles. Note the blunt, bilobed tip of the central follicle formed by the apical part of the adaxial crests, ×2.—18. IU 15703-4167. Isolated follicle with distorted stalk and blunt tip. Note penetration of sediment through the adaxial suture, ×2.—19. IU 15703-4157. Detail of apex of dorsi-ventrally compressed follicle showing blunt bilobed tip formed by the adaxial crests. Note median longitudinal groove in the abaxial surface of the follicle, ×4.—20. IU 15703-2318′. Detail of follicle base showing stalk and expanded attachment area, ×4.—21. IU 15703-2317. Detail of Figure 14 showing transverse cracks interpreted as cracks between the endocarp fibers, and small, slit-shaped depressions caused by resin-bodies in the follicle wall. Note the longitudinal ridge in the abaxial follicle surface, ×10.

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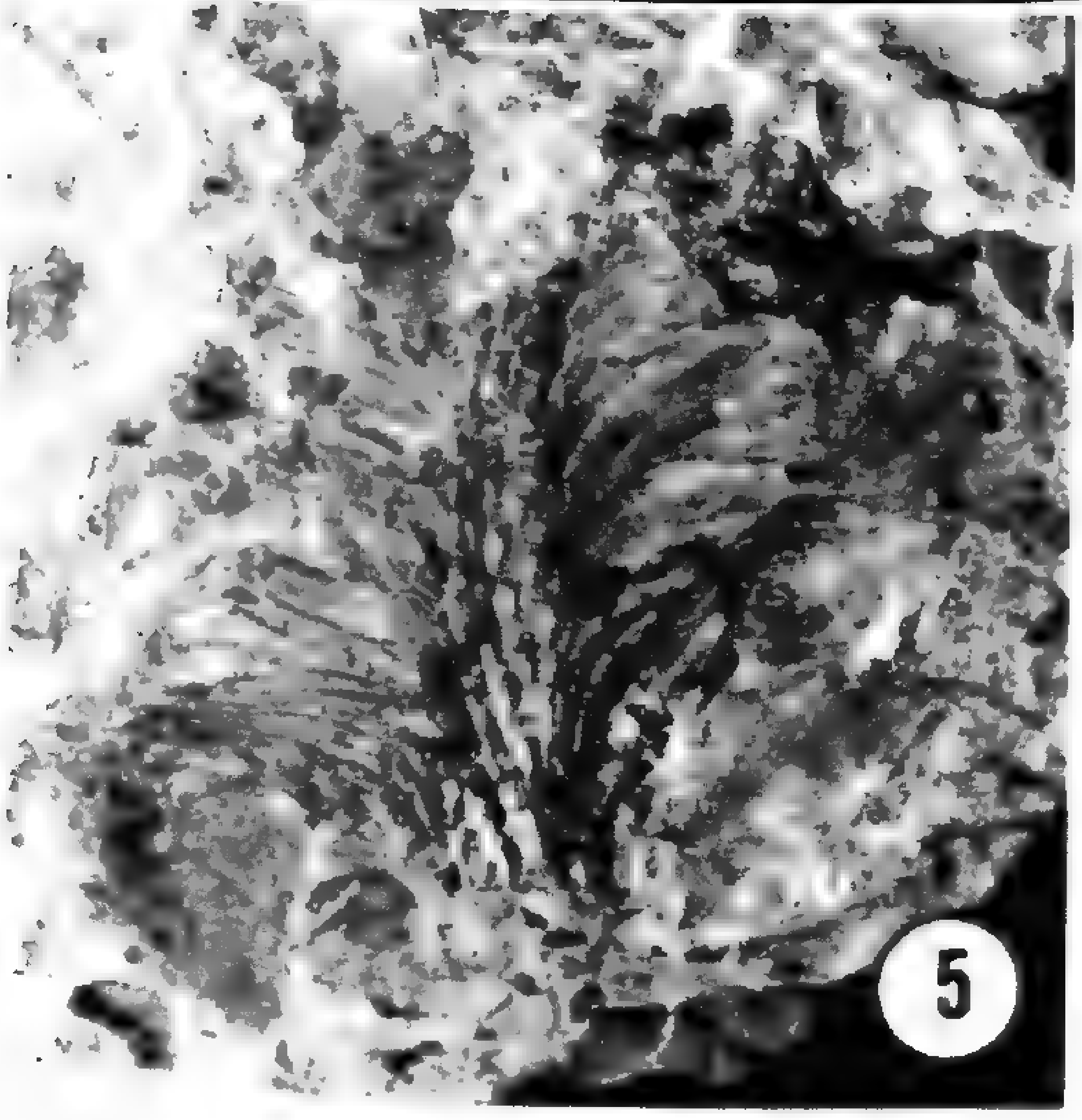

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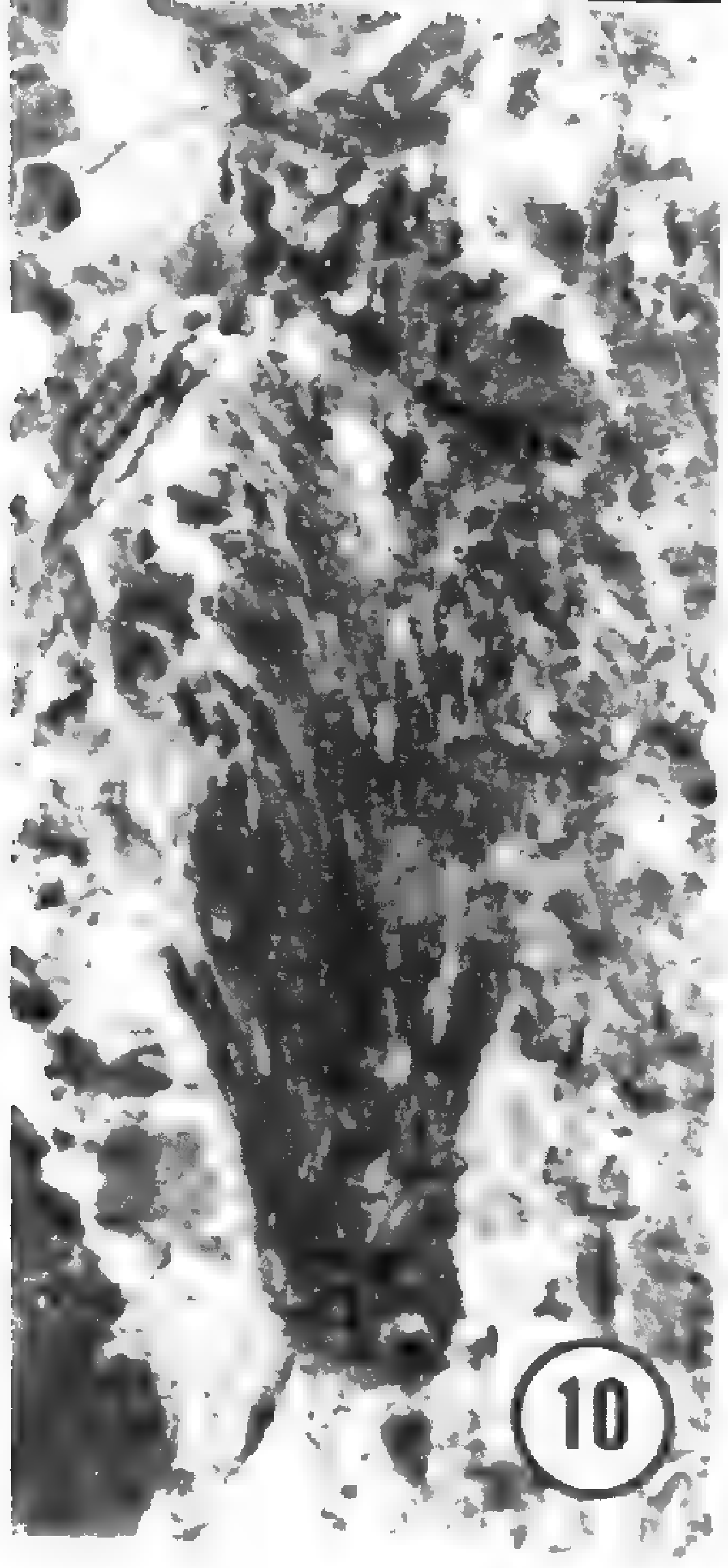
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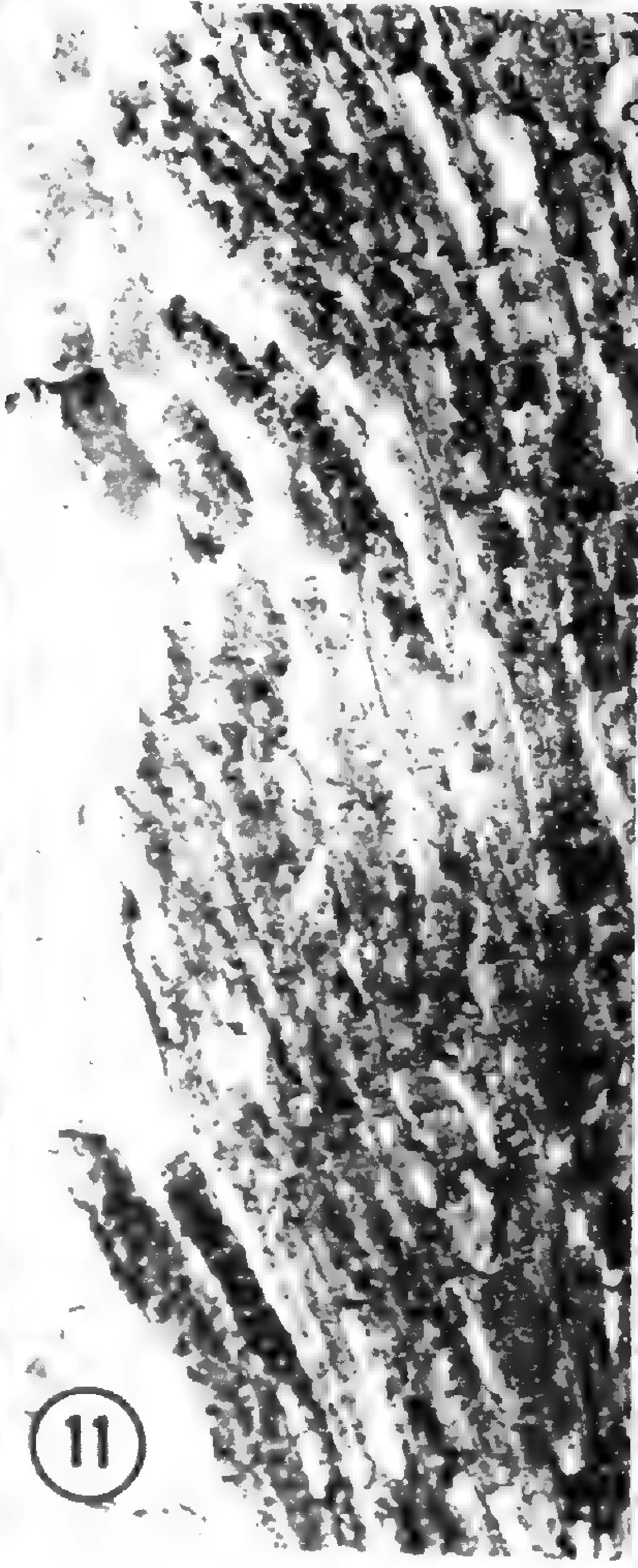
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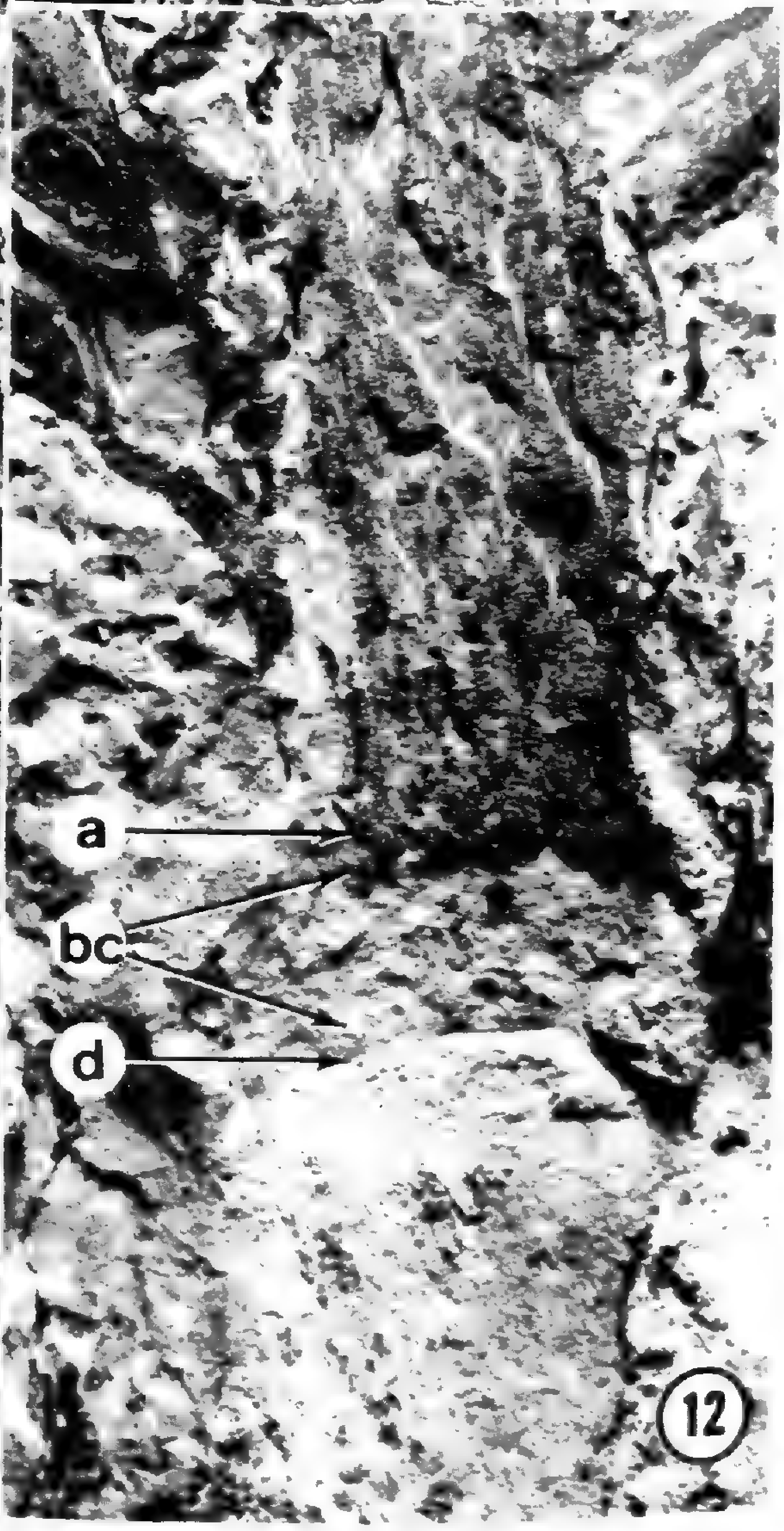
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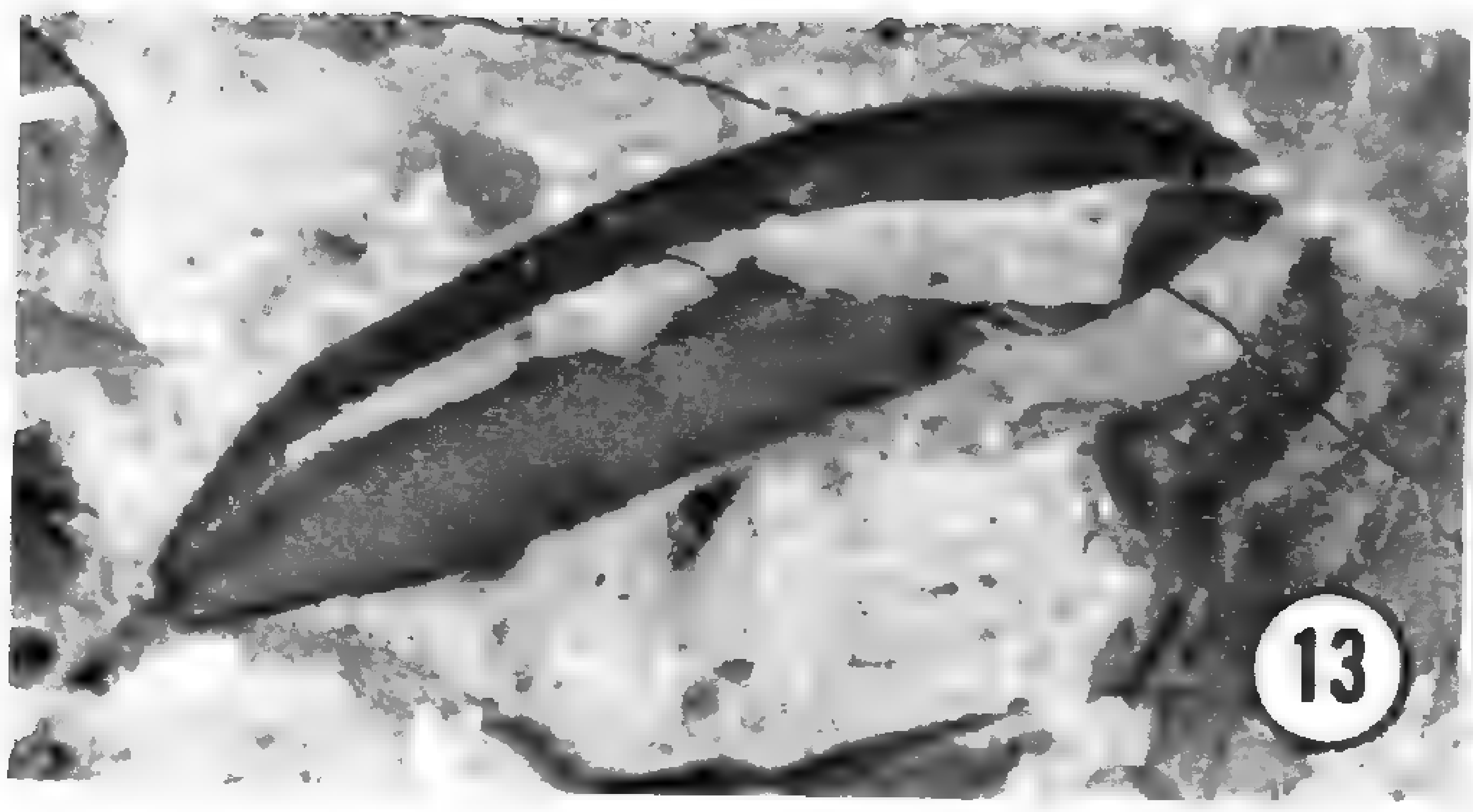
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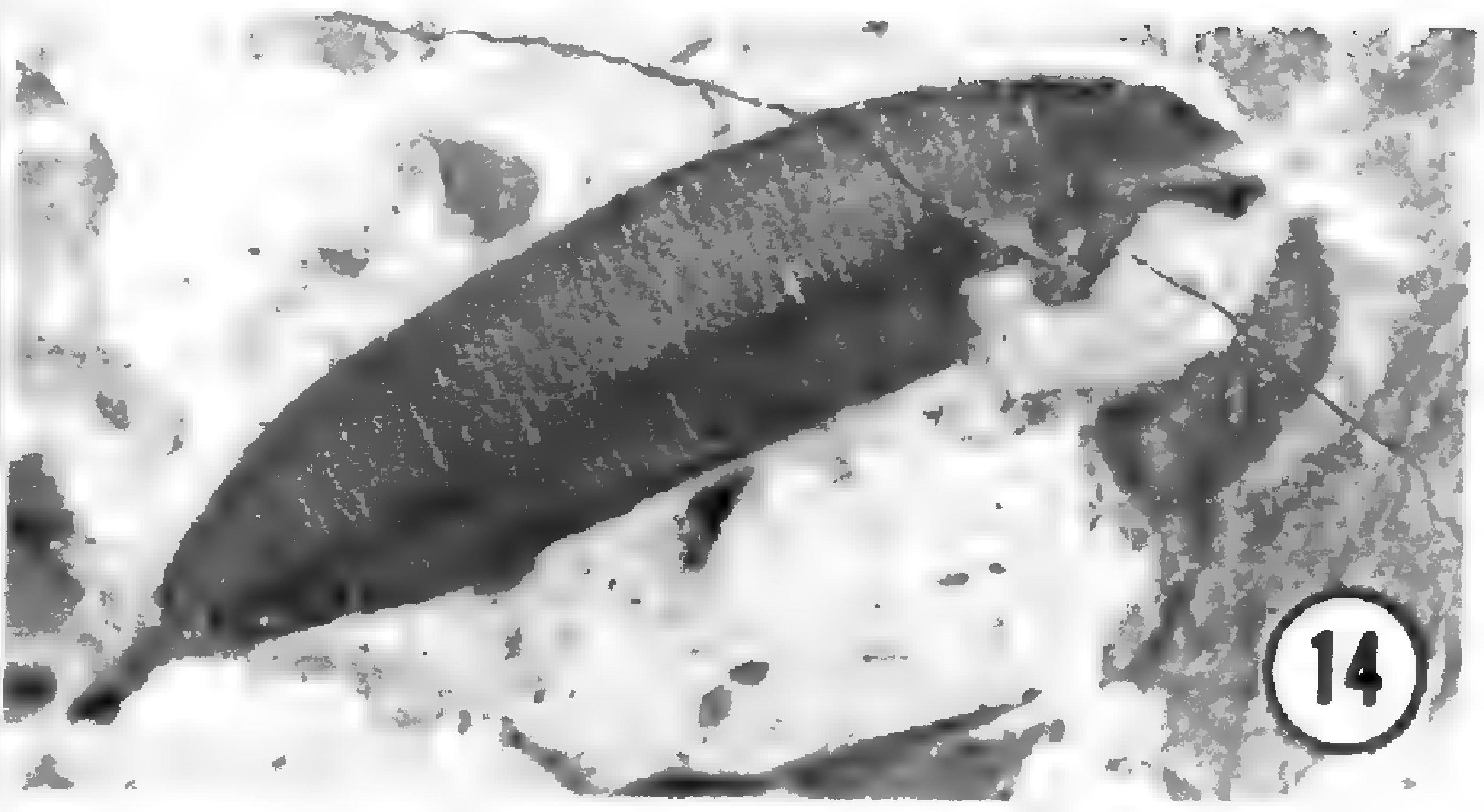
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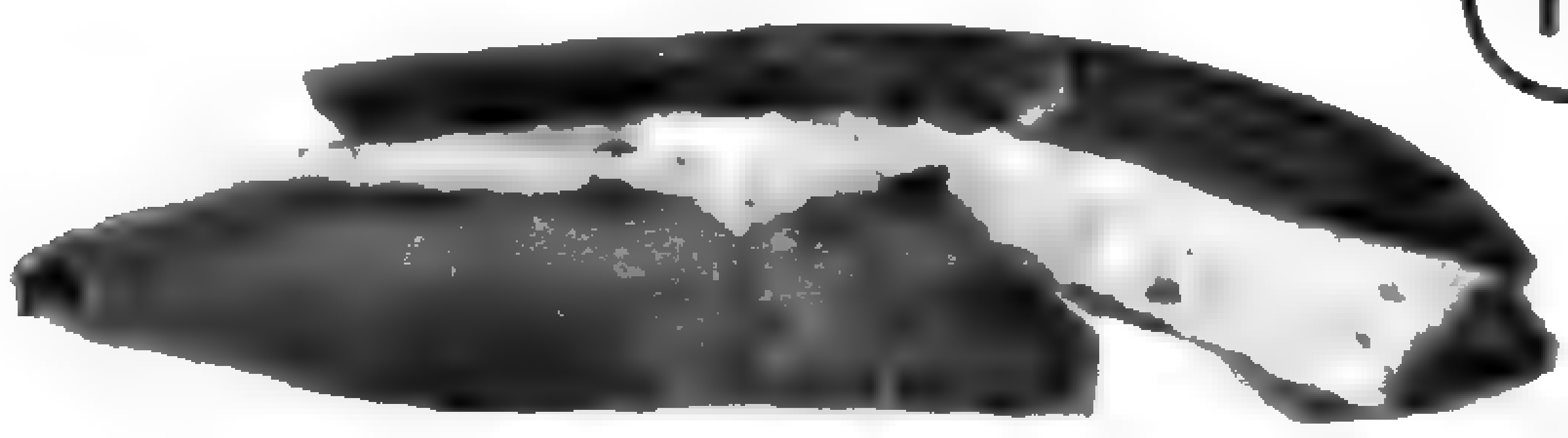
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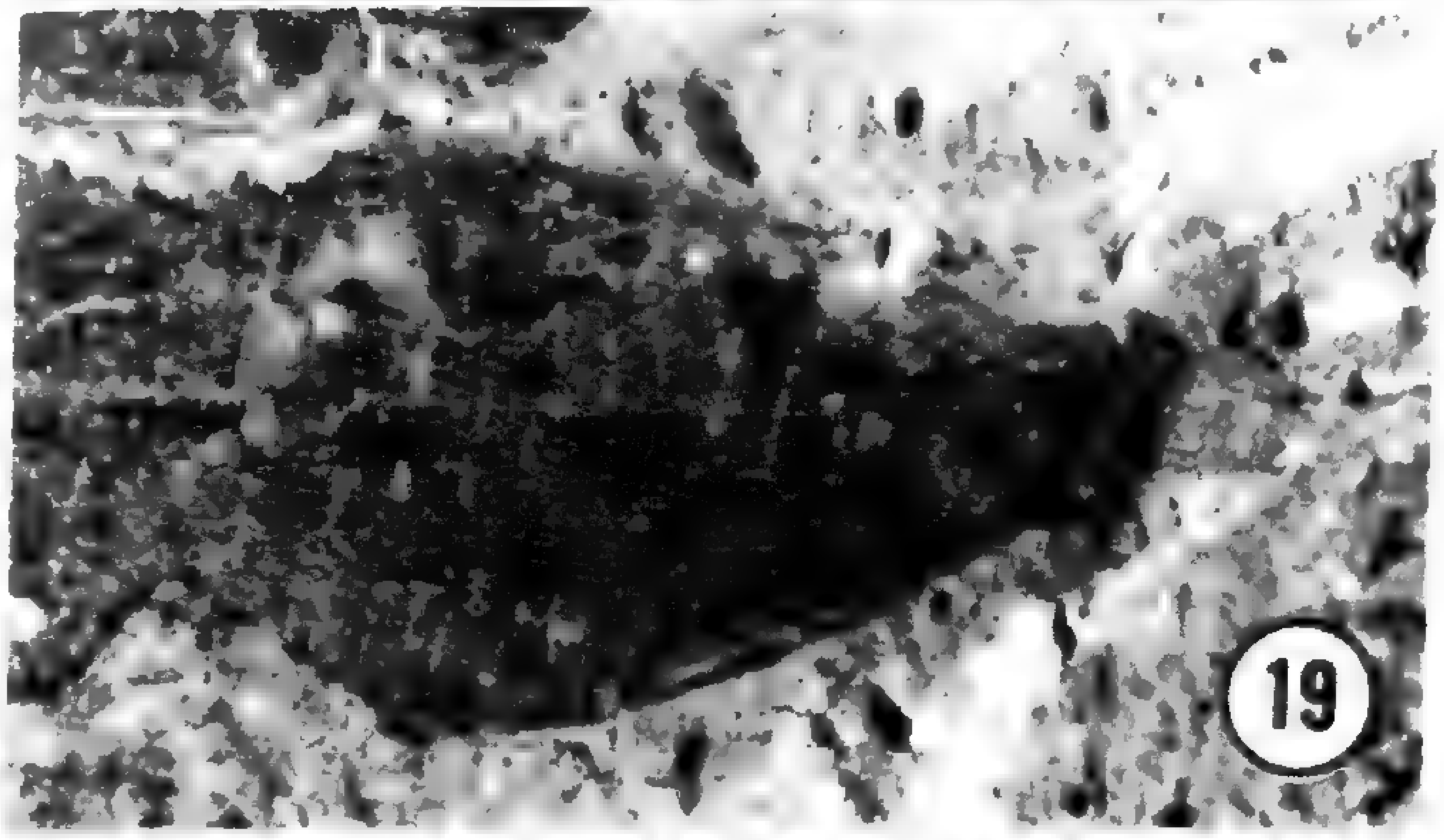
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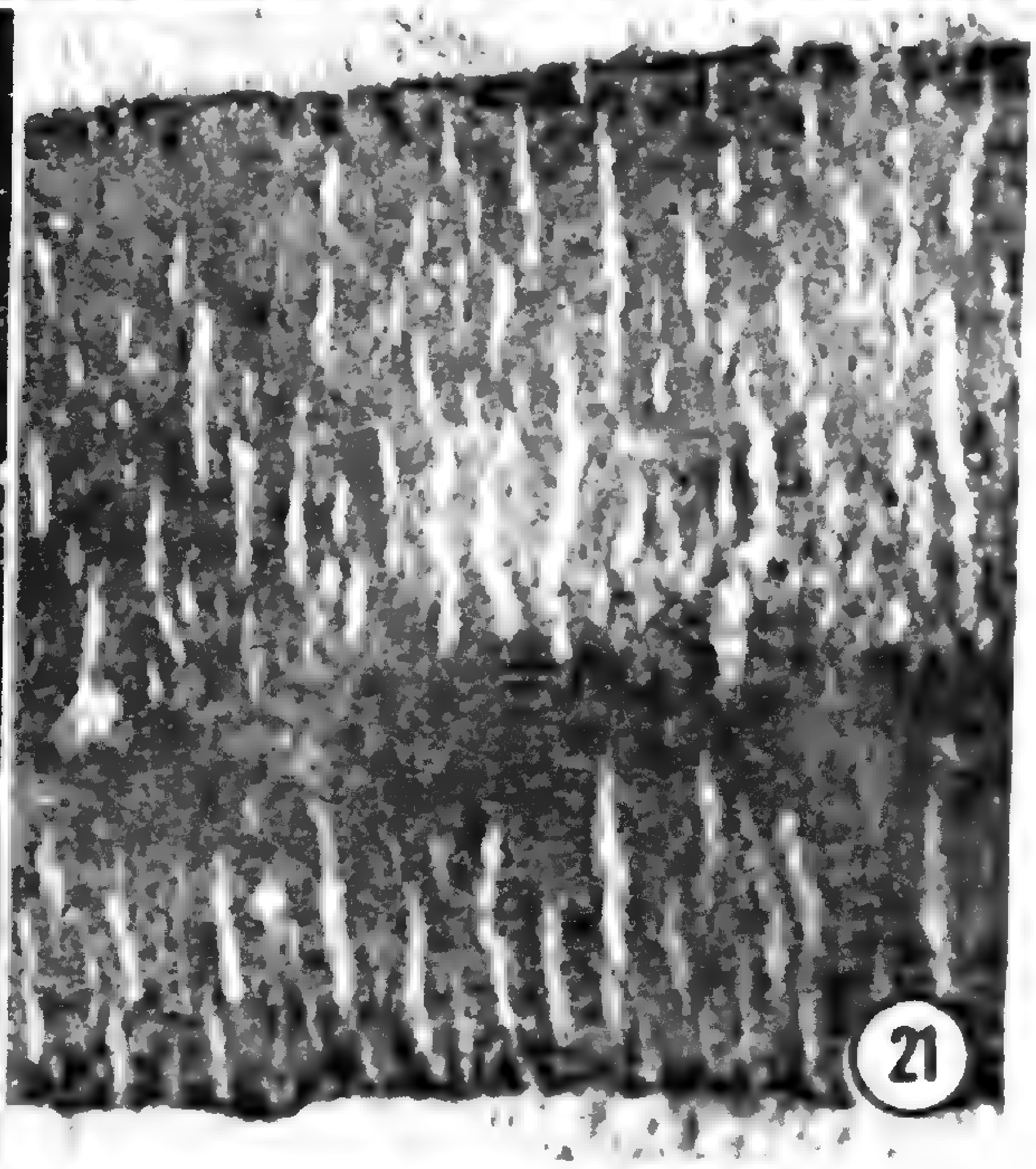
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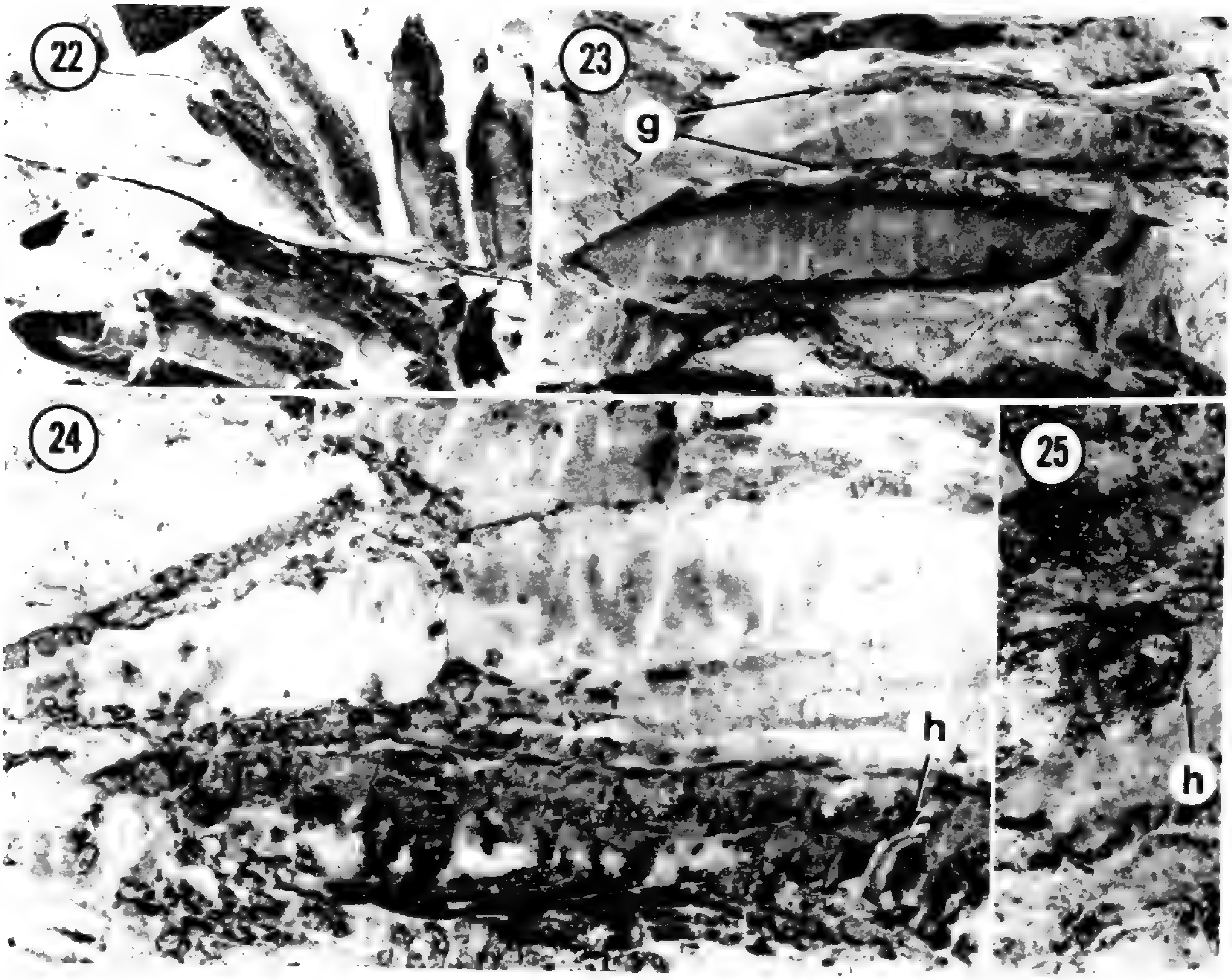


FIGURES 22–25. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov.—22. IU 15703-2318. Showing several follicles. Note the blunt follicle apices, ×1.—23. IU 15703-2300″. Detail of two laterally compressed follicles showing adaxial crests (g) and oval outlines attributed to the position of seeds. Note the restriction of seed outlines to the upper part of the follicle, ×3.—24. IU 15703-2300′. Detail of two laterally compressed follicles showing irregular outlines of seeds and one possible seed in situ (h), × 6.—25. IU 15703-2300′. Detail of follicle showing possible in situ seed (h), ×10.

with a single cutinized membrane, showing distinct cell outlines, delimited by very finely undulating anticlinal flanges. Pointed end heavily cutinized toward the tip, cell outlines more or less square, ca. 10 μm in both dimensions. Blunt end with a distinct, regular, oval to circular perforation, ca. 80 μm diam. Cell outlines in the median part of the membrane and near to the perforation elongated, 20–30 μm long, 5–10 μm wide.

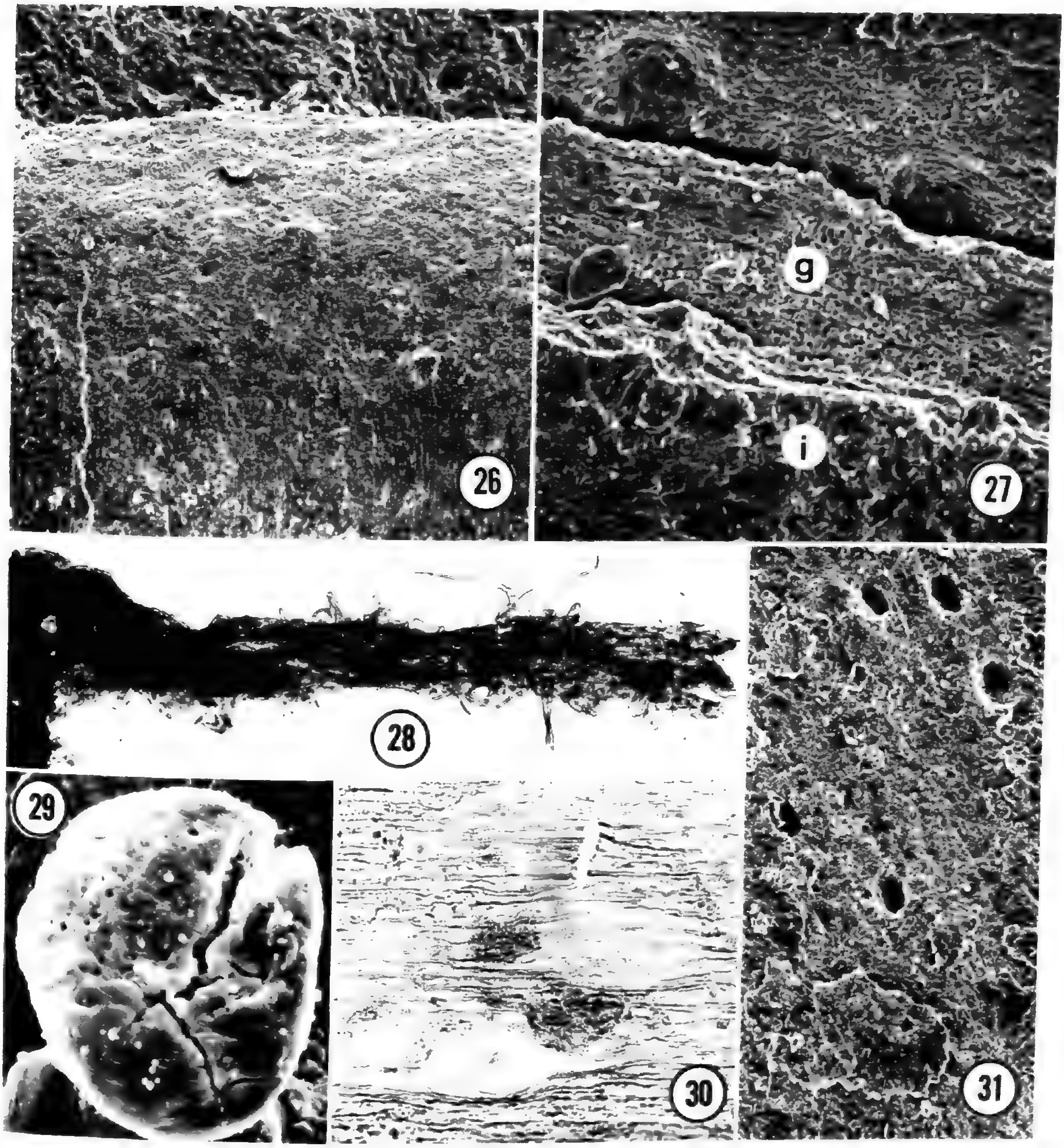
Carpels, receptacle, and branches all contain numerous, yellow-brown lustrous, resin-bodies, (60–)70–100(–120) μm diam.

DISCUSSION: *Archaeanthus linnenbergeri* is known from 44 specimens, all preserved as compressions in a sandy, silty, brown-gray clay. Many have appreciable organic material remaining and have yielded anatomical details.

Three specimens (Figs. 1–4, 9, 12) show the manner in which the clusters of follicles (multifollicles) and, hence, flowers were borne singly at the apex of a stout, presumably woody axis. They suggest that the multifollicles may not have been shed at maturity. The three helically arranged scars on the vegetative branch (Fig. 1) are the correct size and shape to correspond to inflated, petiole bases, such as those of small *Liriophyllum* leaves. The upper scar is substantially larger than the lower two and presumably bore a larger leaf.

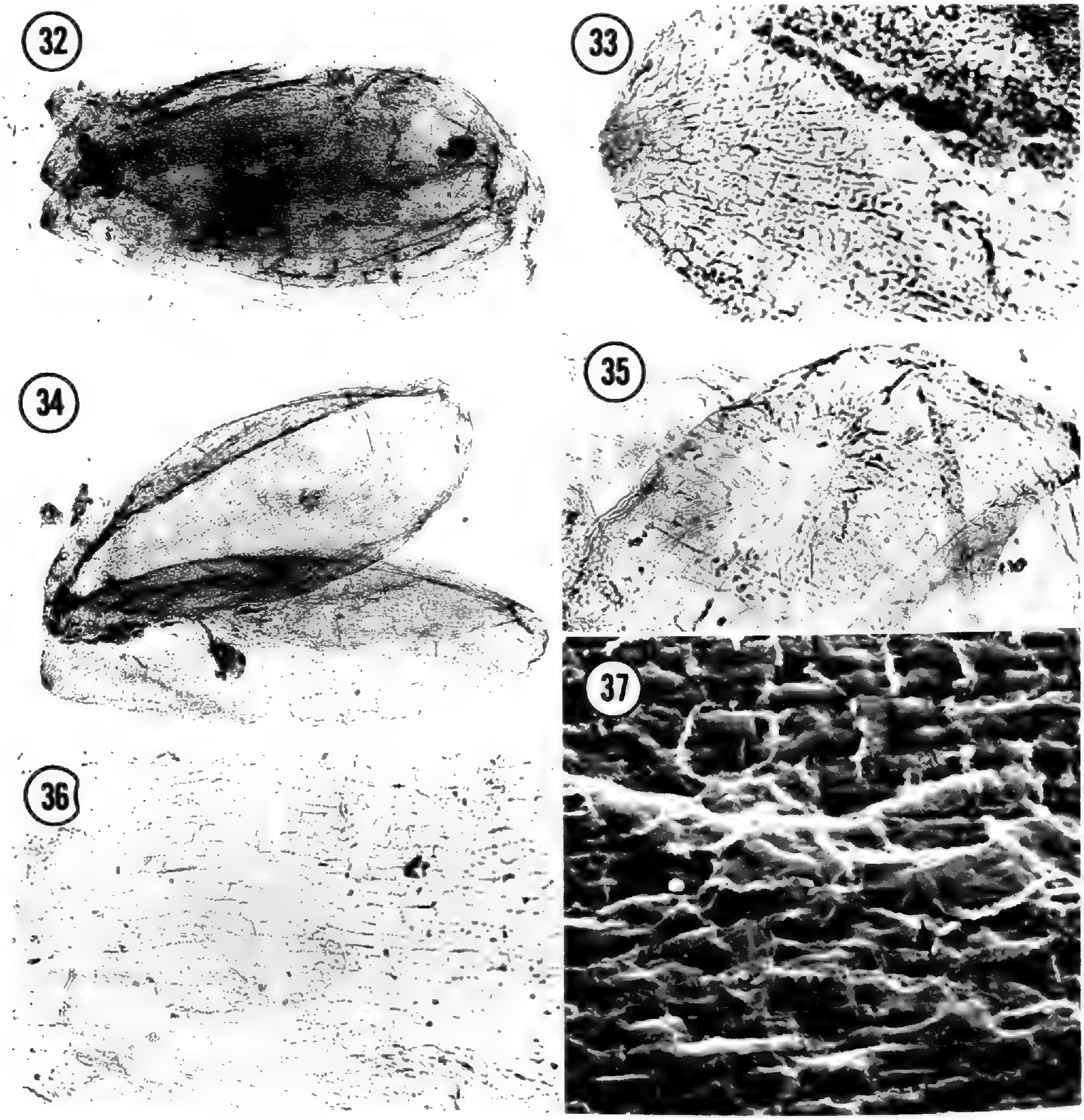
Two specimens (Figs. 10, 11, and IU 15703-4533) are immature, presumably aborted, gynoecial portions of the receptacle and are very similar to the '*Magnolia*' receptacle figured by Lesquereux (1883: 73, pl. 11, fig. 6). These specimens show that the gynoecium was elongated early in development and elongated further, perhaps passing through a stage represented by IU 15703-4136 (Fig. 5) as the fruits and seeds matured.

The organization of the receptacle at maturity



FIGURES 26–31. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov.—26. IU 15703-2300. Scanning electron micrograph showing impressions of fibers on the surface of a locule cast, ×50.—27. IU 15703-2300. Scanning electron micrograph showing impression of adaxial crest (g) and follicle wall (i). Note the difference in texture between the two areas and the two hemispherical depressions caused by resin-bodies, ×125.—28. IU 15703-2300. Light micrograph of cuticle isolated from an adaxial flange showing numerous simple trichomes, ×50.—29. IU 15703-2300. Scanning electron micrograph of a resin-body isolated from a follicle, ×450.—30. IU 15703-4105. Cuticle of locule surface showing elongated cell outlines and the distortions caused by resin-bodies, ×300.—31. IU 15703-4105. Scanning electron micrograph of surface of locule cast showing hemispherical depressions caused by resin-bodies, ×50.

is clear in the three specimens (Figs. 1–4, 9, 12) that have the base of the receptacle preserved, although none of our specimens show the complete length of the mature gynoecium with attached follicles. The most information can be seen on the axis with the lower part of a receptacle preserved on IU 15703-2300 (Figs. 3, 4). This axis has no attached follicles but is identified with *A. linnenbergeri* by the numerous resin-bodies which it contains. It may be the lower part of the well-preserved gynoecium with attached follicles to which it is adjacent. By comparison with IU 15703-4150 (Figs. 9, 12), we interpret the four semicircular marks at the broken upper edge of this specimen (Fig. 4) to be the base of the gynoecial zone. Immediately be-



FIGURES 32–37. *Archaeanthus linnenbergeri* Dilcher & Crane, gen. et sp. nov.—32. IU 15703-4105. Membranes macerated from follicle fragment interpreted as the nucellar or inner integumentary membrane of seeds or aborted ovules. Note the closely overlapping membranes, the strongly cutinized pointed tips interpreted as the micropylar ends, and the rounded bases with a circular perforation interpreted as the chalazal ends, ×30.—33. IU 15703-4105. Detail of micropylar end of ovule membrane showing cutinized tip and more or less isodiametric cell outlines, ×200.—34. IU 15703-4105. Two ovule membranes, ×30.—35. IU 15703-4105. Detail of circular chalazal perforation, ×200.—36. IU 15703-4105. Detail of cells from central portion of ovule membrane showing finely undulating cell outlines, ×200.—37. Scanning electron micrograph of ovule membrane showing finely undulating cell outlines, ×500.

low these marks are laterally elongated elliptical scars; about 12 are clearly visible, and we estimate that this zone of the receptacle probably contained 50–60 such scars. We interpret them as indicating the former position of stamens. Below this point on the receptacle is another zone of larger scars in which two pairs are clearly visible. We estimate that in life there may have been 6–9 such scars around the receptacle and interpret them as indicating the former position of inner perianth parts. At the base of the flower there is an elliptical mark similar to the scars seen at the base of the flower in Figures 2 and 12. These are particularly distinct in IU 15703-4152 (Fig. 2) and suggest that there was a whorl of three narrowly elliptical scars around the receptacle base. These scars are similar to that at the base of *Archaepetala beekeri* (Fig. 38). IU 15703-4152 (Fig. 2) and 2300 (Fig. 4) show a distinct ridge on the pedicel 20–25 mm below the base of the flower. In both specimens there is a suggestion that the ridge bore two scars. By analogy with extant *Liriodendron tulipifera* (Fig. 63) and *Magnolia tripetala* (Figs. 61, 66), we interpret the ridge as the position of calyptra-like bud-scales. Below this ridge, IU 15703-4152 shows no branching or evidence of other flowers; IU 15703-2300 (Fig. 3), however, shows a large concave scar which we interpret as a branch point.

The two specimens of aborted receptacles show that the immature carpels were long, narrow, and had rounded tips (Figs. 10, 11). As they ripened, they increased both in length and width to become ellipsoidal at maturity.

Individual follicles are occasionally found separated from the receptacle, and there may have been a tendency for them to be shed at maturity. They broke away at the very base of each fruit stalk (Fig. 20) to leave clear scars on the receptacle (Fig. 6). A few carpels show one or several transverse cracks on their stalk, corresponding to the groove reported by Dilcher et al. (1976). They are not, however, consistent or significant morphological features, and there is no evidence for any structures subtending the individual carpels in this region or at the base of the stalk. We therefore reject any interpretation of *A. linnenbergeri* as a raceme of unifollicular flowers (Krassilov, 1977).

The follicles clearly dehisced along an adaxial suture, and the locule of many is filled with sediment (Figs. 13–16, 18). There is a prominent adaxial ridge on most of the better preserved follicles (Figs. 23, 24), and some carpel apices clearly show that this adaxial flange continued over the apex, wrapping around the end and giving a bilobed appearance to the carpel tips (Figs. 17, 19). SEM examinations of sediment with impressions of the flange show that it had a different texture to the outer follicle wall (Fig. 27). Cuticle preparations show that both flanges were furnished with long, simple hairs, perhaps related to the stigmatic surface in younger carpels (Fig. 28).

We have obtained only a thin cuticle from the inner surface of the endocarp (Fig. 30), but there are clearly at least two layers in the follicle wall. An inner layer of transverse fibers is indicated by the fine transverse striations seen on the internal locule casts of some specimens (Fig. 26) as well as the transverse cracks (Fig. 21), which we interpret as splits between the fibers. The cuticle of the inner follicle surface shows elongated cells with obvious distortions made by resin-bodies compressed into it (Fig. 30). Many of the resin-bodies are more or less spherical (Figs. 29, 31); others are elongated and seem themselves to have been distorted by the endocarp fibers (Figs. 21, 30). Where organic material or impressions of the outer carpel surface are preserved, they show no obvious cellular detail.

A few specimens of *A. linnenbergeri* show 10–18 more or less oval areas along the length of the follicles (Figs. 3, 23). These are always restricted to the adaxial two-thirds, or half, of laterally compressed follicles and may appear as depressions or raised areas, depending on how the fracture plane passed through the compression, and the extent to which the locule was filled with sediment. We interpret these areas as bulges and constrictions in the follicle wall caused by seeds, and suggest that about ten to 18 seeds matured in each pod. Some of the seed outlines are slightly pointed toward the adaxial margin, perhaps indicating attachment. Seed outlines are seen in relatively few specimens, and where present vary considerably in the regularity with which they are developed; in some follicles they are very regular, but in others the outlines are more confused and overlap, perhaps indicating more than one row of seeds compressed on top of each other. Only two follicles (Figs. 24, 25) show what may be seeds in situ, but they add nothing to our knowledge of their morphology. We have not been able to confidently recognize dispersed seeds in our collections.

The membranes that we have isolated from the carpels are small (Figs. 32–37), and crowded together (Fig. 32). They are variable in size; some may correspond to the seed outlines discussed above while others may be the remains of aborted ovules. Each membrane is a single structure that we suggest is probably the outer cuticle of the nucellus, or possibly the remains of the inner integument, which is extremely thin in extant *Magnolia* (Earle, 1938). Macerations of aborted ovules from *Magnolia tripetala* have yielded similar internal membranes from around the nucellus (Fig. 68). There is no megaspore membrane (Harris, 1954; Hill & Crane, 1982). We are not certain whether the ovules were anatropous or orthotropous. None of our specimens show a raphe, but neither do the membranes from the anatropous ovules of *M. tripetala*. As far as we can tell, the ovules were oriented with the chalazal scar directed away from the suture and were therefore probably anatropous.

The ovules were attached below the base of the adaxial flanges and, like the seed outlines, are restricted to the upper half of the follicle. The ovules were numerous and borne overlapping (Fig. 32), presumably on either side of the suture. We estimate that each carpel probably contained about 100 ovules, but none of the locule casts show any indication of placental scars.

Archaepetala Dilcher & Crane, gen. nov. TYPE: *Archaepetala beekeri* Dilcher & Crane, sp. nov.

DIAGNOSIS: Simple, laminar, entire-margined, isolated, fossil petal-like structures.

DERIVATION: From *archae*—Greek, meaning beginning or first; *petalos*—Greek, meaning broad, flat, outspread.

DISCUSSION: This genus is established as a broad form-genus for accommodating isolated, fossil petal-like structures with the above morphology.

Archaepetala beekeri Dilcher & Crane, sp. nov. HOLOTYPE: IU 15703-3179.

DIAGNOSIS: Lamina elliptical, length-to-width ratio approximately 2:1. Base with a prominent attachment area, apex rounded. Lamina with a broad rib running from the base to the apex.

OTHER MATERIAL: IU 15703-3882.

NUMBER OF SPECIMENS EXAMINED: 2.

FIGURES: 38, 41, 44, 60d.

DERIVATION: After Mr. Charles Beeker, who helped collect much of the material from Linnenberger Ranch.

DESCRIPTION: Lamina simple, elliptical, 70–80 mm long, ca. 40 mm wide (maximum); length-to-width ratio approximately 2:1. Margin entire. Base with a prominent scar that is rounded above, straight below, and pointed at either end; 14 mm wide, 5 mm high. Apex rounded. Lamina with a broad midrib of numerous fine striations running from the attachment area at the base to the apex (further details of venation not seen). Midrib the same width as the attachment area proximally, narrowing distally, 4–6 mm wide in the central part of the lamina. Surface of lamina wrinkled with fine, irregular areolae ca. 0.3–0.8 mm diam. and with numerous spherical resin-bodies (60–)80–100(–110) μm diam.

DISCUSSION: *Archaepetala beekeri* is known from only two specimens (Figs. 38, 41), but both are almost complete. They show evidence of having been at least partially rigid with some three-dimensional curvature in life. The surface texture imparted by the wrinkles and irregular small areolae is distinctive and like that seen in *Kalymmanthus walkeri,* making fragmentary specimens difficult to separate. We are uncertain as to the cause of these areolae, but they could result from clusters of harder cells, such as sclerenchyma, in the lamina.

The shape and size of the attachment area on *A. beekeri* is very similar to the three scars that occur at the base of the receptacle in *Archaeanthus linnenbergeri.* For this and other reasons discussed later (see Reconstruction of the *Archaeanthus* Plant), we suggest that *A. beekeri* are the outer perianth parts of *Archaeanthus* flowers. The irregular wrinkled surface is similar to that of certain dried *Magnolia* perianth parts.

Archaepetala obscura Dilcher & Crane, sp. nov. HOLOTYPE: IU 15703-2266.

DIAGNOSIS: Lamina obovate, length-to-width ratio approximately 1.5:1; ca. 18 evenly spaced, more or less parallel veins diverging slightly from the base.

NUMBER OF SPECIMENS EXAMINED: 1.

FIGURES: 40, 45, 60c.

DERIVATION: From *obscurus*—Latin, meaning

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FIGURES 38–46. Other organs attributed to the *Archaeanthus linnenbergeri* plant.—38. *Archaepetala beekeri* Dilcher & Crane, gen. et. sp. nov., IU 15703-3179. Showing broad midrib and attachment point at the base, ×1.—39. *Kalymmanthus walkeri* Dilcher & Crane, gen. et sp. nov., IU 15703-2747. Showing bilobed apex and narrow midrib, ×1.—40. *Archaepetala obscura* Dilcher & Crane, sp. nov., IU 15703-2266. Showing poorly defined, straight, veins diverging toward the apex, ×1.—41. *Archaepetala beekeri* Dilcher & Crane, gen. et sp. nov., IU 15703-3822. Poorly preserved specimen showing broad midrib, ×1.—42. *Kalymmanthus walkeri* Dilcher & Crane, gen. et sp. nov., IU 15703-4115. Showing bilobed apex, broad midrib, and concave point of attachment, ×1.—43. *Kalymmanthus walkeri* Dilcher & Crane, gen. et sp. nov., IU 15703-4114. Showing bilobed


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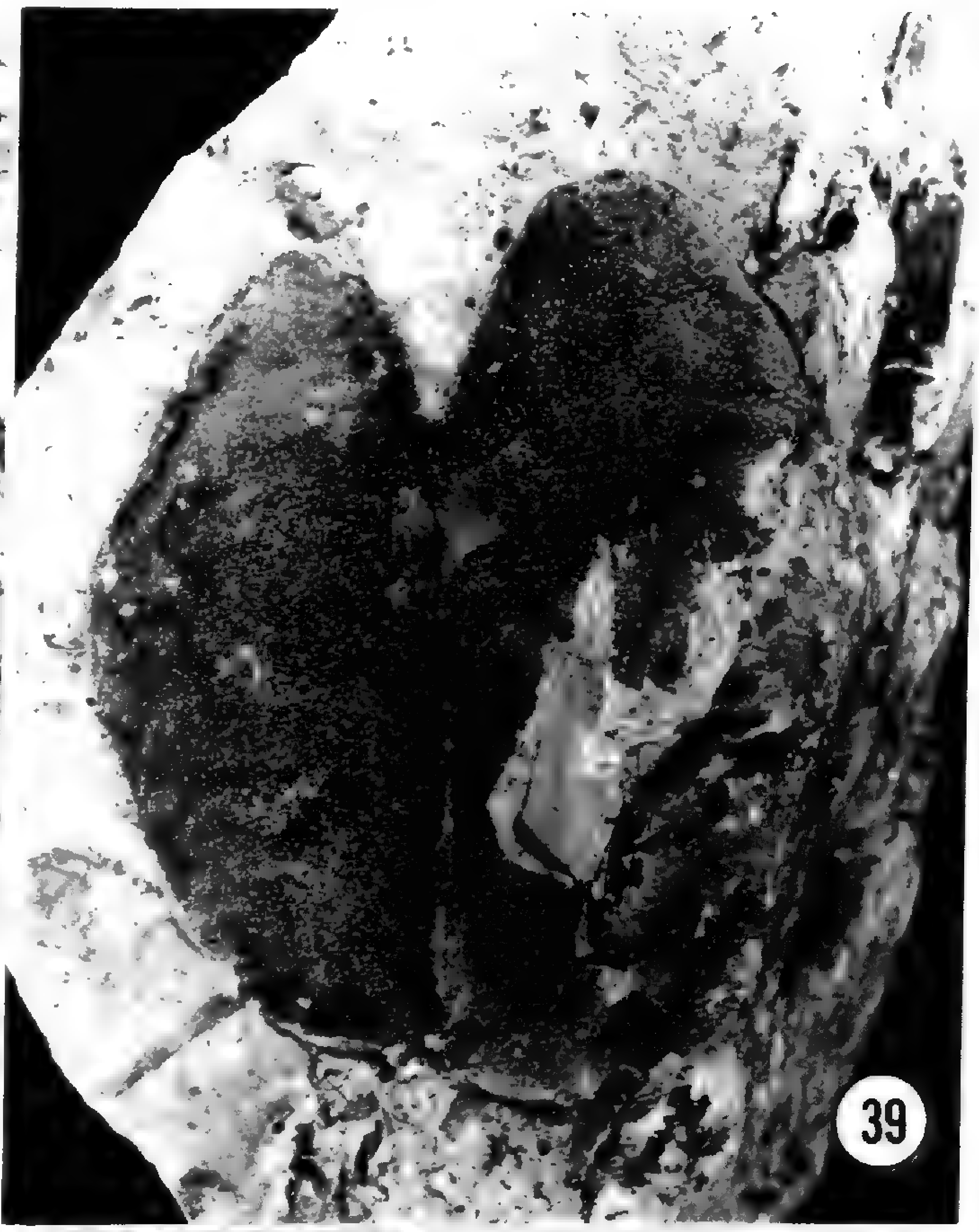
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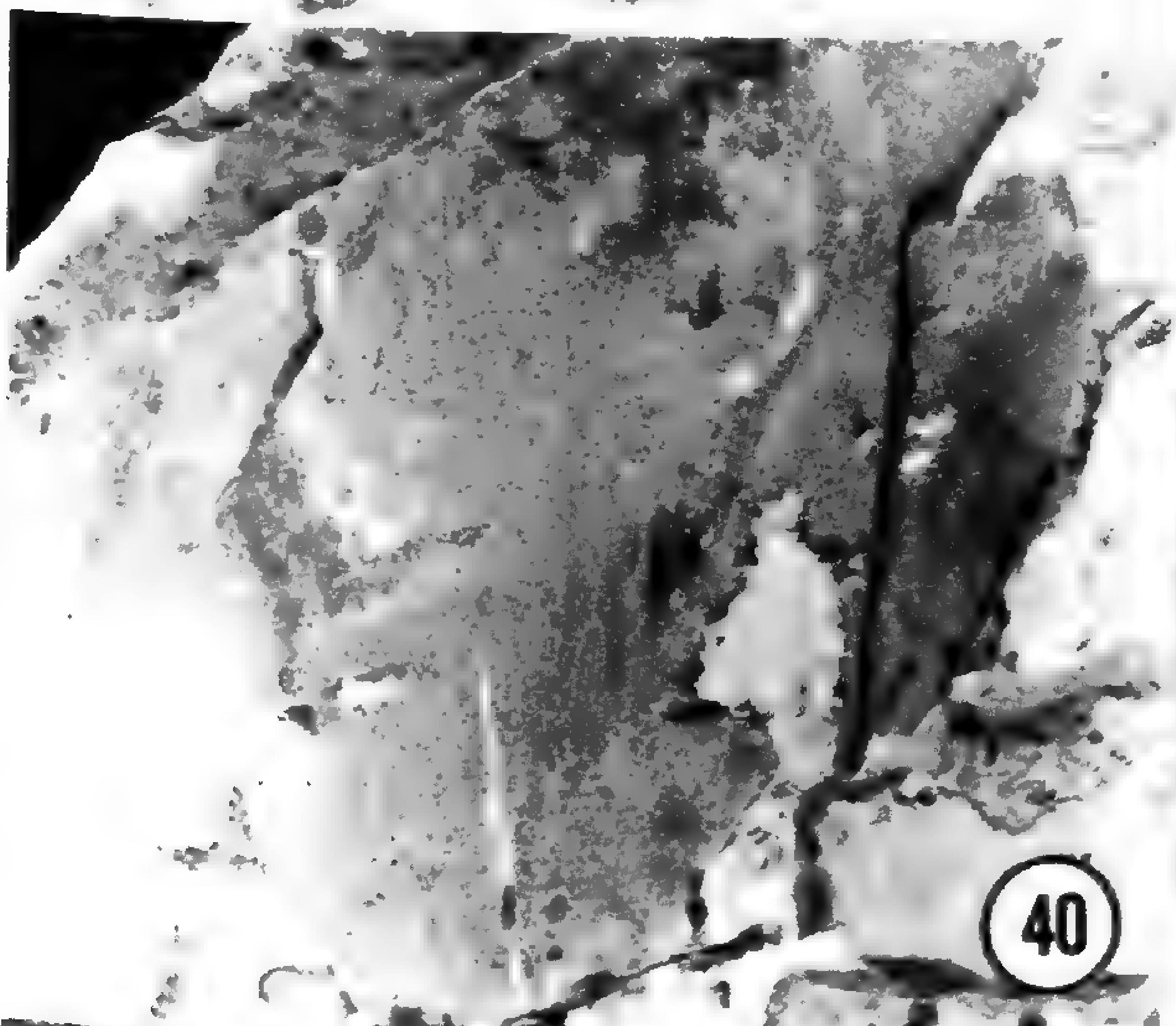
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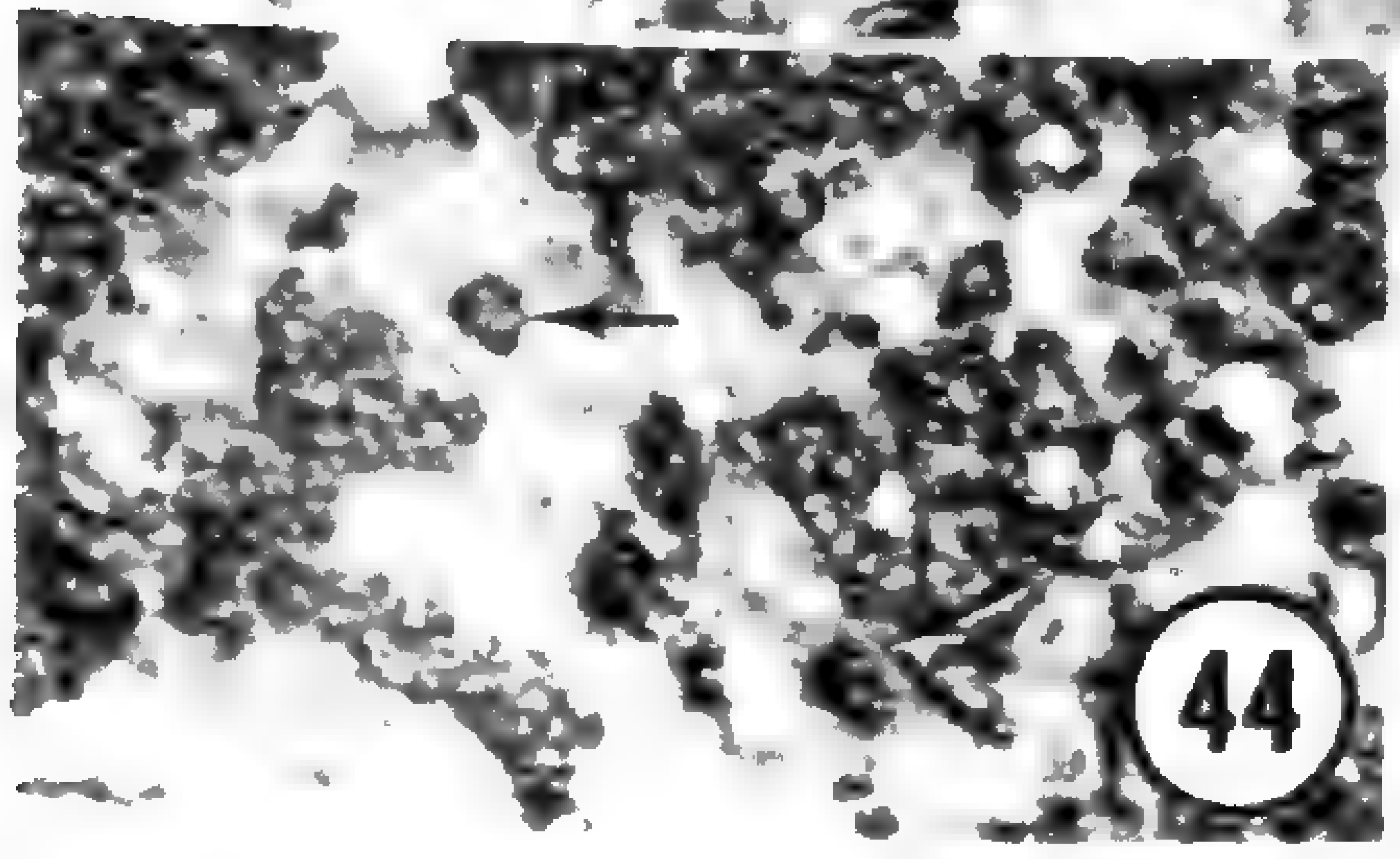
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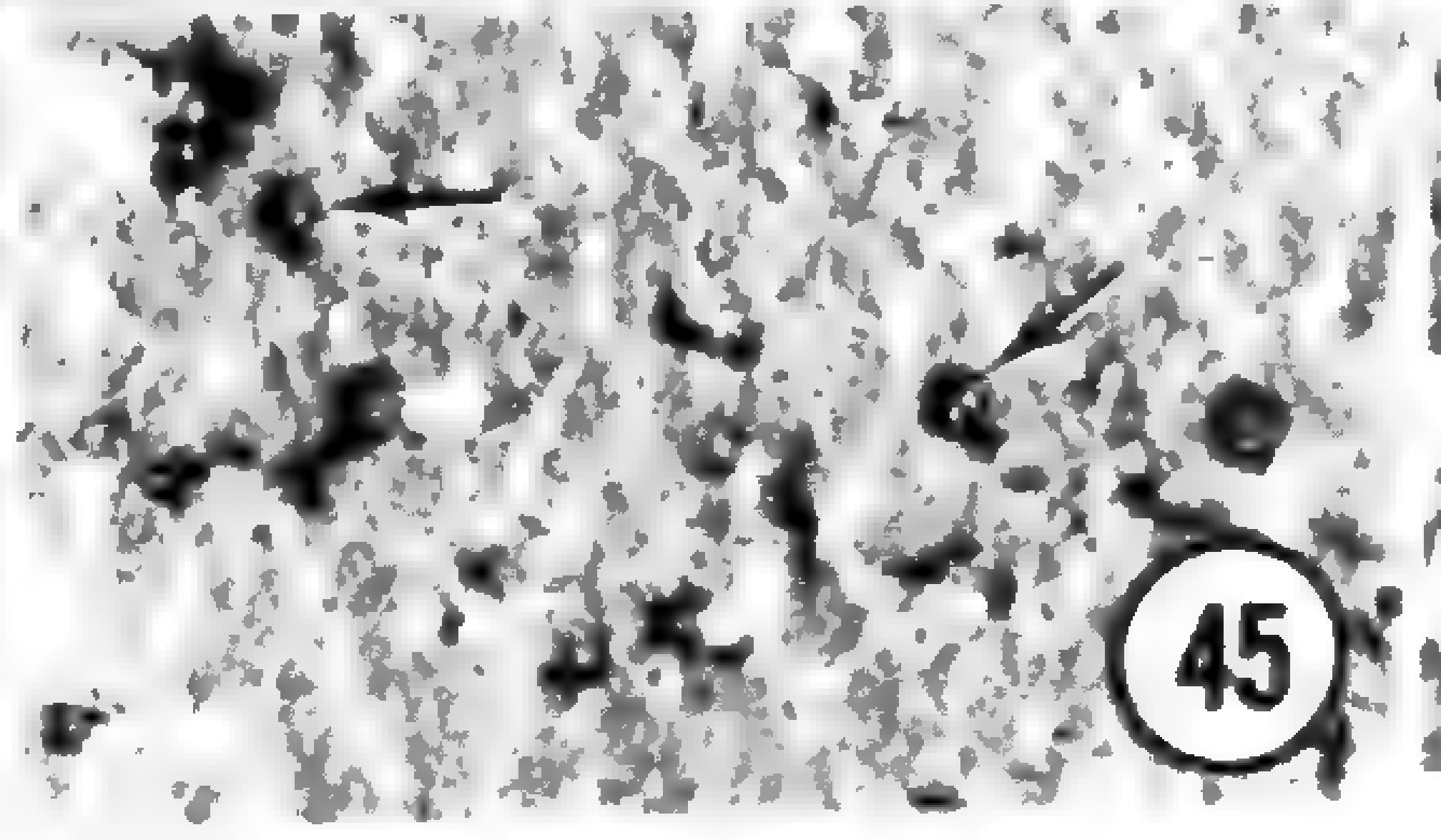
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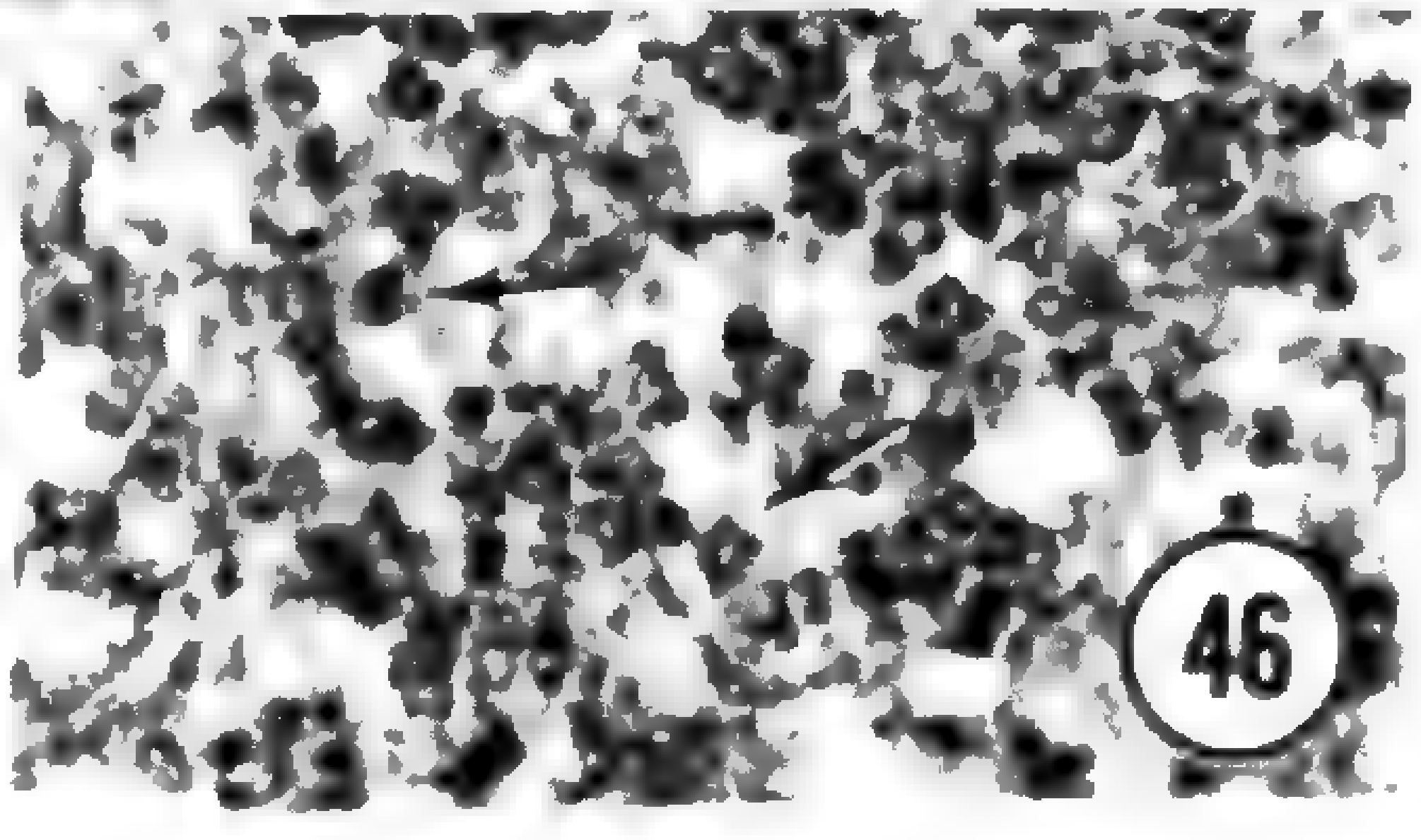
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apex and the split along the line of the midrib, ×1.5.—44. *Archaepetala beekeri* Dilcher & Crane, gen. et sp. nov., IU 15703-3179. Detail showing resin-bodies (arrows), ×15.—45. *Archaepetala obscura* Dilcher & Crane, sp. nov., IU 15703-2266. Detail showing resin-bodies (arrows), ×15.—46. *Kalymmanthus walkeri* Dilcher & Crane, gen. et sp. nov., IU 15703-2747. Detail showing resin-bodies (arrows), ×15.

indistinct, and referring to the unknown apex and base of the holotype.

DESCRIPTION: Lamina simple, obovate, estimated lamina length 80 mm, ca. 50 mm wide (maximum); length-to-width ratio approximately 1.5 : 1. Margin entire (base and apex unknown). Lamina with ca. 9 prominent, more or less parallel veins diverging slightly from the base. A single, more weakly developed vein present in each space between the more prominent veins. Prominent veins linked by a reticulum in the distal part of the lamina. Texture of lamina smooth; the substance of the lamina thin and containing numerous spherical resin-bodies, (80–)90–100(–130) μm diam.

DISCUSSION: *Archaepetala obscura* is known from only a single fragmentary but distinctive specimen (Fig. 40), which was folded prior to compression. The shape and venation of *A. obscura* is very petal-like, but we cannot be certain of its botanical nature. However, we suggest that it may have formed an inner perianth immediately above the three large scars that, in our view, bore the *A. beekeri* parts.

Kalymmanthus Dilcher & Crane, gen. nov. TYPE: *Kalymmanthus walkeri* Dilcher & Crane, sp. nov.

DIAGNOSIS: Lamina broadly elliptical to broadly ovate, bilobed. Length-to-width ratio approximately 1.2 : 1. Base straight or slightly concave, lacking an obvious attachment area. Apices of lobes broadly rounded. Lamina with a rib running from the base of the sinus.

DERIVATION: From *kalymma*—Greek, meaning a covering or hood; *anthos*—Greek, meaning flower.

DISCUSSION: This genus is established as a broad form-genus for accommodating isolated, fossil bud-scale, stipule, or calyptra-like structures.

Kalymmanthus walkeri Dilcher & Crane, sp. nov.

HOLOTYPE: IU 15703-2747.

DIAGNOSIS: As for the genus.

OTHER MATERIAL: IU 15703-4114, IU 15703-4115.

NUMBER OF SPECIMENS EXAMINED: 3.

FIGURES: 39, 42, 43, 46, 60e.

DERIVATION: After Mr. Merle Walker, who aided in the discovery of the Linnenberger Ranch locality and has given us considerable assistance during our collecting in central Kansas.

DESCRIPTION: Lamina broadly elliptical to broadly ovate, bilobed; 26–65 mm long, 21–50 mm wide. Length-to-width ratio approximately 1.2 : 1. Margin entire with a prominent lip 0.5 mm wide. Base straight or slightly concave 6–15 mm wide, lacking an obvious attachment scar. Apices of lobes broadly rounded; lobes typically 0.3–0.2 of the lamina length, but sometimes splitting beyond the original sinus to the base of the lamina. Lamina with a midrib running from the base to the sinus, midrib either narrow, ca. 1 mm wide, or slightly broader and tapering distally. Surface of lamina wrinkled with fine, irregular areolae ca. 0.3–0.8 mm diam., and with numerous resin-bodies typically (60–)80–100 (–110) μm diam.

DISCUSSION: *Kalymmanthus walkeri* is known from three specimens (Figs. 39, 42, 43). Other specimens with the distinctive areolate surface texture do occur at the Linnenberger locality, and although they cannot be confidently distinguished from fragments of *A. beekeri,* some do show a marginal lip, like that in *K. walkeri.* In IU 15703-4115 (Fig. 42), however, this marginal lip is not clearly visible, and the same specimen has a broad rib running from the base to the sinus somewhat similar to that in *A. beekeri.* We interpret *K. walkeri* as bud-scales, probably of both vegetative and flowering shoots. At maturity, the extent of the split along the line of the sinus was probably variable. By analogy with living *Magnolia,* the bud-scales may be of stipular origin, although none of our specimens show any sign of a leaf lamina attached to an extended midrib. Our specimens are unlike the putative bud-scale described and figured by MacNeal (1958) from the Cenomanian Woodbine Sand flora of Denton County, Texas.

Liriophyllum Lesq. (1878) emend. Dilcher & Crane. TYPE: *Liriophyllum populoides* Lesq. (designated by Berry, 1902a: 55).

EMENDED GENERIC DIAGNOSIS: Leaf petiolate, bilobed, deeply divided for at least half its length. Venation pinnate. Midrib stout extending to the base of the sinus and forking into two prominent veins, distinct from the secondary veins below, which form the leaf margin typically for about 0.3–0.16 of the lobe length. Above this point the lamina arches away from the vein into the sinus and broadens distally to form each lobe.

SPECIES EXCLUDED FROM THE GENUS: *Liriophyllum obcordatum* Lesq. (1883: 77).

Liriophyllum obcordatum Lesq. (1892: 210, pl. 28, fig. 7).

Liriophyllum sachalinense Krysht. (1937: 85, pl. 12, figs. 4–6).

Liriophyllum populoides Lesq. emend. Dilcher & Crane. HOLOTYPE: USNM 2079.

EMENDED DIAGNOSIS: Petiole with a proximal, laminar, alate appendage in its lower part. Appendage attached along its full length, entire margined, rounded and tapering above.

SYNONYM: *Liriophyllum beckwithii* Lesq.

REFERENCES: *Liriophyllum beckwithii* Lesq. (1878: 482–483, brief description).

Liriophyllum populoides Lesq. (1878: 482–483, brief description).

Liriophyllum beckwithii Lesq. (1883: 75, pl. 10, fig. 1, generic diagnosis, specific diagnosis, discussion, and line drawing).

Liriophyllum populoides Lesq. (1883: 76, pl. 11, figs. 1–2, specific diagnosis, description, and line drawings).

Liriophyllum beckwithii Lesq. (1892: 210, mention only).

Liriophyllum populoides Lesq. (1892: 211, mention only).

Liriophyllum populoides Lesq. (Hollick, 1894: 470–471, pl. 221, brief description, discussion, and line drawing).

Liriophyllum populoides Lesq. (Holm, 1895: 316, brief discussion of affinities).

Liriophyllum populoides Lesq. (Hollick, 1896: 249, pl. 269, fig. 2, brief discussion and line drawing).

Liriophyllum Lesq. (Berry, 1902a: 47–56, brief discussion and comparison with putative fossil *Liriodendron,* p. 55, takes *Liriophyllum populoides* as the type species of the genus).

OTHER MATERIAL: Morrison, Colorado, USNM 2076, 2078 (two leaves), 2080, 2135, 2142; HU 2881, 2882, 2883, 2884, 2885, 2888, 2892, 2897.

NUMBER OF SPECIMENS EXAMINED: 15.

FIGURES: 47–50.

DESCRIPTION: Leaves petiolate. Outline of lamina square to broadly ovate, 90–185 mm long, 85–240 mm wide, broadest in the lower quarter of the lamina. Lamina bilobed, deeply divided for at least half its length. Midrib stout 1–2 mm wide, 23–36 mm long, extending to the base of the sinus and forking at an angle of 45–70° into two prominent veins that form the leaf margin in the lower part of the sinus. Veins contiguous with the sinus margin for 8–25 mm, typically about 0.25–0.16 of the lobe length. Above this the lamina arches away from the veins into the sinus and broadens distally to form each lobe. Each fork of the midrib enters the distal part of the lobe, branching several times, and gradually becoming finer. Apex of each lobe rounded, lateral margins more or less straight, slightly convex or prominently concave, and forming two distinct lobes on either side of the midrib. Leaf base obtuse or acute, straight or decurrent where it joins the petiole.

Secondary venation pinnate, camptodromous; 2–3 secondary veins on either side of the midrib, alternately arranged, more or less decurrent. Angle of divergence of secondary veins 40–50°. Secondary veins branching well within the margin. (Details of finer venation not preserved.) Extreme base of lamina with two basal veins of secondary or intermediate secondary-tertiary order. Petiole to 27 mm long (longest specimen incomplete) with a proximal, laminar, alate appendage in its lower part. Appendage 13 mm wide, including the petiole, attached along its entire length; entire margined, rounded and tapering above.

Liriophyllum kansense Dilcher & Crane, sp. nov. HOLOTYPE: IU 15703-2272.

SPECIFIC DIAGNOSIS: Petiole simple, lacking a proximal, laminar, alate appendage.

REFERENCES: *Liriophyllum beckwithii* Lesq. Dilcher et al. (1976: 854–856, fig. 1e, f, description, discussion, and photograph).

Liriophyllum Lesq. Dilcher et al. (1978: 11, brief mention and line drawing).

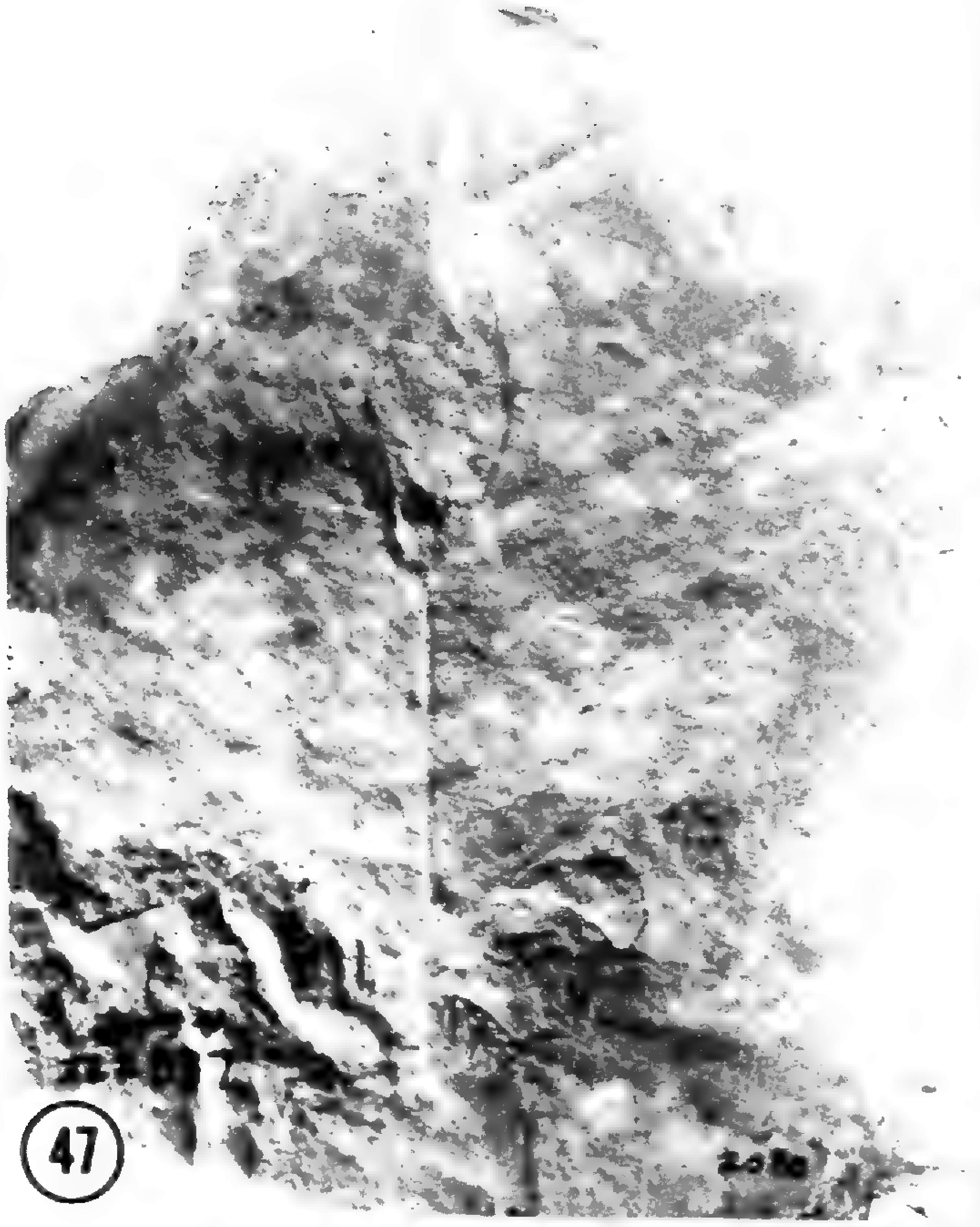
Liriophyllum sp. Retallack and Dilcher (1981c: 39, figs. 2–14, brief mention and photograph).

OTHER MATERIAL: Linnenberger's Ranch IU 15703; 2267, 2271–2277, 2309, 2456, 2463–2466, 2469–2471, 2473, 2475–2477, 2479, 2480, 2482, 2484, 2485, 2487, 2488, 2492, 2493, 2679, 2948, 3443, 3813, 3816–3818, 3823, 3826, 3827, 3836, 3839, 3859, 3885, 3886, 3890, 3894, 3895, 3992, 4028, 4029, 4051, 4120.

NUMBER OF SPECIMENS EXAMINED: Fort Harker, Kansas, USNM 2718. Fifty-four and numerous other fragments.

FIGURES: 51–59, 60b.

DESCRIPTION: Leaves petiolate. Outline of lamina square to very broadly ovate, (60–)100(–140) mm long, (64–)120(–186) mm wide, typically broadest in the lower quarter of the lamina. Lamina bilobed, deeply divided for at least half its length. Midrib stout 1–3 mm wide (10–)20–30 (–44) mm long extending to the base of the sinus and forking at an angle of (40–)60–70(–80)° into two prominent veins that form the leaf margin in the lower part of the sinus. Veins forming the sinus margin for (15–)25(–48) mm, typically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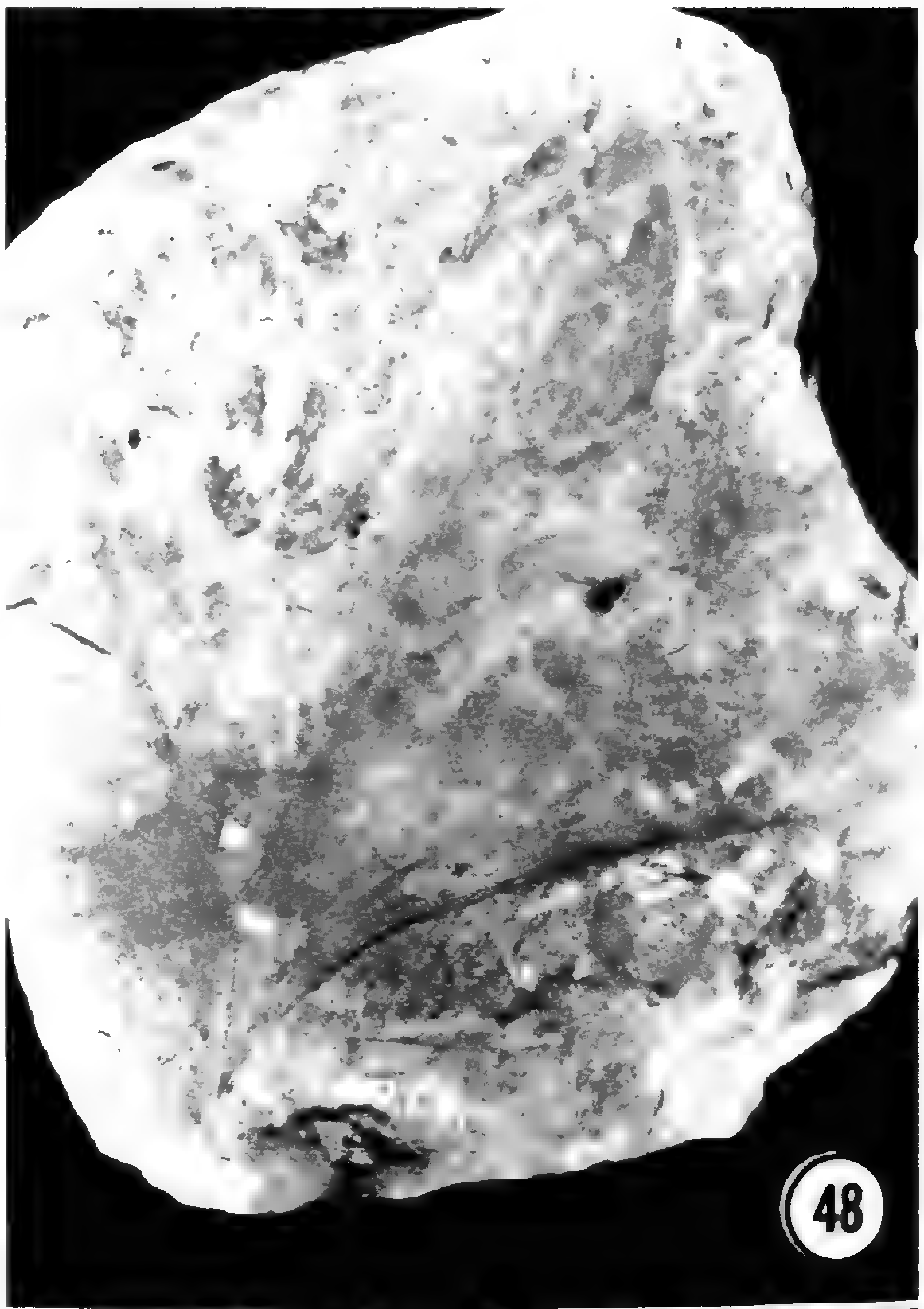
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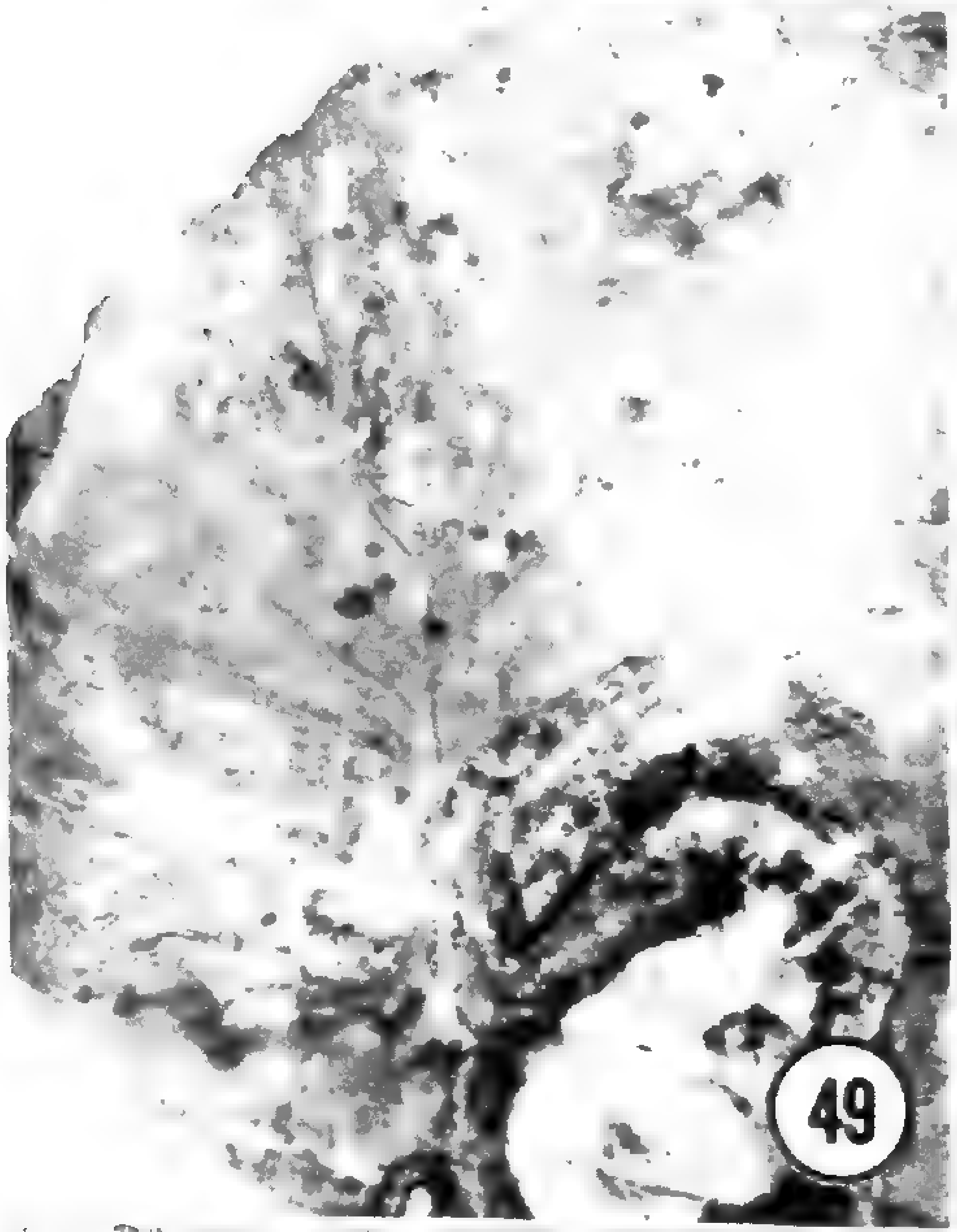
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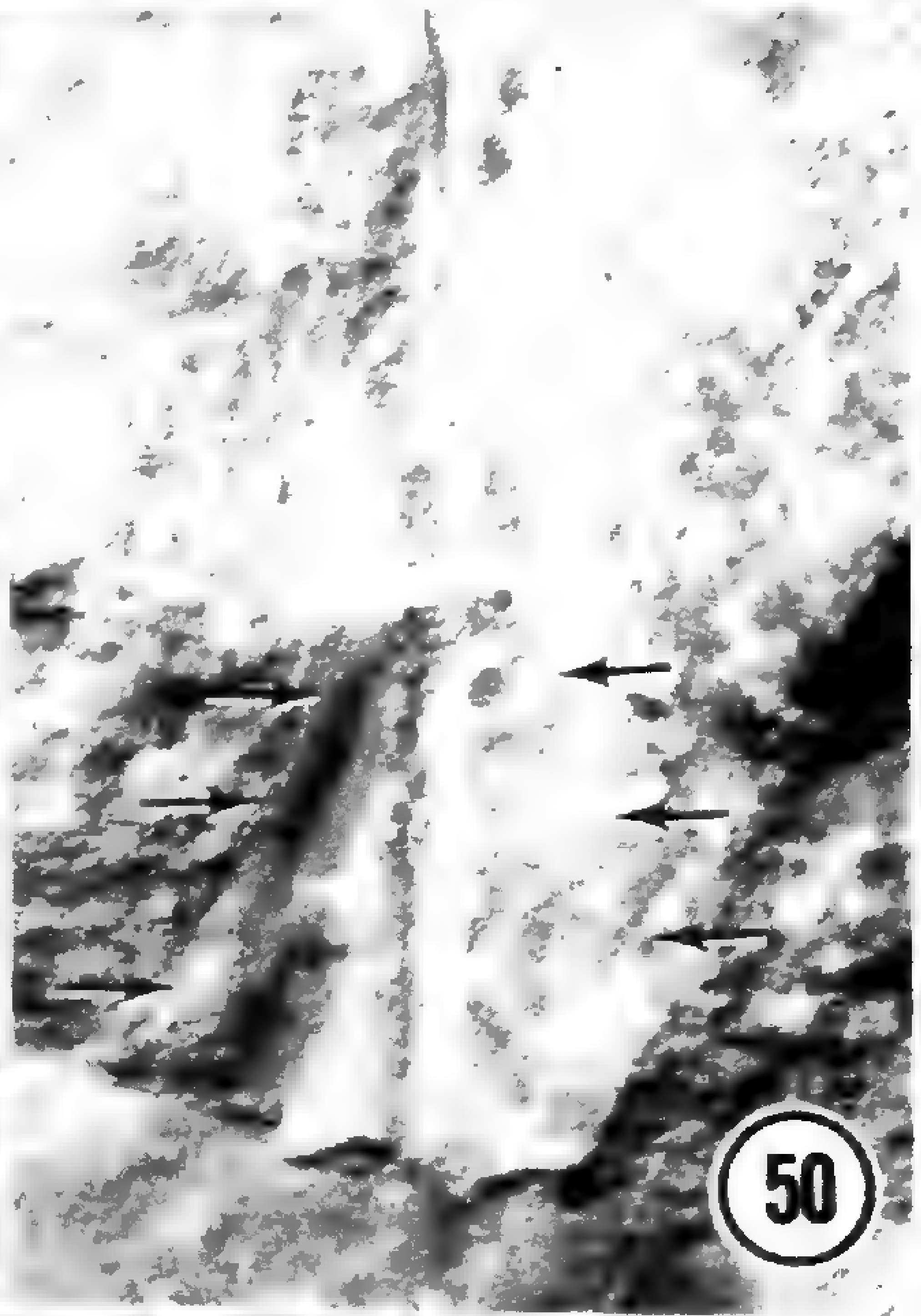
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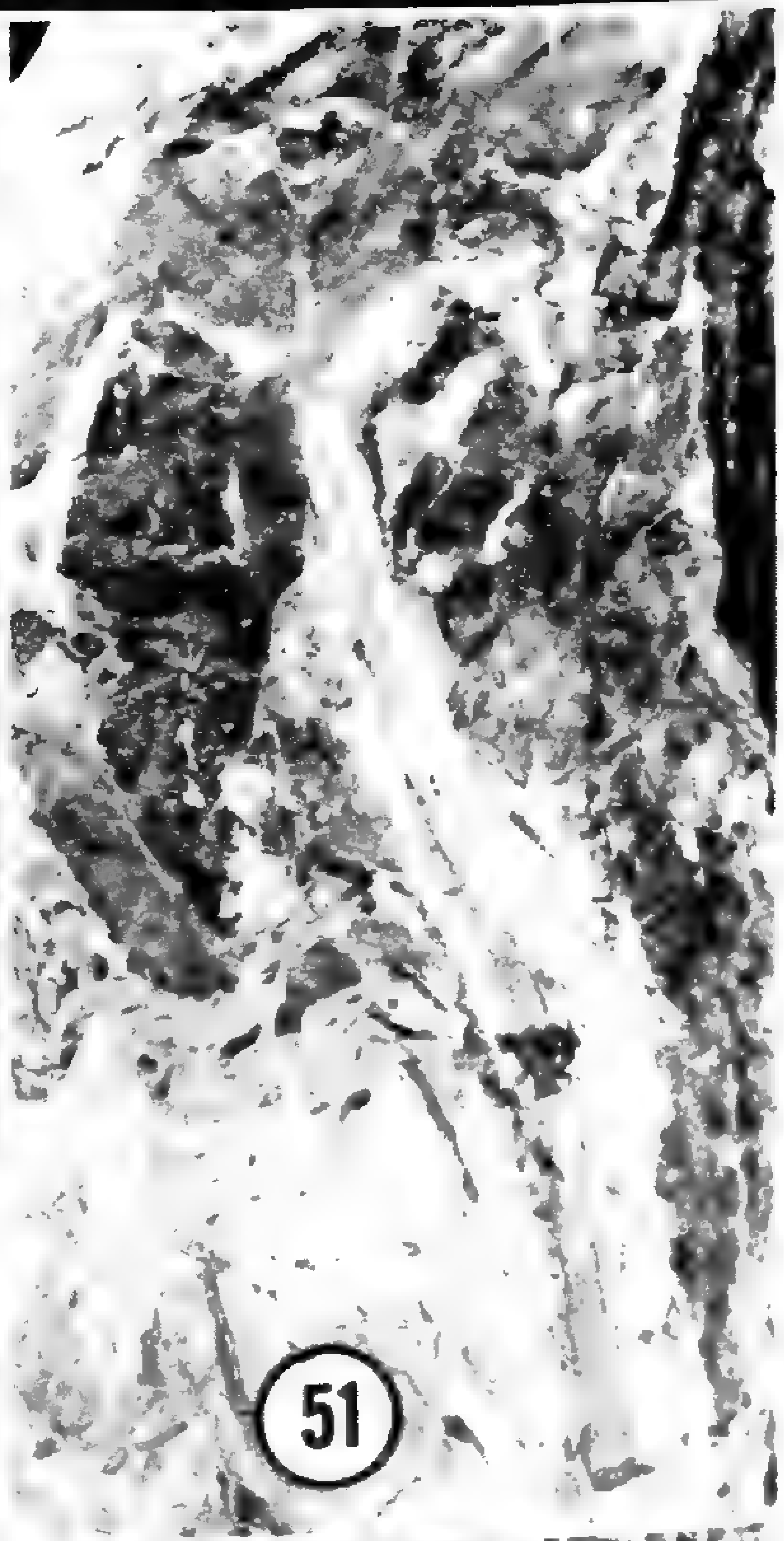
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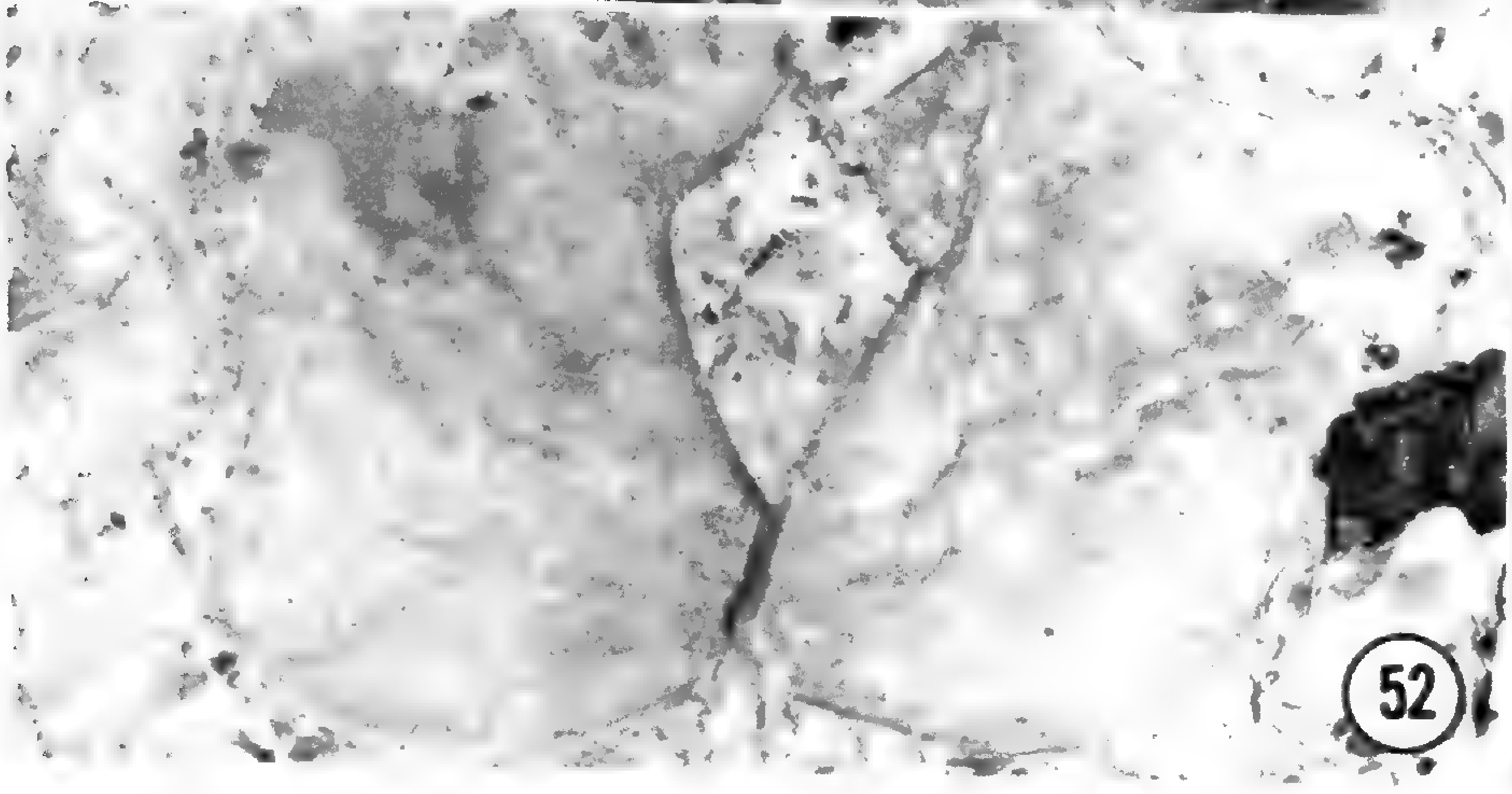
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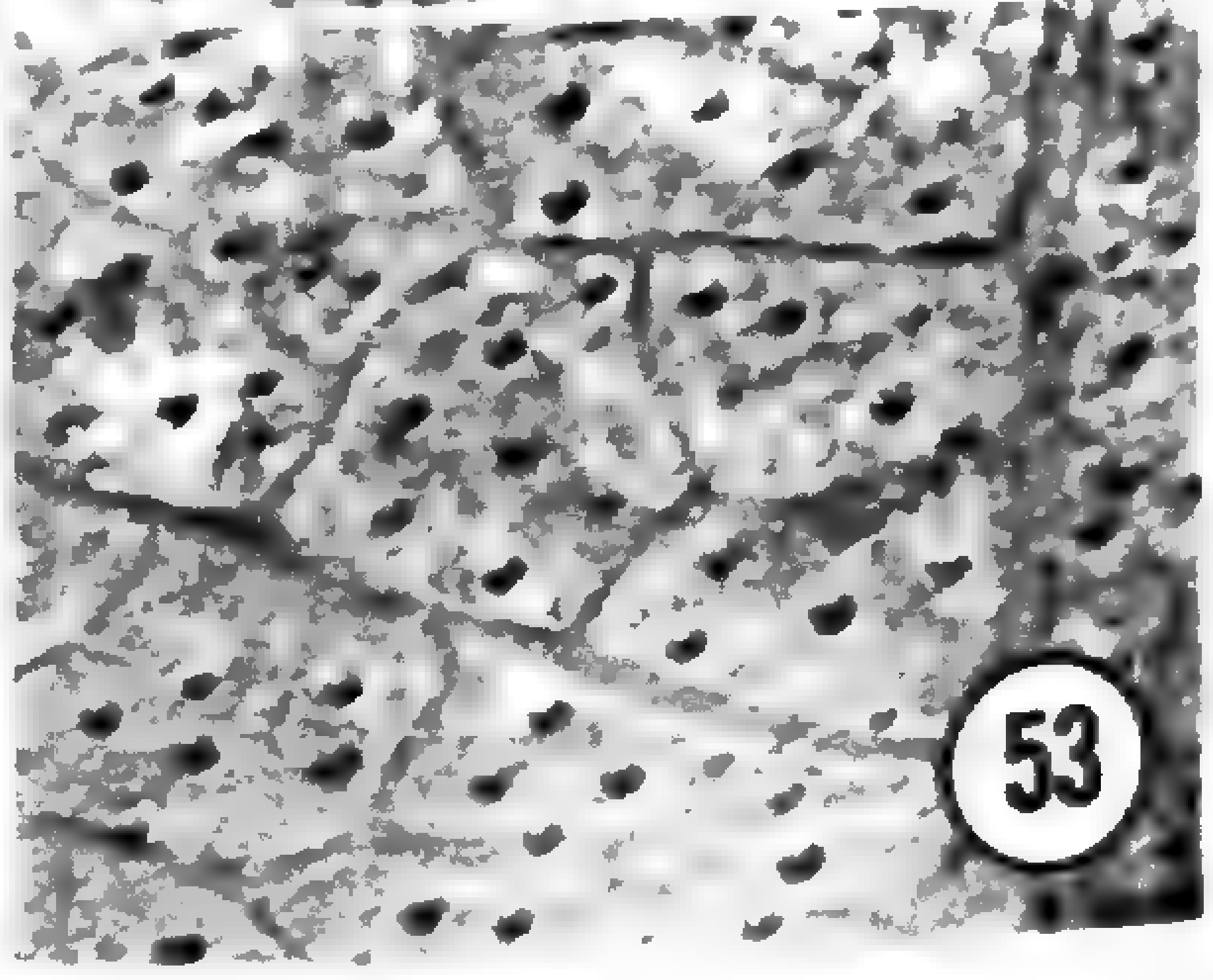
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FIGURES 47–53. 47. *Liriophyllum populoides* Lesq., USNM 2080. Figured by Lesquereux (1883, pl. 11, fig. 2). Note also the structure at the bottom right, *Carpites liriophylli* Lesquereux (1883, pl. 11, fig. 5), which may be an isolated *Archaeanthus* follicle, ×0.75.—48. *L. populoides* Lesq., USNM 2078. Figured by Lesquereux (1883, pl. 10, fig. 1). Note the two lobes in the right side of the lamina, ×0.3.—49. *L. populoides* Lesq., USNM 2078. Specimen on the reverse of block in Figure 48, not figured by Lesquereux. Note the long petiole, ×0.5.—

about 0.3–0.25 of the lobe length. Above this the lamina arches away from the veins into the sinus and broadens distally to form each lobe. Each fork of the midrib enters the distal part of the lobe, branching 4 or 5 times and gradually becoming finer. Apex of each lobe broadly rounded, lateral margins more or less straight, occasionally concave or slightly convex. Leaf base shallowly cordate, acute or obtuse, straight, or more typically decurrent, where it joins the petiole.

Secondary venation pinnate, camptodromous; (2–)4(–5) secondary veins on either side of the midrib, alternately arranged, frequently more or less decurrent. Angle of divergence of secondary veins gradually decreasing apically, up to 90° at the base, ca. 30° distally. Secondary veins branching and becoming finer well within the margin to form weak, camptodromous loops, typically of tertiary order. Extreme base of lamina with 2 basal veins of secondary or intermediate secondary/tertiary order. Angle of divergence of tertiary venation variable, but tertiary veins frequently more or less decurrent where they join the secondaries and the midrib. Toward the margin, tertiary, quaternary, and quinternary veins forming polygonal areolae, frequently more or less elongated toward the center of the leaf; areolae often more regular, pentagonal and orthogonal toward the margin. Areolae open; vein endings simple and compound. Pattern of venation equivalent to leaf rank 2 or 3 (Hickey, 1977). Petiole to 100 mm long, 2–4 mm wide, simple, with no alate appendage, swollen to 6 mm at the base with a terminal crescentic abscission scar. Leaf mesophyll containing spherical, yellow-brown resin-bodies (50–)80–100(–110) μm diam.

DISCUSSION: All of the specimens of *Liriophyllum populoides* are from the Kassler Sandstone of the South Platte Formation near Morrison, Colorado. Lesquereux (1878, 1883) recognized three species in the Kassler Sandstone collection. *Liriophyllum beckwithii* and *L. populoides* have a very distinctive morphology and venation and are synonymized as variants of one species. *Liriophyllum obcordatum* does not show these diagnostic features, particularly the bifurcation of the midrib, and we have excluded it from the genus (Berry, 1902a). We also exclude *Liriophyllum sachalinense* Kryshtofovich (1937), which subsequently has been referred to *Bauhinia* by Vakhrameev (1966), Takhtajan (1974), and Tanai (1979). Lesquereux did not designate a type species for *Liriophyllum,* and although Andrews (1966) cites the first named species *L. beckwithii,* we follow Berry (1902a) in taking *L. populoides* as the type. The specimens of *L. populoides* from the Kassler Sandstone (Figs. 47–50) are poorly preserved but are clearly very similar to the *Liriophyllum* leaves from Kansas. The only significant feature in which they differ is the presence of an alate appendage attached to the proximal part of the petiole in *L. populoides.* Hollick (1894, 1896) was the first to call attention to this feature, but it is also shown by a *Liriophyllum populoides* leaf (Figs. 49, 50) on the same block as one of the specimens figured by Lesquereux (1883). The other specimens in Lesquereux's original collection have too little of the petiole preserved to show whether the appendage was present. None of the *Liriophyllum kansense* specimens, some of which have the complete petiole preserved (Fig. 51), shows any sign of an alate petiolar appendage. Although the two species do show a suggestion of other subtle differences, for example, the pronounced lateral lobes of USNM 2078 (Fig. 48) and variations in the prominence of the forks of the midrib, we have too little *L. populoides* material from Colorado to evaluate the patterns of variation in these characters more carefully. The difference in petiole is our primary reason for formally recognizing two distinct species. The alate petiolar appendage of *L. populoides* has been interpreted by Hollick (1894, 1896) as an early stage in the formation of the prominent stipules of *Liriodendron.* In view of the features of the *Archaeanthus* with which these leaves are now known to be associated (see Reconstruction of the *Archaeanthus* Plant), such a hypothesis seems more plausible. We do not pursue this point further here but merely point out that we have no good evi-

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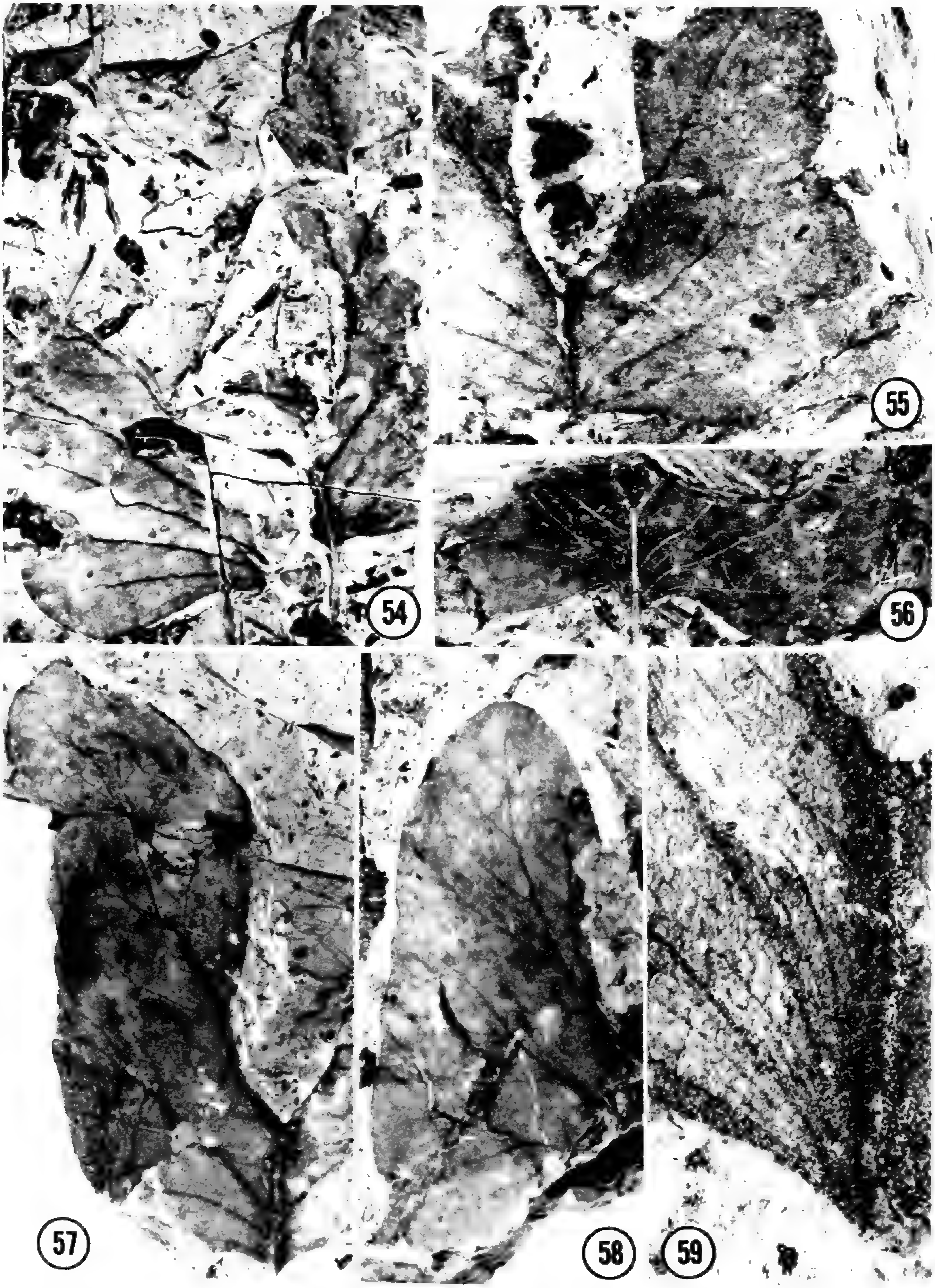
50. *L. populoides* Lesq. Same specimen as Figure 49 showing alate appendage attached to petiole (arrows), ×1.—51. *L. kansense* Dilcher & Crane, sp. nov., IU 15703-4029. Complete petiole showing expanded base and absence of alate appendage, ×0.5.—52. *L. kansense* Dilcher & Crane, sp. nov., IU 15703-2464′. Showing dichotomy of midrib and the veins forming the sinus margins, ×1.—53. *L. kansense* Dilcher & Crane, sp. nov., IU 15703-2317. Detail of leaf fragment from the same block as Figures 13–16 showing ultimate venation and hemispherical depressions caused by resin-bodies, ×15.



FIGURES 54–59. *Liriophyllum kansense* Dilcher & Crane, sp. nov.—54. IU 15703-2272. Large leaf showing characteristic venation, ×0.5.—55. IU 15703-2463. Leaf fragment showing major venation, ×1.—56. IU 15703-2477. Fragment of large leaf base. Note the cordate leaf lobes and the lamina decurrent down the petiole, ×0.5.—57. IU 15703-2469. Leaf lobe with well-preserved venation, ×1.—58. IU 15703-2479. Leaf lobe, ×1.—59. IU 15703-2472. Detail of midrib and fine venation, ×4.5.

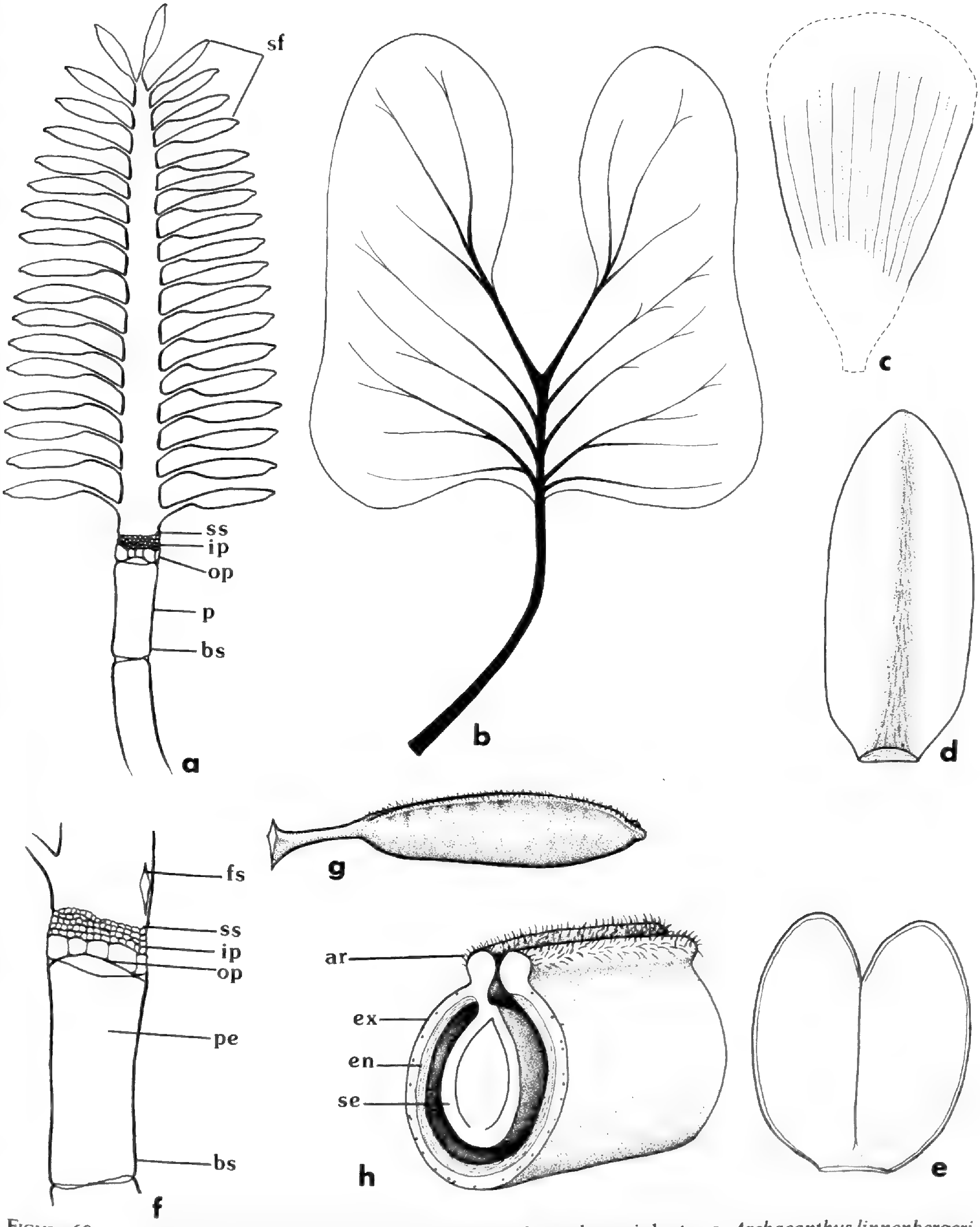


FIGURE 60. Reconstructions of parts of the *Archaeanthus linnenbergeri* plant.—a. *Archaeanthus linnenbergeri*, diagram showing the organization of the multifollicle.—b. *Liriophyllum kansense* leaf showing major venation.—c. *Archaepetala obscura*, inner perianth part.—d. *Archaepetala beekeri*, outer perianth part.—e. *Kalymmanthus walkeri*, bud-scale.—f. *Archaeanthus linnenbergeri*, diagram of the base of the multifollicle.—g. *Archaeanthus linnenbergeri*, reconstruction of a single follicle.—h. *Archaeanthus linnenbergeri*, section through a follicle. sf, stalked follicles; ss, staminal scars; ip, inner perianth scars; op, outer perianth scars; pe, pedicel; bs, bud-scale scars; ar, adaxial ridge; ex, exocarp containing resin-bodies; en, endocarp of transverse fibers; se, anatropous seed borne adaxially.

dence on the vegetative axis of *A. linnenbergeri* for ring-like stipular scars such as occur in Recent Magnoliaceae.

Lesquereux's *Liriophyllum populoides* material consists only of poor impressions in a gray sandstone and exhibits none of the fine details, including the resin-bodies, seen in *L. kansense.* Only the specimens from Linnenberger's Ranch have appreciable organic material preserved with the resin-bodies in situ. Resin-bodies have been seen in over 40 of the 52 specimens of this species. Several other leaf types from the Linnenberger locality have yielded well-preserved cuticles, but we have not been able to obtain these details from *Liriophyllum.* We suggest that the cuticle was probably rather thin in life.

Prominently bilobed leaves are not common in angiosperms but do occur in several genera; for example, *Bauhinia* (Leguminosae) and *Liriodendron* (Magnoliaceae). However, the *Liriophyllum* leaf has a distinctive morphology and none of the living plants known to us are closely similar. We have considered the possibility of a relationship to *Liriodendron* particularly carefully. The morphological variability in the leaves of this genus has been examined in detail by Berry (1901, 1902a, 1902b), Holm (1895), and ourselves, but despite extensive searches including seedling, sucker-shoot, and abnormally developed leaves, we have seen no modern leaf with a strong midrib running to the apex and *dividing into a pair of prominent veins contiguous with the margin.* The same feature also separates *Liriophyllum* from fossil species assigned to *Liriodendron* or *Liriodendropsis* Newb. These species were reviewed by Berry (1902a). We have collected more typical *Liriodendron*-like leaves from the Saline River locality in Russell County, Kansas (IU 15702; see Retallack & Dilcher, 1981b, 1981c, for locality details), and similar specimens are known in the 'Dakota Sandstone Flora' (Lesquereux, 1883, 1892). Such leaves range up into the early Paleogene, where they seem to be replaced by other leaf species even more similar to extant *Liriodendron.* Curiously, only one *Liriophyllum* leaf is known from the 'Dakota Sandstone Flora' of Kansas and Nebraska.

The distinct inequilateral development of the lamina exhibited by *Liriophyllum* also occurs in several other mid-Cretaceous leaves such as *Fontainea grandiflora* (Newberry, 1895: 96, pl. 45), *Halyserites reichii* Sternb., *Halyserites elegans* (Vel.) Knobloch, and *Diplophyllum cretaceum* Vel. & Vin. (Knobloch, 1978). As noted by Rüffle (1970), the same feature is shown by leaves of extant *Helleborus foetidus*; it also occurs in the enigmatic *Scoresbya* (Harris, 1932; Kräusel & Schaarschmidt, 1968). None of these leaves, however, are similar in other respects to *Liriophyllum.*

RECONSTRUCTION OF *ARCHAEANTHUS* PLANT

There is evidence that *Archaeanthus linnenbergeri, Kalymmanthus walkeri, Archaepetala beekeri, Archaepetala obscura,* and *Liriophyllum kansense* are different parts of the same fossil plant. In addition to their association in a narrow horizon of the fossil-bearing sediments at the Linnenberger Ranch, *K. walkeri* and *L. kansense* also occur with an axis and fruiting receptacle similar to *Archaeanthus linnenbergeri* at another central Kansas locality near Hoisington, Barton County (IU 15706; Crane & Dilcher, 1984; see Retallack & Dilcher, 1981b, 1981c, for locality details). One specimen of *L. kansense* is known from the Dakota Sandstone Flora of central Kansas (USNM 2718). The only other known locality for *Liriophyllum* leaves (*L. populoides*) is the Kassler Sandstone at Morrison, Colorado, and it, too, has yielded a probable specimen of *A. linnenbergeri.* One of the blocks figured by Lesquereux (1883, pl. 11, fig. 5) also shows an elongated structure named *Carpites liriophylli* Lesq. (Fig. 47). Lesquereux suggested that this is a fruit of *Liriophyllum,* although he cites no evidence other than their association on the same piece of sandstone. The specimen is poorly preserved, but it is conceivable that it is an *Archaeanthus* follicle. The paucity and preservation of the material, however, precludes establishing the link more securely. The *Magnolia* receptacle, however, figured by Lesquereux (1883) from Morrison is very like the immature specimens (Fig. 10) from Linnenberger's Ranch, and we synonymize it with *Archaeanthus linnenbergeri.*

At Linnenberger's Ranch, *L. kansense* leaves and *A. linnenbergeri* are particularly abundant in a silty, gray clay, with occasional sand stringers, that is ca. 30 cm thick and occurs 3 m below the base of the sandstones which cap the section. In this distinct horizon immediately below the major plant bearing clays, these two species are the commonest plant fossils and occur matted together on the same bedding plane. Considering the Linnenberger flora as a whole, the taxonomic diversity of the plant assemblage is low, and *A.*

linnenbergeri and *L. kansense* are two of the commoner elements in the flora. To judge from the size range of the plant fragments present, the Linnenberger assemblage is mixed and scarcely sorted; Retallack and Dilcher (1981b, 1981c) interpreted the plants as having been deposited close to where they grew.

In addition to evidence of association, *Archaeanthus linnenbergeri, Kalymmanthus walkeri, Archaepetala beekeri, Archaepetala obscura,* and *Liriophyllum kansense* are also linked by the numerous amber-colored resin-bodies that they contain (Figs. 21, 29–31, 44–46, 53). Frequently these protrude from within broken organic fragments of the various organs and can be picked from the surface (Dilcher et al., 1976) or isolated by maceration. Even where other organic material has been lost by oxidation, the resin-bodies, or the small hemispherical depressions that they leave in the matrix, can usually be seen. Very few other types of leaves from the Linnenberger locality contain resin-bodies, but when found they are quite different, being much more compressed, smaller, and lacking the resinous luster. On the basis of association evidence and this structural agreement, we suggest that *A. linnenbergeri, K. walkeri, A. beekeri, A. obscura,* and *L. kansense* were all parts of the same fossil plant species. From their morphology and the scars that they display, we can make some suggestions as to how these various organs may have been attached.

The helically arranged scars on the vegetative axis of IU 15703-4152 are clearly leaf scars and are of similar size to the petiole bases of *L. kansense*. The base of the *K. walkeri* bud-scales corresponds in size and shape to the scar on the pedicel several millimeters below the base of the flower (Fig. 60a, f). By analogy with extant *Magnolia tripetala* (Figs. 61, 66) and *Liriodendron,* we suggest that the bud-scales were attached there and formed a calyptra-like covering over the young developing flower. The attachment area at the base of *A. beekeri* (Fig. 38) corresponds in size and shape to one of the three large scars that delimit the base of the flower (Figs. 2, 4, 12). We suggest that *A. beekeri* was attached in this position and formed an outer perianth of three robust, narrowly elliptical sepals. We interpret *A. obscura* to have been less robust than *A. beekeri* and to have been attached to the more or less circular scars immediately above the three large basal flower scars. The inner perianth probably consisted of relatively few, either six or nine, petals. The male parts of the *Archaeanthus* plant have not been recognized yet, but we envisage that they were borne on the small elliptical scars immediately below the gynoecial zone, and above the scars of the perianth whorl. In Figures 69 and 70 we give our suggestions as to what the *Archaeanthus* flower may have looked like; more detailed reconstructions of the individual parts are given in Figure 60.

BIOLOGY AND ECOLOGY OF THE *ARCHAEANTHUS* PLANT

The reconstruction of the *Archaeanthus linnenbergeri* plant combined with sedimentological data permits some conclusions on the biology and ecology of this mid-Cretaceous angiosperm. During the mid-Cretaceous, a major epicontinental sea extended northward from the Gulf of Mexico into the western interior of North America where, at various times, it linked with a southward extension of the Arctic Sea. Evidence from stratigraphy and sedimentology indicates that the Kansas plant beds were deposited in a range of coastal plain environments adjacent to this seaway and under variable amounts of marine influence. Both the Morrison, Colorado, and Linnenberger material dates approximately from the Albian–Cenomanian boundary: a time of lowered sea-level, bracketed above and below by widespread marine, eustatic transgressive episodes. During this period, both areas were situated at an approximate paleolatitude of 36–37°N (Smith & Briden, 1977) and were experiencing warm-temperate or sub-tropical climates (Kauffman, 1977).

Retallack and Dilcher (1981b, 1981c) interpreted the plant bearing sediments at Linnenberger's Ranch as shales associated with levee deposits in inter-distributary depressions vegetated by swamp woodland. To judge from the almost exclusive angiosperm macrofossil flora, the local vegetation was dominated by flowering plants; although in the palynoflora, angiosperm pollen comprises less than 25% of the total palynomorph assemblage (Dilcher & Zavada, unpubl. data).

Despite the large collections available and the geological proximity of shale and sand facies in the Dakota Formation, only one *Liriophyllum kansense* leaf is known from the classic Dakota Sandstone Flora, which represents a number of localities in and around Ellsworth County, Kansas. Equally many of the characteristic plants of that flora (for example, *Betulites* and the *Platanus-Sassafras* complex) either do not occur or are not common at Linnenberger's Ranch or Hoisington. They are found, however, at other shale localities. Although the fossils known from any locality are an incomplete representation of the living vegetation, where local differences exist (such as those in the Dakota Formation), they may reflect specific associations of plant species in particular environments.

The pollination and dispersal biology of the *Archaeanthus* plant was probably relatively unspecialized. The size of the floral and vegetative organs and the dimensions of the axes that supported them suggests that the plant was woody in life. From the size and features of the leaves, and from the petiole bases, we conclude it was probably a deciduous tree or shrub. The apparently bisexual flowers, and hence the fruits, were borne terminally on leafy, woody axes, probably prominently, beyond or near the margin of the leafy crown. Such a position combined with the large perianth parts indicated by the basal floral scars, and the size of *Archaepetala beekeri* and *A. obscura,* suggests that the flower was probably visually conspicuous and insect-pollinated. Coleoptera, Thysanoptera, and incurvariid Lepidoptera have been recorded as pollinators that feed on pollen in recent 'primitive' angiosperms (Thien, 1974, 1980), and all have a fossil record extending back into the Cretaceous (Thien, 1974, 1980; Whalley, 1978). Following pollination, we suggest that the stamens and perianth parts were shed and that the receptacle elongated as the follicles and seeds matured. Dispersal was probably unspecialized, involving both shedding of the numerous small seeds through the open adaxial suture, and occasional shedding of the complete follicles in a manner analogous to extant *Liriodendron.*

COMPARISON WITH RECENT PLANTS

Vegetative morphology. Similarity in leaf architecture between *Liriophyllum* and certain extant angiosperms has been mentioned already, but we know of no closely comparable Recent leaf. *Asarum* (Aristolochiaceae) shows a similar pattern of venation in which the major veins form the margin of the leaf for some distance before entering the lamina; but in *Asarum* it is the base rather than the apex of the leaf that is involved. Judging from the one axis of *Archaeanthus* in which leaf scars are preserved, the phyllotaxy was helical; a widespread condition generally regarded as primitive in flowering plants.

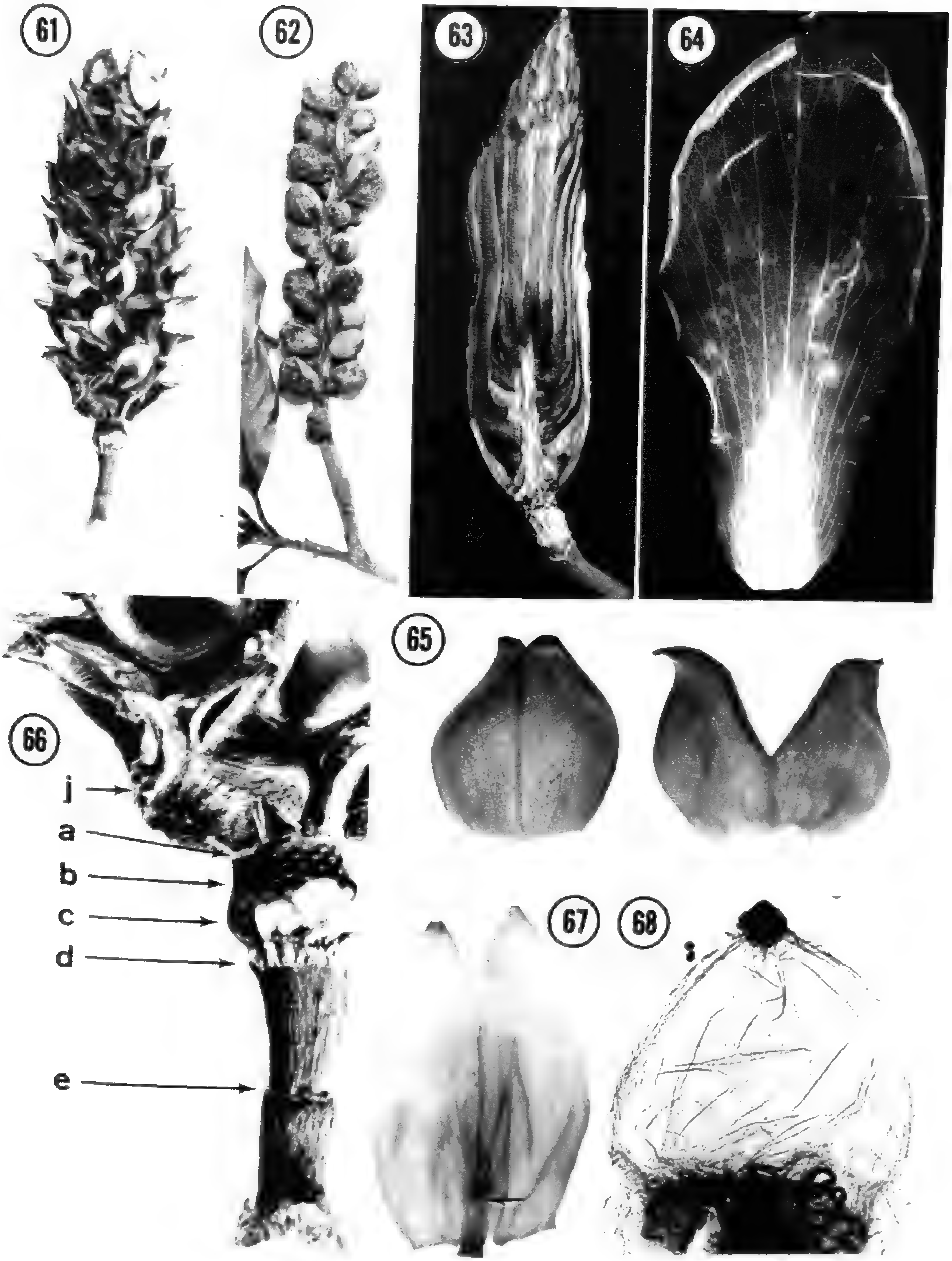
We interpret the resin-bodies preserved throughout the *A. linnenbergeri* plant as the diagenetically altered contents of oil cells. Ethereal oil cells are particularly common in Recent Magnoliidae, especially Magnoliales, Laurales, Piperales, Aristolochiaceae, and Illiciales (Cronquist, 1981), and are frequently preserved in younger fossil material confidently referable to these groups; for example, Tertiary lauraceous leaves.

We assume that the vegetative axes of *Archaeanthus* were woody, but we regrettably have no knowledge of the secondary xylem, which would be of considerable interest.

Floral organization. The basic organization of the *Archaeanthus* flower consists of numerous, helically arranged, separate carpels borne on a stout, elongated receptacle probably with numerous helically arranged stamens below; these are followed in turn below by two kinds of perianth parts arranged in apparent whorls. This combination of features occurs most commonly in the Magnoliidae, but also occurs in a few families of the Ranunculidae and Dilleniidae, such as the Ranunculaceae, Paeoniaceae, and the Dilleniaceae, which are often regarded as primitive.

In most magnoliid families the floral receptacle is rather short, but in the Magnoliaceae and some Annonaceae it is frequently elongated, and elongates further during the maturation of the fruits, as we suggest for *A. linnenbergeri* (Figs. 61, 62). Numerous helically arranged stamens occur more widely in flowering plants than helically arranged carpels, but both are nevertheless very common in the Magnoliidae. The lack of a more detailed understanding of the staminate parts of *Archaeanthus* is currently the most conspicuous gap in our knowledge of the plant. Trimerous perianth parts are widespread (for example, in the monocotyledons, Burger, 1977), but they also occur in the Magnoliidae. In the Lactoridaceae (Magnoliales) there are only three tepals, and in *Degeneria,* three sepals. Again, in the Annonaceae and Magnoliaceae, a trimerous arrangement of perianth parts is common.

A calyptra similar to that envisaged for *A. linnenbergeri* occurs in many Magnoliidae. In *Drimys* and *Tasmannia* (Winteraceae) the sepals are connate into a deciduous calyptra. In *Liriodendron* and *Magnolia* the large, frequently lobed, bud-scales enclosing the developing flower are interpreted as stipular in origin (Howard, 1948).



FIGURES 61–68. Extant Magnoliaceae.—61. *Magnolia tripetala* L. Fruiting receptacle (multifollicle) showing closely spaced follicles dehiscing abaxially, ×0.5.—62. *Michellia champaca* L. Luzon, Phillipines, collected by E. D. Merrill, Missouri Bot. Gard. 865046, fruiting receptacle (multifollicle). Note spacing of follicles along the receptacle, ×0.5.—63. *Liriodendron tulipifera* L. Fruiting receptacle (multifollicle) with several samaroid follicles removed to reveal ridged receptacle. Note staminal and perianth scars; the bud-scale scars are just below the base of the flower, ×1.—64. *Magnolia tripetala* L. Cleared petal showing details of venation. Compare with Figure 40, ×1.—65. *Magnolia grandiflora* L. Bud-scales for comparison with Figures 39, 42, and 43. Note the narrow rib and the splitting, ×0.75.—66. *Magnolia tripetala* L. Base of fruiting receptacle (multifollicle) showing follicles (j), the base of the gynoecial zone (a), scars of stamens (b), scars of inner (c) and outer perianth (d) parts, and the position of the bud-scales (e), ×4.—67. *Magnolia tripetala* L. Stipular bud-scale. Note the attachment point left by the leaf lamina (arrow), ×0.5.—68. *Magnolia tripetala* L. Nucellar or inner integumentary membrane isolated from an aborted ovule in an immature multifollicle. Compare Figures 32 and 34, ×30.

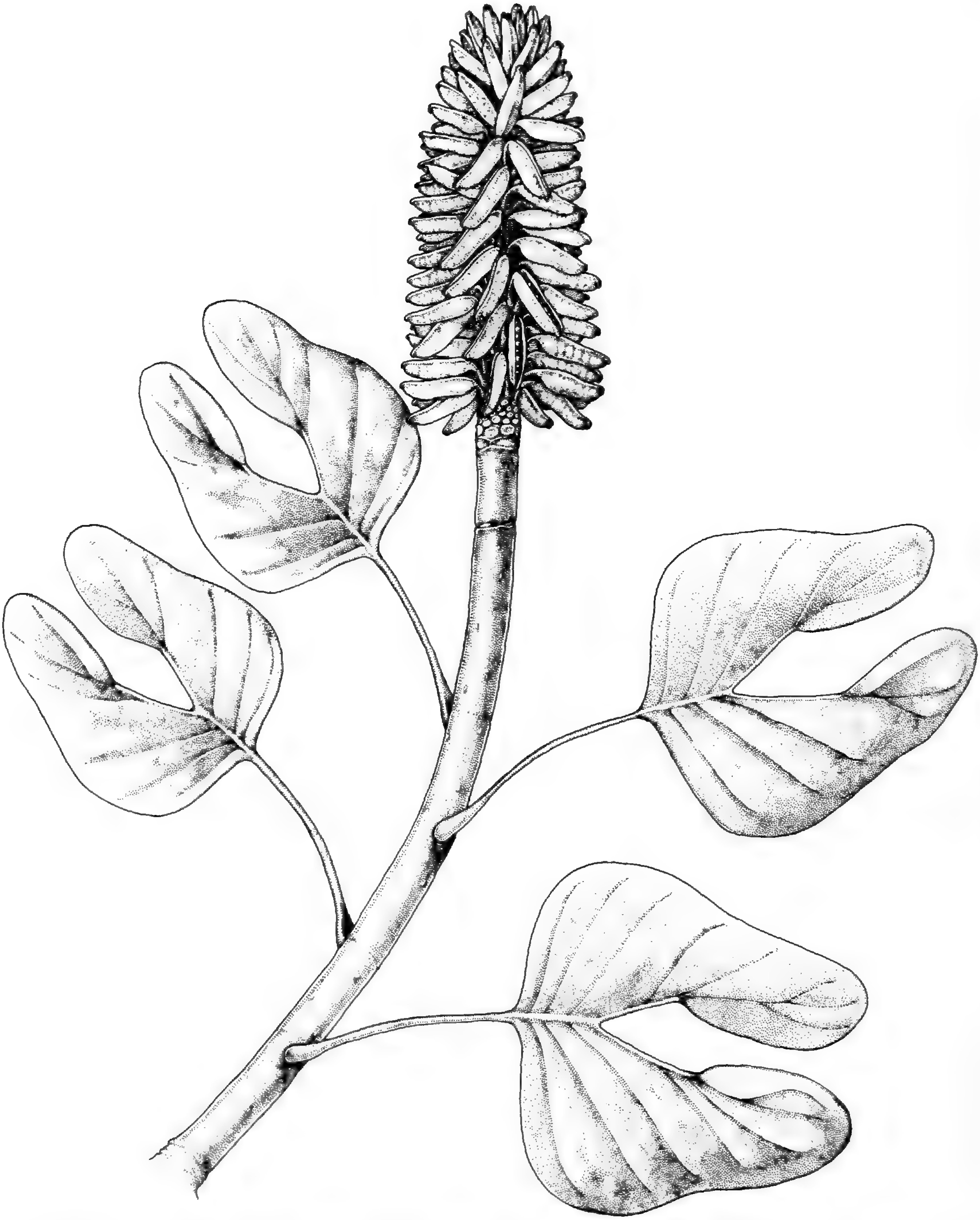


FIGURE 69. *Archaeanthus linnenbergeri.* Reconstruction of leafy twig bearing a multifollicular axis.

Both *Magnolia tripetala* (Figs. 61, 66) and *Liriodendron tulipifera* (Fig. 63) show calyptra scars below the base of the flower.

Follicles and seeds. The follicles of *Archaeanthus* are assumed to have developed from conduplicate carpels with two stigmatic crests along the adaxial surface. Although this kind of carpel is basic in the Magnoliidae, adaxial dehiscence is much less common. In most Magnoliaceae, dehiscence is abaxial but in *Kmeria* the follicle splits adaxially and apically, as it does in *A. linnenbergeri*. Adaxial dehiscence also oc-

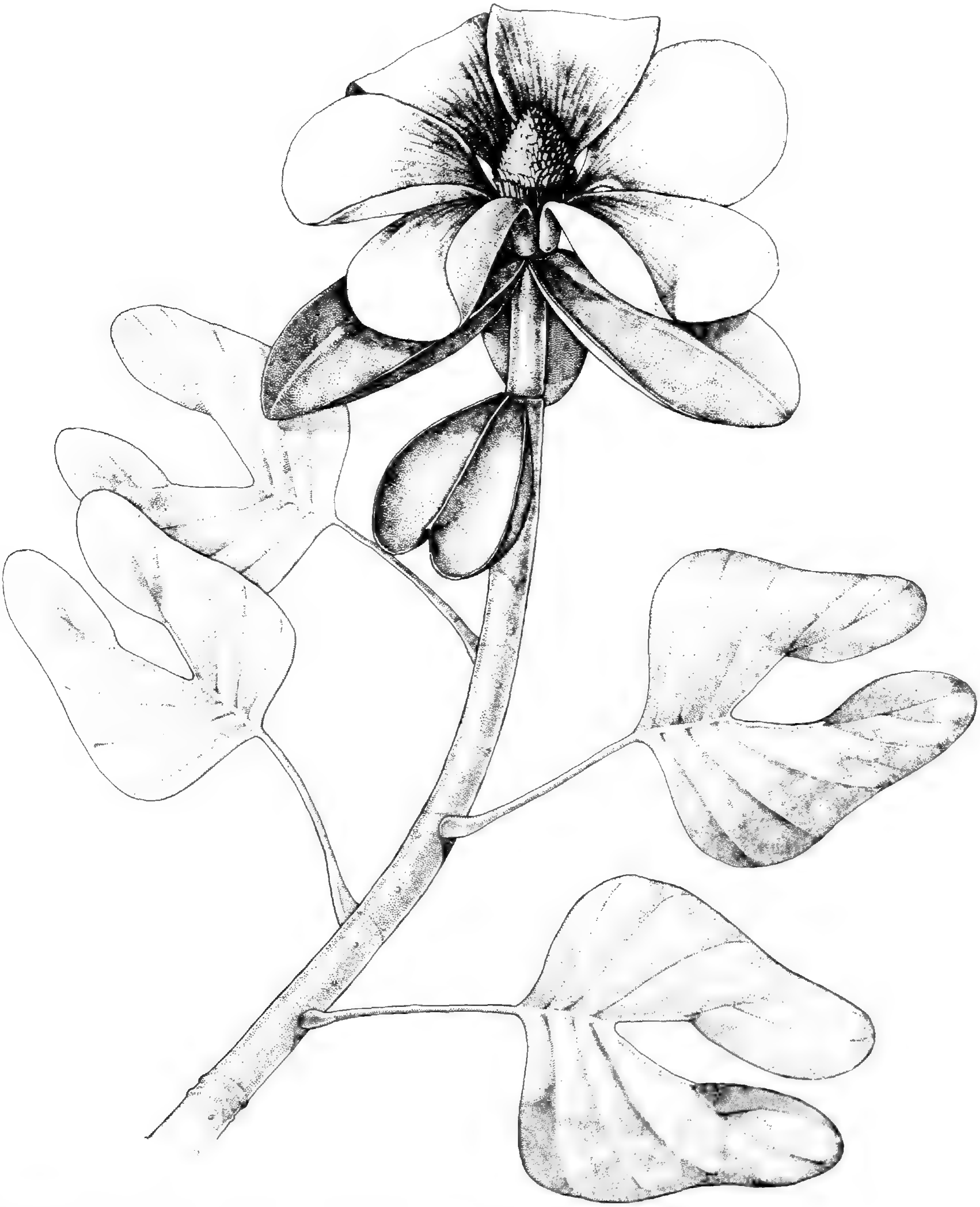


FIGURE 70. *Archaeanthus linnenbergeri.* Reconstruction of leafy twig and flower.

curs in *Illicium,* as well as in a few Ranunculidae and Hamamelidae.

Prominently stalked follicles like those in *Archaeanthus* occur in many Annonaceae such as *Anaxagorea, Guatteria, Unonopsis, Xylopia* (Fries, 1930, 1931, 1934, 1937, 1939), as well as *Austrobaileya, Drimys* (Winteraceae), and *Degeneria.* In the Magnoliaceae the carpels are generally tightly fused to the receptacle (Fig. 61) and often more or less concrescent. Several of the annonaceous genera cited above have follicles that break away from the receptacle at the base of the stalk at maturity, but the closest analogy to the dispersed fruits observed in *Archaeanthus* is in *Liriodendron,* in which the two-seeded, indehiscent follicle acts as the unit of dispersal and separates from the receptacle leaving narrow diamond-shaped scars (Fig. 63). Both the shape of the follicle bases and the scars are similar to those in *A. linnenbergeri.*

The number of seeds borne in the *A. linnenbergeri* follicles is higher than in most Recent Magnoliaceae. Multi-seeded follicles do, however, occur in *Degeneria,* some Annonaceae, and a few other groups of Magnoliidae.

Conclusions. *Archaeanthus* is clearly most similar to extant Magnoliidae and shares some features with supposedly primitive members of the Hamamelidae and Dilleniidae. A summary of the similarities with a range of families is given in Table 1. All of the characters of the fossil with the possible exception of the unusual form and venation of *Liriophyllum* occur in the Magnoliidae, but no living species comes close to the combination of features that *Archaeanthus* displays. Within the Magnoliidae it seems most closely related to the Magnoliales sensu Cronquist (1981), viz. Annonaceae, Austrobaileyaceae, Canellaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae, Lactoridaceae, Magnoliaceae, Myristicaceae, and Winteraceae. However, we do not believe that *Archaeanthus* usefully can be assigned to any extant family; *Archaeanthus* is a unique and extinct genus of fossil angiosperms.

EVOLUTIONARY SIGNIFICANCE

The occurrence of *Archaeanthus* and the floral structure it exhibits, as early in flowering plant evolution as the mid-Cretaceous, is of considerable relevance to concepts of flowering plant evolution. The late Albian to mid-Cenomanian age established for *Archaeanthus* places it approximately 10 to 15 Ma after the first generally accepted angiosperm fossils appear in the fossil record (Hughes et al., 1979). *Archaeanthus* is one of the most completely known of all early angiosperms, and in the characters that it exhibits it comes close to the hypothetical angiosperm archetype developed by adherents of classical magnoliid floral theory over the last 80 years. This archetype, although admittedly hypothetical, has been most explicitly elaborated by Takhtajan (1969) and is summarized in Table 2. The reasoning behind the magnoliid theory is largely based upon neontological data, and a range of approaches have been utilized in formulating the concepts of primitive and advanced characters (Sporne, 1956). In view of this historical decoupling of paleontological and neontological data, the correspondence that exists between the hypothetical archetype and *Archaeanthus* is significant. The details of this similarity are summarized in Table 2, from which it is clear that *Archaeanthus* displays many characters generally regarded as 'primitive' or generalized among Recent plants. There are, however, differences: for example, *Archaeanthus* was probably deciduous rather than evergreen, had small rather than large seeds, and had a lobed rather than a simple leaf; but probably *Archaeanthus* combines more 'primitive' features than any living plant. In terms of magnoliid theory it demonstrates that many of these generalized characters are also ancient. It would be easy to interpret *Archaeanthus* as an ancestor to a range of extant plant groups, but we can see little value in such a naive exercise. Its real significance is in conclusively establishing that the basic magnoliid flower was one of the earliest kinds of floral organization to be developed during the mid-Cretaceous radiation of flowering plants.

Taken in the broader context of mid-Cretaceous fossil flowers, *Archaeanthus* fits well into a pattern that is rapidly becoming established. Other magnoliid flowers similar to *Archaeanthus* occur in the Dakota Sandstone Flora, the Janssen Clay of Hoisington, Kansas (Crane & Dilcher, 1984), the Amboy Clays of New Jersey, and the Crowsnest Formation of southern Alberta (Crane & Dilcher, 1984). None of this material occurs earlier than sub-zone IIC or possibly sub-zone IIB of the palynological zonation established for the mid-Cretaceous of the Atlantic coastal plain (Brenner, 1963; Doyle, 1969; Doyle & Robbins, 1977). However, there is evidence of similar floral morphology as early as zone I. The floral axis figured by Fontaine (1889, pl. 137, fig. 4) and Dilcher (1979, fig. 28) is a cluster of follicles borne on the swollen apex of a simple axis. Other than the swelling at the apex and faint indications of a few scars, no differentiation into receptacle and pedicel is clear. The specimen does, however, show that clusters of follicles are among the earliest of all angiosperm fossil fruit types. Slightly later, Vakhrameev and Krassilov (1979) described *Caspiocarpus paniculiger* from the middle Albian of Kazakhstan, which is thought to be equivalent to zone IIB in the Atlantic coastal

TABLE 1. Comparison of the *Archaeanthus linnenbergeri* plant with selected Recent families of Magnoliidae, Ranunculidae, and Hamamelidae. Data for extant families from D. A. Young (1981). + indicates that at least some members of the extant family display the character indicated.

	Magnoliidae											Ranunculidae		Hamamelidae			Dilleniidae	
	Austrobaileyaceae	Magnoliaceae	Winteraceae	Degeneriaceae	Himantandraceae	Annonaceae	Myristicaceae	Canellaceae	Eupomatiaceae	Amborellaceae	Monimiaceae	Illiciaceae	Schizandraceae	Tetracentraceae	Trochodendraceae	Cercidiphyllaceae	Dilleniaceae	Paeoniaceae
Characters of Fossil Plant																		
1 Flowers Bisexual	+	+	+	+	+	+	0	+	+	0	0	+	0	+	+	0	+	+
2 Receptacle Flat or Convex	+	+	+	+	+	+	+	+	+	0	0	+	+	0	+	+	+	+
3 Perianth Parts Spirally Arranged	0	+	+	0	0	0	0	0	0	+	0	+	+	0	0	0	+	+
4 Perianth Well-Differentiated into Sepals and Petals	0	0	0	+	+	+	+	+	+	0	0	0	0	0	0	0	+	+
5 Stamens Numerous	+	+	+	+	+	+	+	0	+	+	+	+	+	0	+	+	+	+
6 Carpels free	+	0	+	+	0	+	+	0	0	+	+	+	+	0	0	+	+	+
7 Carpel Dehiscence Adaxial	+	0	0	0	0	+	0	0	0	0	0	+	0	+	+	0	+	+
8 Carpels More Than Five	+	+	0	0	+	+	0	0	+	+	+	+	+	0	+	+	+	0
9 Ovules More Than Two Per Carpel	+	+	+	+	0	+	0	+	+	0	0	+	0	+	+	+	+	+
10 Style Absent, Stigma Sessile	0	+	+	+	0	+	+	+	+	+	+	0	+	+	+	+	0	+
11 Leaves Simple	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	0
12 Phyllotaxy Helical	0	+	+	+	+	+	+	+	+	+	0	+	+	+	+	+	+	+
13 Reproductive Shoot Well-Defined	+	+	+	+	+	+	+	+	+	+	0	+	+	+	+	+	0	0
14 Flowers Solitary on a Leafy Cyme	+	+	+	+	+	0	+	+	+	0	+	+	+	0	0	0	+	+

TABLE 2. Comparison of the *Archaeanthus linnenbergeri* plant with the angiosperm morphotype elaborated by Takhtajan (1969). + indicates agreement. − indicates disagreement. ? indicates character unknown in *A. linnenbergeri*. ( ) indicates uncertainty but possible agreement.

	Vegetative		Reproductive
+	Woody	(+)	Flowers Entomophilous
−	Evergreen	+	Radially Symmetrical
+	Leaves Simple	(+)	Bisexual
+	Leaf Margin Entire	+	Flowers Terminal on Leafy Branches
+	Leaves Pinnately Veined	+	Receptacle Elongated
?	Leaves Glabrous	−	Perianth Parts Numerous
?	Stomata Paracytic	−	Perianth Parts Passing Gradually into Foliage Leaves
?	Multilacunar Nodes with a Median Double Trace	(+)	Stamens Numerous
		?	Stamens Laminar
?	Vessels Absent	?	Microsporangia Long and Narrow
?	Tracheids with Scalariform Pits	?	Pollen Monosulcate
?	Wood Parenchyma Absent or Diffuse Apotracheal	+	Carpels Numerous—Helically Arranged
		+	Carpels Large
?	Rays Multiseriate with High Uniseriate Wings	+	Carpels Stalked
?	Phloem Companion Cells Absent	+	Carpels Conduplicate—Suture Adaxial
		(+)	Carpels Incompletely Closed
		+	Fruits Multifollicles
		+	Ovules Numerous
		(+)	Ovules Anatropous
		?	Ovules Bitegmic
		(+)	Ovules Borne Between Median and Lateral Carpel Veins
		−	Seeds Large
		?	Endosperm Abundant
		?	Embryo Small and Undifferentiated

plain zonation. This, too, shows follicles, but they are apparently borne in a unisexual, panicle-like cluster.

From these records alone it is clear that follicles were a very early innovation in flowering plant evolution and that the origin of the conduplicate carpel remains an important issue in angiosperm phylogeny. Contemporaneous with these species, however, are other kinds of floral organs that are very different. A well-preserved pentamerous flower is known from the Janssen Clay Member of southern Nebraska and also occurs at the Linnenberger Ranch locality (Basinger & Dilcher, 1984; Dilcher & Basinger, unpubl. data). Each flower had five loosely fused carpels with abaxial dehiscence. Leaves and reproductive structures very similar to those of extant *Platanus* are common in the Dakota Formation (Dilcher, 1979) and also occur as early as subzone IIB (Krassilov, 1977; G. Upchurch, pers. comm.; Dilcher & Schwartzwalder, unpubl. data). Other mid-Cretaceous angiosperm reproductive structures may also have been unisexual (Dilcher, 1979; Retallack & Dilcher, 1981b). Such plants clearly demonstrate that on present evidence the magnoliid floral organization seen in *Archaeanthus* does not predate other very different kinds of flowers, including apparently unisexual forms, in the fossil record. *Archaeanthus* does, however, add significantly to our knowledge of early angiosperm reproductive diversity and demonstrates the existence of a well-differentiated, relatively sophisticated floral organization during the mid-Cretaceous. *Archaeanthus* demonstrates conclusively that magnoliid flowers are among the earliest known, and that magnoliid-like plants were an early development in angiosperm evolution.

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LESQUERIA: AN EARLY ANGIOSPERM FRUITING AXIS FROM THE MID-CRETACEOUS[1]

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ABSTRACT

Lesqueria elocata (Lesq.) Crane & Dilcher, an early angiosperm fruiting axis, is described from the mid-Cretaceous (Upper Albian–Middle Cenomanian) Dakota Formation of central Kansas and the Woodbine Formation of northeastern Texas. The species is based on three-dimensional molds preserved in sandstone. The fruits (multifollicles) comprise 175–250 follicles borne helically, in a tight, more or less spherical or ovoid head. The receptacle below the gynoecium is cylindrical, elongated, and bears numerous, helically arranged, persistent laminar flaps. The bases of these flaps are diamond-shaped at their attachment to the receptacle, but it is not known whether they are stamens or perianth parts. The follicles are short stalked, with two terminal prolongations, and dehisced along a single adaxial suture. The follicles contained 10–20 seeds arranged in two longitudinal rows. The former assignment of *L. elocata* to *Williamsonia* (Bennettitales) is rejected and *Lesqueria* is shown to be most similar to Recent magnoliid angiosperms. *Lesqueria* is one of a diverse group of extinct mid-Cretaceous magnoliid flowering plants.

Until recently, knowledge of early angiosperms has been almost exclusively restricted to isolated pollen grains and leaves. Although some conclusions may be drawn about the systematic relationships of the plants from which these organs were derived, progress in interpreting the systematic affinities of the earliest flowering plants has been considerably inhibited by a lack of knowledge of their reproductive structures. In this paper we describe an early angiosperm fruit from the mid-Cretaceous of central United States. The fruit (multifollicle) comprises a receptacle with a terminal cluster of tightly packed follicles. We discuss its systematic relationships and briefly evaluate its evolutionary significance in relation to the known fossil record of early angiosperm reproductive structures.

One element in the early formulation of magnoliid floral theory was the superficial similarity of generalized *Magnolia*-like flowers to the 'flowers' of the Bennettitales (Arber & Parkin, 1907). Although it is now clear that these two kinds of reproductive organs are very different in detailed structure, their superficial similarity creates some difficulties for the determination of imperfectly known fossil material. In his review of the bennettitalean genus *Williamsonia,* Seward (1917) excluded several species, including *W. elocata* Lesq. from the Dakota Sandstone Flora of Kansas. Wieland (1928) described a species similar to *W. elocata* from the same flora as *W. hespera* and also expressed doubt as to its relationship with *Williamsonia.* In this paper we reinterpret both of these species based on five specimens from the Dakota Sandstone Flora, including the type material of *W. hespera,* and two specimens from the Woodbine Formation of Texas. Both are interpreted as angiosperm fruits and united as a single species *Lesqueria elocata* (Lesq.) Crane & Dilcher.

MATERIAL

The seven specimens described in this paper are preserved as three-dimensional molds in sandstone. Five are from the classic Dakota Sandstone Flora of Kansas, the other two are from the Woodbine Formation of Texas.

Almost all of the large plant fossil collections

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from the Dakota Sandstone (Dakota Formation) are preserved as impressions or molds in a fine- to medium-grained ferruginous sandstone. Although we have seen similarly preserved material in situ in sandstones at various central Kansas localities, the specimens considered here are from the collections of the University of Kansas at Lawrence (UKDSC), the Field Museum of Natural History, Chicago (FM-P), the Peabody Museum of Natural History, Yale University, New Haven (PMNH), and the United States National Museum (USNM). Large collections of the 'Dakota Sandstone Flora' were assembled by Sternberg and others in the mid-nineteenth century (see Andrews, 1980) principally from surface weathered sandstone blocks in Ellsworth County. The locality for these specimens is often simply given as Ellsworth County, with no further details. Brief descriptions and discussions of the Dakota Sandstone Flora are given by Meek and Hayden (1858), Newberry (1859, 1860a, 1860b), Heer (1861), Marcou (1864), Capellini and Heer (1867), Bartsch (1896), Gould (1900a, 1900b, 1901), Berry (1920), Tester (1931), and Baxter (1954). More extensive reports and illustrations were given by Lesquereux (1868, 1874, 1878, 1883, 1892), Newberry (1868), and Gress 1922). The flora is dominated by angiosperm leaves and over 400 species have been described (Lesquereux, 1892).

Despite considerable lateral sedimentological variation, the Dakota Formation in Kansas is generally divided into two members, neither of which constitute mappable units (Franks, 1975); the Terra Cotta Clay Member below and the Janssen Clay Member above (Plummer & Romary, 1942). Sandstones occur throughout both members but the classic Dakota Sandstone Flora is probably principally from the sandstone facies of the Janssen Clay Member. The age of the Dakota Formation in Kansas is firmly bracketed as no older than late Albian (Scott, 1970a, 1970b; Ward, 1981) and no younger than Cenomanian (Hattin, 1965, 1967; Eicher, 1975). It seems likely that the Dakota Formation in this area straddles the Upper and Lower Cretaceous boundary (Zeller, 1968; Kauffman et al., 1976).

Two specimens of *L. elocata* are known from the Woodbine Formation (Woodbine Sand) of northeast Texas. One was kindly donated by Ms. V. Hamilton (IU 15726-4419); and the other (USNM 326817) was identified by Brown (1958: 359) as *Isoetites* sp. Fossil plants from the Woodbine Formation have been described by Knowlton (1901), Berry (1912, 1917, 1922), Winton (1925), and MacNeal (1958). The flora is dominated by angiosperms, and over 80 species of leaves and other organs have been recognized (MacNeal, 1958). The Woodbine Formation comprises diverse sediments divided into four members, from the base upward; the Dexter Member, the Euless Member (more or less laterally equivalent to the Red Branch Member), the Lewisville Member, and the Templeton Member. The Templeton, Lewisville, and Euless Members are predominantly marine in origin, whereas the Red Branch and Dexter Members are predominantly non-marine sands, clays, and carbonaceous shales. Most of the plants, and probably our specimens, are from the Red Branch or Dexter Members. Although there are some plant species unique to the Woodbine Formation, the flora is very similar to the typical 'Dakota Sandstone Flora' of Kansas and Nebraska (MacNeal, 1958). Marine and brackish water invertebrates from the upper part of the Janssen Clay Member suggest a correlation with the Woodbine Formation in northeast Texas (Hattin, 1965). The age of the Woodbine Formation is generally regarded as Cenomanian (Stephenson, 1952; Hedlund, 1966; Pessagno, 1969). All of the material described in this paper, therefore, comes from sediments of similar age, probably equivalent to zone III, of the palynological zonation established by Brenner (1963), Doyle (1969), Doyle and Robbins (1977), and others for the mid-Cretaceous of the Atlantic Coastal Plain.

SYSTEMATICS

The measurements given in the description are based on all seven specimens, with ranges and common dimensions given whenever possible.

Lesqueria Crane & Dilcher, gen. nov. TYPE: *Lesqueria elocata* (Lesq.) Crane & Dilcher.

DIAGNOSIS: Fruit consisting of a receptacle bearing a tight, ovoid, cluster of follicles at the apex, and other floral organs below. Receptacle stout, elongated, consisting of a distal, swollen, ovoid, gynoecial zone bearing follicles; with an elongated, more or less cylindrical zone below, bearing numerous helically arranged laminar flaps. Bases of the flaps diamond-shaped, forming a distinctive pattern on the receptacle. Base of flower delimited by a narrow transverse ridge. Follicles narrowly ellipsoidal with a distinct adaxial suture; very short stalked and with elongated bifid tips.

DERIVATION: After Leo Lesquereux who originally described the type species.

Lesqueria elocata (Lesq.) Crane & Dilcher, comb. nov. NEOTYPE: UKDSC 203—Ellsworth County, Kansas.

DIAGNOSIS: As for the genus.

SYNONYMS: *Williamsonia elocata* Lesq.

Williamsonia (?) *hespera* Wieland.

REFERENCES: *Williamsonia elocata* Lesquereux (1892: 89, pl. 2, figs. 9, 9a) (brief description, discussion, and line drawings).

Williamsonia elocata Lesq. (Wieland, 1928: 39–41, fig. 5) (discussion and line drawing).

Williamsonia (?) *hespera* Wieland (1928: 41–47, figs. 7–10) (description, discussion, and photographs).

Williamsonia elongata Lesq. (Seward, 1917: 462) (rejects the assignment to *Williamsonia*; orthographic error).

Isoetites sp. (Brown, 1958: 359) (brief mention).

OTHER MATERIAL: PMNH 2403–2405, Dakota Formation, Kansas; FM-P3056, Dakota Formation, Ellsworth County, Kansas; USNM 2782, Dakota Sandstone, Fort Harker, Kansas; USNM 50598, Dakota Formation, Ellsworth County, Kansas; USNM 326817, Woodbine Formation, 5 miles SE of Dexter, Texas; IU 15726-4419, Woodbine Formation, Denton County, Texas.

NUMBER OF SPECIMENS EXAMINED: 7.

FIGURES: 1–32, 42A–G, 47.

DESCRIPTION: Fruit borne at the apex of a stout vegetative axis, ca. 10 mm diam., which also shows the bases, or former attachment, of 4 other fruits. Surface of axis with a few transverse grooves and ridges immediately below the re-

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FIGURES 1–3. *Lesqueria elocata* Crane & Dilcher, comb. nov., UKDSC 203, Dakota Sandstone, central Kansas.—1. Ovoid head of clustered, narrowly elliptical, follicles prior to fracturing, A–A indicates plane of fracture; bases of follicles and their attachment to the receptacle missing; ×2.5.—2. Longitudinal fracture of a three-dimensional mold, showing curved follicles borne on the terminal, swollen, gynoecial zone of a long receptacle. Below the gynoecial zone note: the bases of the numerous helically arranged flaps and the penetration of sandstone matrix approximately midway along the cylindrical portion of the receptacle (B), the constriction at the receptacle base and point of attachment to the vegetative branch (C); ×1.5.—3. Counterpart of Figure 2, note the attachment of the receptacle to the vegetative branch and the bases of other receptacles projecting into the sediment, see Figure 8 for details; ×1.5.

FIGURES 4–8. *Lesqueria elocata* Crane & Dilcher, comb. nov., UKDSC 203, Dakota Sandstone, central Kansas.—4. Ovoid head of follicles seen obliquely from above after the transverse fracture along A–A (Fig. 1) but before longitudinal fracture. Note the diamond-shaped bases of the flaps on the upper part of the cylindrical receptacle, and the molds of individual follicles; ×1.—5. Counterpart of transverse fracture in Figure 4 seen from below, showing molds and locule casts of individual follicles; ×1.—6. Detail of transverse fracture plane in Figure 4, showing paired, triangular cavities caused by the curved, double follicle tips. Note the lower parts of two follicle molds showing the groove (D) caused by the abaxial follicle surface which diverges at the apex into the two follicle tips; ×5.—7. Detail of longitudinal fracture in Figure 2 showing the gradual change in the shape of the flap bases along the cylindrical receptacle. Note the short flaps (E) toward the base of the receptacle; at the apex the longest flaps (F) form a collar around the base of the head of follicles; ×2.5.—8. Composite photograph, from different orientations of the specimen in Figure 3 showing (C) the base of the receptacle and (G) the bases or attachment points of three other receptacles; ×2.

FIGURES 9–14. *Lesqueria elocata* Crane & Dilcher, comb. nov., UKDSC 203, Dakota Sandstone, central Kansas.—9. Detail of transverse fracture plane in Figure 5 (A–A, Fig. 1) showing several follicles seen from below. Note the variable extent to which sediment has penetrated the follicles both adaxially and apically to form the locule casts, and therefore the extent to which internal and external features of the follicles can be interpreted from the specimen. The paired triangular cavities are formed by the upcurved double tips of follicles attached lower down on the receptacle; ×5.—10. Part of Figure 9 in different orientation showing cavities in a locule cast interpreted as those of seeds (H); ×5.—11. Part of Figure 9 in different orientation showing the outline of a seed in the locule cast formed by the distorted fruit wall (I), and the fine double groove formed by the two external adaxial ridges on the follicles (J); ×5.—12. Detail of part of Figure 9 showing the impressions of the two adaxial ridges; ×30.—13. Detail of part of the specimen in Figure 9 seen obliquely from below and showing the grooves (J) left by the adaxial ridges of the follicles, and penetration of sediment through the adaxial suture; ×5.—14. Detail of part of Figure 1 showing sections of the cavities left by follicles. Note in each follicle the impressions of two adaxial ridges which comprise the adaxial crest, one abaxial ridge, and two lateral ridges; ×4.


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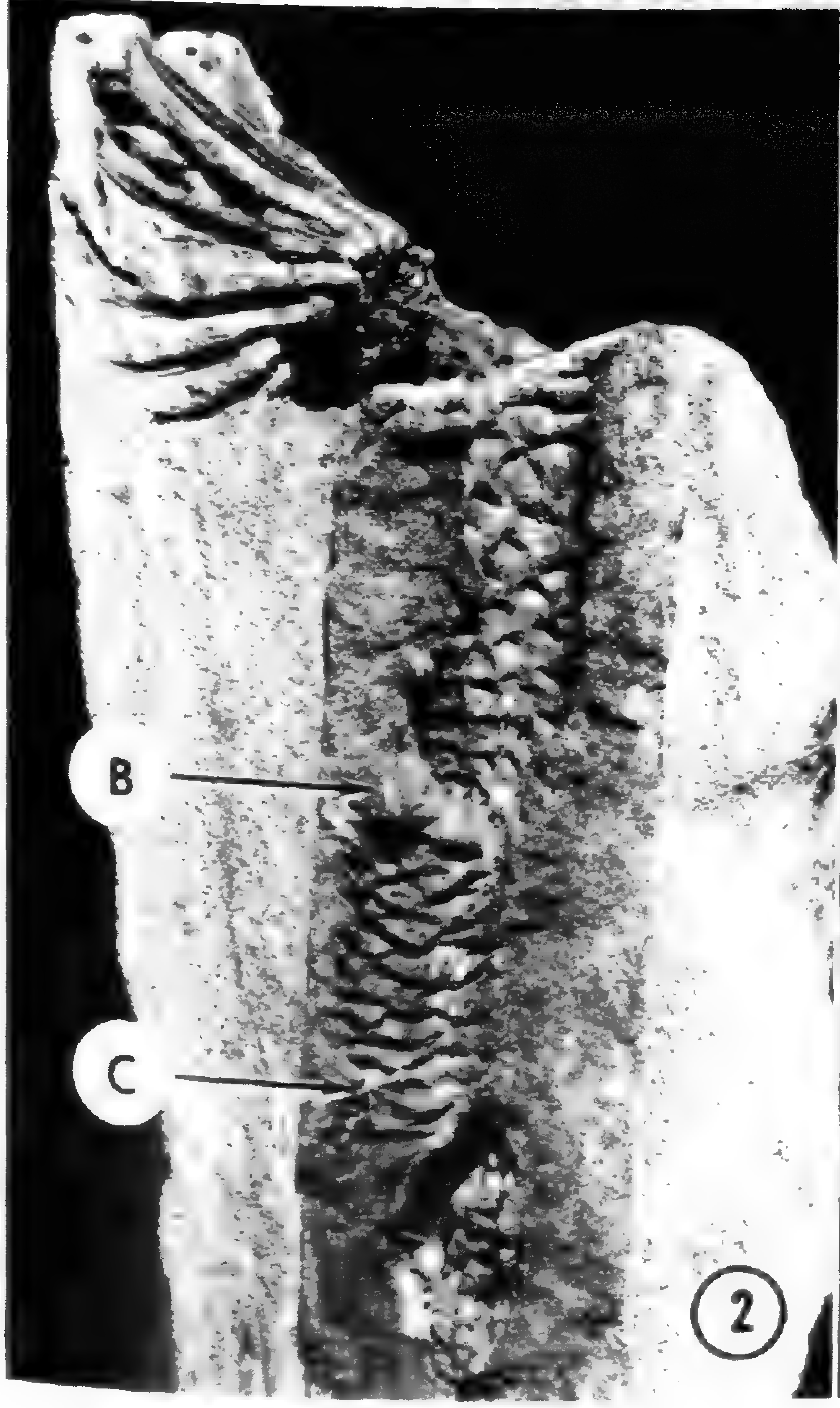
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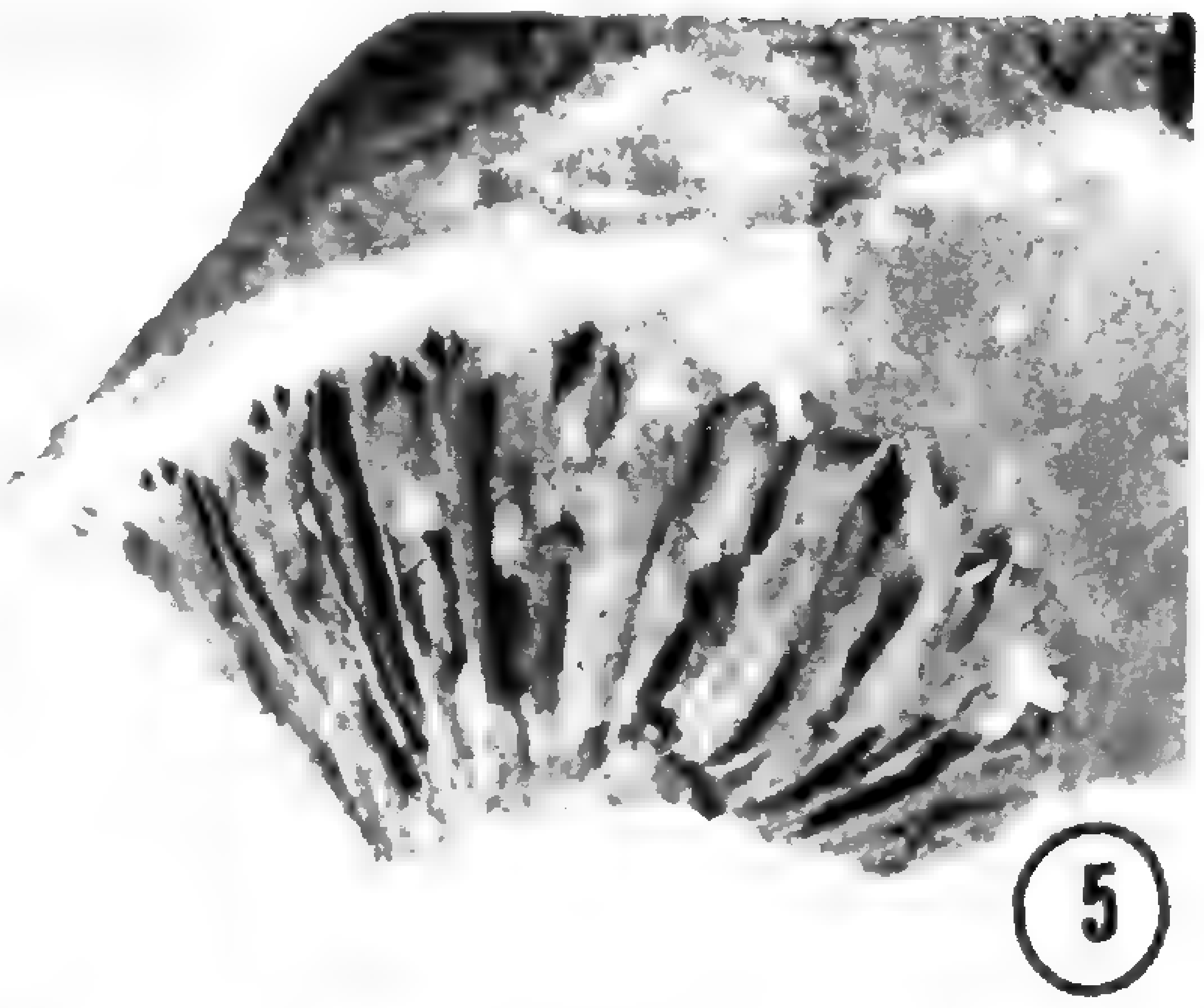

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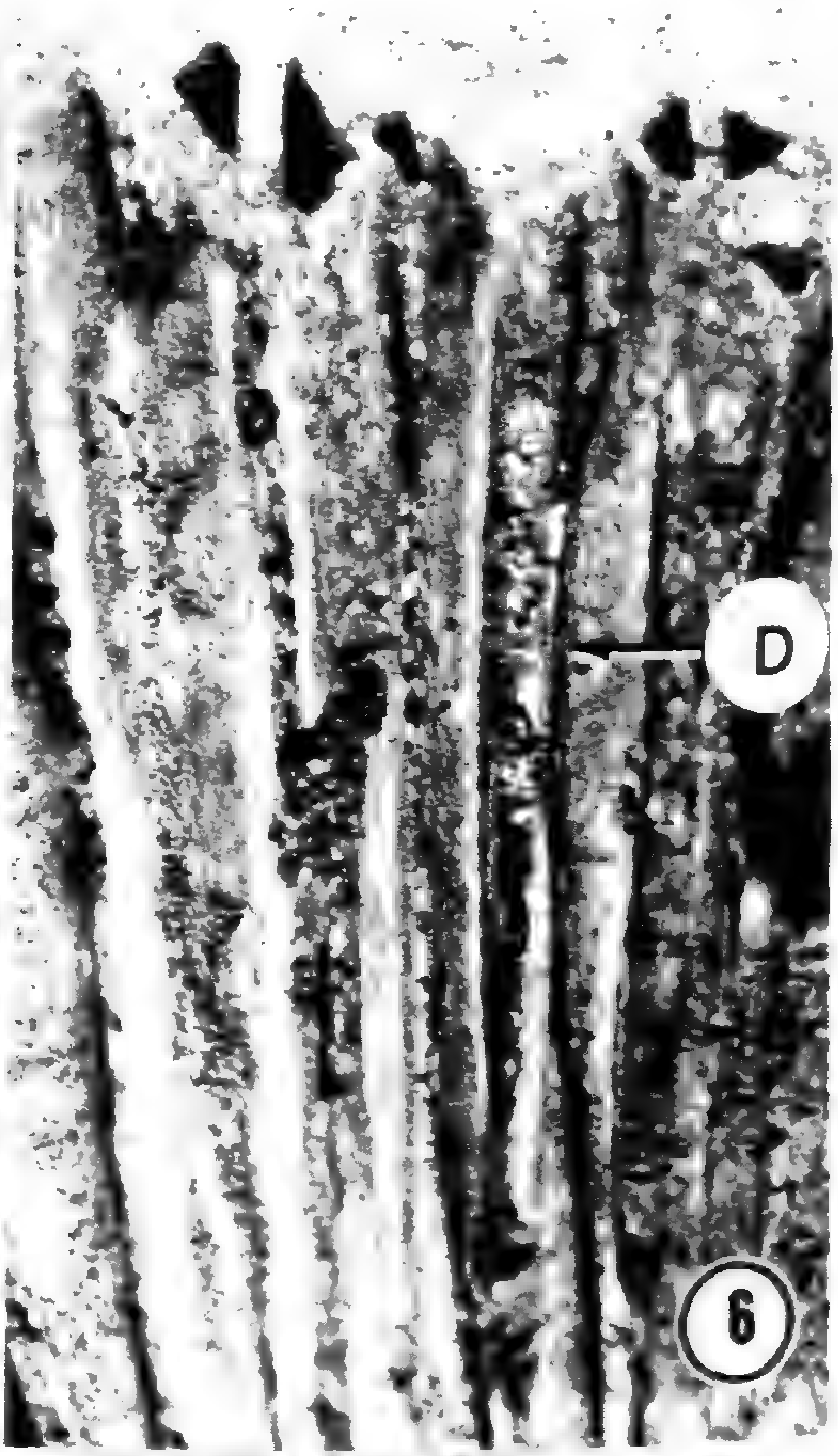

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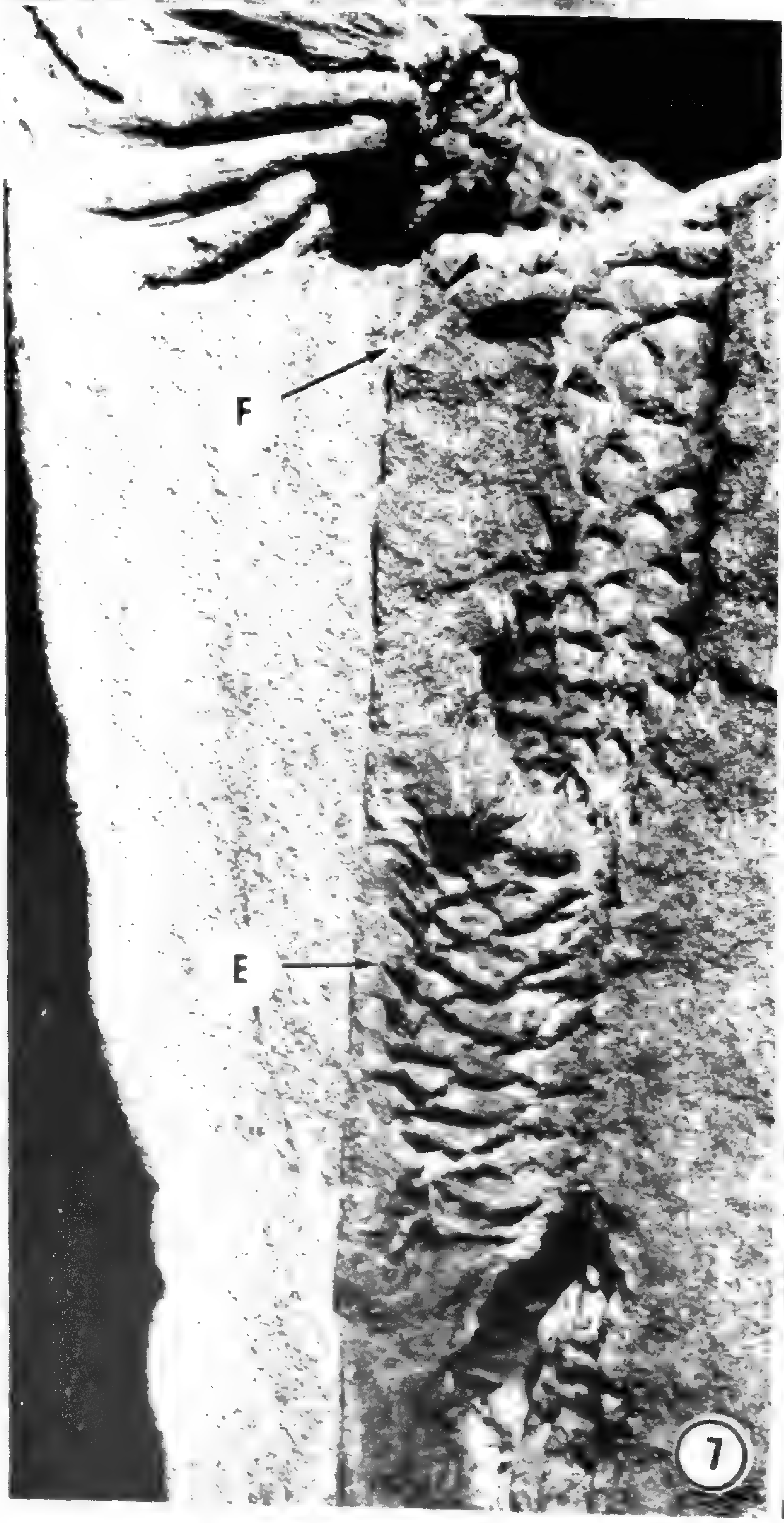

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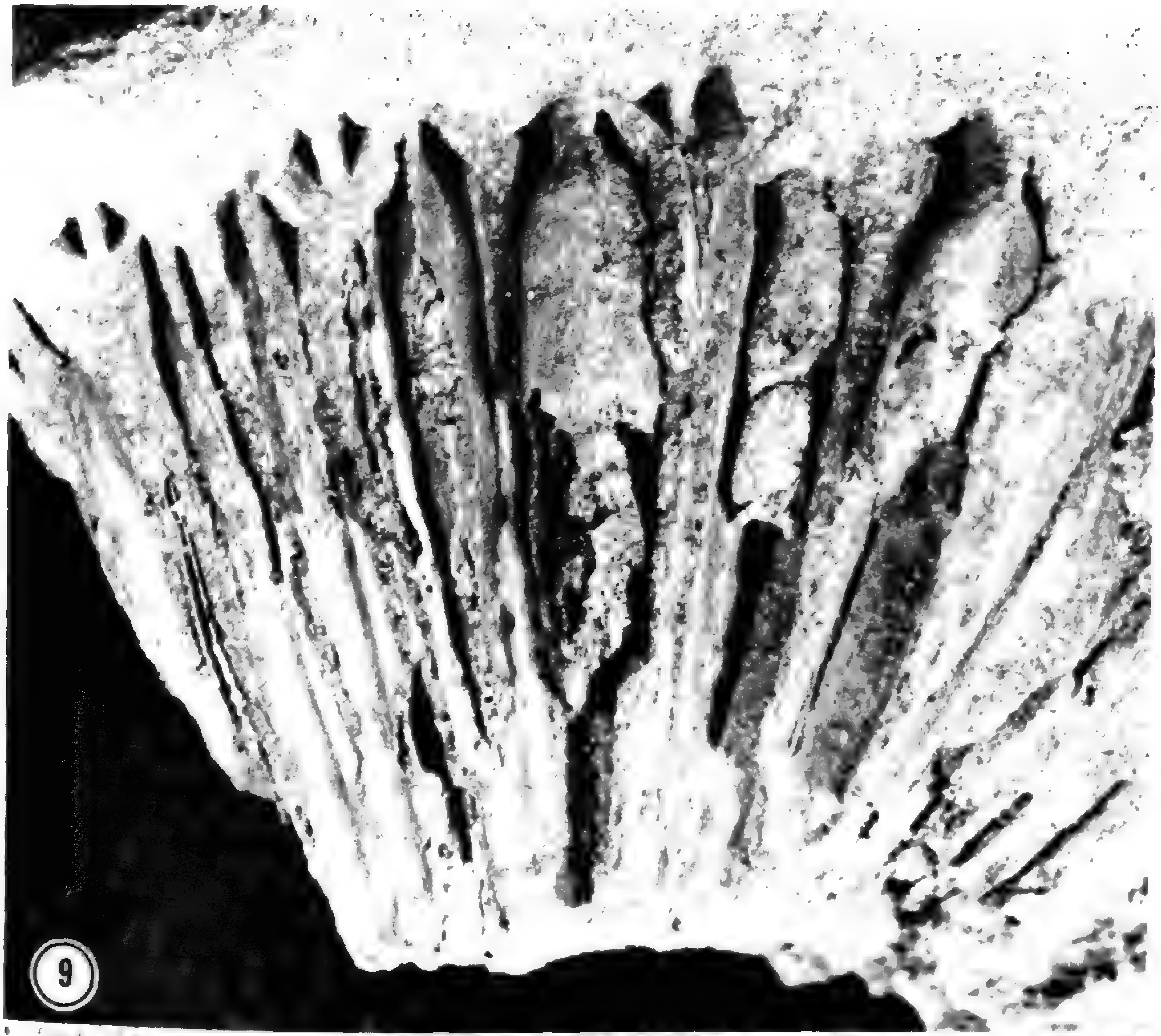
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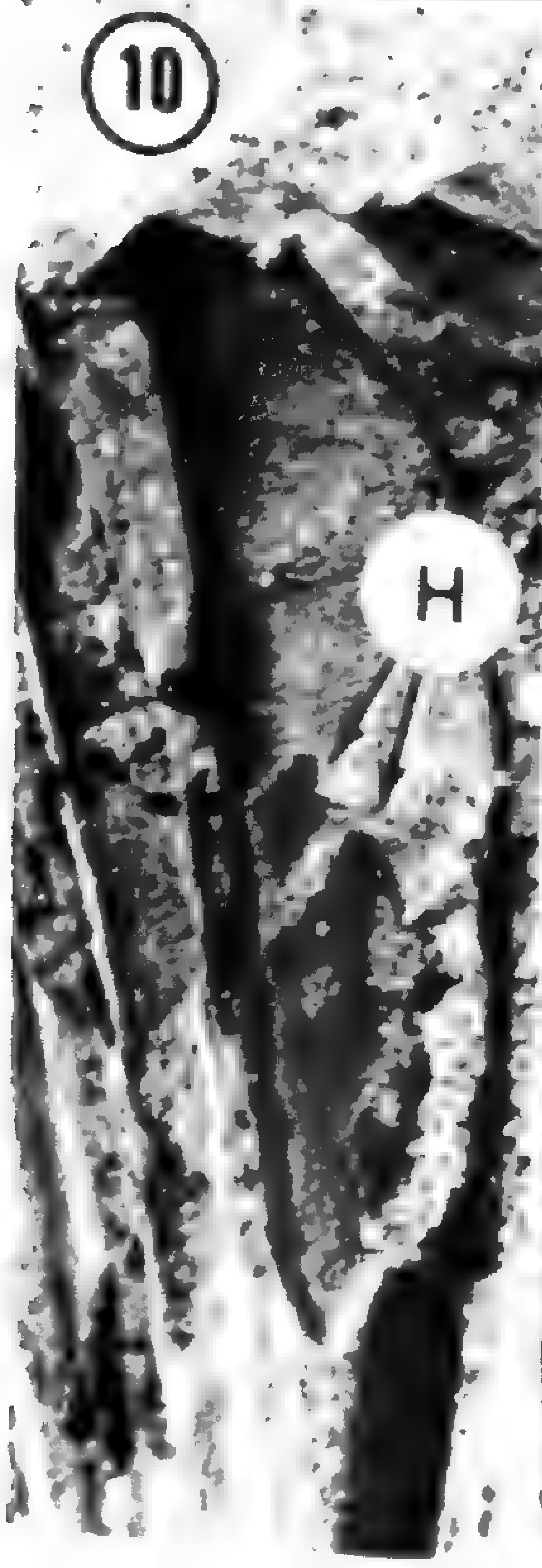
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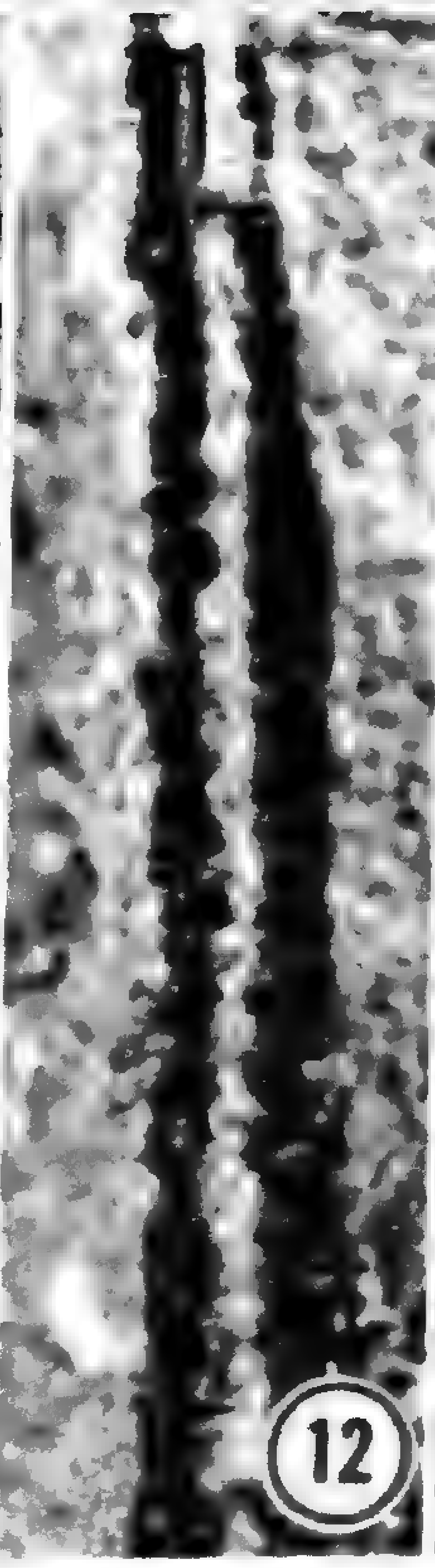
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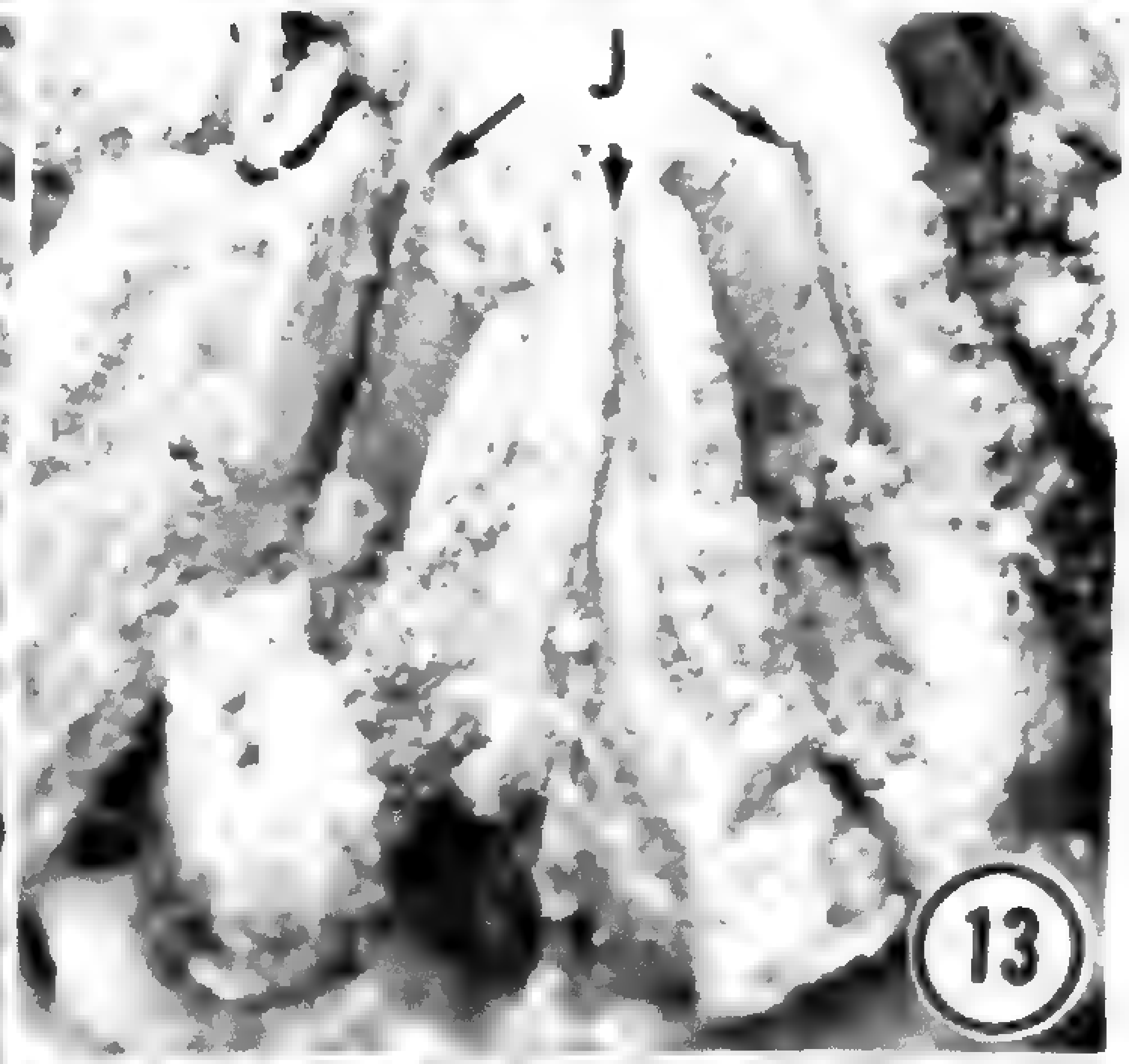
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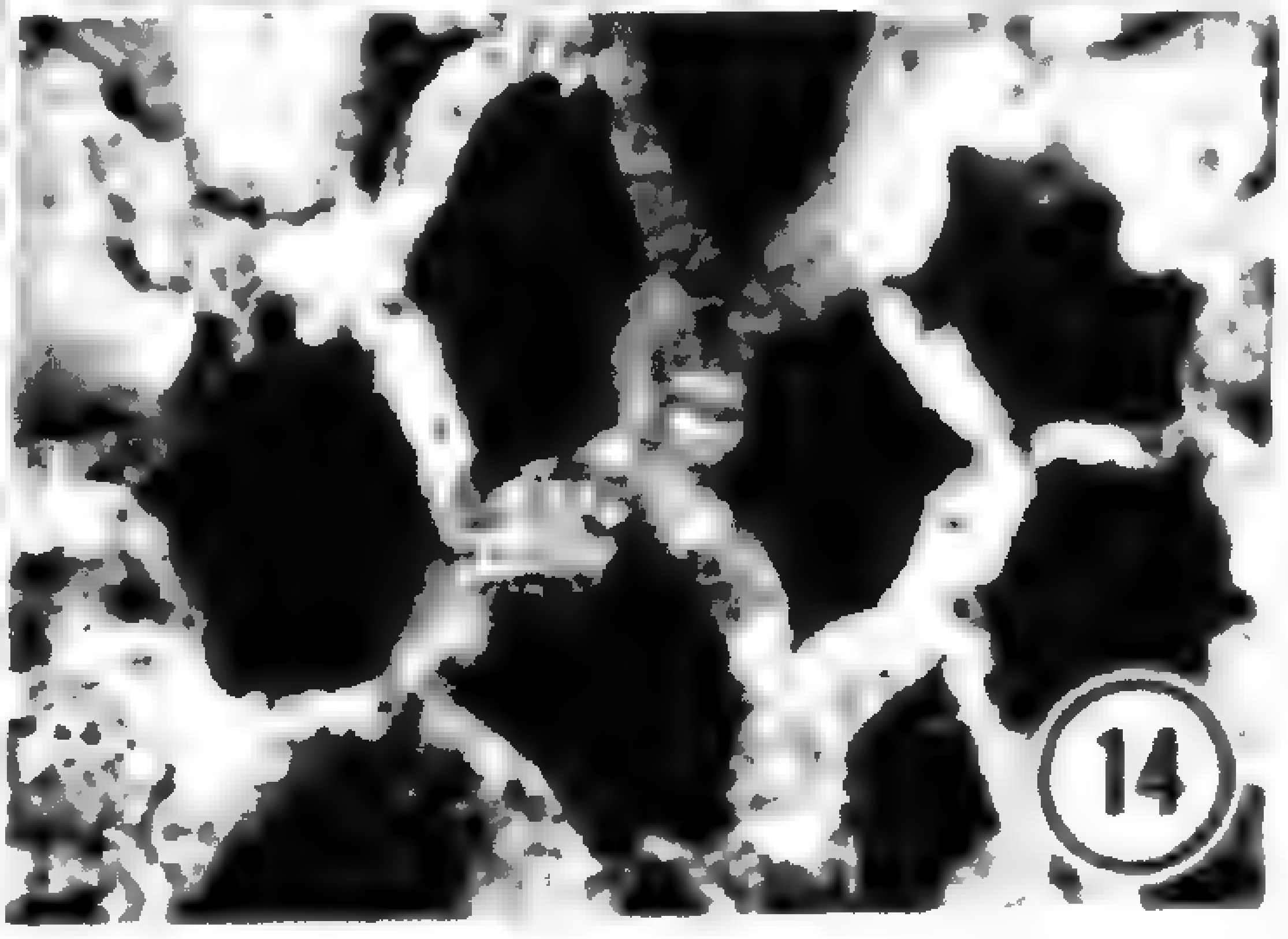
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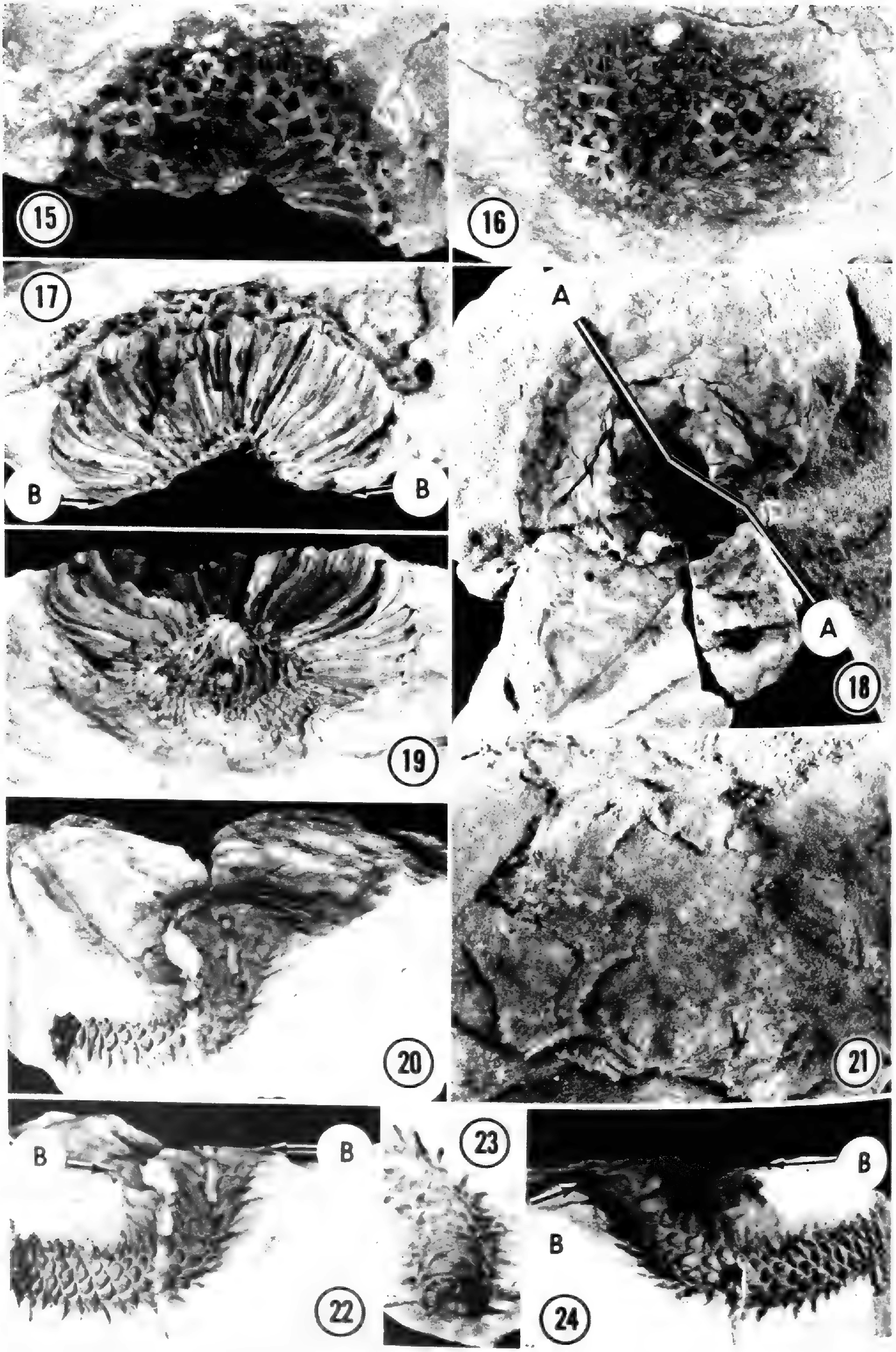

FIGURES 15–24. *Lesqueria elocata* Crane & Dilcher, comb. nov., Dakota Sandstone, central Kansas.—15. PMNH 2403, transverse fracture of a head of follicles seen from above, showing cavities left by follicles and the paired cavities formed by the double follicle tips; ×1.—16. FM-P3056, transverse fracture through a head of curved follicles: notice that the fractures become increasingly tangential toward the circumference of the head.

ceptacle, otherwise more or less smooth. Maximum length of vegetative axis preserved, 28 mm. Total length of longest specimen seen, 88 mm.

Receptacle stout, elongated, to 56 mm long; comprising a distal, swollen, ovoid, gynoecial zone bearing follicles, with an elongated more or less cylindrical zone below. Gynoecial zone of receptacle to 14 mm long, to 25 mm diam. (maximum), bearing ca. 175–250 follicles tightly packed into a more or less spherical or ovoid head, ca. 37–65 mm diam., and to 35 mm high. Follicles borne helically, diamond-shaped in section at their attachment to the receptacle. Gynoecial zone abruptly or gradually tapered into the apex of the cylindrical zone below.

Receptacle below the gynoecial zone 40–42 mm long, ca. 8 mm diam., broadening slightly where it joins the gynoecial zone and bearing 110–150 helically arranged laminar flaps which have distinctive diamond-shaped bases where they are attached to the receptacle. Diamond-shaped bases 2–4 mm high, 2–4.5 mm wide distally; generally about as wide as high, occasionally higher than wide; gradually becoming shorter and wider toward the base where they are 1.5–3 mm high, 3.5–6 mm wide.

Distal flaps expanded at their apex into a prominent lamina to 20 mm long, and to 17 mm wide (largest flap incomplete in length and width), occasionally with a weak adaxial keel. Proximal flaps short, to 2 mm long (always incomplete). Upper flaps crowded and imbricate, forming a persistent irregular collar below the gynoecial zone. Lamina surface with a fine granular texture, showing no obvious venation or other morphological features.

Base of receptacle constricted where it joins the vegetative axis and with a narrow transverse ridge below. Base of receptacle showing a central pith surrounded by 10 xylem wedges. Xylem cylinder surrounded by softer tissue.

Follicles narrowly ellipsoidal, more or less straight or with strong upward curvature in the distal third, particularly toward the base of the follicle cluster. Individual follicles 9–24 mm long, 1.5–4 mm wide. Follicles contracted just above the attachment to the receptacle into a very short stalk-like constriction 2 mm long, and extended apically into an elongated bifid tip. Stalk 1 mm wide at its midpoint, broadening proximally to a diamond-shaped attachment to the receptacle, 1–2 mm high, 1–2 mm wide. Follicles with two narrow terminal prolongations 3–5 mm long forming a distinct bifid tip. Each prolongation triangular in cross section, ca. 0.5–1 mm thick (maximum); the inner surface of each pair parallel, and ca. 0.5 mm apart. Follicles attached to the receptacle at high angles of ca. 70–90°.

Follicles with a median, longitudinal, adaxial suture along the entire length, flanked on either side by a low ridge ca. 0.2 mm high, and 0.2 mm broad, forming an adaxial crest. Follicles dehiscing adaxially from the distal end along the suture; also splitting apically between the 2 prolongations. Follicles diamond-shaped in transverse section, to 4 mm high, slightly higher than broad. Abaxial follicle surface generally featureless externally or with a single ridge, frequently with a weak median groove internally. Lateral margins with a prominent ridge in their median part; ridge less conspicuous toward the apex and base. Internal locule surface smooth or rugulate-striate. Locule uninterrupted.

Follicle wall ca. 0.2 mm thick, thickening at

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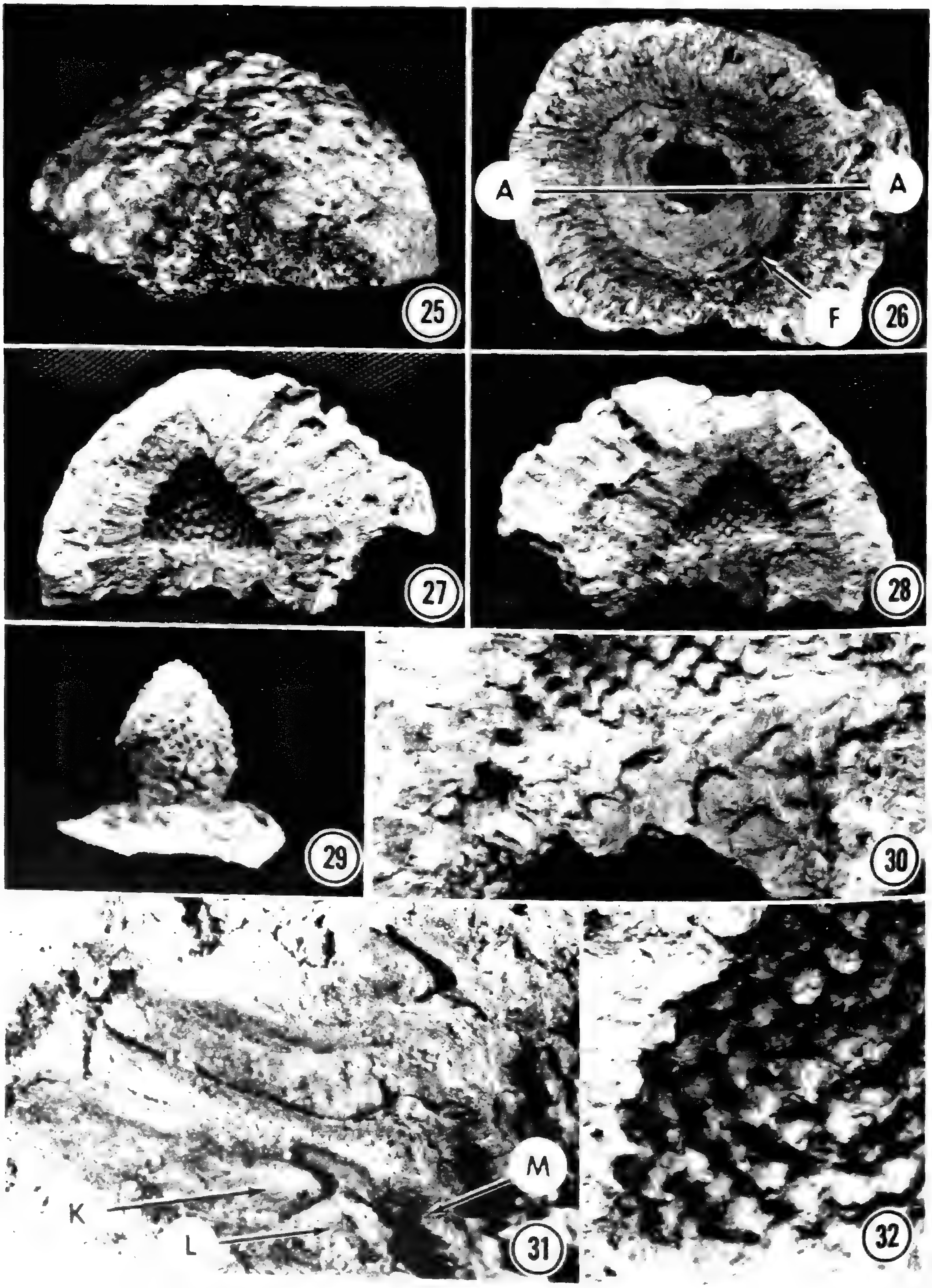
×1.—17. Specimen in Figure 15 rotated through approximately 90°, showing lateral views of numerous curved follicles, and position of fracture surface in Figure 18 (B–B); ×1.—18. PMNH 2403-5 seen from above, showing the position of various fragments and the section, A–A. The exposed fracture surface shows a collar formed by the laminae of persistent flaps attached immediately below the gynoecial zone (line B–B in Figs. 17, 24); ×1.—19. Specimen in Figure 17 rotated through approximately 45°, showing numerous curved follicles radiating from the receptacle; ×1.—20. PMNH 2405, fracture surface B–B (Figs. 17, 18, 22) seen obliquely from above showing the cylindrical portion of the receptacle with the bases of numerous helically arranged flaps, the upper flaps form the prominent, persistent, overlapping flaps of the collar, as seen in face view in Figure 18; ×1.—21. Surface detail of flap laminae showing a granular texture finer than that of the sandstone matrix, ×2.5.—22. Specimen in Figure 20 rotated through approximately 45°, showing a lateral view of the surface of section A–A, the curved cylindrical portion of the receptacle and the position of fracture plane B–B; ×1.—23. PMNH 2405, same specimen as Figure 22 showing the base of the receptacle from above, note the differential penetration of sediment into the receptacle base which shows three zones: a central core interpreted as pith, a ring of discrete wedges interpreted as xylem, and an outer zone interpreted as cortex; ×1.—24. PMNH 2404, counterpart of Figure 22, showing a lateral view of the surface of section A–A, the curved cylindrical portion of the receptacle and the position of the fracture plane B–B; ×1.



FIGURES 25–32. *Lesqueria elocata* Crane & Dilcher, comb. nov., IU 15726-4419, Woodbine Formation, Denton County, northeast Texas.—25. Lateral view showing abraded outer surface; ×1.—26. Specimen seen from below showing radiating follicles and receptacle cavity, note the remains of the flaps (F) between the follicles and the cylindrical portion of receptacle: A–A line of fracture surface; ×1.—27. Fracture of specimen along line A–A (Fig. 26), showing the cavity formed by the swollen gynoecial zone of the receptacle, radiating follicles, and the upper part of the cylindrical portion of the receptacle; ×1.—28. Counterpart of fracture plane in Figure 27; ×1.—29. Latex rubber cast showing the ovoid gynoecial zone of the receptacle and the bases of numerous helically arranged follicles; ×1.—30. Detail of Figure 28 showing the bases of the upper flaps borne on the

the distal end. Seeds 10–20, borne in 2 rows along either side of the median line, slanted adaxially to abaxially, proximal to distal, 3 mm long, 1.5 mm wide.

DISCUSSION: None of the specimens have plant tissues preserved, either organically, or in mineralized form, and all of the details reported in the diagnosis and description are preserved as cavities or impressions in the encasing sandstone matrix. In places, particularly in IU 15726-4419, there is a fine-grained ferruginous sheath surrounding the cavities left by the plant tissue, similar to that reported by Spicer (1977) for Dakota Sandstone leaf fossils and leaves from Recent depositional environments. None of the impressions, however, have yielded cellular detail. Although there has been some distortion, none of the specimens were significantly compressed during fossilization.

Only UKDSC 203 shows the way in which the flowers were borne on the vegetative axis (Figs. 3, 8). At the apex of this vegetative axis there are the bases, or positions of attachment of four other floral receptacles in addition to the one more or less complete fruit (Figs. 7, 8). One of these receptacle bases is 12 mm long and clearly shows the attachment of the proximal flaps to the receptacle. The others are 4 mm long or less and abruptly truncated, suggesting that the fruits frequently abscised at the receptacle base when mature. PMNH 2405 clearly became detached at this point (Figs. 22–24), and the manner in which the sediment differentially penetrated the base of the receptacle (Fig. 23) has provided some information on the anatomical structure at the base of the flower (Fig. 42D).

In addition to the receptacles or receptacle attachments, on UKDSC 203 there are three other projections into the matrix from the apex of the vegetative axis. They are smooth walled, taper distally, and are all less than 10 mm long. They may have been formed by buds, or in the case of the smallest, perhaps by a petiole base. At least one of these holes seems to subtend a floral axis, but the others do not clearly show a similar relationship.

The complete proximal cylindrical zone of the receptacle is preserved in UKDSC 203 (Figs. 2, 3), PMNH 2405 (Figs. 20, 22, 24), and USNM 2782, 50598 but the distal gynoecial zone is most complete in IU 15726-4419 (Figs. 27, 28). The two specimens from Texas show slight differences from the Kansas specimens, for example IU 15726-4419 has straighter follicles, and the very short cylindrical portion of the receptacle preserved in USNM 326817 shows no sign of laminar flaps. However, the evidence to separate these two specimens is weak and we include them with the Kansas material of *L. elocata*.

The gynoecial zone of IU 15726-4419 is slightly compressed laterally from what we assume was originally a symmetrical rounded cone but merges gradually at the base with the zone below (Figs. 27, 28, 30). In UKDSC 203 and USNM 50598 the transition into the cylindrical portion of the receptacle is more abrupt (Figs. 2, 3).

The cylindrical portion of the receptacle is probably equivalent to the "cylindrical scaly pedicel" mentioned by Lesquereux (1892). The bases of these flaps, which produce the characteristic diamond-shaped pattern on the receptacle, change in size and shape from the apex to the base (Figs. 7, 22), but the transition is gradual. In UKDSC 203 the receptacle is interrupted approximately in the middle of this zone and was blocked by a small plug of sandstone that must have penetrated through a line of weakness in the rotting receptacle relatively early in fossilization (Fig. 7).

The impressions formed in the matrix by the flaps gradually become thinner away from their attachment, and there is no indication of a regular abscission layer (Fig. 7). We imagine that the flaps were persistent and rotted or withered while still attached to the receptacle. A few of the flaps on PMNH 2405 show a weak adaxial keel at their base. Their morphology is otherwise unclear and they show no sign either of pollen sacs or venation (Figs. 18, 21, 42B, C). We do not know their original size or shape, but certainly those immediately below the flower were substantial and formed a prominent collar around the base of the gynoecium (Figs. 18, 20, 22, 42A). The largest collar of persistent flaps is seen in

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receptacle immediately below the follicles; ×3.—31. Detail of Figure 28 showing longitudinal fracture through three follicles. Note locule casts (K), very short constrictions forming the stalk (L) and the expanded follicle bases (M); ×6.—32. Detail of Figure 27 showing molds of expanded follicle bases; ×4.

PMNH 2405, but smaller flaps occur in USNM 50598, IU 15726-4419 (Fig. 26), and UKDSC 203 (Fig. 7). A specimen figured by Lesquereux (1892, pl. 2, fig. 9a) may be the base of the gynoecial zone, and its collar of persistent flaps, seen from below.

The transition that the bases of the flaps exhibit along the receptacle could reflect a gradual change in the size and shape of the lamina. Two interpretations seem possible to us: either there was a gradual transition between two kinds of perianth parts, or a transition from stamens with broad laminar filaments to tepals. We have no data to favor one explanation over the other and have seen no evidence of pollen sacs on the upper flaps. A bisexual flower would be more consistent with our interpretation of the systematic affinities of *Lesqueria* based on the number and arrangement of the carpels. Unisexuality is relatively uncommon among living plants with polycarpic flowers, but this possibility cannot be excluded.

The expanded bases of the follicles, the short stalks, and their attachment to the receptacle are best seen in IU 15726-4419, which clearly shows them arranged in helices (Figs. 27, 28, 31, 32). The follicle bases are similar in PMNH 2405 but less well preserved. Other details of the follicles are well preserved in UKDSC 203 (Figs. 4–6, 9) although the apices are also seen in USNM 2782, 50598, 326817, FM-P3056 (Fig. 16), and PMNH 2405 (Figs. 15, 17). These specimens show narrow bilobed terminal prolongations of the follicles that probably correspond to the 'bristles' mentioned and figured by Lesquereux (1892, pl. 2, fig. 9). In a few follicles the extreme apex of each style-like prolongation is slightly expanded, and it is possible that this swelling, and perhaps also the adaxial crest, may have been stigmatic. The two style-like prolongations occur in both dehisced and non-dehisced follicles so we discount the idea that they are formed by splitting of a single elongated style at maturity.

In dehisced follicles the matrix penetrated through the open adaxial suture and also distally between the two apical prolongations (Fig. 9). Where a complete cast of the locule is formed in this way, both internal and external features of the follicle and the thickness of the follicle wall can be interpreted (Fig. 9). Two follicles on UKDSC 203 show irregular holes in the locule fill arranged in a single line on either side of the median plane (Figs. 10, 42G). They are slanted from proximal to distal, adaxially to abaxially, and we interpret these as molds of seeds. We estimate there would have been approximately ten to 20 seeds in each follicle. In his original description of the species Lesquereux (1892) mentioned transverse undulations in some follicles that may also reflect the positions of seeds. In USNM 326817, the cast of the inner locule surface shows a distinctive rugulate-striate pattern oriented proximally to distally, adaxially to abaxially, but in all other specimens the locule surface is smooth. Reconstructions of the *Lesqueria* follicles are given in Figure 42E–G.

In his discussion of *W. hespera* Wieland (1928: 46) mentioned "three scale-like bodies about each sporophyll or unit." Each of these sporophylls is equivalent to what we interpret as follicles. We have seen no good evidence of any organs at the base of each follicle but the cavities that Wieland interpreted as 'scale-like bodies' are visible on FM-P3056, and in his original specimen PMNH 2405 (Figs. 15, 16). In our view these cavities are spaces remaining between the follicles that were not filled by either sand or mineral deposition during fossilization, and they are quite different from the cavities formed as molds around the plant tissues. In places mineralization seems to have followed the plant surfaces but did not completely fill the cavities between them, particularly where no sand had penetrated. Similar cavities occur occasionally between the two terminal prolongations of the follicles, an unlikely position for scales. Where they occur, these cavities are irregularly arranged and are completely absent from USNM 2782, 50598, and UKDSC 203.

COMPARISON WITH FOSSIL PLANTS

Although the holotype of *Williamsonia elocata* Lesq. is lost, from the original description and illustration we have no hesitation in assigning our specimens to this species and establishing UKDSC 203 from the same geological formation and the same geographical area as a neotype. *Williamsonia hespera* Wieland (1928) and *Isoetites* sp. (Brown, 1958) are clearly the same species. Seward (1917) and Wieland (1928) questioned the assignment of *W. elocata* and *W. hespera* respectively to the genus *Williamsonia*. We confirm their opinions and have no doubt that both species belong neither in *Williamsonia* nor the Bennettitales. The structures at the apex of the receptacle are follicles with a distinct longitudinal adaxial suture and contain seeds. In *Williamsonia* we would expect 'interseminal' scales among stalked ovules, with bracts ('perianth') below (Harris, 1969). In our view *Lesqueria elocata* is clearly a multifollicular angiosperm fruit.

The reassignment of "*Williamsonia*" *elocata* to the angiosperms calls into question the relationship of other poorly understood Cretaceous *Williamsonia*-like plant organs for example: *Palaeanthus hollickii* Seward & Conway (1935a) from the Upper Cretaceous of Kingigtock, West Greenland; *Palaeanthus tenuistriatus* Seward & Conway (1935b) from the Upper Cretaceous of Igdlokunguak in the same area; *Palaeanthus* sp. Seward & Edwards (1941) from the Palaeocene of Kangerdlugssuak, East Greenland; *Palaeanthus prindlei* Hollick (1936) from the Palaeocene of Alaska; *Williamsonia cretacea* Heer (1880) from the Upper Cretaceous of Atanikerdluk, West Greenland; *Williamsonia reisii* Hollick (1906; Leppik, 1963) from the Upper Cretaceous of Staten Island; *Williamsonia delawarensis* Berry (1916) from the Upper Cretaceous of Maryland; *Velenovskia opatovicensis* Knobloch (1974) from the Cenomanian of Czechoslovakia; and many other poorly known species that might be interpreted as angiosperms just as easily as bennettitaleans on the data available. We have seen none of the original specimens, but these and similar species would be worth reexamining. We have, however, examined specimens of two *Williamsonia*-like fossils, *Williamsonia*? *recentior* Dawson and the type species of *Palaeanthus, P. problematicus* Newb.

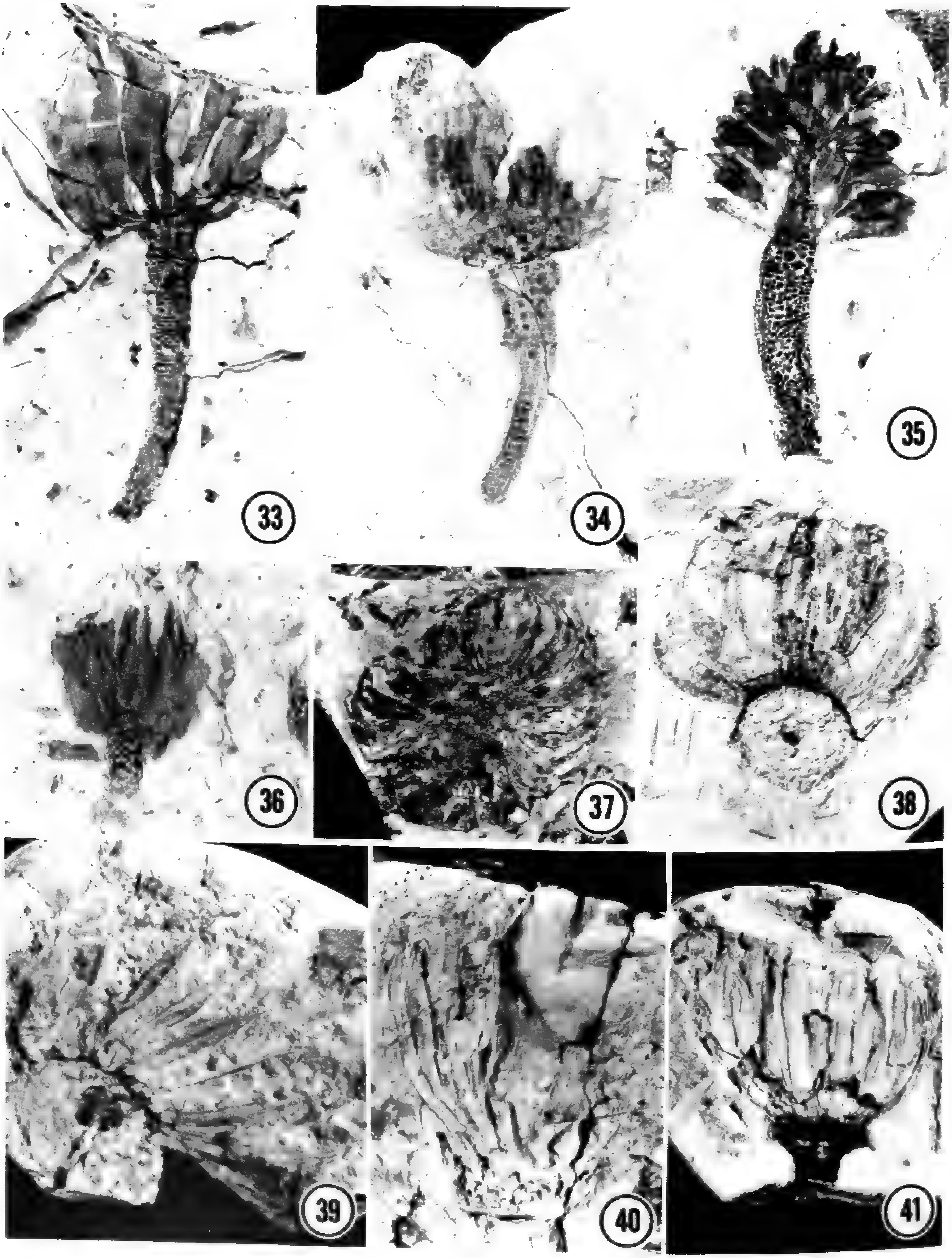
Williamsonia? *recentior* Dawson (1886; Seward, 1917; Bell, 1956) is from the 'Upper Blairmore Flora' of southwestern Alberta, generally accepted as of Albian age (Glaister, 1959; Norris, 1964; Rudkin, 1964; Mellon, 1967; Price & Mountjoy, 1970; Stelk, 1975; Stott, 1975; and Singh, 1975). The holotype of the species (Fig. 37) is preserved as a compression in an indurated grey shale. It shows a head of numerous, apparently helically arranged, follicles with indications of scars below. The follicles show curvature similar to those of *Lesqueria*. We estimate that the gynoecial zone bore about 150 to 200 follicles. The general appearance of the head (but not of the remainder of the receptacle) is similar to *L. elocata*. The scars and remainder of the receptacle are more similar to *Archaeanthus linnenbergi* (Dilcher & Crane, 1984).

The original material of *Palaeanthus problematicus* described by Newberry (1886, 1895) is from the Amboy Clays (Raritan Formation) of New Jersey, which are generally regarded as of Middle to Upper Cenomanian age (Christopher, 1979 and references cited therein). We have not seen the specimens described later from Gay Head, Martha's Vineyard (Hollick, 1896, 1906) and Glen Cove, Long Island (Hollick, 1912) but from the illustrations judge that they may be a different taxon. The specimens from New Jersey (Figs. 38–41) are preserved in a grey micaceous silty-clay, and although organic material may once have been present, most of it is now missing. However, the impressions show heads of about 50 to 80 follicles, some with a longitudinal adaxial suture; these are surrounded by another zone of more or less linear, to narrowly triangular, structures. Two of the best of these structures on one specimen (New York Botanical Garden, 11420G, now at PMNH) show a prominent bilobed expansion at the apex. Several authors have discussed the botanical relationships of *P. problematicus* (Newberry, 1895; Stebbins, 1940; Cronquist, 1955) and suggestions for closest relatives have ranged from *Williamsonia* to the Compositae. In our view, *P. problematicus* is an angiosperm fruit of many follicles and is very similar to material collected from the Dakota Formation of Hoisington, Barton County, central Kansas (IU 15706) (Figs. 33, 34, 36). One specimen from Hoisington (Fig. 35) is more similar to *Archaeanthus linnenbergeri* (Dilcher & Crane, 1984). *Liriophyllum* leaves, probably belonging to the *Archaeanthus* plant, also occur at the Hoisington locality.

Palaeanthus problematicus and "*Williamsonia*" *recentior* taken in conjunction with *Lesqueria elocata* and *Archaeanthus linnenbergeri* unambiguously demonstrate the diversity and ubiquity of polycarpic flowers among mid-Cretaceous early angiosperms.

COMPARISON WITH RECENT PLANTS

Among Recent angiosperms, *Lesqueria* is most similar to polycarpic taxa, most of which occur in the Magnoliidae. The *Lesqueria* head of follicles most closely resembles those of *Magnelietia* (Magnoliaceae; Canright, 1960) and *Talauma* (Magnoliaceae). *Magnelietia hainanensis* has a tight ovoid cluster of carpels borne on a swollen distal portion of the receptacle. The receptacle in *Himantandra* is similar but much smaller. In *Talauma* (Fig. 46) the cluster of carpels at flowering stage is very similar to the head of follicles in *Lesqueria*. *Annona, Dugetia* (Figs. 43, 44) (Annonaceae; Fries, 1931, 1934), and *Schizandra* (Smith, 1947) also show tight clusters of car-



FIGURES 33–41. Mid-Cretaceous angiosperm fruits showing clusters of follicles. 33–36. Unnamed specimens from the Dakota Formation, central Kansas. 37. "*Williamsonia*" *recentior* Dawson from the Blairmore Group (Albian) of Alberta. 38–41. *Palaeanthus problematicus* Newberry from the Amboy Clays (Raritan—middle to late Cenomanian of New Jersey).—33. IU 15706-3078; ×1.—34. IU 15706-3077; ×1.—35. IU 15706-3084; ×0.5.—36. IU 15706-3083; ×1.—37. Geological Survey of Canada 5105; ×1.—38. New York Botanical Garden (NYBG) *s.n.*; ×1.—39. NYBG 11447G, Newberry (1895, pl. 35, fig. 7); ×1.—40. NYBG 11420G, Newberry (1895, pl. 35, fig. 6); ×1.—41. NYBG *s.n.*, Newberry (1895, pl. 35, fig. 2); ×1.

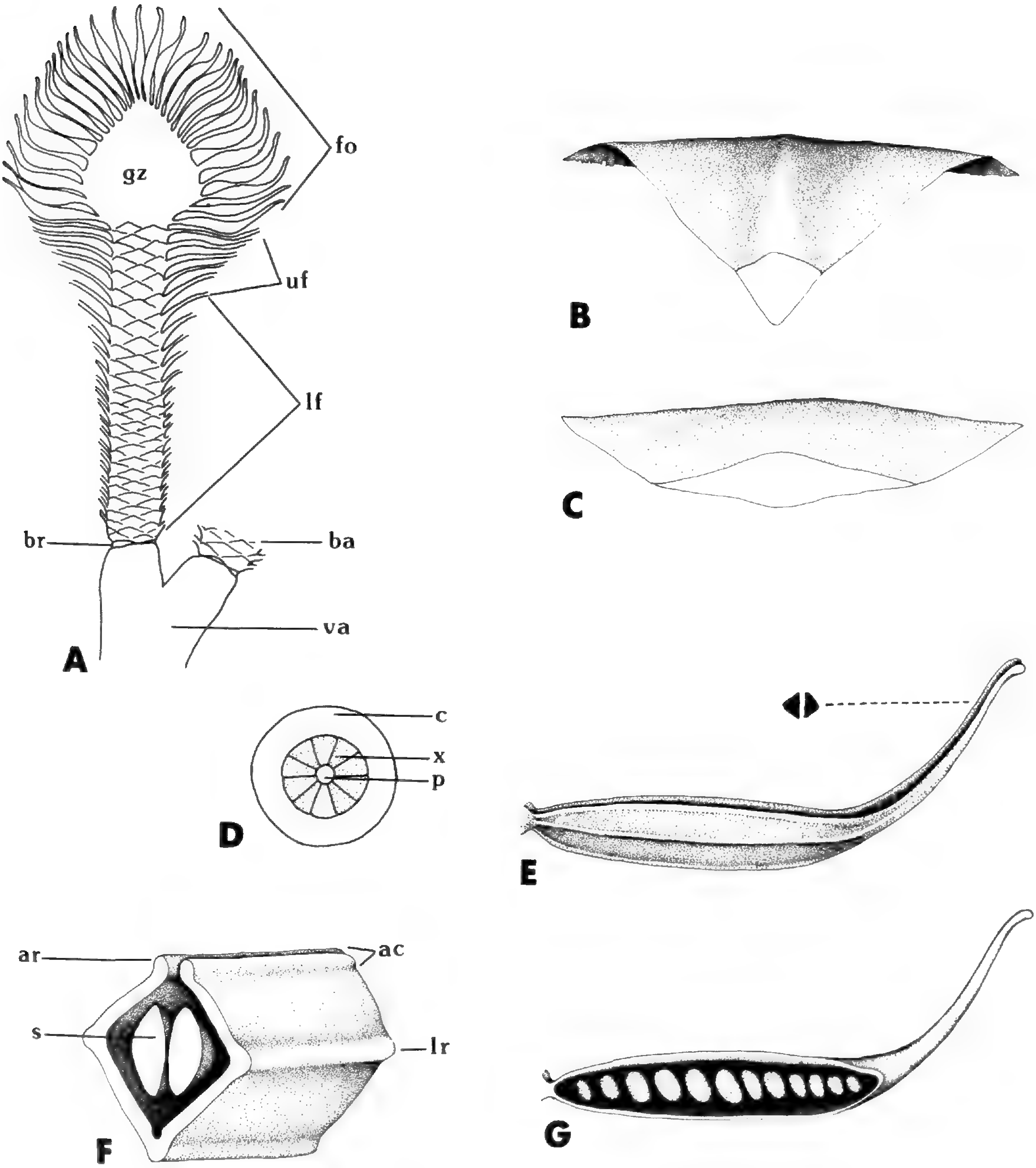
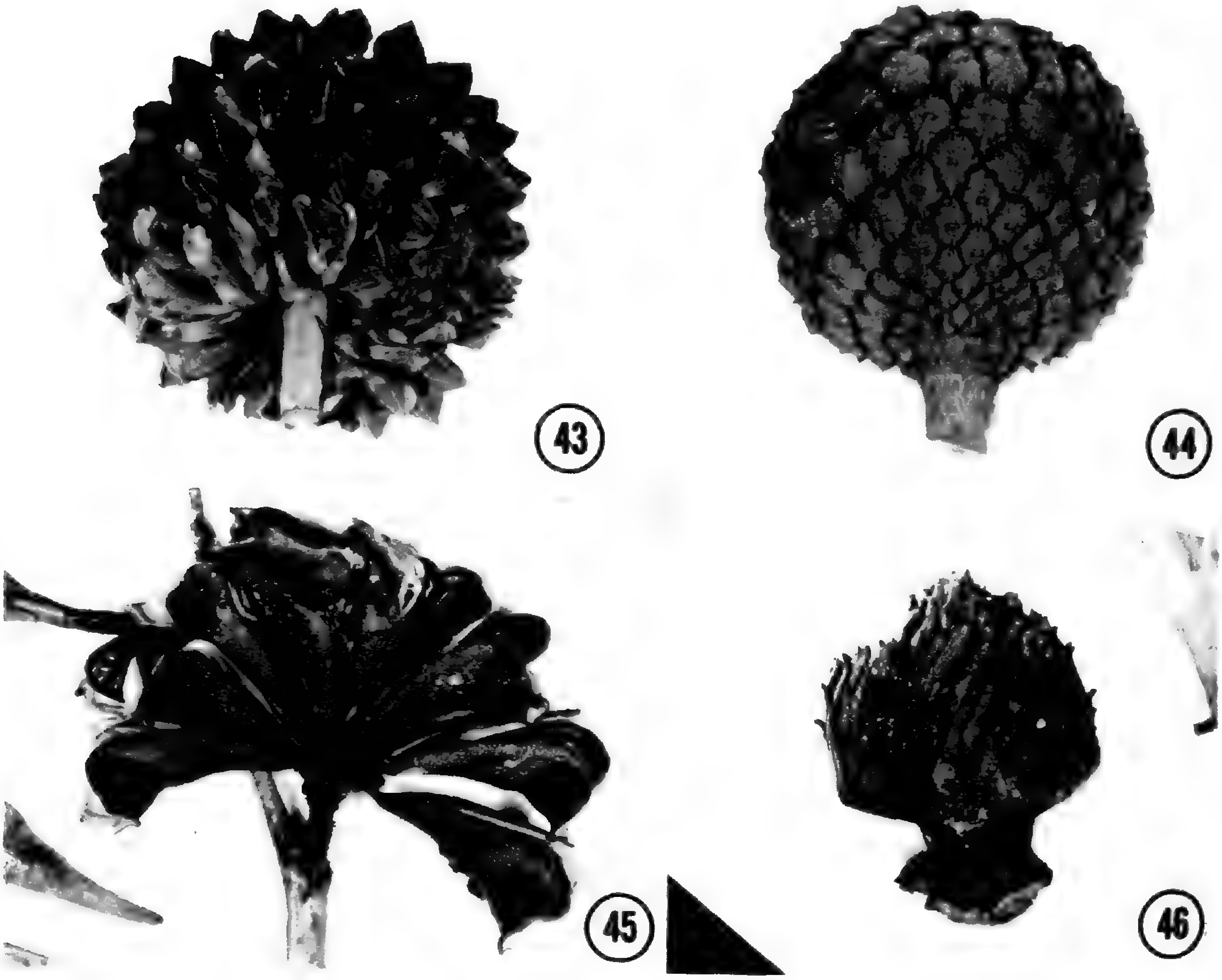


FIGURE 42. *Lesqueria elocata* Crane & Dilchor, comb. nov.—A. Diagram of the *Lesqueria* receptacle and attached organs: fo, tight clusters of follicles; gz, swollen gynoecial zone of the receptacle; uf, upper flaps forming a collar; lf, lower flaps; br, constriction at the base of the receptacle; ba, broken base of another receptacle; va, vegetative axis.—B. Drawing of an upper flap in the collar region removed from the receptacle.—C. Drawing of lower flap removed from the receptacle.—D. Diagram showing the anatomical structure of the receptacle base: c, cortex; x, xylem; p, pith.—E. Reconstruction of a single follicle.—F. Section through follicle: ac, adaxial crest; ar, abaxial ridge; lr, lateral ridge; s, seed.—G. Diagrammatic median longitudinal section of a single follicle showing position of seeds.

pels, but in *Schizandra* the receptacle elongates dramatically at maturity. None of these genera, however, have the gynoecial zone at the apex of a long cylindrical receptacle, such as occurs in *Lesqueria*. All, however, are bisexual and would be consistent with an interpretation of the persistent upper flaps in *Lesqueria* as stamens. Whatever the botanical nature of these flaps,



FIGURES 43–46. Fruits of Recent plants with numerous follicles. MO, herbarium of the Missouri Botanical Garden.—43. *Dugetia uniflora* (Dun.) Mart., Brazil, MO 2765089; ×1.—44. *Dugetia cordata* R. E. Fries, Brazil, MO 2873354; ×1.—45. *Anaxagorea* sp., Venezuela, MO 2726969; ×1.—46. Young multifollicle of *Talauma* sp., Panama, MO 2778717; ×1.

gradual transitions between different floral organs are common in plants with numerous floral parts. Gradual transitions of stamens into tepals occur, for example, in *Eupomatia, Paeonia,* and the nymphaeaceous genera *Euryale, Nymphaea,* and *Victoria* (Moseley, 1958). However, we know of no Recent angiosperm in which the length of the non-gynoecial portion of the receptacle is as elongated as it is in *Lesqueria.* Another unusual feature is the persistence of the flap-like floral organs below the follicles. Many parallels exist in the Magnoliidae, however, for the clustered arrangement of flowers in *Lesqueria.* The irregular cymose inflorescences of some Annonaceae, for example, are quite similar.

The double follicle tip in *Lesqueria* is similar to the double style of *Austrobaileya* (Endress, 1980) and *Goniothalamus* (Annonaceae). The fruits of these genera are not follicles, however, and the two styles do not persist to fruit maturity.

Although it is clear from this brief review that some Magnoliidae have various features that are similar to those of *Lesqueria,* we know of no Recent plant that has the combination of numerous, helically arranged, dehiscent follicles with bifid tips borne in a swollen head at the apex of a long receptacle bearing numerous, persistent, spirally arranged, laminar structures. Further comparison of *Lesqueria* with Recent angiosperms is limited by lack of knowledge of other parts of the plant, including wood, leaves, staminate floral parts, and particularly by the uncertainties over the interpretation of the laminar flaps. However, it is clear that *Lesqueria* is a fruit comprised of many follicles and that the *Lesqueria* plant is an extinct angiosperm, probably most closely related to the magnolialean group of the Magnoliidae.

CONCLUSIONS—EVOLUTIONARY SIGNIFICANCE

Lesqueria elocata contributes significantly to our knowledge of the reproductive diversity of early flowering plants. Along with *Archaeanthus* (Dilcher & Crane, 1984), *Palaeanthus proble-*

maticus, and "*Williamsonia*" *recentior,* it demonstrates that the basic floral organization, consisting of numerous, adaxially dehiscent, follicles borne helically on the distal part of a receptacle with another floral organ(s) below, was widespread and common at an early stage in angiosperm evolution. These plants also illustrate the diversity that magnoliid plants had attained some ten to 15 Ma after the first apparently unequivocal angiosperm leaves and pollen appear in the fossil record (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Doyle, 1978; Hughes et al., 1979). Today the Magnoliidae are extremely diverse and heterogeneous, exhibiting various mosaics of primitive and advanced characters (Takhtajan, 1969; Cronquist, 1981). The fossil evidence from *Archaeanthus, Lesqueria, Palaeanthus problematicus,* "*Williamsonia*" *recentior,* and other material suggests that the Magnoliidae were also diverse during the mid-Cretaceous. Extinction of some of the mid-Cretaceous magnoliid diversity may well account for some of the large morphological gaps that separate the Recent genera and families in this group.

It is important to recognize that these magnoliid flowers occur contemporaneously with other very different kinds of angiosperms, including bisexual, unisexual, and evidently insect and wind pollinated forms (Dilcher, 1979; Vakhrameev & Krassilov, 1979; Retallack & Dilcher, 1981; Dilcher & Crane, 1984). However the mid-Cretaceous magnoliids are of particular interest in relation to concepts of the primitive angiosperm flower. The current, most widely accepted view, based almost entirely on comparative studies of living plants, is that the Magnoliidae, and in particular the Magnoliales, are the most primitive living group, and that the primitive angiosperm flower was of generalized magnoliid construction (Bessey, 1897; Arber & Parkin, 1907; Bessey, 1915; Cronquist, 1968; Takhtajan, 1969; Hutchinson, 1973; Cronquist, 1981). The hypothetical primitive flower is envisaged as radially symmetrical, bisexual, and entomophilous. The receptacle would have been elongated, bearing numerous helically arranged, undifferentiated perianth parts, numerous laminar stamens, and numerous free, conduplicate carpels that dehisced at maturity along an adaxial suture. The carpels would have contained numerous ovules that developed into many large seeds (Takhtajan, 1969). Although no known fossil plant shows precisely this hypothetical combination of characters, *Lesqueria, Archaeanthus, Palaeanthus problematicus,* and "*Williamsonia*" *recentior* conclusively establish that some of these allegedly primitive features are also ancient.

FIGURE 47. Reconstruction of the *Lesqueria elocata* fruiting axis.

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PRELIMINARY REPORT OF UPPER CRETACEOUS ANGIOSPERM REPRODUCTIVE ORGANS FROM SWEDEN AND THEIR LEVEL OF ORGANIZATION[1]

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ABSTRACT

Well-preserved fossil angiosperm reproductive organs from the Upper Cretaceous of Sweden provide increased knowledge of structure and evolutionary relationships of Cretaceous angiosperms. The material includes a diverse assemblage of angiosperm flowers, fruits, seeds, and anthers representing more than 100 taxa. This paper focuses on the level of organization of the reproductive organs with special attention directed to the various types of flowers. The flowers are all very small, usually actinomorphic and bisexual. The position of the perianth is hypogynous or, more commonly, epigynous. Some of the flowers are of simple construction with only one whorl of perianth parts, apparently adapted to wind-pollination. Others have well-developed calyx and corolla, sometimes together with the presence of a disk, suggesting adaption to insect-pollination. A number of floral diagrams are presented for the fossil flowers of Sweden, and their systematical position is discussed.

Theories of evolutionary relationships within the angiosperms are largely based on comparative studies of the flower structure. The study of fossil flowers is therefore essential to the understanding of the origin and evolution of the angiosperms. However, angiosperm flowers are rare in the fossil record, and less than 200 species have been described so far.

The amount of information obtainable from these fossils is variable, depending largely on the mode of preservation. Floral structures and arrangement of parts are best studied in three-dimensionally preserved flowers, but few flowers are known in this state of preservation. Plant material usually has collapsed in varying degree during incorporation into sediments and so becomes preserved as compressions or, if completely decayed, as impressions. Such material usually yields very incomplete information on the floral details, but the recent application of transfer techniques and electron microscopy has revealed the considerable potential for studies of compressed flowers such as those from the Eocene of North America (Crepet & Dilcher, 1977; Crepet & Daghlian, 1980; Crepet et al., 1980; Daghlian et al., 1980).

The majority of fossil flowers are known from Tertiary deposits, and only about 20 different species have been described from the Cretaceous. The most important source of information on Tertiary fossil flowers is probably the Paleogene Baltic Amber, which accounts for about one-third of the known record. Owing to the amorphous texture of the amber and that it was fluid at the time of incorporation of the fossils, very fine details have been preserved (Goeppert & Berendt, 1845; Caspary, 1872, 1881a, 1881b; Conwentz, 1886; Larsson, 1978). The amber fossils are strictly molds, with very little organic material remaining, and thus anatomical details are scarce. Because of extensive information existing on the morphology and the structure of the fossils, however, it has been possible to establish the botanical affinity for a large proportion of the amber flowers (Conwentz, 1886).

Anatomical information is usually obtainable from petrifactions, but reconstructions of arrangement of parts may be surprisingly problematic, and establishment of the botanical affinity is often uncertain. One of the few petrified flowers is *Palaeorosa similkameensis* Basinger (1976) from the Eocene of British Columbia. This is

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probably the most fully known of these petrified structures. Few other species were described from the Intertrappean beds in Deccan, India, probably of Eocene age (Shukla, 1944; Prakash, 1956; Chitaley & Patel, 1975, for example). *Cretovarium japonicum* Stopes & Fujii (1911) is imperfectly preserved but is significant in being the only petrified floral structure described from the Cretaceous.

No fossil angiospermous flowers have been described yet from the Lower Cretaceous, but from fossil fructifications we know that reproductive structures were diverse by the late early Cretaceous (Dilcher et al., 1976; Dilcher, 1979; Vachrameev & Krassilov, 1979). In the early Upper Cretaceous (Cenomanian) the diversity is documented by fruiting as well as floral structures from Europe (Velenovský, 1889; Bayer, 1914; Velenovský & Viniklář, 1926, 1927, 1929, 1931) and from North America (Dilcher, 1979; Dilcher & Basinger, 1980; Dilcher & Crane, 1984; Crane & Dilcher, 1984).

From the Uppermost Cretaceous (Senonian), small angiosperm flowers have recently been discovered from eastern North America (Tiffney, 1982 and pers. comm.; Hueber, pers. comm.) and from Scania, southern Sweden (Friis & Skarby, 1981, 1982; Friis, 1983). This review is an attempt to illustrate the diversity in structure of the Upper Cretaceous angiosperms based on the study of the well-preserved Swedish material. Special attention is directed to the various organizational levels of the fossil flowers, and floral diagrams of the main basic types are presented (Figs. 1–9). Although the taxonomic study of the Swedish material is still at an early stage, it has been possible to demonstrate relationships between some of the fossil taxa and modern plant groups at the family or ordinal level.

MATERIAL

The angiosperm fossils described here were collected from the upper part of the fluviatile sequence in Höganäs AB's clay pit at Åsen, southern Sweden. The age of the sediments is probably Upper Santonian or Lower Campanian (Friis & Skarby, 1982).

The fossils were obtained from unconsolidated clays and sands by sieving in water. They were then cleaned in hydrofluoric and hydrochloric acid.

The material comprises a diverse assemblage of leaf fragments, twigs, megaspores, sporangia, flowers, fruits, seeds, and anthers (Friis & Skarby, 1981, 1982; Friis, 1983). The majority of fossils represents angiospermous plants, and more than 100 taxa have so far been recognized. The commonest of the angiosperm fossils are fruits and seeds, but the floral structures also constitute an important element of the flora.

The fossils are mainly preserved as three-dimensional charcoal fossils, probably formed as a result of a forest fire (Friis & Skarby, 1981). Their excellent preservation allows detailed study of arrangement of parts. However, the material shows certain limitations. The fossil flowers are generally found isolated from the rest of the plant and the orientation and inflorescence structure is thus unknown. The lack of parts in some flowers may be primary, but could also be caused by shedding before fossilization. Very delicate or protruding parts such as stamens and petals may be broken in open flowers and the study of such parts is often referred to fragments or scars or to flower buds when present. In spite of these limitations, the material yields useful information on the organization of the flower structure reached by the uppermost Cretaceous and represents a significant addition to the known record of angiosperm flowers.

DIMENSIONS OF THE ANGIOSPERM FOSSILS FROM SWEDEN

The fossil angiosperm flowers, fruits, and seeds from Åsen are all of small size, the largest flower being about 4 mm long, and the dimensions of the fruits and seeds range from 0.2 to 5 mm. No fragments of larger fruits and seeds have been observed among the fossils, but larger fragments of twigs and wood are common in some samples. The size distribution of the fossils is apparently independent of the texture of the sediment and the absence of larger fruits and seeds cannot be explained by sorting.

The small size of the Swedish fossils is consistent with the dimensions quoted for fruits and seeds of most other Upper Cretaceous floras of Europe (Vangerow, 1954; Knobloch, 1964, 1971, 1977; Colin, 1973; Jung et al., 1978), Greenland (Miner, 1935), and North America (Schemel, 1950; Hall, 1963). A few fossil floras including large angiosperm fruits and seeds have been reported from the Cenomanian of Europe (Velenovský & Viniklář, 1926) and North America

(Dilcher, 1979), and from the Upper Campanian or Maastrichtian of Africa (Monteillet & Lappartient, 1981).

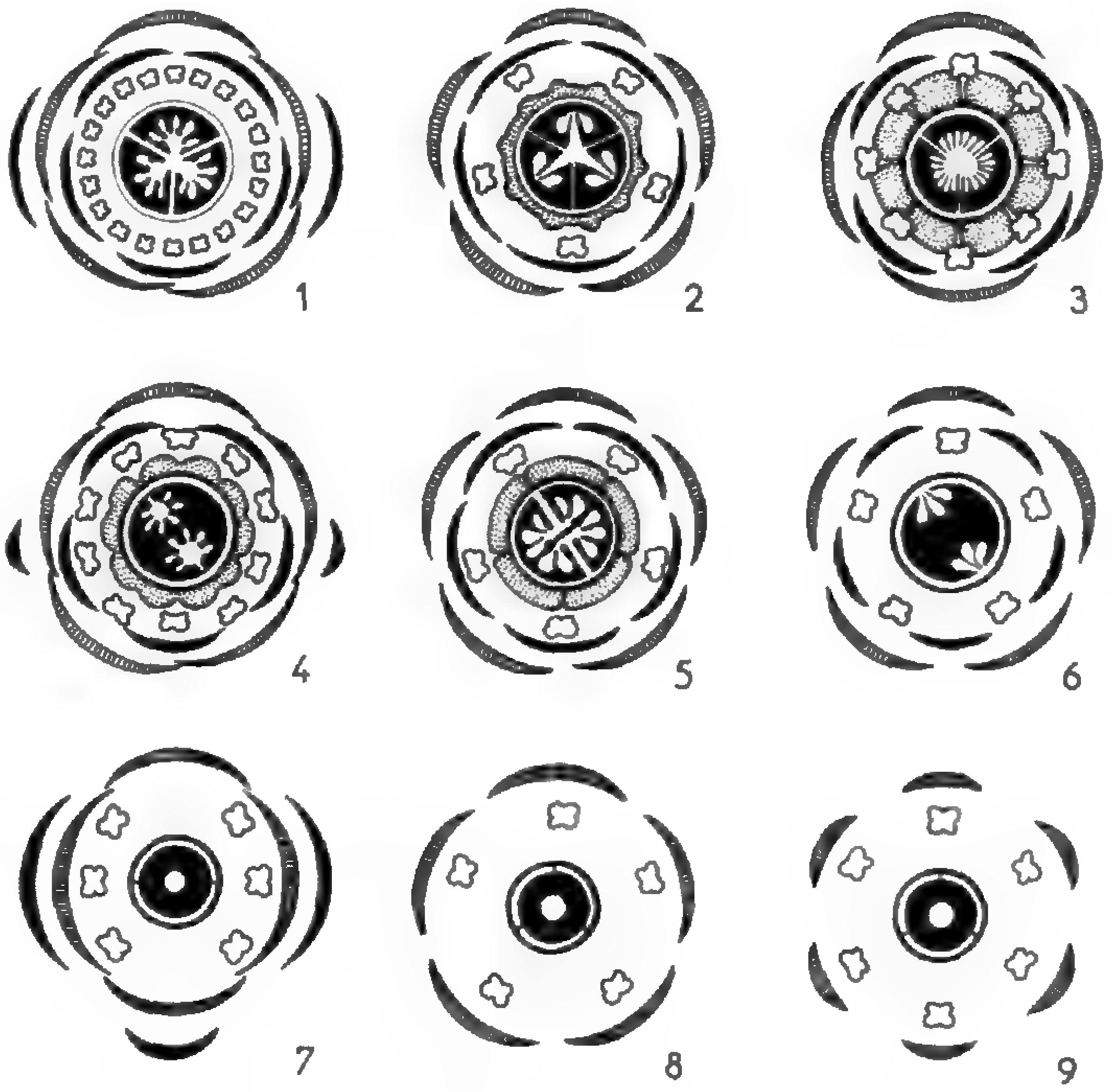
In Recent plants very small seeds are characteristic of epiphytes, saprophytes, and parasites. Small seeds are also common among herbs as well as woody plants inhabiting open country and are especially common in plants of early stages in vegetation succession (Harper et al., 1970; Stebbins, 1974). It is possible that the small size of the fossil fruits and seeds in many of the Cretaceous floras might be explained by paleoecological conditions. However, a number of other factors should also be considered (see Tiffney, 1984).

Level of Organization of the Fossil Flowers from Sweden

The Swedish material includes more than 20 different floral structures. The fossil flowers are apparently all bisexual and cyclic with a definite number of parts in each whorl. The perianth is well developed in the majority of the flowers, differentiated into calyx and corolla (heterochlamydous), or consisting of only one perianth whorl (monochlamydous). A single fossil flower type is apparently naked (achlamydous or apochlamydous). The position of the perianth is hypogynous or more commonly epigynous. A variety of fruit types has been recognized, including follicles, capsules, nuts, and drupes. There is a great diversity in number of locules, placentation, and number of seeds. The vast majority of the seeds are anatropous. So far only a few orthotropous and amphitropous taxa have been found. The seed coat varies from a thin membraneous layer, apparently formed from one integument, to a thick, sclerenchymatous wall formed from one or two integuments.

Some of the basic floral types found in the Swedish material are described below more closely, including, if possible, description of fruits and seeds; the organizational level of the different flowers is illustrated with floral diagrams, and their systematical position is discussed.

1. Heterochlamydous flowers. Flowers with well-developed calyx and corolla are the most common among the Swedish floral structures. They are all actinomorphic, including hypogynous as well as epigynous flowers. The sepals and petals are generally free, but in a few flowers the sepals are fused at the bases. Some of the flowers bear a disk and were probably nectar producing, adapted to insect-pollination. The flowers are generally pentamerous (Figs. 1, 2, 4–6). One flower type differs in being tetramerous (Fig. 3), and a small triangular fruit with persistent calyx indicates that also trimerous floral types were present.



Figures 1–9. Floral diagrams of the basic floral types found among the Upper Cretaceous fossils from Åsen, Sweden.—1–2. Heterochlamydous, hypogynous flowers.—3–6. Heterochlamydous, epigynous flowers.—7–9. Monochlamydous, epigynous flowers.

1.1. Hypogynous flowers with multistaminal androecium. One fossil genus including hypogynous flowers with a multistaminal androecium has been recovered among the Swedish fossils (Figs. 1, 10–13). It is represented mostly by fragmentary specimens. The flowers are small, about 4 mm long, borne on a thick peduncle. There are two thick bracteoles, five free, coriaceous sepals (Figs. 12, 13), and five free petals. The androecium is composed of 20 stamens in one whorl. The filaments are broad with slightly narrowing bases and a pronounced contraction at the apex. The anthers are elongated and almost as long as the filaments; they are apparently ventrifixed and open by longitudinal slits (Fig. 11). The surface of the anthers has distinctive epidermal cells and short, spiny hairs (Fig. 11). None of the anthers have pollen preserved. The ovary is superior and three-loculed (Fig. 13), formed by three carpels and with three free styles. The surface of the ovary is covered with densely spaced, stiff hairs.

Each locule contains many ovules on pronounced, axile placentae. The characters of the fossil flowers seem to indicate a relationship with modern plants of the Theales, such as members of the Ternstroemioideae (Theaceae).

Three-loculed capsules with a hairy surface, similar to that of the ovary in the fossil flowers, may represent the mature fruits of similar flowers. They enclose many small seeds. The same seed type is very common in the samples from Åsen, found separate from the fruits. The seeds are about 1 mm long, anatropous, with a distinct raphe, micropyle, and chalaza (Figs. 18–20). The seed coat is composed of two layers of cells. The outer epidermis is built of thick-walled cells with strongly pitted cell walls. Several different species, probably referable to a single genus, have been recognized. The species may be distinguished from each other by the size and shape of the surface cells, the number of cell rows, and the thickness of the seed coat. Two different species are shown in Figures 18 and 20. The organization and structure of the fossil fruits and seeds also seem to indicate a relationship with some modern Theaceae. Although campylotropous or amphitropous seeds are the most common seed type among modern Theaceae, anatropous seeds are found in some genera. The outer epidermis of the seed coat in many modern Theaceae is similar to that seen in the fossil seeds in having thickened and strongly pitted cell walls.

Another group of seeds possibly related to the Theaceae has been recovered among the Swedish fossils. The seeds are anatropous and about 1.5 mm long. The raphe is embedded in the sclerotic mesotesta (Fig. 22). The embryo cavity is elongated ellipsoidal in shape, marked on the outer surface by distinct cell rows (Fig. 21). The inner layer of testa consists of lignified cells with angular lumina, which suggests that they once contained inorganic crystals. Similar seed types also occur in the Lythraceae, but the fossil seems to differ from members of this family by the lack of a fibrous inner layer.

1.2. Hypogynous flowers with haplostemonous androecium. A few other hypogynous, pentamerous floral structures are present in the fossil flora, but they are mostly incompletely preserved, and reconstructions of the complete structures have not yet been possible. One of these flowers is shown in Figures 16 and 17. It has five elongated, coriaceous sepals, fused in the basal part, and apparently five petals and five stamens. The ovary is composed of three fused carpels and there are three pronounced, plate-like placentae with many anatropous ovules. At

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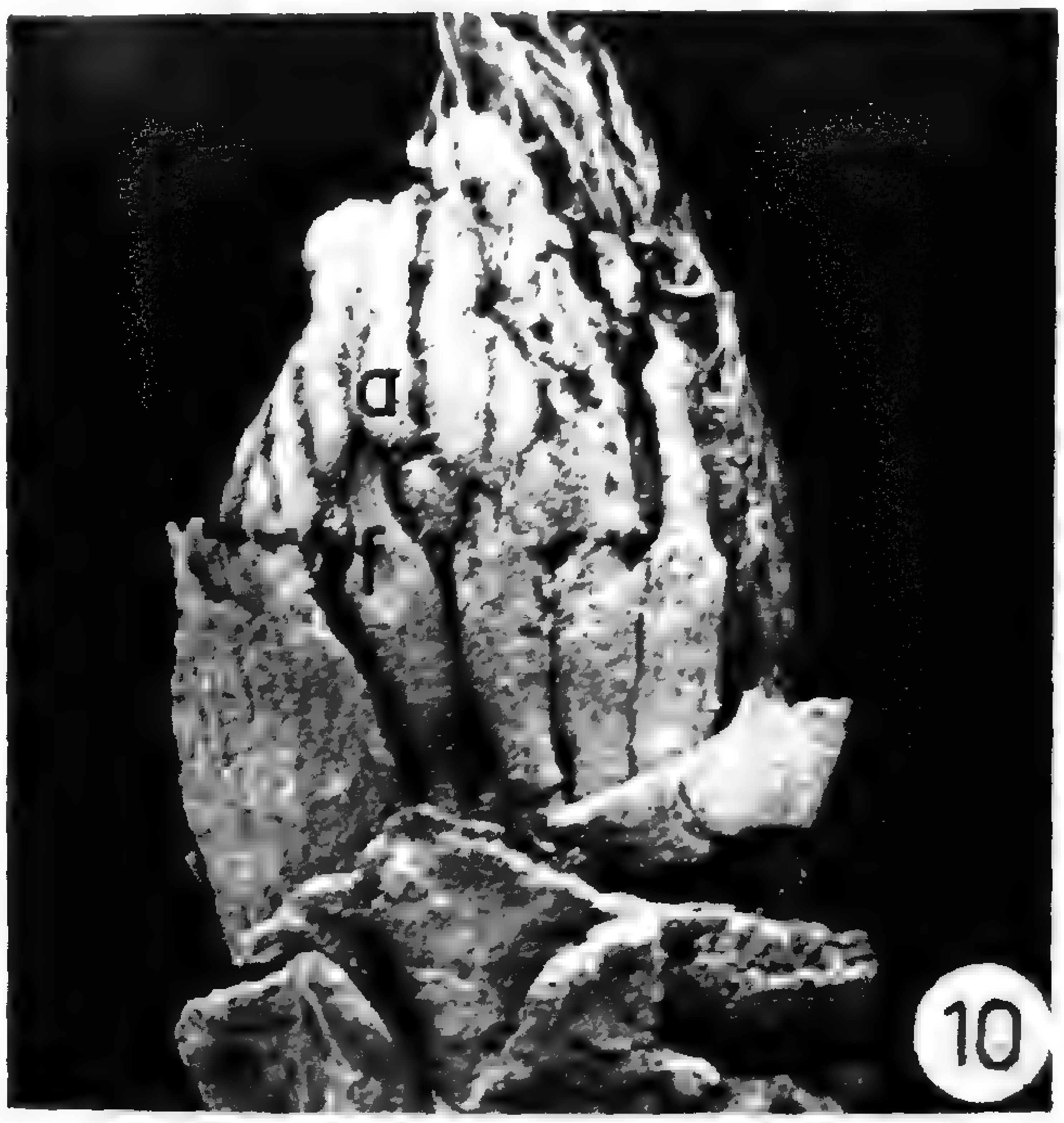
FIGURES 10–15. Fossil flowers from the Upper Cretaceous of Sweden. 10–13. Heterochlamydous, hypogynous flower with multistaminal androecium (floral diagram see Fig. 1).—10. Flower with stamens preserved (a = anther, f = filament); SEM-136$_1$, ×40.—11. Stamens enlarged showing hairy surface of anthers, ×175.—12. Flower with ovary partly preserved showing coriaceous sepals and bracts; SEM-202, ×25.—13. Ovary enlarged showing three locules and many ovules; same specimen as Figure 12, ×45.—14. Small perigynous flower with hairy ovary and three stigmas preserved; SEM-209$_3$, ×70.—15. Pollen from surface of ovary; same specimen as Figure 14, ×3,500.

FIGURES 16–22. Fossil flowers and seeds from the Upper Cretaceous of Sweden. 16–17. Heterochlamydous and hypogynous flower with haplostemonous androecium (floral diagram see Fig. 2).—16. Specimen with ovary and sepals partly preserved; SEM-196$_1$, ×60.—17. Specimen with floral parts abraded showing ten-lobed disk surrounding tripartite gynoecium; SEM-197$_3$, ×65.—18–20. Anatropous seeds probably related to the Theaceae.—18. External view of seed with narrow surface cells; SEM-130$_2$, ×65.—19. Internal view of seed similar to Figure 18, showing hilum (h), raphe (r), chalaza (ch), and micropyle (m); SEM-130$_6$, ×65.—20. External view of seed with large surface cells; SEM-163$_1$, ×65. 21–22. Anatropous seeds probably related to the Theaceae.—21. External view of seed showing surface cells; SEM-206$_4$, ×40.—22. Section of seed showing raphe (r) and embryo cavity (e); SEM-206$_2$, ×35.

FIGURES 23–28. Fossil flowers from the Upper Cretaceous of Sweden related to the Saxifragales. (a = anthers, d = disk; f = filament; p = petal; s = sepal; st = style). 23–24. *Scandianthus* Friis & Skarby, heterochlamydous and epigynous flowers (floral diagram see Fig. 4).—23. *Scandianthus costatus* Friis & Skarby; SEM-210$_2$, ×55.—24. *Scandianthus major* Friis & Skarby; SEM-210$_1$, ×30. 25–28. Heterochlamydous, epigynous flower with haplostemonous androecium (floral diagram see Fig. 5).—25. Imperfectly preserved flower bud showing stamens and styles; SEM-181; ×50.—26. Flower showing disk, sepals, remnants of stamens and styles; SEM-189$_3$; ×80.—27. Stamen enlarged; same specimen as Figure 25; ×190.—28. Section of ovary showing many anatropous ovules on axile placenta; SEM-189$_2$, ×155.



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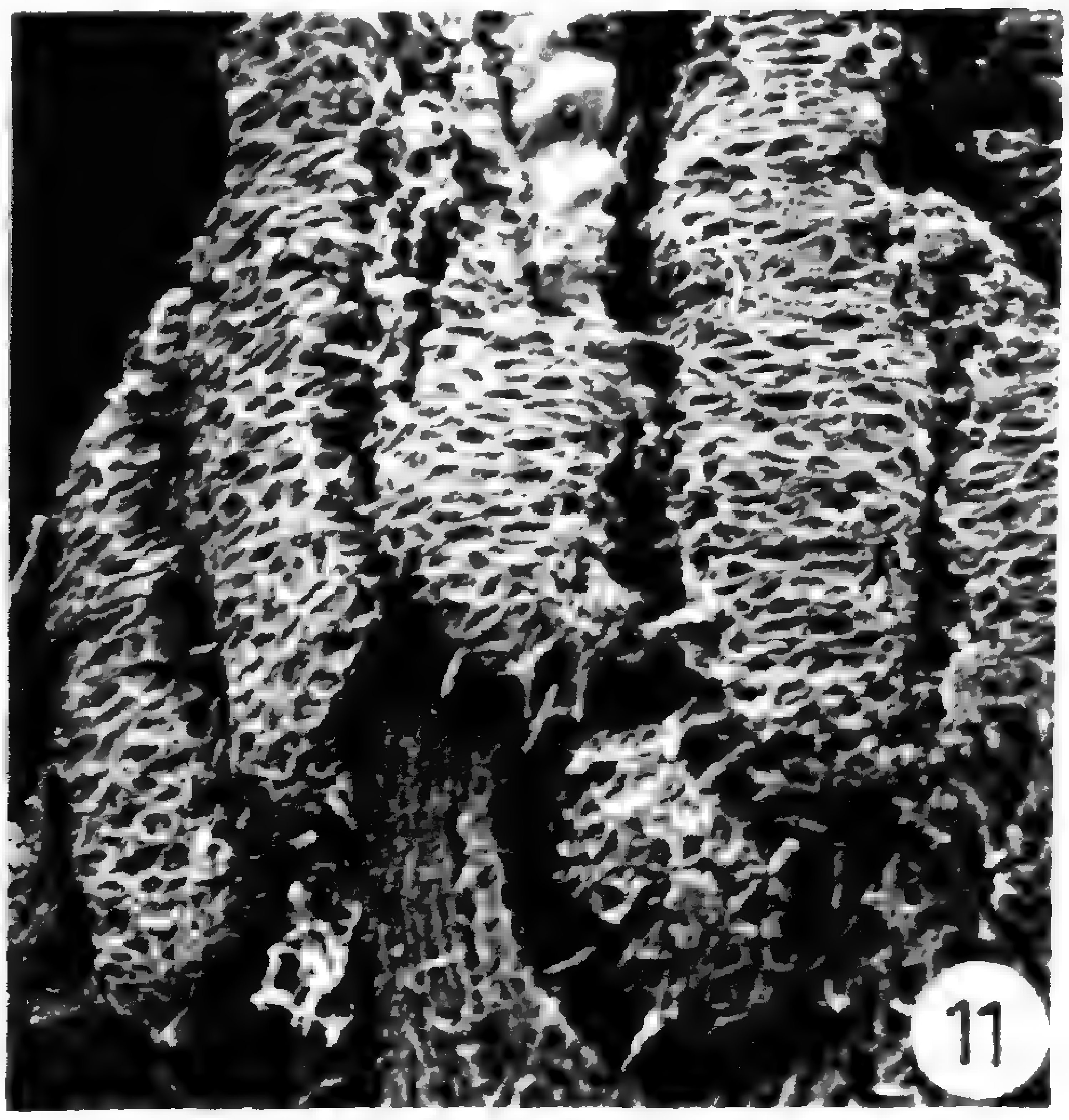

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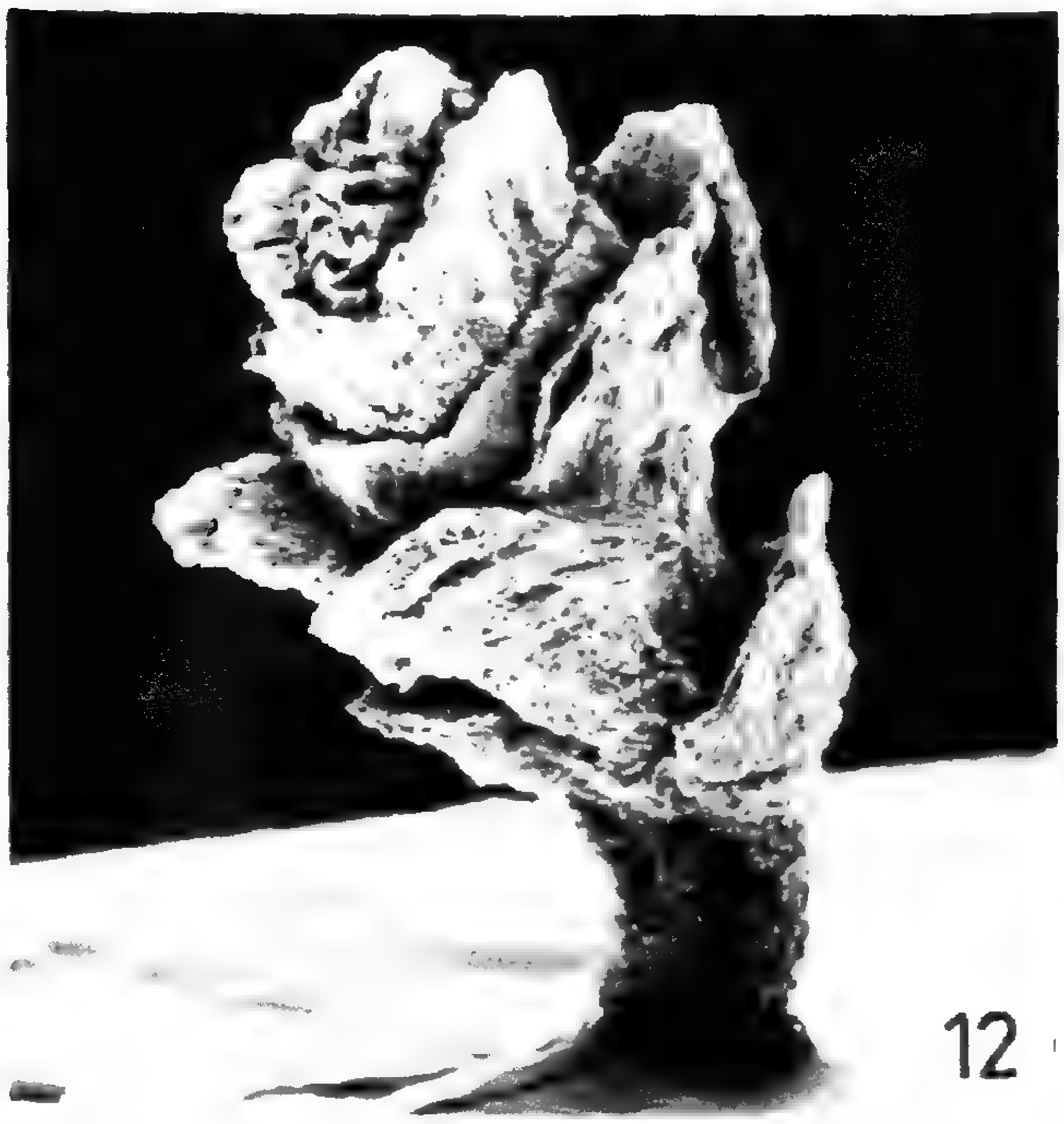

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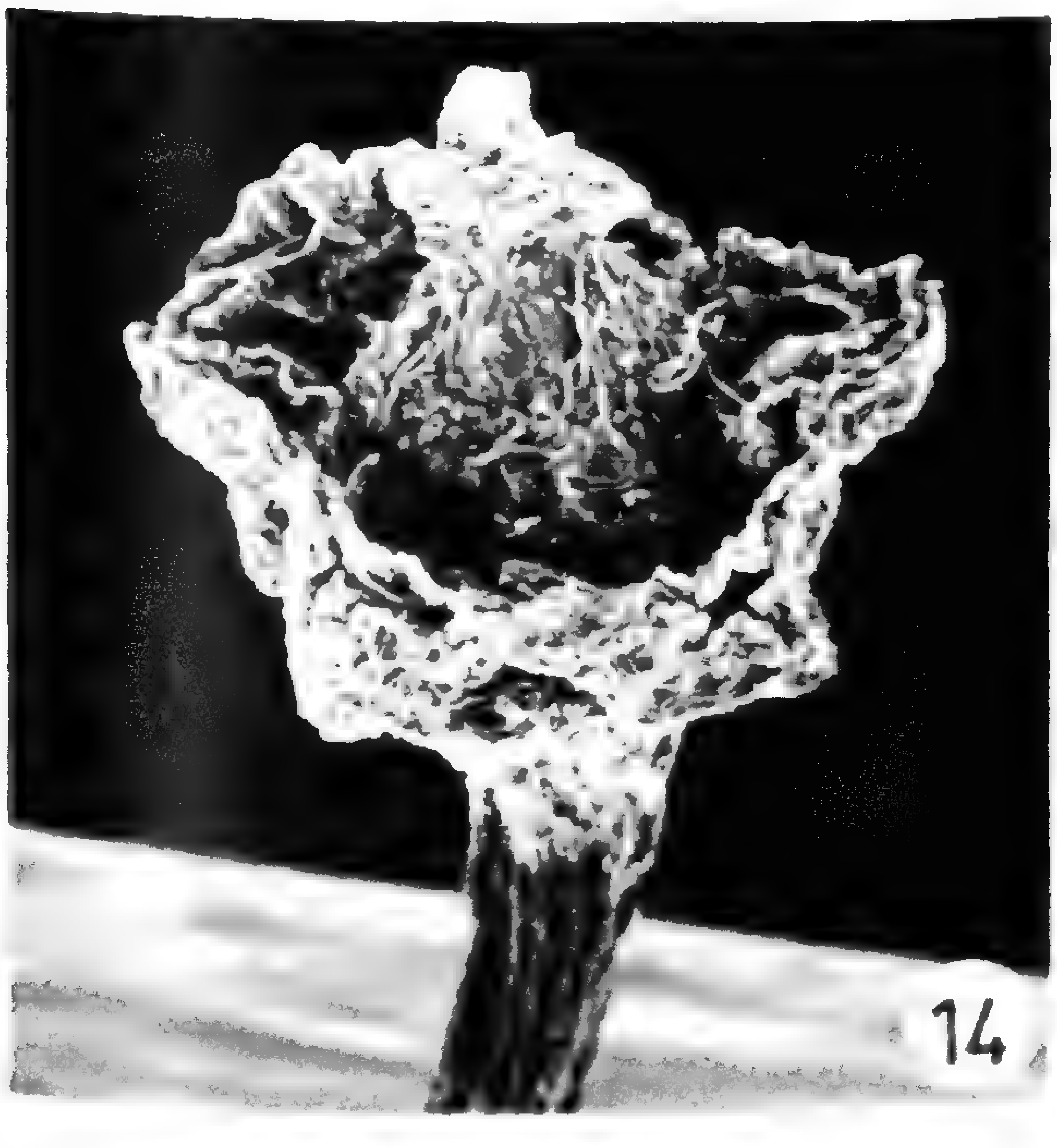

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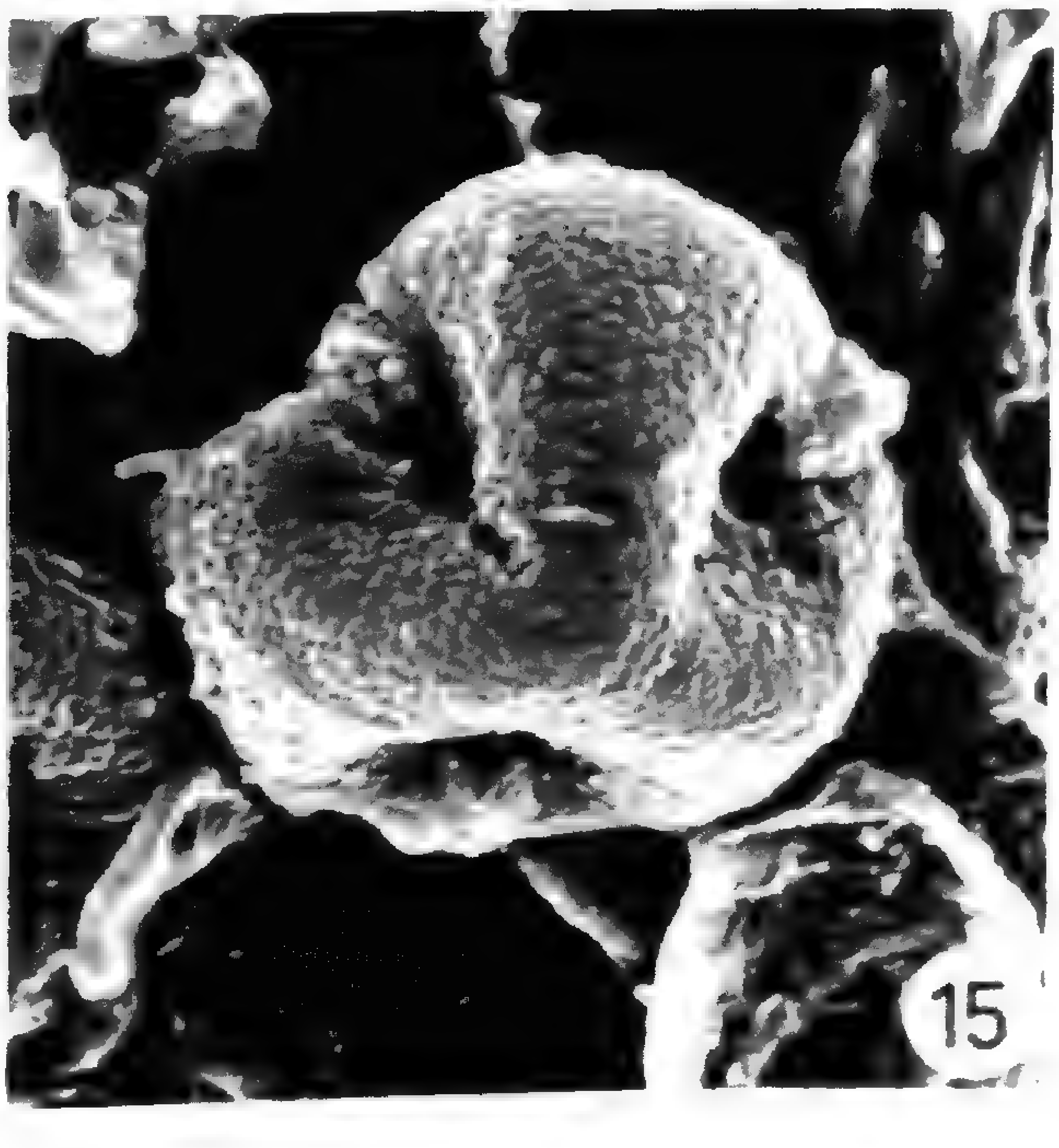

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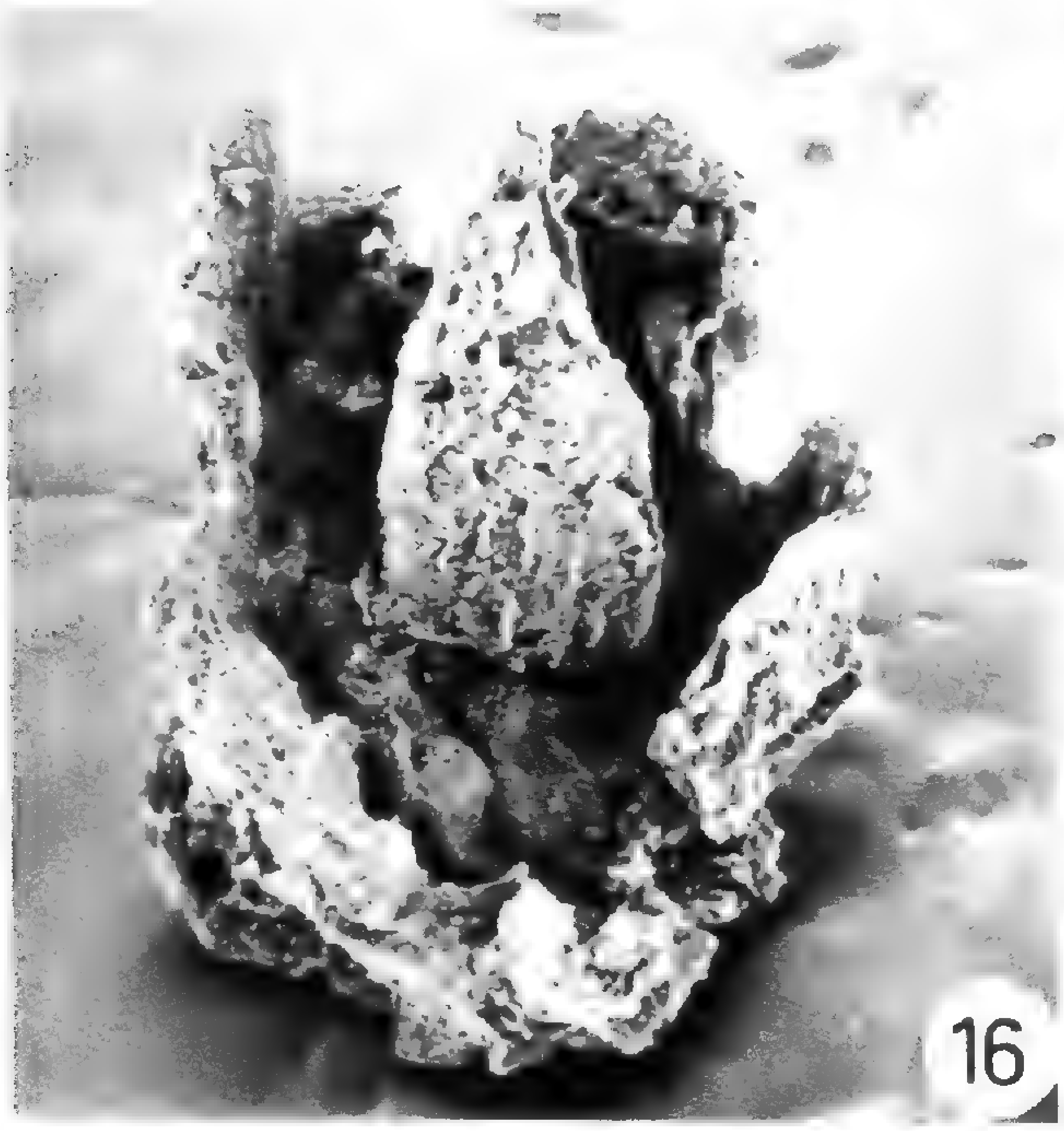
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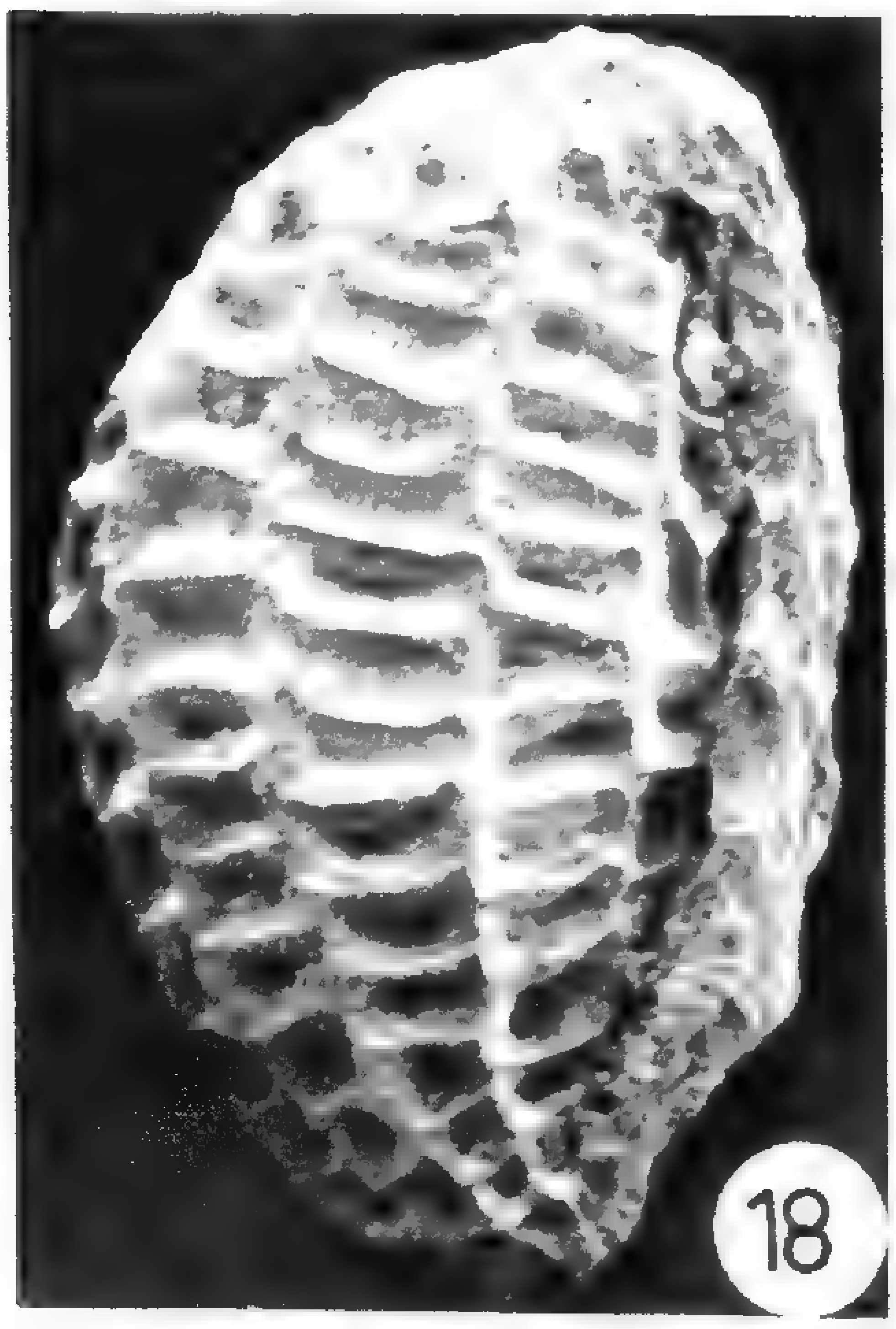
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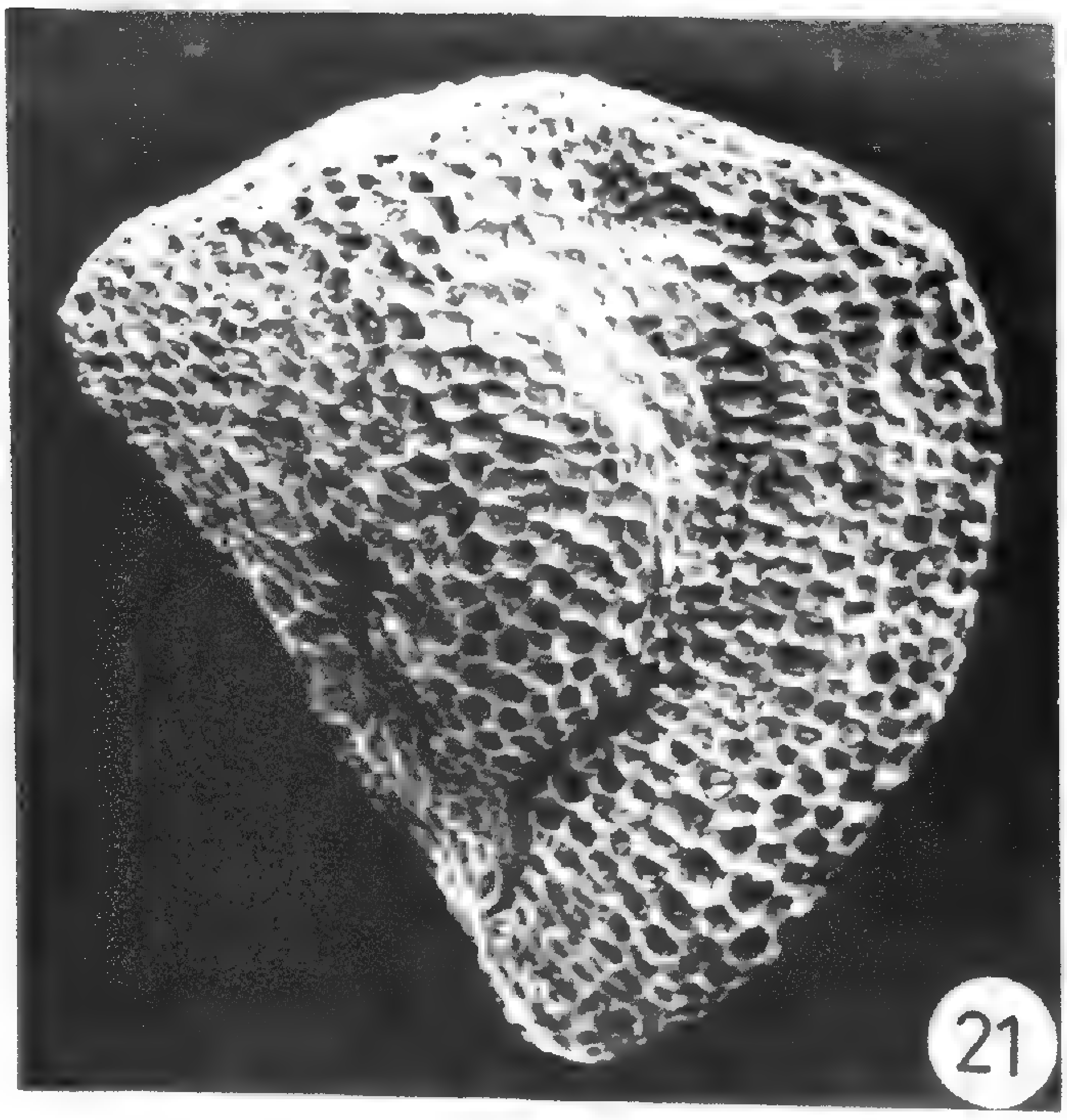
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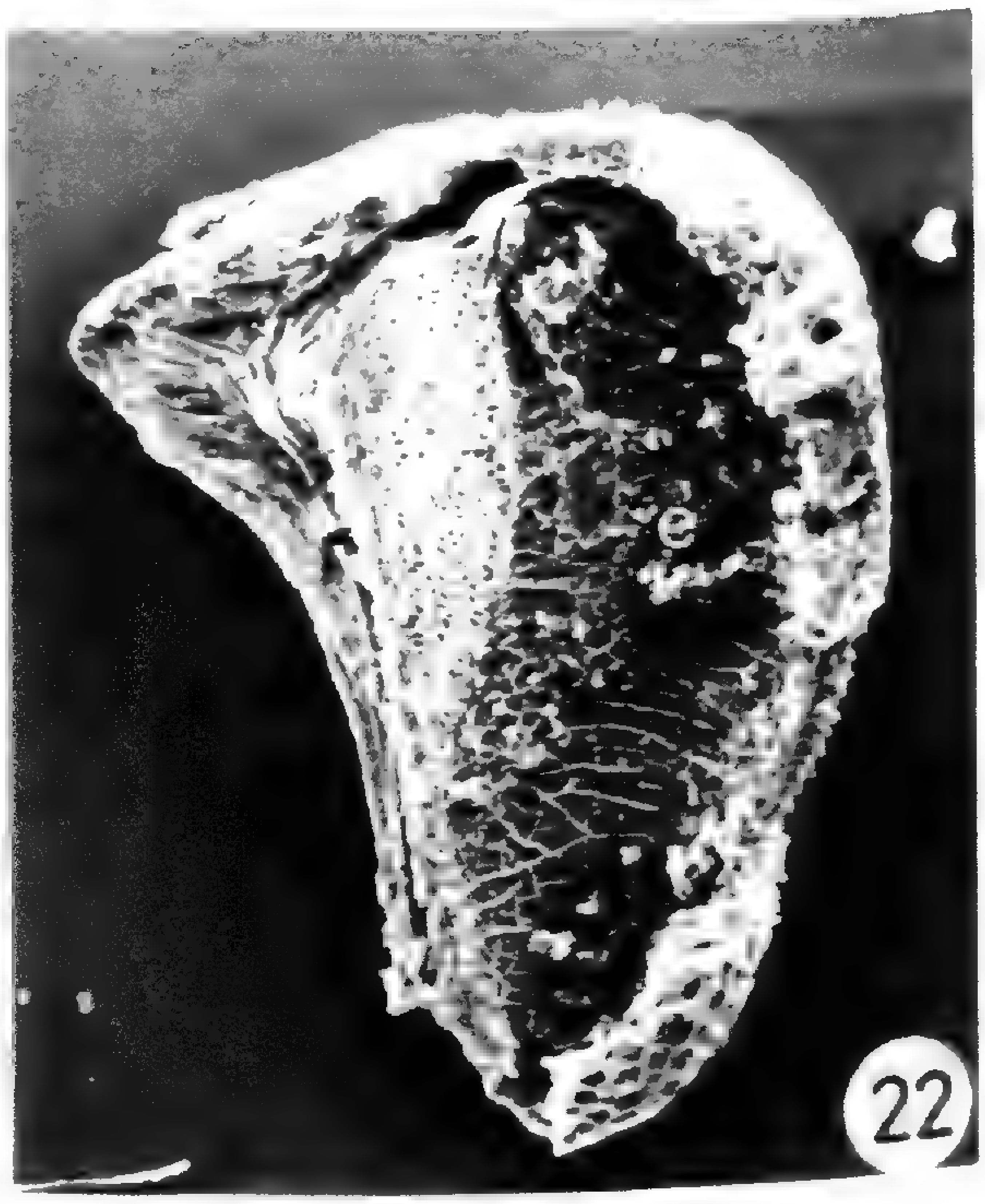

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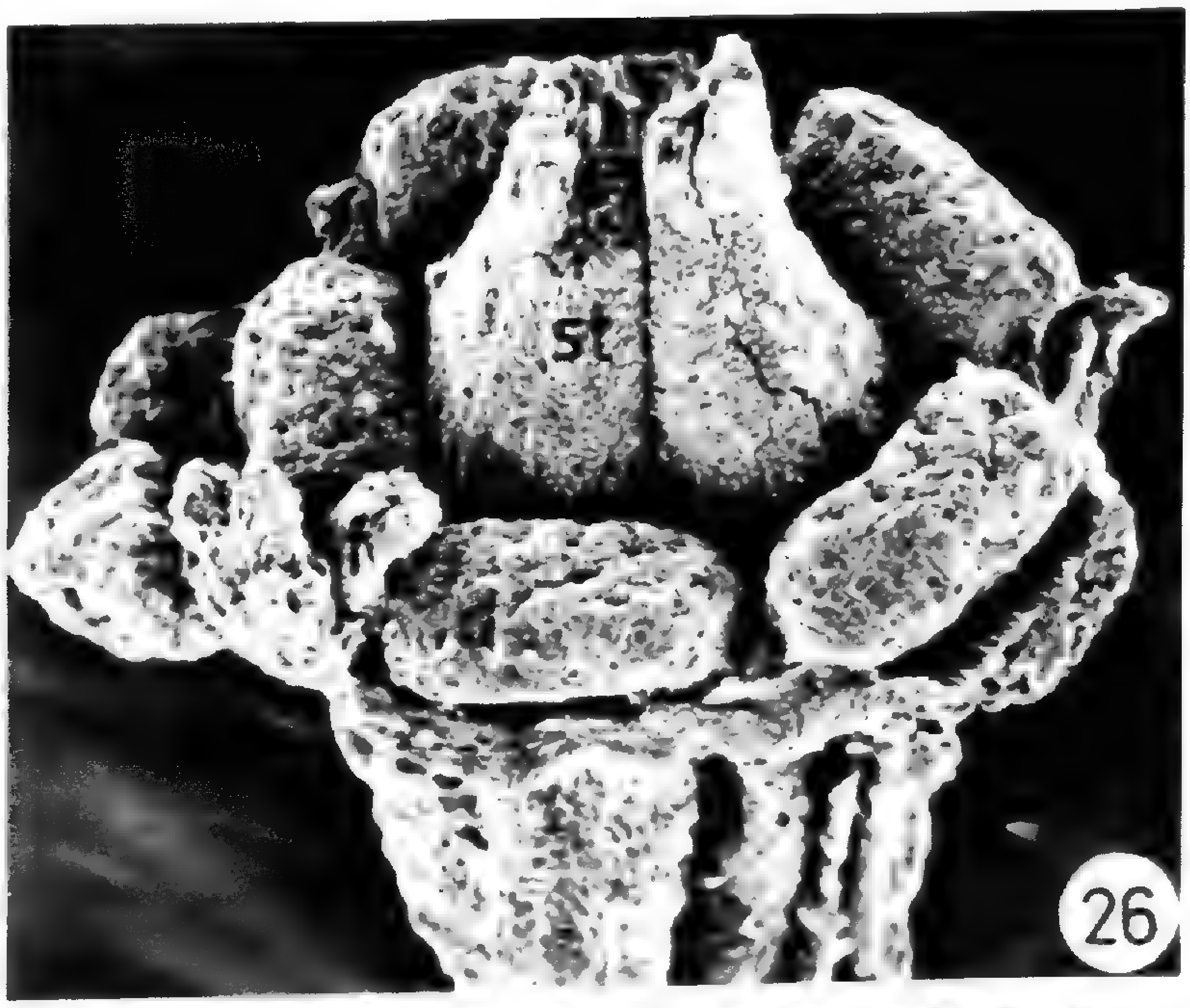

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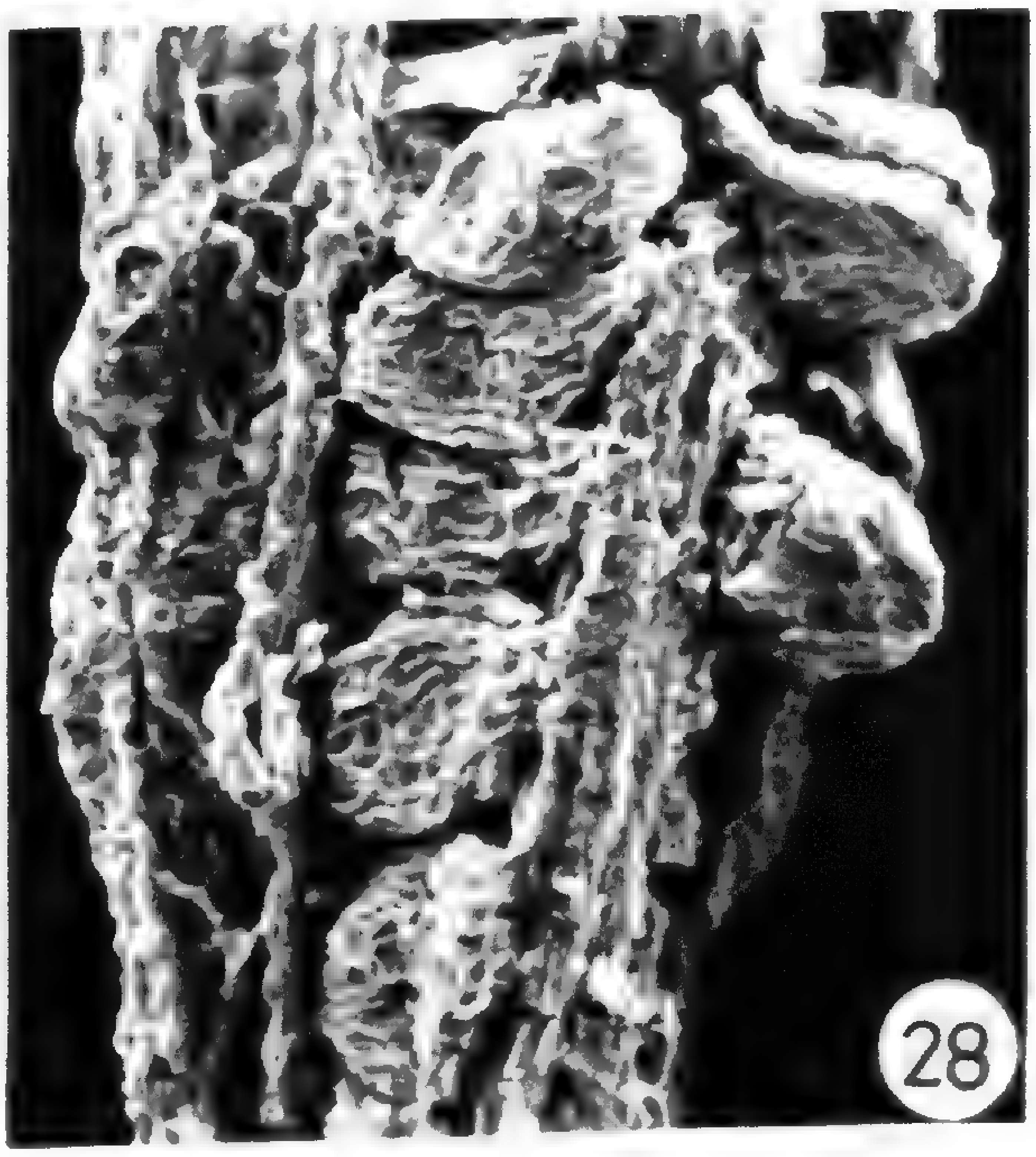

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the base of the ovary there is a ten-lobed disk (Fig. 17). A preliminary floral diagram of the fossil flower is shown in Figure 2.

Two or three other pentamerous flowers with their ovary composed of three carpels have been found. A single hypogynous type with a pentamerous gynoecium has also been recognized. Figure 14 shows a minute perigynous flower, about 1.2 mm long with three stigmatic branches and a hairy ovary. Several tricolporate pollen grains have been observed on the surface of the ovary. This type is represented by a few, incompletely preserved specimens and their botanical affinity has not yet been examined.

1.3. Epigynous flowers with diplostemonous androecium. 1.3.1. Pentamerous flowers. Probably the most fully known flowers from the Cretaceous of Sweden are those of *Scandianthus* Friis & Skarby (1982). The flowers are small, about 1–2.5 mm long, bisexual, with radial symmetry (Figs. 4, 23, 24). They are epigynous with five free sepals and five free petals (Figs. 23, 24). There are ten stamens in two whorls, diplostemonously arranged. The anthers are dorsifixed and open by longitudinal slits. The pollen grains are small, about 10 microns in diameter, tricolporate, and tectate. There is a pronounced ten-lobed disk between the stamens and the gynoecium. The ovary is inferior and unilocular, formed by two fused carpels, and with two free styles. The placentae are apical-parietal and pendant, with many anatropous ovules. The fruit is a capsule dehiscing apically between the styles. The seeds are small, about 0.2 mm long, with a thin seed coat possibly formed by only one integument. The presence of a disk and the very small size of the pollen grains suggest that the fossil flowers were insect-pollinated.

Small insect-pollinated flowers of similar construction are common in a number of modern Saxifragalean families, and comparison with modern plant groups indicates a close relationship to the Saxifragales. The best correlation is with members of the families Hydrangeaceae, Vahliaceae, Escalloniaceae, and Saxifragaceae (Friis & Skarby, 1981, 1982). Although the most common organization of the androecium within the Saxifragales is obdiplostemonous or haplostemonous, diplostemonous types occur within the group.

1.3.2. Tetramerous flowers. A single tetramerous flower type has been recovered among the Swedish fossils (Figs. 3, 35, 36). The flowers have four sepals, four petals, and eight stamens, apparently diplostemonously arranged. Between the stamens there is an eight-lobed disk-like structure (Fig. 36). The ovary is semi-inferior and three-loculed, with numerous ovules. There are three free thick styles. The flower type is represented by only a few incompletely preserved specimens and the structure is not fully known. The characters of the fossils suggest, however, a close relationship with some modern plants of the Saxifragales, e.g., the Hydrangeaceae.

1.4. Epigynous flowers with haplostemonous androecium. 1.4.1. Anthers antipetalous. The fossil flowers illustrated in Figures 25–28 were partly described by Friis and Skarby (1982). Additional material has since provided information on the corolla and the androecium. The flowers are small (about 3 mm long), bisexual, and actinomorphic, with an almost epigynous perianth insertion. There are five free sepals and five free petals, which are rarely preserved. The androecium is composed of five antipetalous stamens in one whorl; the anthers are dorsifixed and open by longitudinal slits (Figs. 25, 27). Pollen grains have not been observed yet. There is a pronounced five-lobed disk (Fig. 26). The ovary is inferior, two-loculed, and formed by two fused carpels. There are two free, thick styles (Fig. 26). The placentation is central with many anatropous ovules (Fig. 28). The surface of the ovary is characterized by distinct longitudinal ridges. Like *Scandianthus*, the fossil flower is believed to have been pollinated by insects because of the pronounced, perhaps nectariferous disk. This floral type also shares many characters with modern members of the Saxifragales and is believed to belong to this group.

1.4.2. Anthers antisepalous. Among the Swedish fossils two different flower types with antisepalous stamens have been recognized. The flower type shown in Figures 29 and 30 is probably also related to the Saxifragales. The flowers are small (1–2 mm long), bisexual, and with a more or less epigynous perianth insertion. The perianth is composed of five free petals and five free sepals of open aestivation. There are five antisepalous stamens; the filaments are triangular, almost of the same size as the petals (Fig. 29). Anthers have not been found attached to the filaments. The pistil is bicarpellary; its ovary is semi-inferior and one-loculed, and its style is simple. The fruit is a capsule dehiscing along the midline of the carpels. The placentae are parietal with many anatropous ovules (Fig. 34). The seeds are small and have a thin seed coat.

The fossil flowers have many characters in common with those of *Scandianthus,* but differ in having only one whorl of stamens and a single style. Flowers of similar construction also occur in some modern plants of the Saxifragalean complex, and these fossil flowers should probably also be referred to this group. However, a more detailed study of their systematical affinity is needed before the final affiliation can be made.

Another group of flowers from the Swedish material represented by many well-preserved specimens is illustrated in Figures 31–33. The flowers are about 1–2 mm long, bisexual with radial symmetry. The perianth is epigynous composed of five free sepals and five free petals. There is one whorl of antisepalous stamens. The filaments are thread-like and the dorsifixed anthers open by longitudinal slits (Fig. 33). Pollen grains have not been observed. Between the stamens and style there is apparently a broad disk. The ovary is inferior and unilocular, formed by two carpels, and with one style. The placentae are parietal and marginal, with few anatropous ovules (Fig. 32). The mature fruit is an elongated capsule, apparently with only one or two seeds. It dehisced along the midline of the carpels starting at the base. Figure 34 illustrates a minute epigynous, pentamerous flower about 0.7 mm long with well-preserved stamens. It possibly represents an immature stage of the flowers described above. The flowers show some features comparable to those of some modern plants of the Rosanae and Myrtanae, but a detailed comparative study has not yet been carried out.

2. *Monochlamydous flowers.* The Swedish material includes a few floral types that bear only one whorl of perianth parts. They are all epigynous with a one-loculed ovary, and one basal and orthotropous seed. They produced small triporate pollen grains assignable to the Normapolles complex. The flowers are probably closely related and belong to the same group. Based on the number of parts and floral symmetry, they are grouped into three different genera. The simple construction of the flowers and the structure of the pollen grains indicate that these flowers were adapted to wind-pollination.

Dispersed pollen forms included in the Normapolles complex (Pflug, 1953; Góczán et al., 1967) occur as significant elements of many Upper Cretaceous and Lower Tertiary palynofloras of Europe and North America (Góczán et al., 1967; Zaklinskaya, 1981; Tschudy, 1981). Pollen grains of the Normapolles type are also abundant in the Upper Cretaceous fluviatile deposits of Sweden (Skarby, 1968), and anthers including Normapolles pollen have been recovered among the megafossil plants from Sweden. The fossil flowers from Sweden represent the first megafossil evidence of plants producing this stratigraphical important pollen group.

Comparison with modern plant groups shows that the fossil flowers and fruits share characters with modern Juglandales (Juglandaceae and Rhoipteleaceae) and Myricales (Myricaceae). These families generally include unisexual flowers, but bisexual flowers occur in *Rhoiptelea* (Rhoipteleaceae) and *Canacomyrica* (Myricaceae). However, the fossils cannot with certainty be placed in any of these families, and it is thought that they represent an intermediate, perhaps ancestral, group with bisexual flowers (Friis, 1983).

2.1. *Epigynous, pentamerous flowers with radial flower symmetry.* This organizational type is represented in the Swedish material by one species of *Manningia* Friis (1983) (Figs. 7, 37–39). The structure is known from several developmental stages from small flowers to mature fruits. The flowers are bisexual and actinomorphic with an epigynous perianth composed of five free tepals in one whorl. The androecium is composed of five antitepalous stamens. No anthers in the preserved material are attached to the filaments of the flower, but fragments of pollen sacs with pollen and numerous dispersed pollen grains have been found inside the perianth of many flowers (Fig. 39). The pollen grains all belong to the same type. They are peroblate and triangular, about 20 microns in equatorial diameter, with pronounced thickenings at the inner apertures and with elongated outer apertures. They are assignable to the Normapolles genus *Trudopollis* Pflug (1953).

The ovary is inferior, one-loculed, and formed by three fused carpels. There is one thick style with three elongated stigmatic branches. The fruit is a nut with a single basal and orthotropous seed.

2.2. *Epigynous, hexamerous flowers with radial symmetry.* One fossil species, *Antiquocarya verruculosa* Friis (1983), representing this structural type has been recovered among the Swedish fossils (Figs. 8, 43, 44). The flowers are bisexual and actinomorphic, with an epigynous perianth composed of six small, apparently reduced tepals (Fig. 43). The androecium is haplostemonous with six antitepalous stamens. The stamens are represented only by remnants of filaments: anthers have not been observed. In a single specimen, pollen grains referable to the Normapolles group have been observed attached to the surface of the styles. The ovary is epigynous, one-loculed, and composed of three fused carpels. There are three very short styles, the stigmatic parts of which have not been preserved (Fig. 44). The fruit is a nut with one basal, orthotropous seed.

A very similar floral structure has been observed in the fossil flowers illustrated in Figures 45 and 46, but these flowers are apparently naked. Traces of a perianth have not been observed in any of the specimens studied (more than 50), and it is believed that they represent a reduced (apochlamydous) form of the flower illustrated in Figures 43 and 44. The flowers bear remnants of six stamens at the top of the ovary (Fig. 46), but anthers have not been preserved. Pollen grains referable to the Normapolles group have also been found in these flowers, attached to the surface of the apical part. The ovary is one-loculed, formed by three carpels, and has one orthotropous and basal ovule.

2.3. Epigynous, bimerous and bisymmetrical flowers. This floral type has been studied from numerous small nuts with persistent floral parts (Figs. 9, 40–42). It is very common in certain horizons of the fluviatile sequence and so far several thousands of specimens have been found. The material includes three species apparently in one genus, *Caryanthus* Friis (1983). The flowers are bisexual and bisymmetrical with epigynous perianth insertion. The ovary is enclosed by two thick bracteoles and a small bract united with the base of the ovary. The perianth is epigynous with four tepals in two decussate pairs. The androecium is composed of six stamens. No anthers have been observed attached to the filaments, but pollen grains of the Normapolles type have been found inside the perianth of many specimens (Fig. 40). The pollen grains are peroblate, triangular, with protruding apertures. The outer apertures are elongated and there is a triradiate fold over the polar area. These grains are referable to the Normapolles genus *Plicapollis.*

The ovary is inferior and one-loculed, formed by two fused carpels. The carpels are apparently transverse. There are two styles or stigmatic branches and a single basal and orthotropous seed. The seed coat is thin and membraneous.

DISCUSSION

The examination of the plant megafossils from Åsen demonstrates the existence in the Upper Cretaceous of a great morphological diversification of the angiosperm reproductive structure. The fossil flowers studied are mainly actino-

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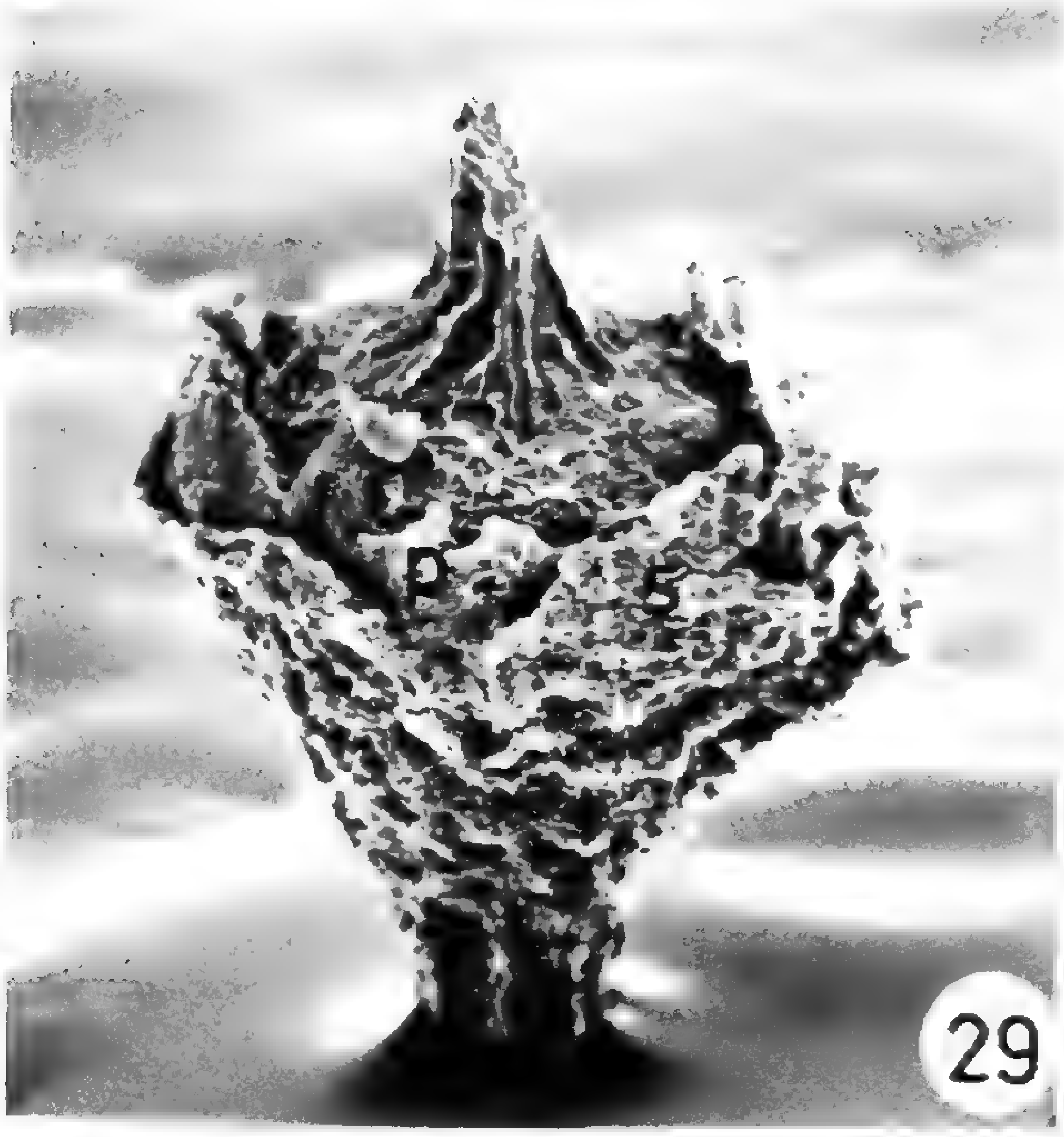
FIGURES 29–34. Fossil flowers from the Upper Cretaceous of Sweden. 29–30. Heterochlamydous, epigynous flower with haplostemonous androecium (floral diagram see Fig. 6).—29. Flower with remnants of sepals (s), petals (p), and stamens (f) preserved; SEM-197$_2$, ×75.—30. Section of flower showing parietal placenta with many anatropous seeds; SEM-203$_7$, ×85. 31–33. Heterochlamydous, epigynous flower with haplostemonous androecium.—31. Flower with single stamen preserved; SEM-192, ×70.—32. Section of flower showing parietal placenta with anatropous ovules; SEM-197$_1$, ×75.—33. Apical view of flower showing petals (p) and stamen (f and a); same specimen as Figure 31, ×85.—34. Small flower bud with stamens and style; SEM-198, ×180.

FIGURES 35–40. Fossil flowers, fruits and pollen from the Upper Cretaceous of Sweden. 35–36. Heterochlamydous, epigynous and tetramerous flower (floral diagram see Fig. 3).—35. Flower with sepal (s) and petal (p) preserved; SEM-214$_1$, ×45.—36. Apical view of flower showing remnants of petals (p), stamens (f), and styles (st); SEM-213$_4$, ×20. 37–39. *Manningia crassa* Friis, monochlamydous flower with pentamerous perianth (floral diagram see Fig. 8).—37. Flower bud with tepals (t) and clusters of pollen preserved; SEM-176$_1$, ×40.—38. Apical view of fruit with remnants of tepals (t) and stamens (f); SEM-179$_1$, ×85.—39. Pollen grains of the Normapolles type (*Trudopollis*) from apical part of flower bud; same specimen as Figure 37, ×1,700.—40. Pollen grains of the Normapolles type (*Plicapollis*) from apical part of *Caryanthus knoblochii*; SEM-164$_3$, ×3,850.

FIGURES 41–46. Fossil flowers and fruits from the Upper Cretaceous of Sweden. 41–42. *Caryanthus knoblochii* Friis, monochlamydous, epigynous and bimerous flower (floral diagram see Fig. 7).—41. Fruit with remnants of bracteoles (b), tepals (t), and stamens (f); SEM-164$_1$, ×55.—42. Apical view of fruit with remnants of six stamens (f); SEM-165$_3$, ×70. 43–44. *Antiquocarya verruculosa* Friis, monochlamydous, epigynous and hexamerous flower (floral diagram see Fig. 9).—43. Fruit with persistent tepals (t) and remnants of stamens; SEM-212$_1$, ×55.—44. Apical view of fruit showing position of perianth and stamens; same specimen as Figure 43, ×100. 45–46. *Antiquocarya nuda,* apochlamydous flower (?).—45. Fruit with scars from stamens (f); SEM-200$_3$, ×45.—46. Apical view of fruit showing position of stamens and three styles; SEM-200$_1$, ×45.



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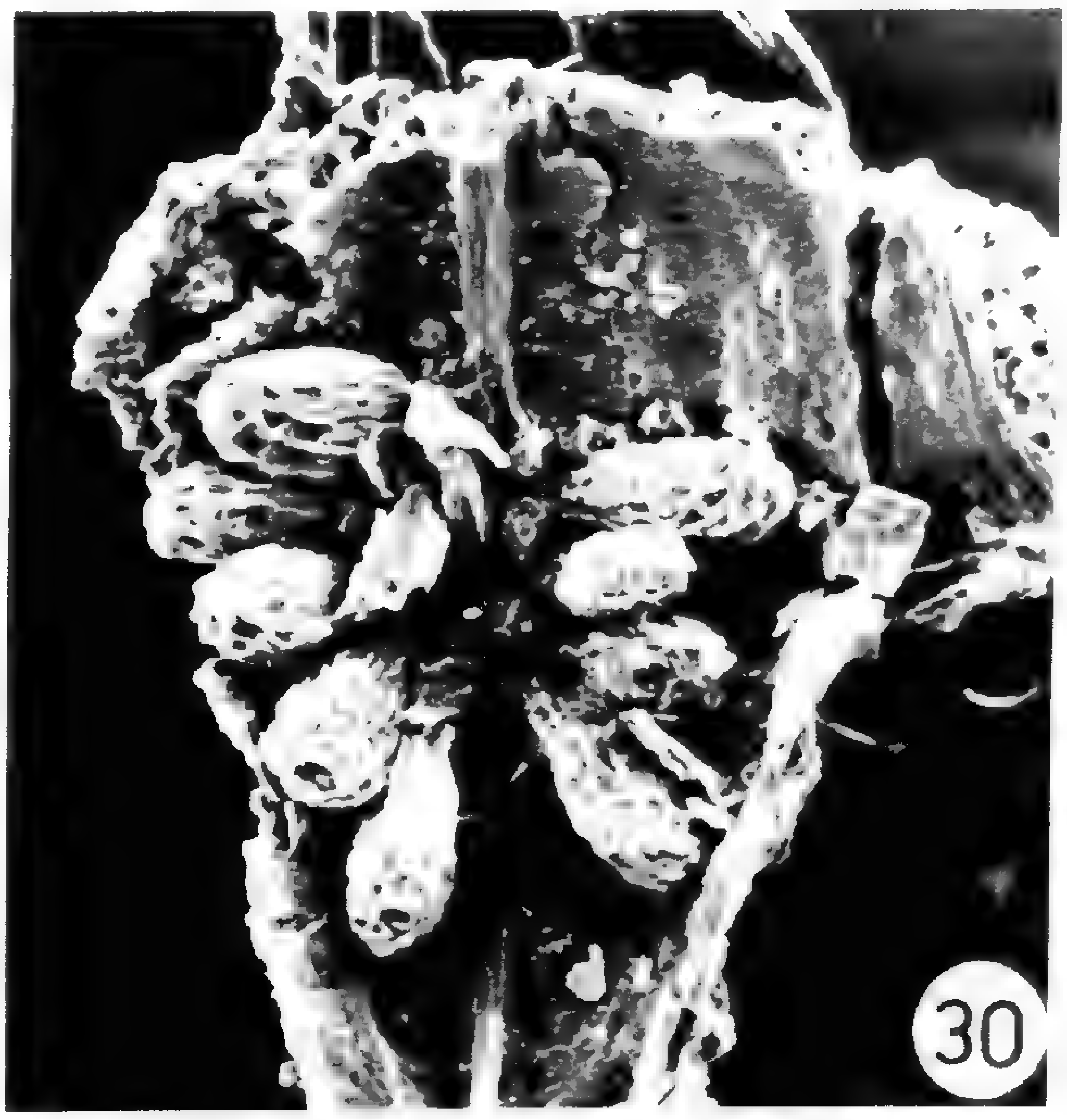

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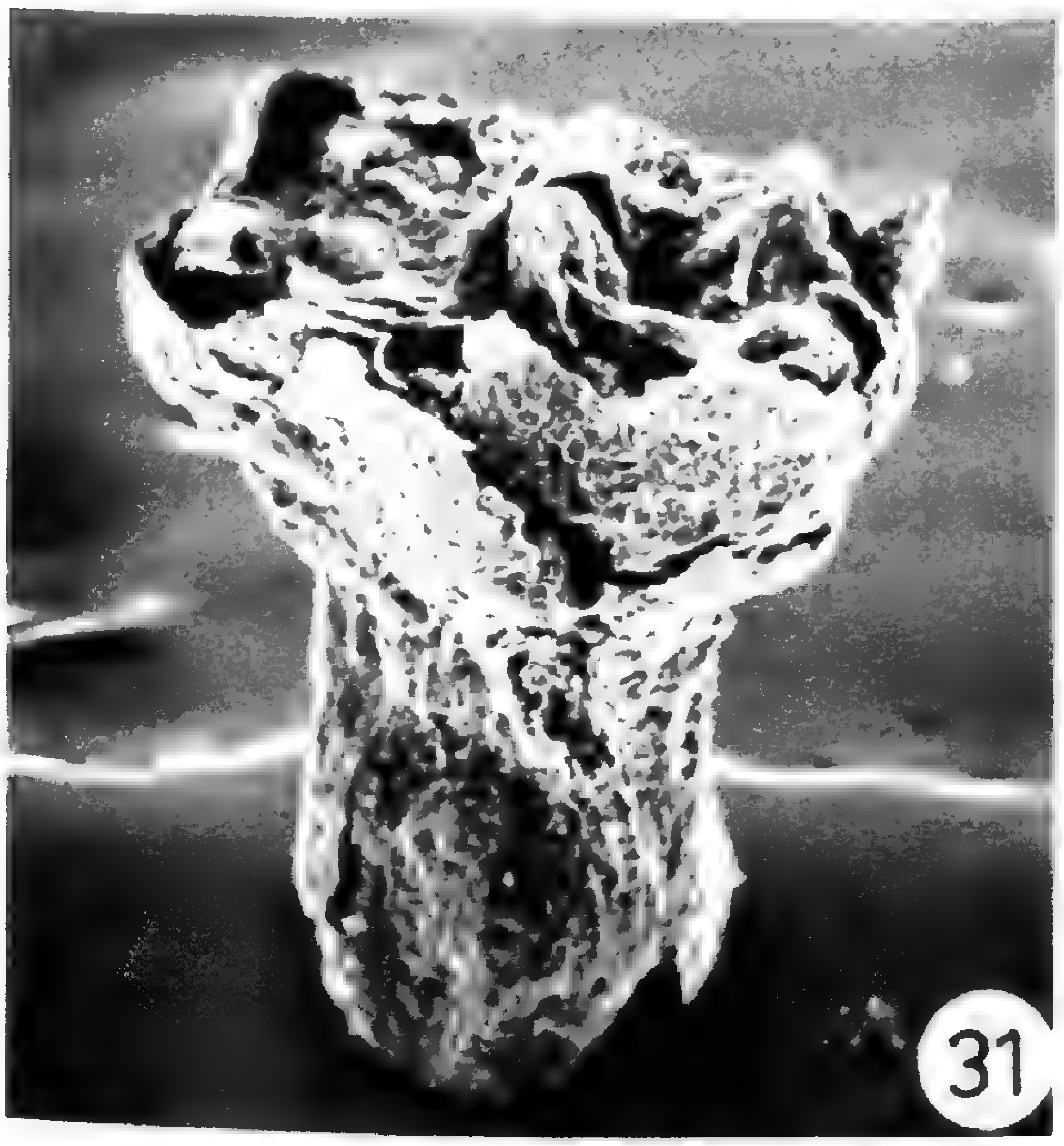

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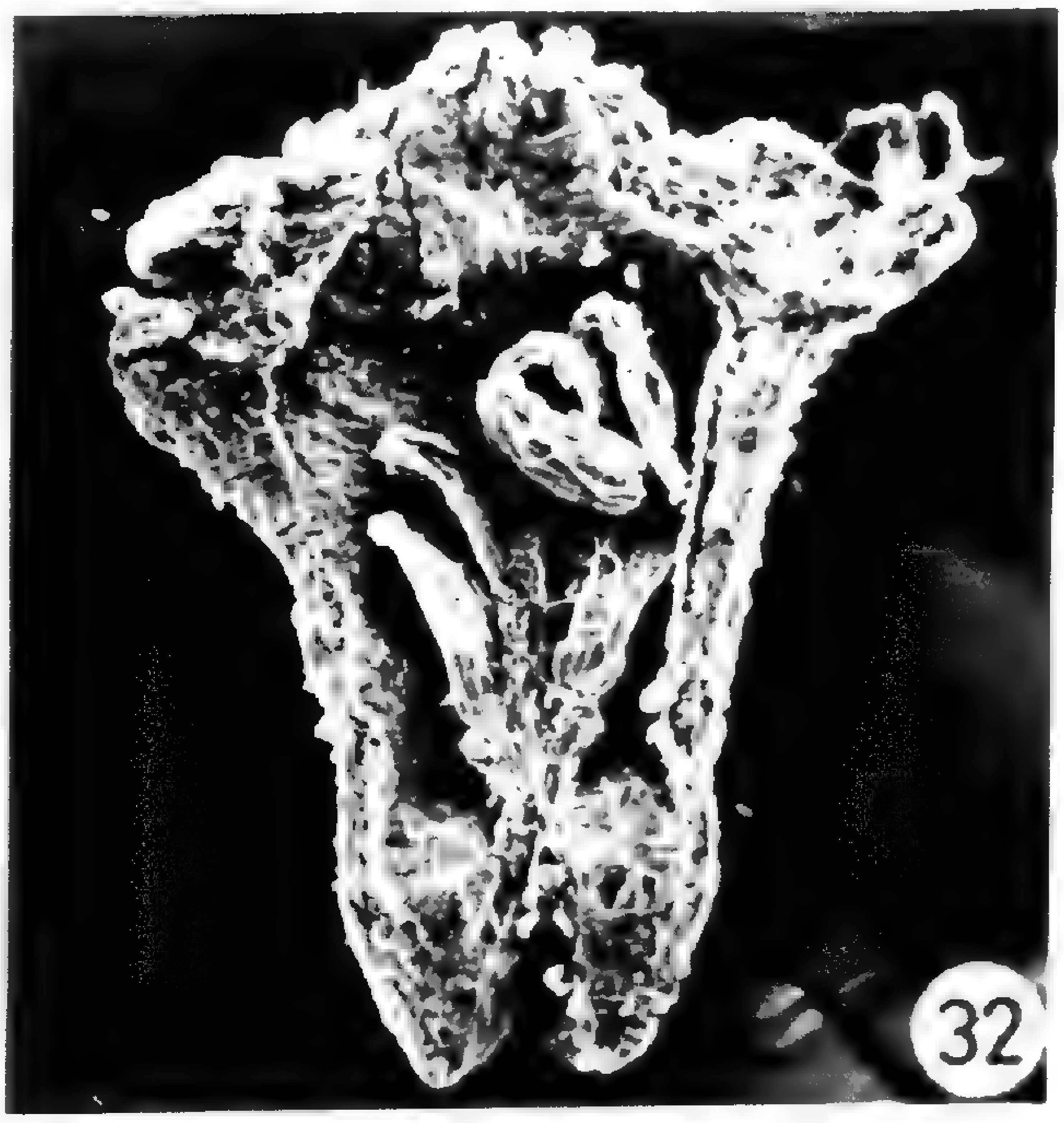

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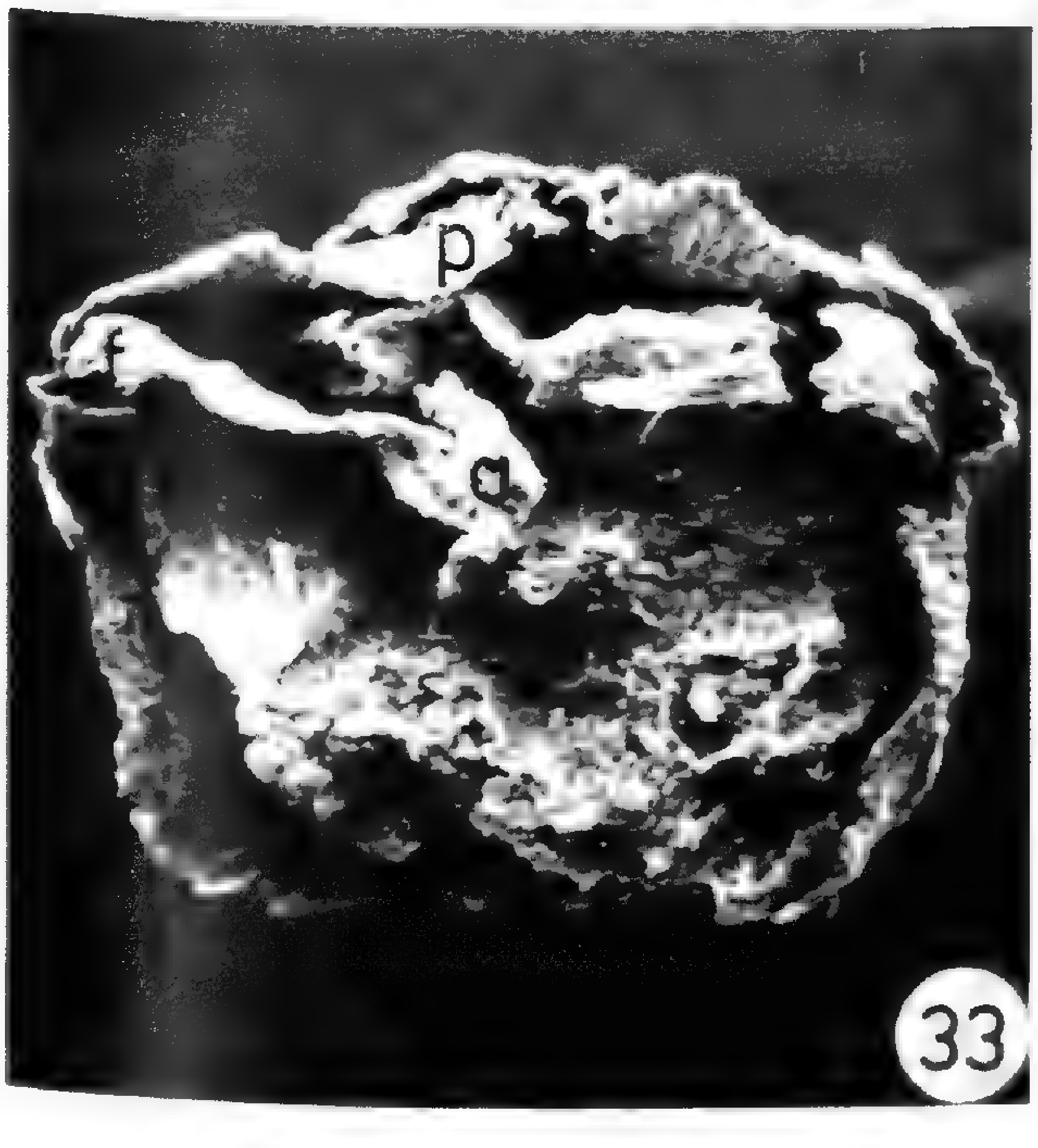

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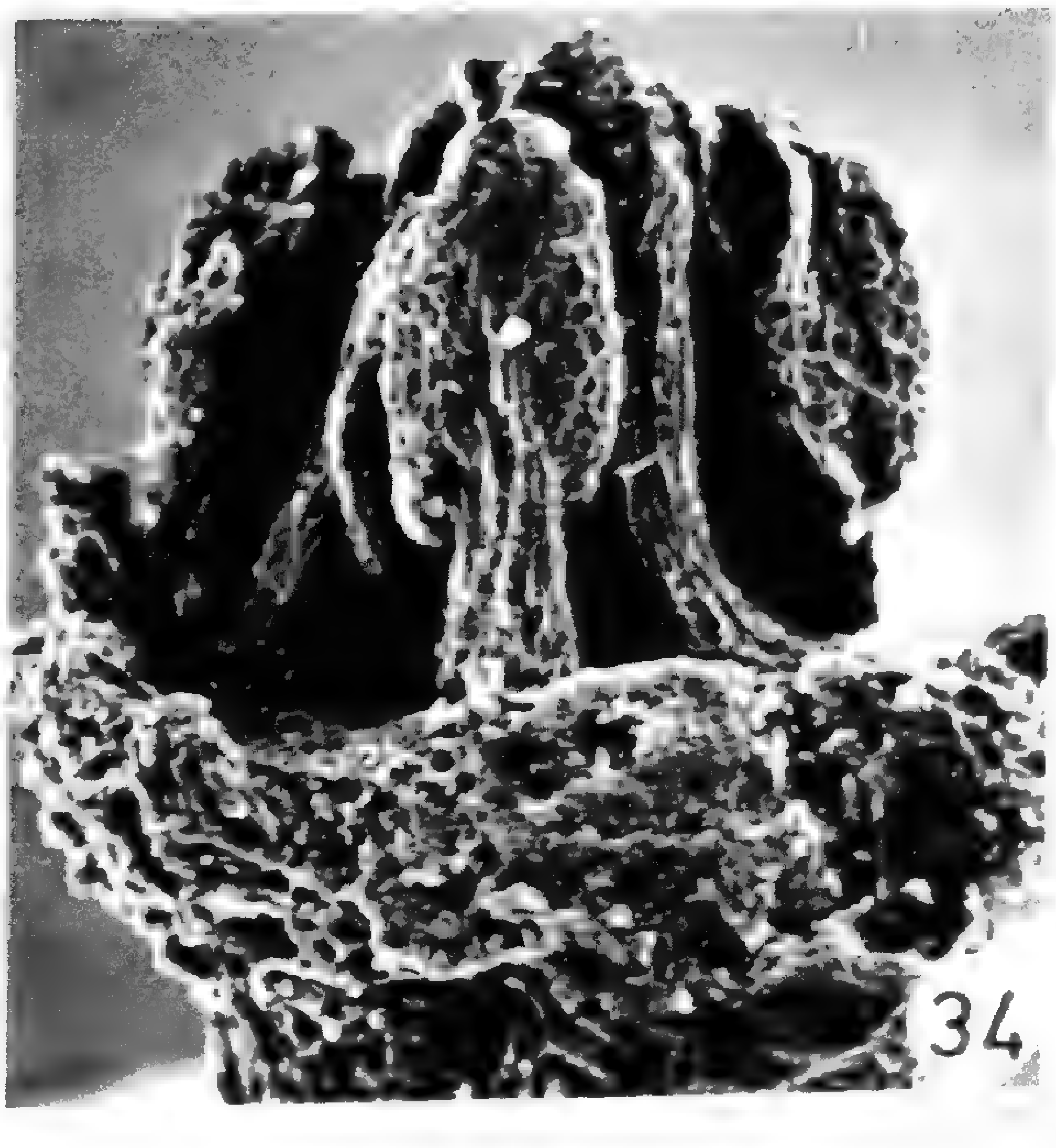

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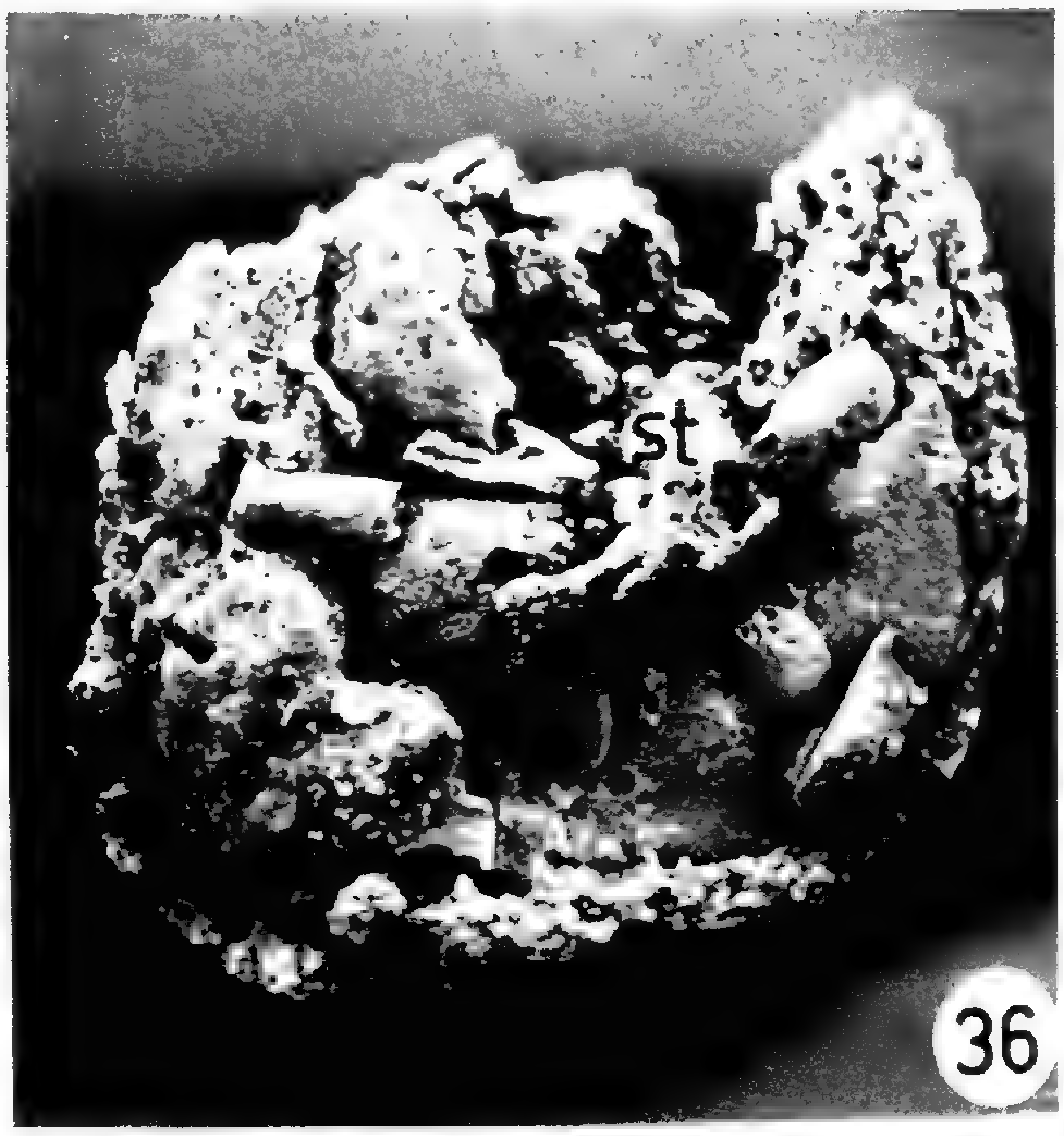

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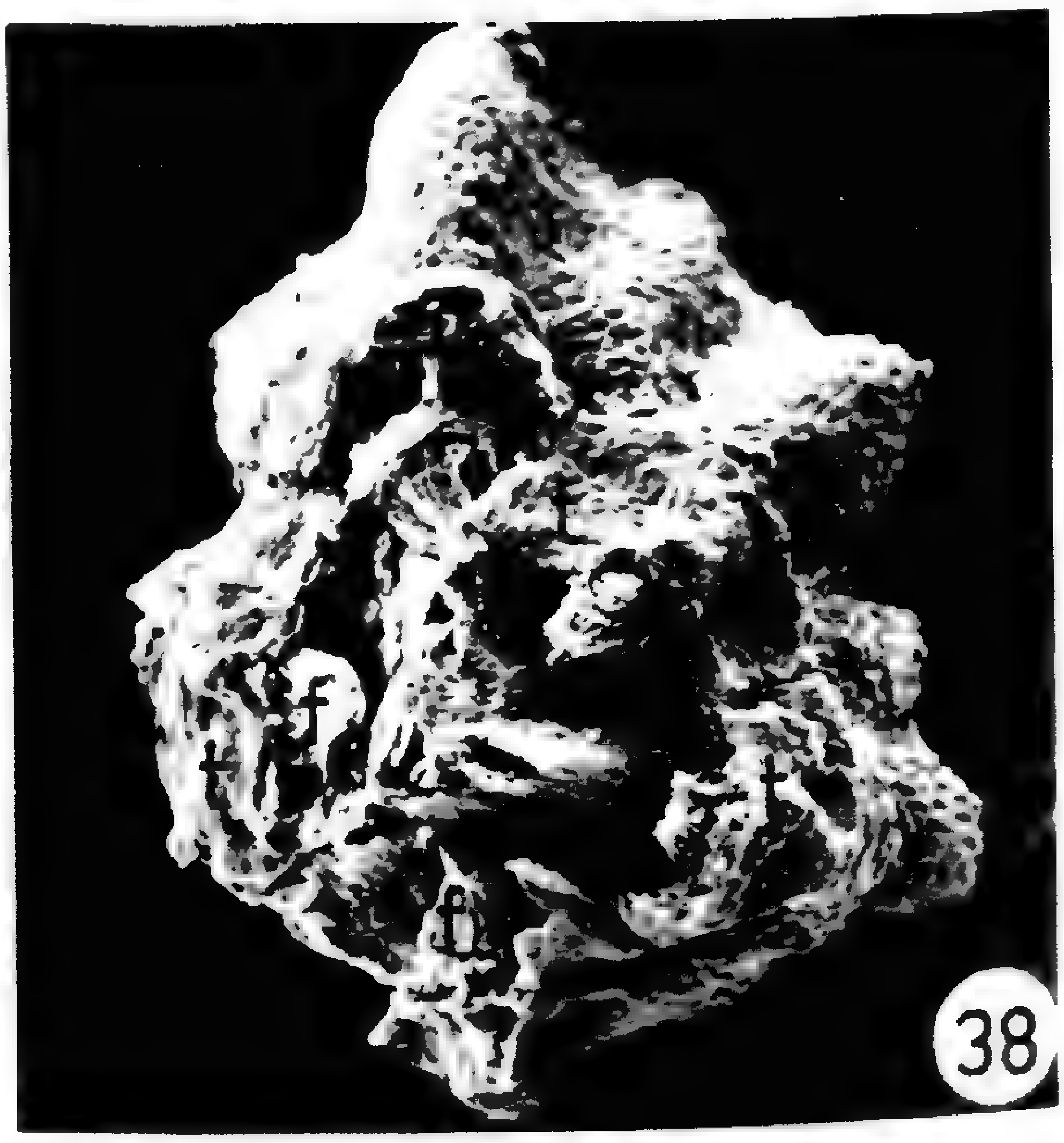

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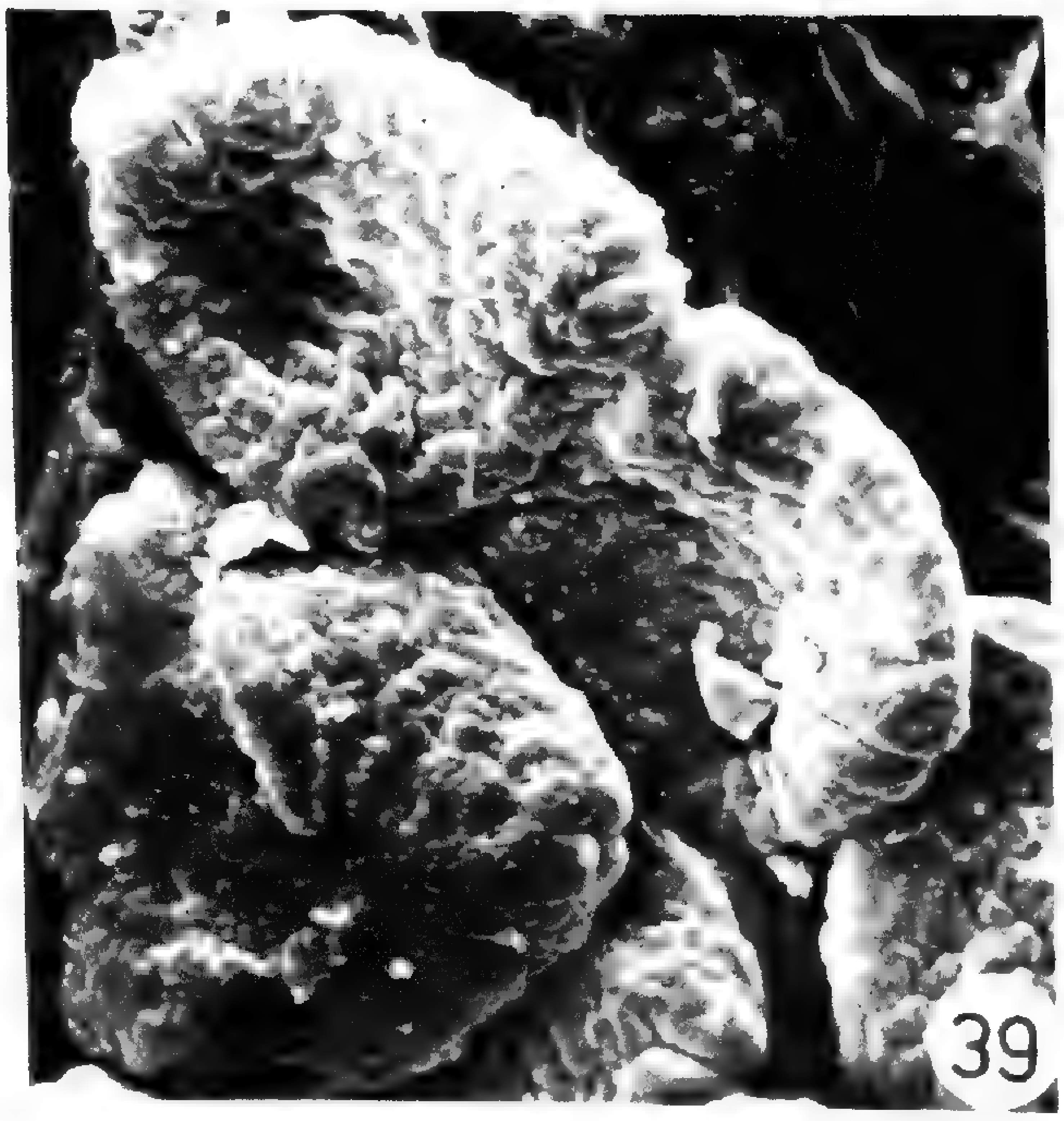
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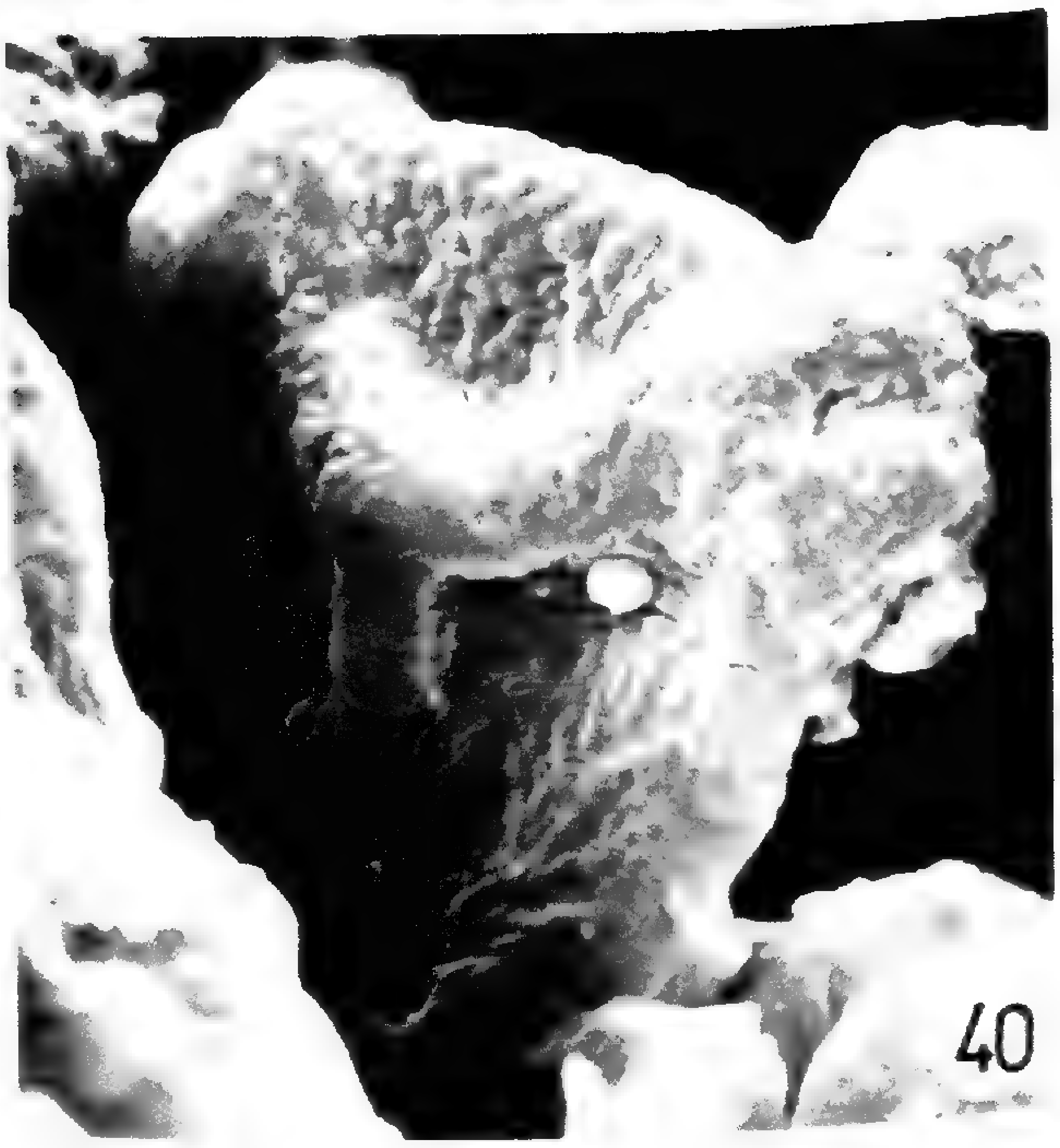
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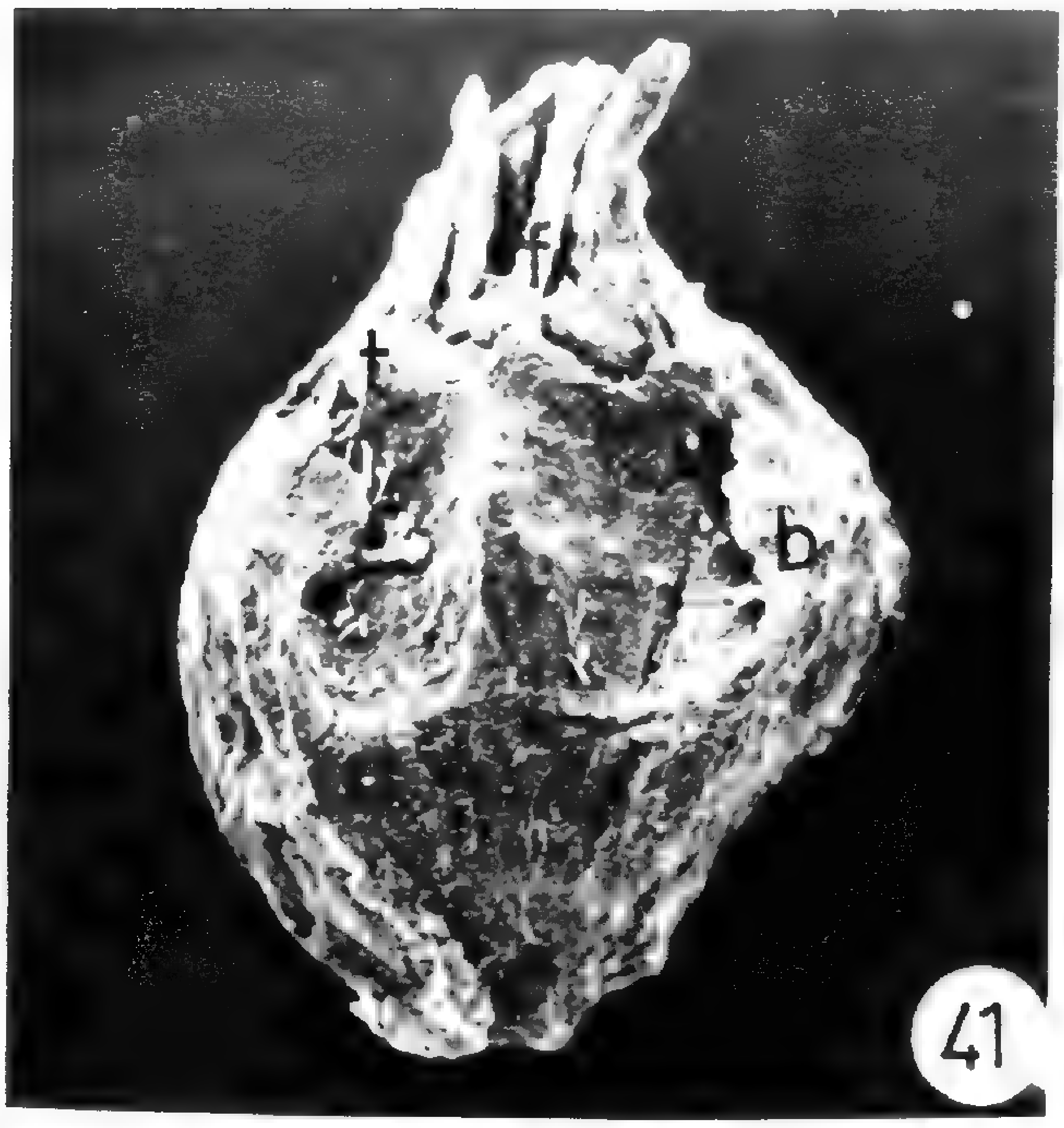
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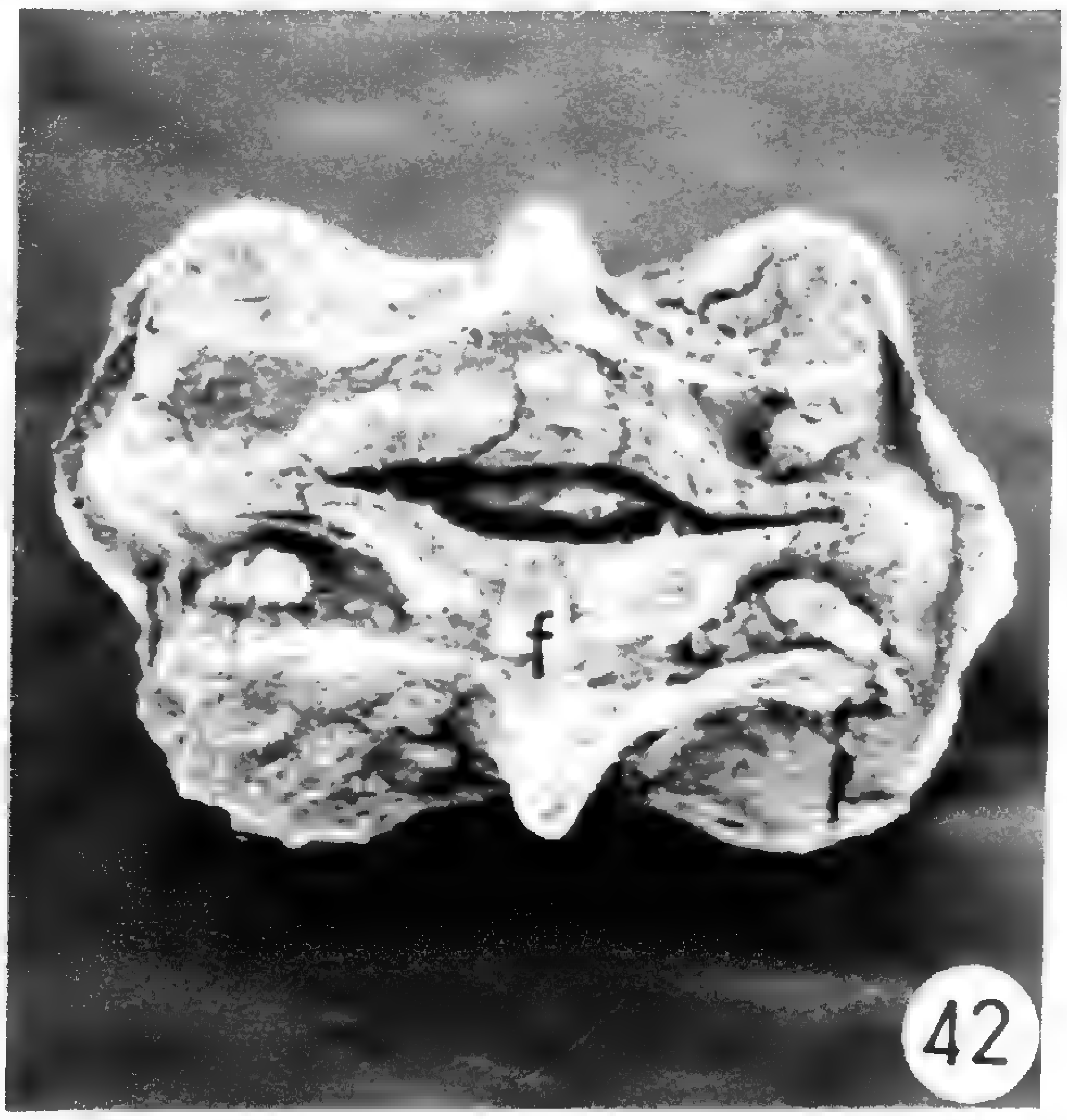
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morphic. One group of bisymmetrical flowers with a simple perianth represents, so far, the first occurrence of this type of floral symmetry. According to Dilcher (1979), all mid-Cretaceous floral structures found exhibit radial symmetry (actinomorphic). No zygomorphic or asymmetrical fossil flowers have been described yet. However, evidence from fossil fruits and pollen may indicate that zygomorphic flowers developed during the Maastrichtian and early Tertiary (e.g., Caesalpinaceae, Chandler, 1961; Muller, 1981), and that asymmetrical flower types appeared late in the Tertiary (e.g., Valerianaceae, Łańcucka-Środoniowa, 1979; Muller, 1981).

The fossil flowers from Åsen are all cyclic with a definite number of parts. Polymerous flowers with helically arranged parts generally considered the ancestral type of the angiosperms (e.g., Dahlgren, 1983) have not been recognized. However, the presence of small, stalked follicles with decurrent stigmas comparable to fruits of some modern Ranunculaceae may suggest that this flower type also existed in the Upper Cretaceous flora of Sweden. Records of an elongated fruiting axis with helically arranged follicles indicate that this flower type had developed in the late early Cretaceous (Dilcher, 1979; Vachrameev & Krassilov, 1979).

The majority of fossil flowers from Åsen are epigynous, and the material includes only a single perigynous and a few hypogynous types. They differ in this respect from the mid-Cretaceous floral structures, which are generally hypogynous. However, the record of a fossil fruit with persistent calyx, *Kalinaia decapetala* Bayer (1914), from Czechoslovakia may indicate that epigynous flowers had evolved as early as the Cenomanian.

The fossil material includes heterochlamydous flowers with a well-developed disk indicating adaptation to insect-pollination as well as simple constructed monochlamydous flowers apparently adapted to wind-pollination.

Although there is no indication of unisexual flowers among the Upper Cretaceous fossils from Sweden, several mid- and Upper Cretaceous records of small flowers in spikes or heads referred to e.g., the Platanaceae and the Myricaceae (Velenovský, 1889; Velenovský & Viniklář, 1926, 1929; Krassilov, 1973, 1977; Dilcher, 1979) indicate that unisexual flowers developed early in the history of the angiosperms.

The present investigation has revealed a variety of floral types, which mainly represent the subclasses Rosidae and Hamamelidae (sensu Takhtajan, 1980). The Dilleniidae is represented by a single flower type related to the Theaceae. This is consistent with the taxonomical results obtained from the study of the fossil pollen record (Muller, 1970, 1981). According to Muller (1981), the period Coniacian-Campanian (Muller's floral phase IIIb) is characterized by a strong diversification of the Hamamelidae and to a lesser degree diversification of the Rosidae, and also by the appearance of the Dilleniidae. Thus, the fossil flowers studied probably reveal the major morphological diversification of the angiosperm flower reached by the mid-Senonian.

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SIGNIFICANCE OF FOSSIL POLLEN FOR ANGIOSPERM HISTORY[1]

JAN MULLER†

ABSTRACT

The significance of fossil pollen evidence for 139 families for understanding the evolutionary history of the angiosperms is discussed. Deficiencies in the fossil record and uncertainties in its interpretation are stressed. The transition from gymnospermous ancestors is as yet unknown. The earliest lower Cretaceous angiosperm pollen types, although few in number, indicate considerable taxonomic diversity. The succeeding progressive differentiation is clearly shown by the pollen as well as by the macrofossil record. The competitive replacement of ancient gymnosperms and ferns by angiosperms was largely completed in the Turonian. Strong differentiation takes place in the Maestrichtian and most higher taxonomic categories were present by the end of the Cretaceous. Differentiation at lower taxonomic levels continued in the Tertiary. Some taxa are discussed more in detail and are shown to have different timing and patterns of development. Dicotyledonous herbaceous types appear relatively late and, in the monocotyledons, the woody palms are a secondary development. In general, a positive correlation exists between advancement index and time of first appearance. Some evidence for evolution by gradual development, as well as by punctuated equilibria, is discussed.

The significance of fossil pollen for the study of an angiosperm evolution is based primarily upon its abundance and its characteristic and diversified morphology. The first provides us with a nearly continuous, often independently dated stratigraphical record and the second with a biased and incomplete taxonomical record.

Let us look at this bias first. It is evident that some pollen types have a better chance of being preserved in the fossil record than others, and this depends mainly on quantity produced and distance between source area and place of sedimentation. Thus, a wind pollinated dominant in the coastal vegetation is more likely to leave a fossil pollen record than a rare, montane, insect pollinated plant. Based on this, it has been argued by Axelrod (1970) and Stebbins (1974) that the pollen record essentially shows only the penetration of angiosperms into the lowland and coastal environment but that they must have originated elsewhere and that the main features of fossil pollen evolution only reflect adaptation to advanced pollination syndromes.

To a certain extent this is true and tends to indicate a first date that is too young, unless the fossil evidence indicates that the transition from an ancestral type has taken place in or close to the area of sedimentation, as in Juglandaceae or Sonneratiaceae. Pollen evolution itself is only partly related to pollination, however. Recent studies by Heslop-Harrison (1976), Muller (1979), Payne (1981), Bolick (1981), and Hesse (1981) have indicated a large diversity of functions for the exine, such as adaptations to harmomegathy, storage of recognition substances and of lipids, which have been linked, next to pollination, to the extreme diversity of present-day exine structure in angiosperms. It was already apparent from the first investigations of the fossil pollen record that the evolution from simple to complex types in response to these factors can be traced in surprising detail. In fact, a close analysis of the morphology of fossil types in comparison with form and function in recent equivalents will allow us to detect the evolution of many adaptations in the reproductive sphere.

To demonstrate how far function may determine the morphology of the exine, two series of photomicrographs of Recent pollen types, with contrasting morphology are presented. First, alder pollen (Fig. 1a, b) is relatively small, dry, thin walled, with 4 or 5 small pores and an intragranular exine structure. Here the main harmomegathic movements are being absorbed by the ridge-enclosed flexible wall, which is quite typical of anemophilous pollen in general. Next, *Cobaea* (Fig. 1c–f) has a large, periporate pollen grain obviously adapted to insect pollination. It has a thick, rigid wall, in which stress is absorbed all over equally, resulting in a spherical shape.

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[1] The author is much indebted to M. Zandee (Department for Theoretical Biology, University of Leiden) for the statistical evaluation of the relation between age and advancement index. Requests for reprints should be addressed to the Director, Rijksherbarium, Schelpenkade 6, 2313 ZT Leiden, The Netherlands.

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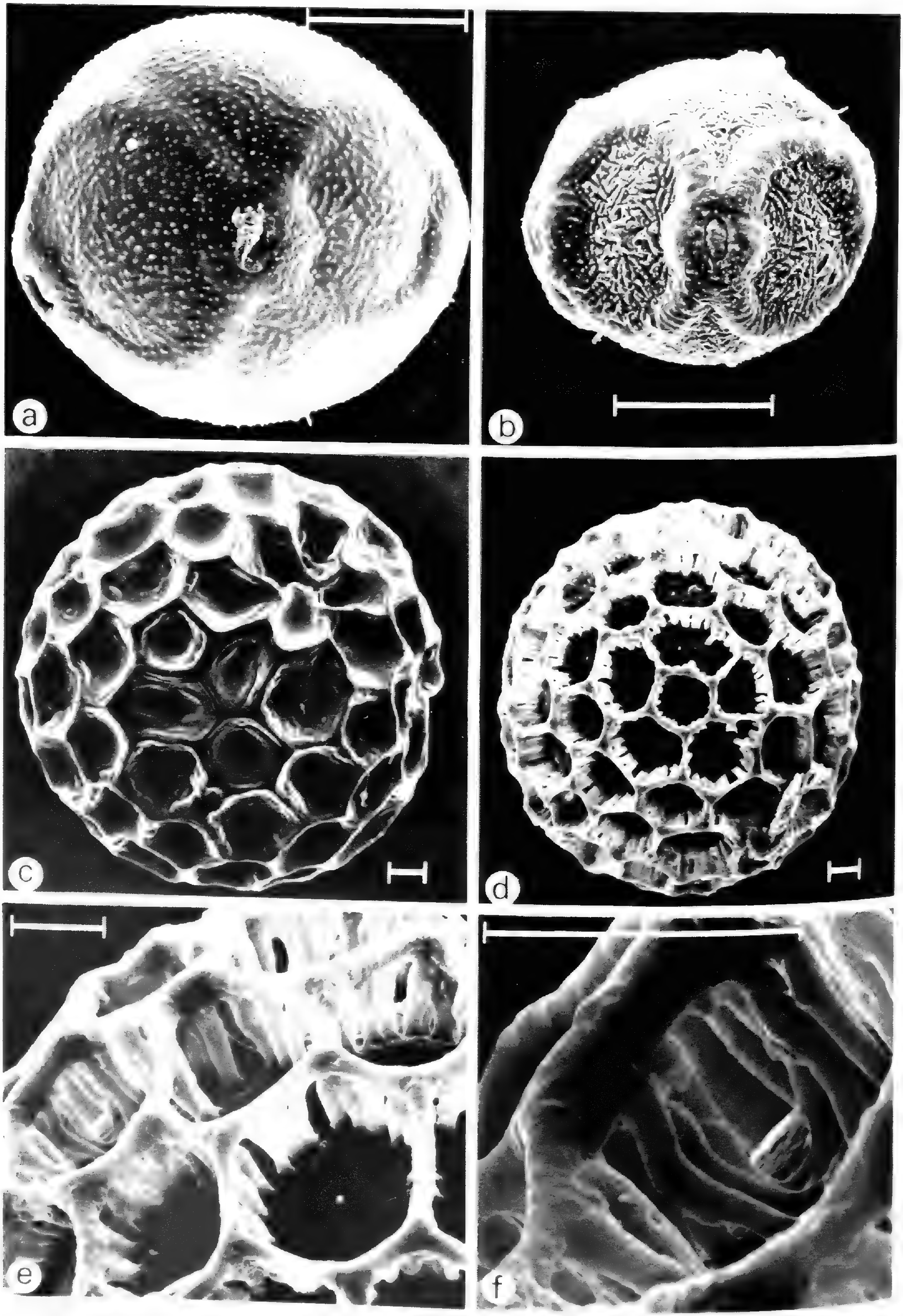

FIGURE 1. a–b. *Alnus glutinosa* pollen (Betulaceae), fresh, exine surface dry.—a. Expanded, upon release from anther, × 2,500.—b. Contracted after two days exposure to sunny atmosphere, causing the arcuate thickenings to stand out as a rigid framework supporting the withdrawn, thin, and flexible exine. The apertures are

The beautiful open structure of the exine is, in the living state, covered with oil, making the grain both sticky and insulated against water loss. It may have evolved both in response to stress accommodation and oil retention. These examples show that many structures of fossil pollen grains can be interpreted better if comparable Recent pollen types are studied more in detail with regard to their functioning.

However, there is also a non-functional (nomothetical) element in pollen morphology that arises as a consequence of limitations and repetitions in design due to certain mathematical plus physical restraining factors during development (Muller, 1980; Melville, 1981). Such characters are, in their evolution, more independent of biological functioning, and thus are probably more useful for recognition of taxa and their phylogenetic relationships, as first shown by Van Campo (1967) in her study of the successiform series.

Although taxonomic identification will rely on as many independent characters as possible, it is clear that morphologically specialized pollen types stand a better chance of being recognized and that families of angiosperms that have retained an unspecialized pollen type are consequently underrepresented in the fossil record. This is especially serious if pollen specialization lagged behind the evolution of other characters due to mosaic evolution (heterobathmy). It will be clear that the factors influencing pollen evolution are quite distinct from those acting on anatomical, leaf, fruit, or seed characters. This, however, can rarely be proven in the fossil record, although most of the cases in which a discrepancy in time of first occurrence has been found between macro- and microrecords are probably due to this phenomenon. It may be significant that in the few fossil flowers found with pollen, some showed a combination of characters not known in the Recent relatives.

The most clear-cut case is perhaps *Burretia* from the Miocene of Europe, described by Mai (1961). The flower characters indicate affinity with the subfamily Brownlowioideae of Tiliaceae, whereas the pollen is of the *Tilia* type, restricted at present to the subfamily Tilioideae. In *Fagopsis* from the lower Oligocene of the United States (Wolfe, 1973), *Quercus* type pollen is found in betulaceous staminate inflorescences, associated with fagaceous leaves. Tiffney (1977) has found a flower in the upper Cretaceous that contains tricolpate pollen but has a combination of characters that cannot be matched in the living angiosperm flora. From the mid-Cretaceous, Dilcher (1979) has reported monocolpate-reticulate pollen from catkins of an amentiferous type, a most unusual association, almost suggesting that the older the fossil, the more unusual the combination. Some of these fossils undoubtedly belong to extinct taxa, which may or may not have given rise to lineages leading to Recent ones.

In general, it may be stated that the degree of precision in identification decreases in proportion to the age of the fossils. This is not to be confused with the chance for an erroneous identification, but rather that the circle of possible affinity increases. Thus, although in the Tertiary generic identification is often possible, in the Cretaceous we may only be sure of affinity at the family or even higher taxonomic level.

In the following discussion all these potential sources of error have been taken into account as far as possible. It proceeds, in general, on the assumption that with a large, statistically significant number of identifications per taxon, at least some estimate of time of origin and development is possible. Whereas in 1970 (Muller) only 74 families with 135 pollen types could be identified based on fossil pollen, in 1981 (Muller) 139 families with a total number of 332 pollen types could be identified. The present account will deal principally with the general results of this last compilation, with the addition of some important new records published recently.

It is self-evident that these pollen records should be combined with macrofossil evidence for a final interpretation, and it is hoped that critical lists for leaf, seed, fruit, and wood remains will become available in the near future.

Some remarks on nomenclature and classification of fossil angiosperm pollen should be added because this will have to reflect the degree of precision of the identification. Apart from those rare cases in which a fossil pollen grain can be

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well protected against collapse by the annular thickenings, ×2,500. c–f. *Cobaea scandens* pollen (Polemoniaceae).—c. Fresh, covered with a sticky, oily deposit ("pollenkitt"), ×500.—d–f. Acetolyzed, showing the open, columellate structure, supporting the inner wall in which regularly distributed circular pores are located at the bottom of the smaller lumina. d, ×500; e, ×1,500; f, ×4,000. Line equals 10 μm.

identified with a living species, it should be placed as a form species in either a Recent genus, a form genus, a Recent family, or a higher taxonomic category. In the case of extinct groups of pollen, the higher taxonomic category must be circumscribed exclusively on the fossil evidence but should be related to the general classification even if only by stating that they are angiospermous. Thus, the group of Normapolles should have at least ordinal rank and can be placed in Hamamelidanae; the genus *Aquilapollenites* plus associated genera could form an extinct monotypic family within Santalales. *Tricolpites micromunus* from the lower Cretaceous can be identified with Magnoliopsida B–G, for which, unfortunately, no taxonomic name exists, and *Wodehouseia* is an extinct incertae sedis genus in the Angiospermae. At the other end of the scale *Florschuetzia trilobata* could represent an extinct genus linking Lythraceae and Sonneratiaceae.

This approach is based on the very sensible recommendations made by Schopf (1969) and allows us to integrate both fossil and Recent angiosperms in one system of knowledge. This approach certainly allows incorporation of corrections when new evidence comes to light and avoids the reproach made against many leaf identifications with Recent genera with its attendant dangers [see Wolfe (1973) and Hughes (1976) for a pertinent critique of this habit].

Of course, neutral names are preferred for fossil pollen types, and names like *Nothofagidites,* or *Santalumidites* should be avoided at all cost, since they, more than anything else, suggest too strongly what can only be tentative suggestions of affinity.

ORIGIN AND EARLY DEVELOPMENT (BARREMIAN–ALBIAN)

Because at this symposium the pollen floras from this period are dealt with in detail by other contributors, and because my approach of tracing Recent pollen types backward in time virtually denies me the possibility, as has been rightly emphasized by Stebbins (1950) and Hughes (1976), of recognizing the vital link between gymnosperms and angiosperms, I must restrict myself to a few remarks only about the earliest phase of angiosperm evolution.

In 1975, Doyle et al. presented their well known scheme that could form a basis for separating fossil gymnospermous from angiospermous exines. However, the discovery by Cornet (1980, 1981), of pollen grains with columellate structure from the Triassic, which are unfortunately not yet described in detail, casts doubt on the validity of at least one criterion leaving only that of the laminated endexine, which is very hard to test in fossil material.

At least three different functions have been proposed for the columellate exine, so beautifully developed in *Cobaea* pollen (Fig. 1c–f). These are: to hold pollenkitt and lipid material in connection with entomophily and for sealing purposes; to store recognition substances for stigmatic germination; and to give structural support in connection with harmomegathy. It will therefore be difficult to determine the ecologic significance of the columellate structure for Cornet's Triassic grains. All known living entomophilous gymnosperms have sticky pollen grains but lack columellate or even alveolate exines, according to Frederiksen (1980). However, Hesse (1980) has recently commented on the lack of pollenkitt in many gymnosperms. In angiosperms pollenkitt deposited on the tectum surface renders the pollen sticky, but if it is deposited in the tectum cavities the pollen becomes powdery (Hesse, 1980). This is contrary to prevailing opinion that the reticulate-columellate exines invariably indicate stickiness and hence entomophily. In this connection it is of interest that Klaus (1979) has found evidence for relicts of columellate structure in *Pinus*. The columellate structure of *Classopollis* is also well known, suggesting that the difference may not be fundamental.

If the Triassic columellate grains have been produced by ancestral angiosperms, then this structure may have been lost, probably because the group became extinct, to reappear with the first undoubted angiosperms in the lowermost Cretaceous. If not, we may have a case of structural parallelism between gymnosperms and angiosperms, likely to be due to structural or stickiness adaptations.

The first recognizable angiosperm pollen type is *Clavatipollenites,* starting in the Barremian. Thanks to detailed studies by Doyle et al. (1977), Hughes et al. (1979), and Walker and Walker (1980), it is clear that different types are involved. At least one form, *C. hughesii* appears to be closely similar to Recent *Ascarina* pollen and can in fact be traced to the Recent area of distribution (Muller, 1981, fig. 1). This pattern indicates a gradual range restriction with an essentially unchanged pollen morphology and hence probably also a similar pollination biology. In

Recent Chloranthaceae, e.g., in *Hedyosmum,* large amounts of pollen are produced and it seems likely that the *Clavatipollenites-Ascarina* lineage may have been adapted to an unspecialized pollination both by wind and indiscriminate insect visitors. According to Dilcher (1979) this may represent a basic and primitive strategy in angiosperms. True anemophily with dry, powdery pollen would be a secondary specialization from this initially indiscriminate system and may, according to Dilcher (1979), already have existed in mid-Cretaceous time.

Of course no evidence exists regarding the other characters of the plants producing these early *Ascarina*-like pollen types; but that they belonged to the ancestral complex of Chloranthaceae, or if one would add some more caution, of Laurales appears highly probable.

Other grains belonging to the *Clavatipollenites* complex may be ancestral to Myristicaceae, according to Walker and Walker (1980), but these have not yet been traced to younger occurrences.

Recently, however, a significant discovery has been made by Walker et al. (1983), who described undoubted Winteraceae pollen tetrads from the late Aptian/early Albian of Israel. This takes the record for this family back another 35 Ma compared to the late Cretaceous record listed in Muller (1981), indicating that taxonomically not closely related members of the Magnoliidae were already present in the lower Cretaceous, thereby suggesting a much earlier, possibly Jurassic origin and differentiation of this primitive subclass of Angiospermae.

The second main angiospermous pollen type to appear is the tricolpate reticulate type in the Aptian. Like *Clavatipollenites,* it is small and similar in the columellate exine structure but has three equatorial colpi. It is more likely that this change in apertures is related to improved harmomegathic efficiency and pollen/stigma interaction rather than to a change in pollination. The small size of the pollen would indicate small flowers (Muller, 1979; Dilcher, 1979: 323), or anemophily (Crepet, 1981).

In contrast to the *Ascarina* type, this group of tricolpate grains can be identified only as having been derived from non-magnoliid dicotyledons. Today, it occurs in Ranunculidae (Menispermaceae predominantly, but also in Berberidaceae, Papaveraceae, and Fumariaceae), lower Hamamelididae (Trochodendraceae, Tetracentraceae, Hamamelidaceae, and Platanaceae), and Dilleniidae (some Dilleniaceae, some Salicaceae, Brassicaceae). It appears to be rarer in Rosidae (some Oxalidaceae and Olacaceae) and very exceptionally is found in Asteridae (some Verbenaceae and Lamiaceae).

Thus the probability that the earliest Cretaceous tricolpate grains represent ancestral Ranunculidae and Hamamelidae appears higher than that they indicate the presence of early Dilleniidae or Rosidae.

The retention of this basic pollen type in so many Recent genera of diverse affinity is another striking example of "stasis" in pollen evolution and presumably also in pollination biology.

Rather soon after the first appearance of the tricolpate type, endoapertures developed in the Albian. The resulting tricolporate-reticulate pollen types represent a significant advance and specialization both in harmomegathic structure and increased efficiency of pollen/stigma interaction because of the presumed development of specialized intine structures. As stressed by Wolfe et al. (1975), this change has probably occurred independently in several lineages of the ancestral tricolpate complex. Menispermaceae, Flacourtiaceae, and Dilleniaceae have retained the transitional stages, the former having advanced less than the latter two families. In Rosidae, however, tricolporate-reticulate types have become dominant today. Thus, identification of these early tricolporate types is possible only in a very general way and probably indicates the presence of ancestral Dilleniidae and especially Rosidae.

The third main early angiosperm pollen type is the monocotyledonous one, recognized already by Doyle in 1973 from the Aptian. Functionally it is similar to the *Clavatipollenites* group of types.

Several other monocolpate types with a peculiar exine structure, such as *Stellatopollis* with a crotonoid pattern, or types found by Hughes et al. (1979) with a dipterocarpoid pattern, might also be monocotyledonous but disappear from the record soon afterwards.

A fourth main category is the periporate group from the Albian, identification of which is also very uncertain at present. This group is probably not related to Caryophyllidae and shows more similarity to *Alisma* (Alismataceae) and *Trimenia* (Monimiaceae), but has not yet been connected with younger types.

Thus, in the Barremian-Albian early phase of angiosperm development a limited number of taxa, but with a rather wide variety in pollen structure, make their appearance, roughly cor-

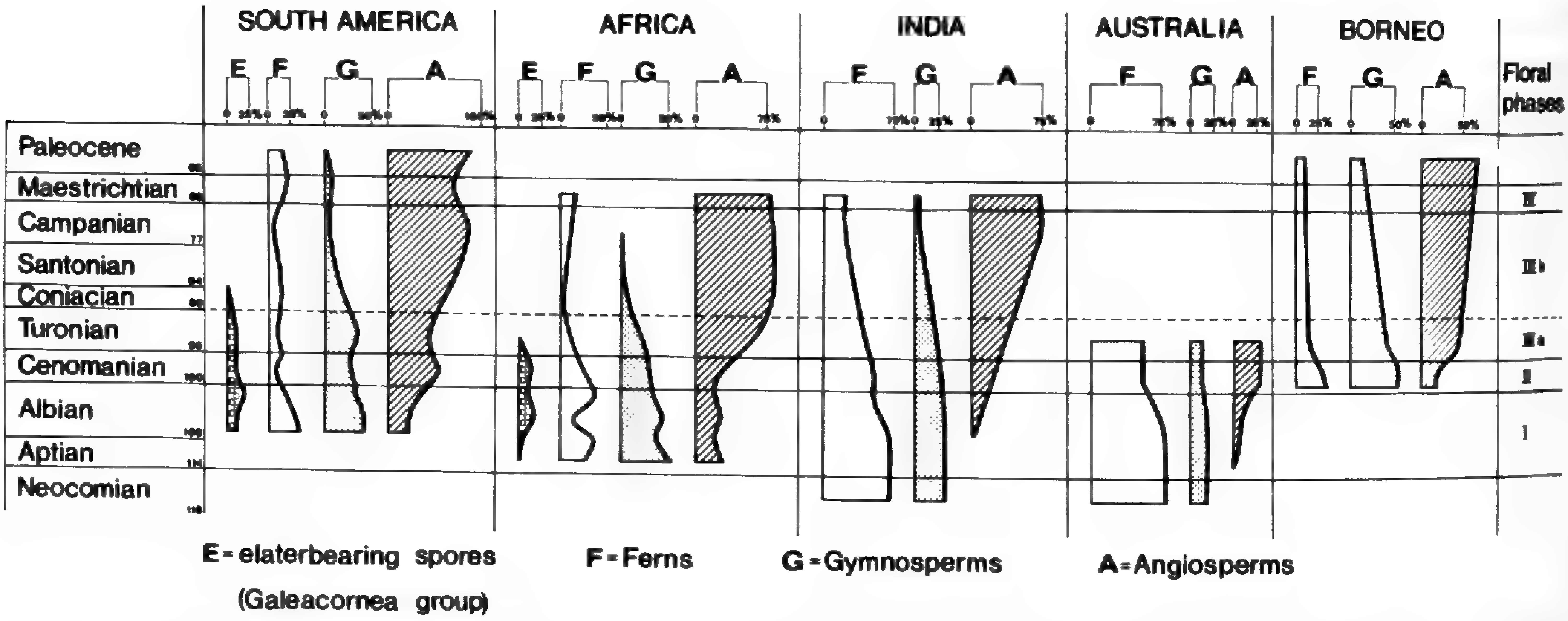

FIGURE 2. Microfloral diversity curves expressed as % species composition for four major categories of spores and pollen. Floral phases based on Muller (1981).

responding with increases in leaf diversity and abundance as Doyle (1977) and Doyle and Hickey (1976) have pointed out. This would appear to invalidate Axelrod's (1970) claim that fossil pollen does not register early angiosperm diversity. But, if, as Stebbins (1974) contends, angiosperm origin took place in a semi-arid dry land environment, admittedly palynology would only rarely detect traces of it, although the abundance of very early angiospermous pollen types in the ancient, probably semi-arid rift valley sediments of Gabon could support Stebbins' views, as already pointed out by Doyle (1977, 1978).

INCREASE IN ABUNDANCE (CENOMANIAN-TURONIAN)

The long known and well established increase in abundance of angiosperm macrofossils in the Cenomanian is accompanied by a comparable increase in pollen abundance and diversity. As shown in Figure 2, pollen diversity curves from many areas, in which no angiosperm macrofossils have been found at all, show a general picture of the intense competition between the young and vigorous angiosperms and the long established gymnosperms and ferns. These curves confirm Raven and Axelrod's (1974) and Doyle's (1978: 23) views of an early development of angiosperms in West Gondwanaland and negate Smith's (1970) and Takhtajan's (1969) view that the area between Assam and Fiji was the cradle of the angiosperms. Both Borneo and Australia appear to have been backwaters, far removed from the mainstream of early angiosperm development and, moreover, as now has been demonstrated by plate tectonics, widely separated at that time. In Australia especially, the delayed entrance of angiosperms, possibly due to a cooler climate, is clear (Dettmann, 1981).

In the Cenomanian, the main new development in pollen evolution is the appearance of triporate types. This has probably taken place independently, in a lineage from tricolporate types via a flattening of the triangular shape and a shortening of the colpi to early Normapolles as first described by Doyle (1969) from the Cenomanian of the gulf coast of the United States and in the Turonian in a separate lineage leading to early triporate celtoid pollen types of which the derivation and place of origin are not yet known (Muller, 1968). The Normapolles group will be shown to have probably given rise to juglandaceous types, and the celtoid types have become fairly early established as Urticales. In both cases, ancestral types to higher Hamamelidae must have been present.

It is mainly in the Turonian that the real increase in pollen morphological diversity becomes obvious and that modern types quite suddenly appear, like that of *Ilex* (Celastranae) and *Gunnera* (Myrtanae). Such sudden appearances without any preceding ancestral types strongly suggest immigration into an environment in which they are more likely to be preserved than the place of their actual origin.

By the end of the Turonian the ecological breakthrough of the angiosperms appears largely to have been completed, but the taxa present were, in most cases, different from Recent ones, as is becoming also more and more clear from the study of macrofossil records. Tiffney (1981) has suggested that this increase is a result of competitive pressure by increasingly efficient angiosperms, after a slow and gradual additive process of evolution during the lower Cretaceous, and has pointed out that many of the more archaic gymnosperms became extinct worldwide at the same time. The fossil pollen evidence is well in accordance with this view.

Maestrichtian Events

In the Maestrichtian, an accelerated development of modern pollen types appears to have taken place indicating increased differentiation at the level of families, orders, and superorders (Muller, 1981, fig. 3). In view of the relative short duration of this period and also because this development clearly antedates the catastrophic events at the Cretaceous-Tertiary boundary, a special explanation appears necessary. Whether the phenomenon is due to a solar radiation maximum as postulated by Hughes (1976) or to coevolution with insects and dispersal agents, the development of chemical defenses, or any other factor, is difficult to decide without further detailed study, although selective pressure on pollen evolution undoubtedly has become high.

The Maestrichtian is also the last period in which, locally, extinct groups of plants, such as those that produced the Normapolles types or *Aquilapollenites* were dominant. In the Australian-Antarctic region, in contrast, no comparable extinction has occurred and the flora developed early into a vegetation type that largely still survives today (Proteaceae, *Nothofagus*).

It is clear that differentiation at ordinal and superordinal level decreases in the succeeding Tertiary, but that at the family level much differentiation still took place, as was also emphasized by Tiffney (1981) for the Paleocene/Eocene and Eocene/Oligocene transitions.

For the ordinal level, this is shown in Figure 3 as a cumulative curve in which we can distinguish an initial slow rate, then a fast, tachytelic phase in the upper Senonian, followed by a slow but steady increase in the Tertiary.

Discussion of Selected Taxa

We can apply this method of analysis to the fossil pollen data, as well as to more restricted taxonomic groups among the angiosperms. This is especially illuminating if abundant and well-preserved pollen records exist that inspire confidence that they reflect taxonomic diversification sufficiently closely. But I must emphasize once more that the primary data, as summarized on the preceding and following diagrams, and discussed more in detail in Muller (1981a), directly reflect only pollen evolution, indirectly reflect adaptive trends in the reproductive sphere, and have mostly no relation to what happened in the rest of the plant body. This emphasizes once more the importance of studying the fossil pollen record, taking into account Recent evidence on form and function, and then integrating such information with macrofossil evidence.

If this is attempted, one can agree with Doyle (1978), Niklas et al. (1980), and Tiffney (1981) that neither the prejudice of Hughes (1976) against the evidence from Recent plants, nor the opinion of Heywood (1977) and Stebbins (1974) that fossil evidence is insignificant for an understanding of angiosperm evolution, will appear justified.

The evidence will be summarized on charts representing the distribution of contrasting groups of fossil pollen types. On these charts more emphasis is laid on the general evolutionary pattern within the group than on first occurrence only, which almost never coincides with origin due to the inherent deficiencies of the fossil record, even for such ubiquitous organs as pollen grains.

HAMAMELIDIDAE

In Figure 4, as in the following, Takhtajan's (1969) taxonomic concepts are followed, but it is realized that inclusion of Didymelaceae is debatable (Köhler, 1980) and that Dahlgren (1980) and Thorne (1976) have quite different concepts for this group.

The pollen types indicated are often abundant in the fossil assemblages due, of course, to the predominance of wind-pollination in many of the taxa included. Also, most of the pollen types are remarkably stable since their first appearance, no doubt because of the uniform, conservative anemophilic environment (cf. Crepet, 1979; Dilcher, 1979). *Alnus* pollen (Fig. 1a, b) is a typical representative of this group, which appears to show little evidence of co-evolution with insects. Anemophily may be responsible also for the frequent occurrence of an infragranulate exine structure.

However, it is clear that the tricolpate-reticulate members of the group shown, especially those commonly referred to as lower Hamamelididae, are underrepresented. As mentioned before, their ancestors could be present as early as

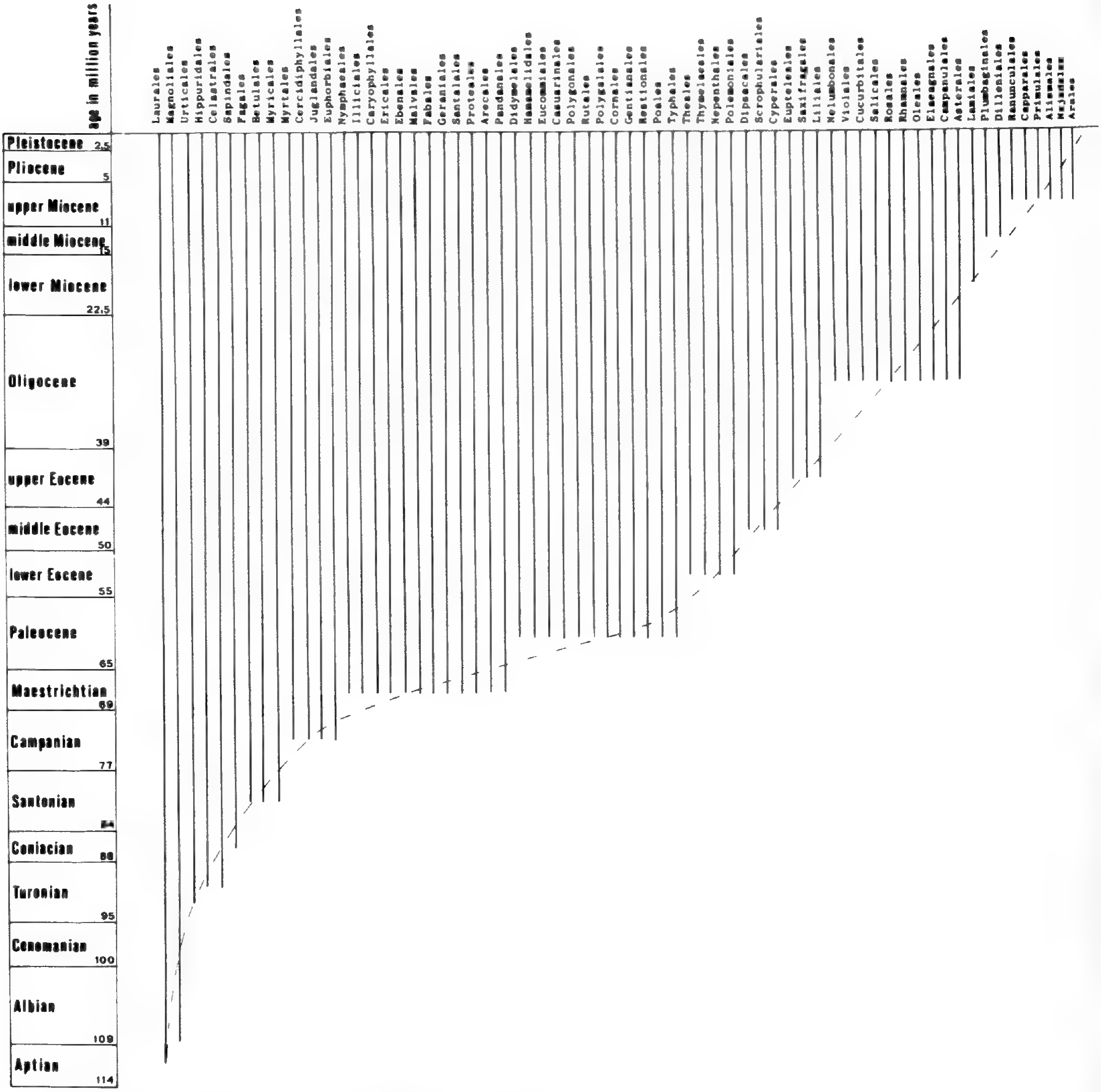

FIGURE 3. Pollen records for angiosperm orders.

the lower Cretaceous, and they may have been adapted to entomophily, since in Recent representatives like *Hamamelis* the reticulum is covered by a large amount of extremely sticky "pollenkitt" (Hesse, 1981).

The problem in the pollen morphological evolution of this group is in the transition from the tricolpate to the triporate "amentiferous" type. As already mentioned, Doyle (1969) and Wolfe et al. (1975) have suggested that the Normapolles could be transitional, but this is probable only for Betulales, Juglandales, Myricales, and Casuarinales, not for Fagales. Urticales also may have had a different origin as mentioned before.

Walker and Doyle (1975) and Wolfe et al. (1975) have also expressed doubts whether the tricolporate, subspherical, columellate-reticulate pollen of the lower Hamamelididae could have given rise to a triangular-oblate, intragranular-smoothly tectate porate anemophilous pollen type via Normapolles. It is clear that the colporate condition, which according to Doyle (1969) has preceded Normapolles development, has been preserved in few present-day higher Hamamelididae, notably in some Fagaceae (*Castanea*, *Lithocarpus*).

However, Endress (1977) has argued for a close connection between Hamamelidales, Fagales, and Betulales and of these, only Betulales conform to the above porate amentiferous pollen type.

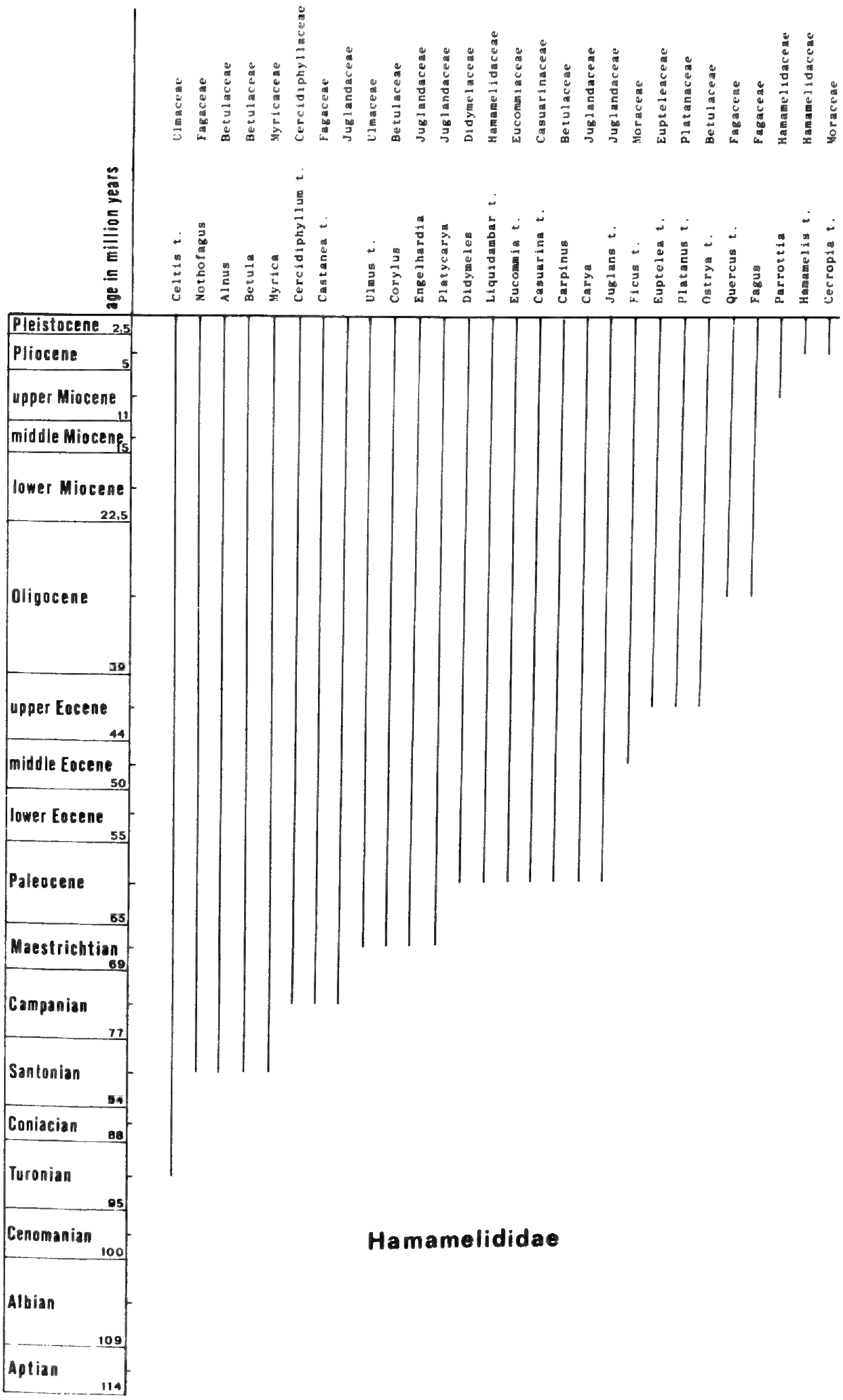

FIGURE 4. Pollen records for Hamamelididae.

Fagales, in fact, have a basically colpate-subprolate type but generally without the reticulate tectum that is so typical for lower Hamamelididae. The loss of the reticulum may be the most direct expression of the change towards anemophily. Within the Fagales, *Nothofagus* has a highly specialized, and deviating pollen type. It is thus unlikely that Fagales went from the basic tricolpate-reticulate type through a Normapolles stage to the Recent types. Rather, a *Castanea* pollen type may be placed at the base. Some of the genera that produce this pollen type, such as *Lithocarpus* and *Castanopsis,* have retained some entomophilous characters; and the pollen type that retains traces of columellar-reticulate structure at the poles is remarkably similar to certain mid-Cretaceous types.

Therefore, it is of great interest that Wolfe et al. (1975) claim, on the basis of foliar morphology, that Juglandales are allied to Rosidae, in which the colporate type is dominant and in which anemophily is rare. Because the closest connection between Normapolles and a Recent taxon is with Juglandales and not with Fagales (Skarby, 1968; Wolfe, 1973; Nichols, 1973), the idea that the Normapolles-Juglandales lineage is intermediate between the Fagales/Betulales/Myricales/Casuarinales on one hand and the Rosidae on the other may seem attractive. It would imply a lower Cretaceous differentiation before the appearance of the first Rosidae and Hamamelididae from the Turonian, and probably even before the first appearance of Normapolles in the Cenomanian. A similar view has recently been expressed by Cronquist (1981).

As already stated, it is considered unlikely that Urticales have developed from Normapolles in view of the early record of *Celtis* type pollen, although Walker and Doyle (1975) judge *Planera* (Ulmaceae) to have colporate pollen and stress the presence of arci both in Normapolles and Ulmaceae. It is likely that further study of the fossil pollen record and especially of transitions between types will provide important new evidence to help solve these questions. In this connection Zavada and Crepet's (1981) description of middle Eocene celtidoid flowers and pollen, which suggest a transitional stage between insect and wind pollination, are significant.

Regarding macrofossil evidence, there is broad agreement in the timing of the early development of at least some major groups. Rüffle (1980) raised the possibility that certain leaf remains from the lower Cretaceous could be referred to Hamamelidales (cf. also Doyle & Hickey, 1976; Hickey & Doyle, 1977), whereas the well known records of *Platanus*-like leaves from the Cenomanian onwards could be said to agree with the regular occurrence of tricolpate-reticulate type pollen in this period.

Fagaceae appear to have roots in the cenomanian, although in general Cretaceous representatives had leaves that deviated considerably from the Tertiary ones; whereas, by the middle Eocene, the family appears to have diversified strongly (Crepet, 1979). *Betula* leaves from the Santonian and betulaceous wood from the Campanian agree remarkably well with the earliest pollen records, which are from the lower Senonian (Cronquist, 1981; Rüffle & Knappe, 1977). For both Juglandaceae and Ulmaceae, the earliest upper Cretaceous pollen records antedate macrofossil finds, which are known only from the Eocene onwards.

Wolfe (1973) stated that forms showing the specialization of modern amentiferous families and orders do not become differentiated until near the end of the late Cretaceous, when pollen morphological differentiation is very pronounced also.

MALVANAE

Within the Dilleniidae, the Malvanae form a fairly well defined taxon, with very morphologically diverse pollen, but with sufficient transitional types to confirm the coherence, and to anticipate phylogenetic junctions, in the fossil record. Anemophily is rare in this group and much of the pollen diversity may have a structural basis or may reflect co-evolution with pollinators, which are known to range from insects to birds and bats. It thus forms a striking contrast with the preceding group.

The timing and mode of development of the pollen record as shown in Figure 5 differ rather strikingly from the previous group. Whereas Hamamelididae are already recorded by pollen as early as the Turonian and even earlier as macrofossils, Malvanae can, on pollen, be traced only to the Campanian and the main development is Tertiary. It is obvious that the cumulative curve is approximately straight, and that all orders included show a similar pattern. This indicates that evolutionary change in pollen characters went on at a steady rate, and suggests the action of a large number of diverse selective forces acting in the reproductive sphere. Obviously the stabilizing force of the wind has been lacking here, in contrast to Hamamelididae. It is also curious that the pollen record does not detect an early, slow phase of development, which presumably remains undetected because of uncharacteristic ancestral pollen types.

According to Walker and Doyle (1975), Elaeocarpaceae are rather primitive in Malvales and have a small, tricolporate, smooth pollen type that could be considered ancestral. Also, the fossil pollen record of Euphorbiaceae is clearly biased towards the more specialized types. Only for Bombacaceae has Wolfe et al. (1975) found evidence for a relatively unspecialized type from which the highly specialized Tertiary pollen types can be derived.

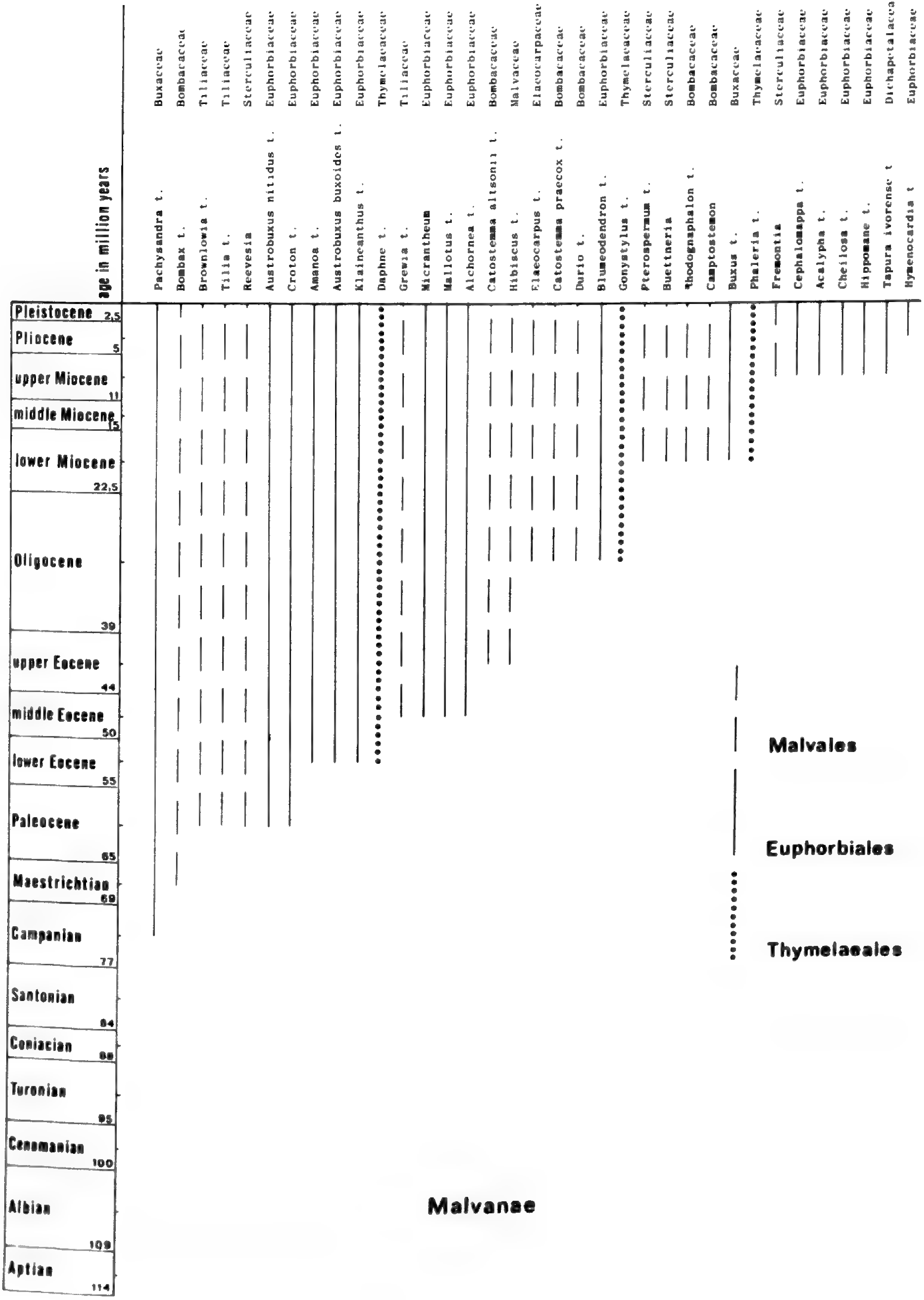

FIGURE 5. Pollen records for Malvanae.

The macrofossil record for Sterculiaceae starts earlier than the pollen record but is mainly based on leaves from the Cretaceous. Macrofossils of Tiliaceae, Malvaceae, Bombacaceae, and Euphorbiaceae, however, start appearing only in the Tertiary, in line with the microfossil evidence. Thus, as a whole the macrofossil record appears to be synchronous with the microfossil record, confirming that the pollen data as summarized in Figure 5 do reflect the general evolutionary radiation of Malvanae.

ASTERIDAE

Figure 6 shows the pollen record for Asteridae, a taxon which is more or less equivalent to the "tubiflorae" of an older generation of angiosperm systems, such as Wettstein's. The pollen

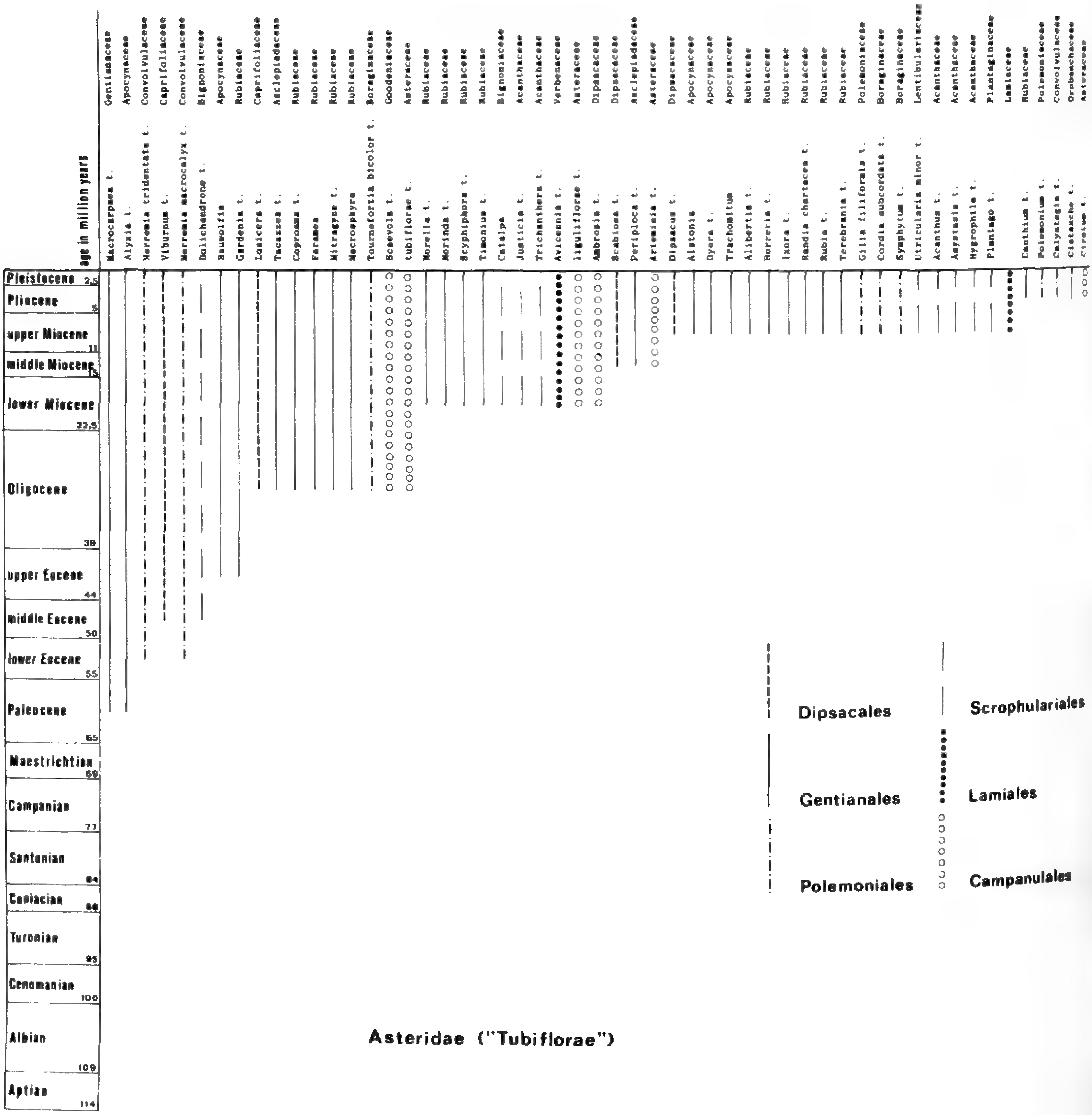

FIGURE 6. Pollen records for Asteridae.

morphological evolution in this group starts slowly in the Paleogene, accelerates markedly in the Neogene, and is probably continuing today. This clearly reflects active evolution in the reproductive sphere, and there seems to be little doubt that it indicates a process of co-evolution with long-tongued insects, although pollen/stigma interactions, germinating efficiency, and harmomegathy may also have been important. Especially in Asteraceae, the latter factor may have been dominant (Bolick, 1981).

There appears to be some difference in timing of main development, with Dipsacales, Gentianales, and Polemoniales appearing earlier than Scrophulariales, Lamiales, and Campanulales.

Macrofossil evidence partly supports the timing suggested by the pollen record, although Caprifoliaceae and Apocynaceae are known from the Cretaceous already.

The presence of Gentianaceae in the Paleocene has recently been documented by Crepet and Daghlian (1981) based on funnel shaped flower remains containing *Pistillipollenites macgregorii* pollen, which is comparable to pollen of the Recent genus *Macrocarpaea*. This record was not quoted in Muller (1981). Caprifoliaceae become abundant in the Tertiary, Boraginaceae are known from the Eocene, Rubiaceae appear in the Eocene, and Bignoniaceae are first recorded from the Oligocene. The macrofossil record of Asteraceae is very limited and appears restricted also to the Tertiary.

The earlier appearance in the macrofossil record of Caprifoliaceae and Apocynaceae agrees with the difference in the microfossil record but is out of phase. This again may indicate mosaic evolution, leaf characters developing earlier than pollen characters, because they are obviously not likely to have been influenced by evolving pollinators, whereas flower evolution in the Asteridae probably started more or less simultaneously with insect evolution. According to Crepet (1979), entomophily was already well developed in the middle Eocene, and fossil flower types from this period indicate the presence of four orders of anthophilous insects, whereas the gentianaceous flower from the Paleocene indicates even earlier bee pollination (Crepet & Daghlian, 1981).

The three cumulative curves from the groups discussed before are shown together in Figure 7 for easy comparison. The significance of the pollen data here is that they suggest differences in timing of evolutionary development in those character complexes related to the reproductive sphere and, in a more general and indirect way, differences in taxonomic diversification. For Hamamelididae, a fast, tachytelic phase in the upper Cretaceous is followed by a bradytelic one characterized by slow diversification. Malvanae show a constant rate of diversification, but an early tachytelic phase may have gone undetected in the pollen record. The curve for Asteridae suggests that this group is still essentially in a tachytelic phase, adapting since the Tertiary to a large variety of environmental conditions.

LEGUMINOSAE (FABALES)

Figure 8 shows the contrasting records for the three main groups of Leguminosae. Caesalpiniaceae appear as the oldest, with a strongly diversified number of pollen types. Macrofossils from the Maestrichtian confirm the earliest occurrence of pollen for this taxon.

Mimosaceae are recognizable as soon as their characteristic polyads appear in the middle Eocene, and tetrad pollen has been found associated with mimosoid flowers from the same period (Crepet & Dilcher, 1977) indicating a phase of active evolution in flower structure. An earlier tricolpate phase of single grains may have gone undetected, however.

Fabaceae are nearly absent in the fossil pollen record, presumably because of the low pollen productivity and lack of characteristic pollen types.

This picture broadly agrees with Raven and Polhill's (1981) views on the development of the legumes as a whole. They assume a Cretaceous development for Caesalpiniaceae with a Paleogene radiation of the main branches of the tropical, woody legumes (Caesalpiniaceae, Mimosaceae, and Fabaceae) and a proliferation of advanced Fabaceae in the Neogene is postulated.

MONOCOTYLEDONS

As may be recalled, the first monocotyledonous pollen types have been recognized in the Aptian, but these cannot be more closely identified, and the same difficulty holds true for most of the succeeding Cretaceous types. It may be significant that the pollen of the first modern groups appears only in the upper Cretaceous, as will now be discussed more in detail.

RESTIONACEAE (COMMELINIDAE)

Among the most intriguing monocotyledonous groups well represented in the fossil pollen record are the Restionaceae, starting in the Maestrichtian. As shown in Figure 9 and discussed recently by Hochuli (1979), the fossil distribution for this taxon is quite different from the Recent one, indicating that the present range is a relict one. A Gondwana origin is likely, however, from which extensions northwards to Europe and North America became possible. The Maestrichtian occurrence in West Africa, coupled with the total absence of restionaceous pollen in the Tertiary of tropical South America and India, indicates that migration northwards took place via Africa. Hochuli (1979) has suggested that *Rhizocaulon*, a macrofossil occurring in the Upper Cretaceous and Tertiary of western Europe, may be related to Restionaceae, but this plant shows rather profound points of difference with the Recent genera of this family, and its pollen has not yet been isolated from its fructifications.

POACEAE (GRAMINEAE)

The first, rather doubtful, fossil grass pollen grains appear in the Campanian. They are scarce

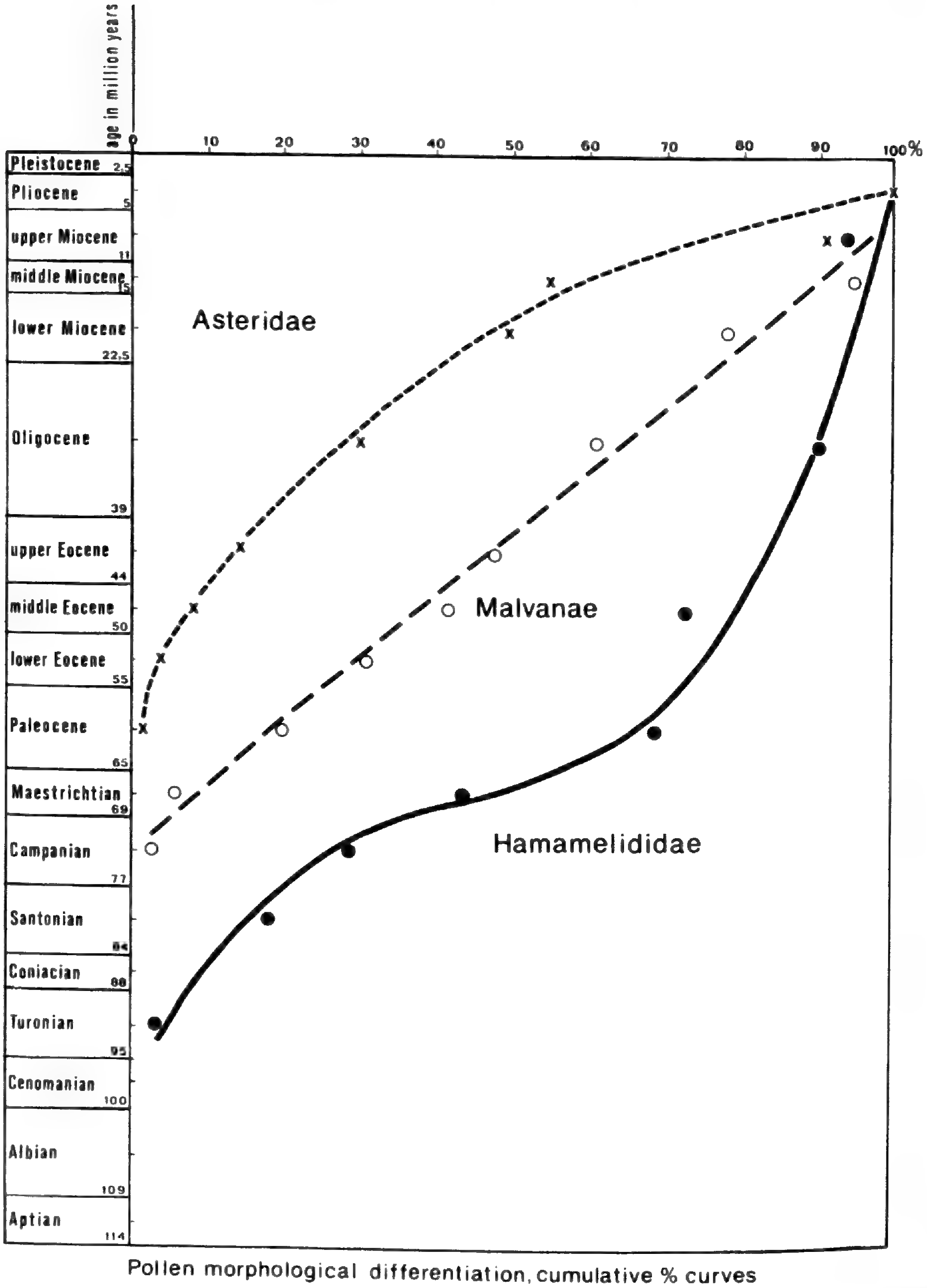

FIGURE 7. Cumulative % curves for Hamamelididae (dots), Malvanae (circles), and Asteridae (crosses).

and badly preserved. Firm records date from the Paleocene and they become increasingly abundant in the course of the Tertiary.

Although macrofossil remains of this family have been described already from the Cretaceous, firm records based on caryopses date only from the Lower Eocene (Daghlian, 1982). This confirms the impression that the main development of the family started only in the earliest Tertiary. Its pollen record, however, partly will reflect the adaptation towards anemophily (cf. Takhtajan, 1969: 238).

CYPERACEAE

The characteristic pollen grains of this family are first found in the Middle Eocene and this agrees well with the macrofossil record, which starts with fruits in the Lower Eocene of England.

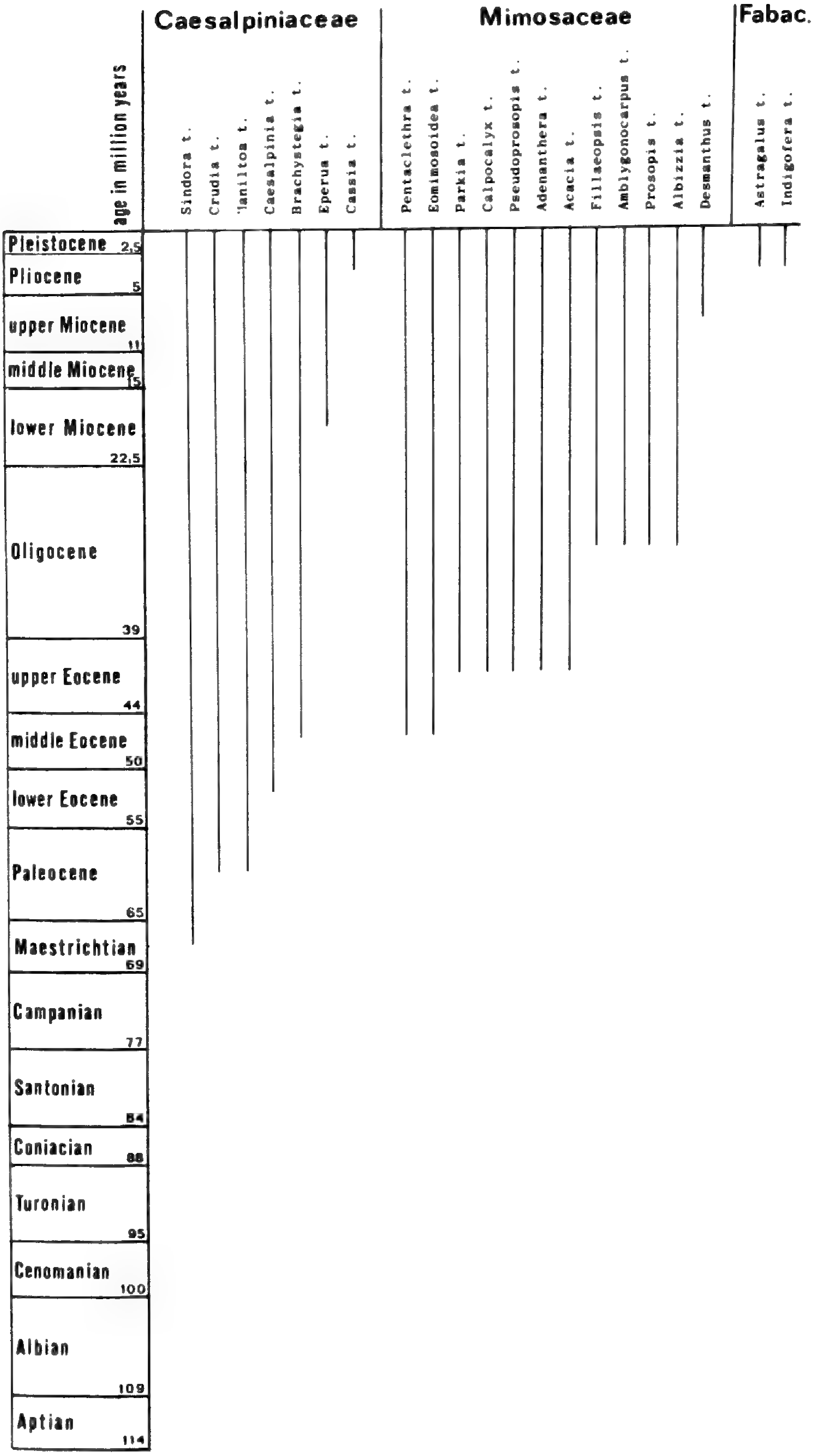

FIGURE 8. Pollen records for Fabales.

Earlier macrofossil records of Cyperaceae are considered dubious (cf. Daghlian, 1981).

ARECACEAE (PALMAE) (ARECIDAE)

Whereas the preceding monocotyledonous families each had a fairly uniform pollen type, Palmae are much more diversified in this respect. The distribution of the recorded types is shown in Figure 10. Again, the more characteristic lepidocaryoid types dominate here, but taking other, less clearly identifiable types into account, the microfossil record suggests a lower Senonian diversification phase in West Gondwanaland, and a second diversification in Southeast Asia must

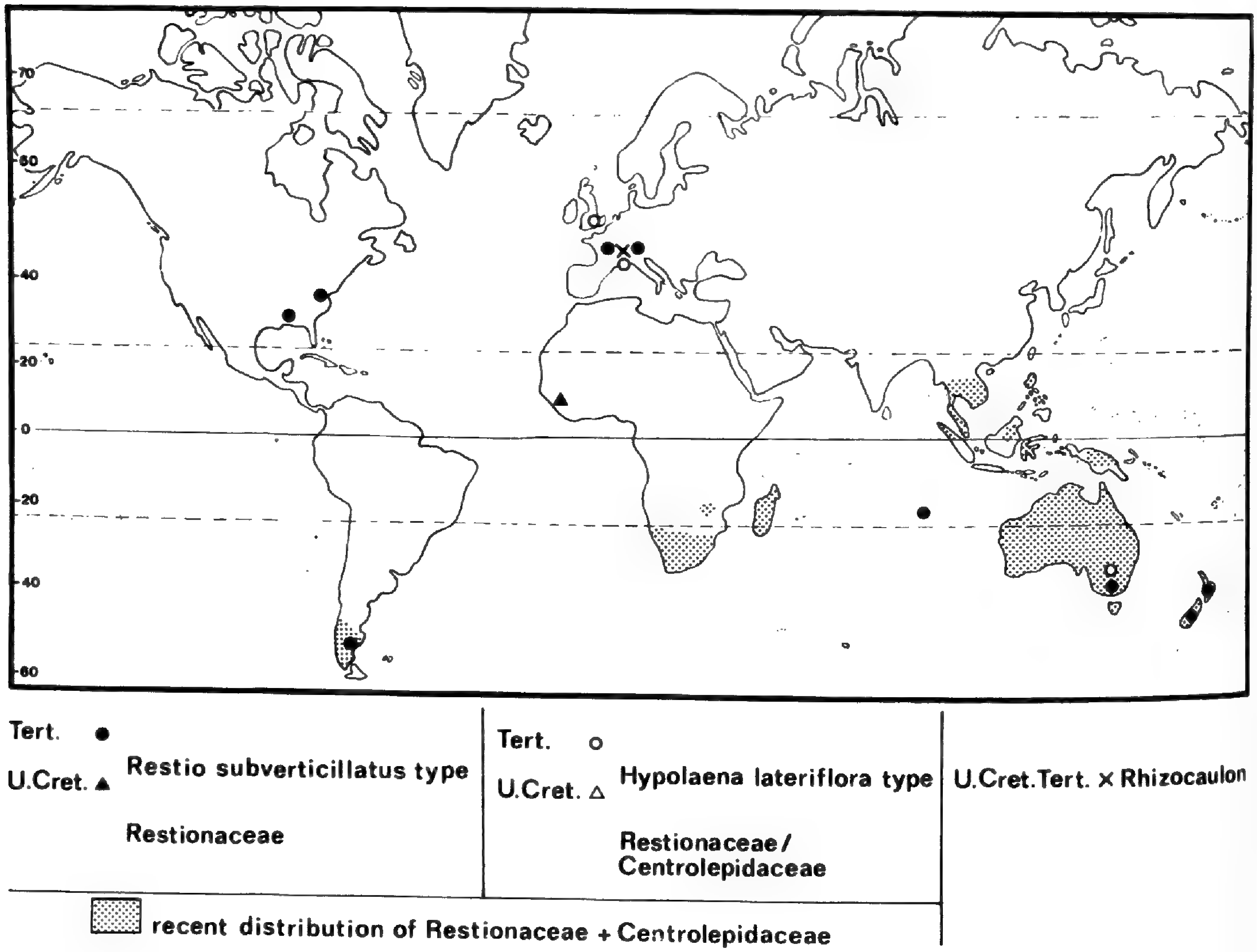

FIGURE 9. Recent and fossil distribution of Restionaceae and Centrolepidaceae.

have taken place in the Tertiary (Muller, 1979b). The macrofossil record supports this picture because fossil palm wood starts appearing regularly in the Senonian, and both leaves and stems occur in the Santonian of North America (Daghlian, 1981).

A Gondwana origin is postulated by Moore (1973) and Dransfield (1981) on the basis of Recent distribution patterns and a revised taxonomy. It is not at all clear what factors have caused this relatively late development, although an obviously secondary development of the only major woody group of monocotyledons, from semiaquatic herbaceous ancestors in the Lower Cretaceous, which has taken considerable time to achieve, is indicated.

PANDANALES

According to the pollen records, this group starts occurring in the Maestrichtian, although fossil fruits have been described from the Lower Eocene of India. These, however, are not certain to belong to Pandanaceae according to Daghlian (1981).

TYPHALES

Tetrad pollen of Typhaceae is recorded from the Paleocene onwards and single grains that can belong either to Typhaceae or Sparganiaceae also date from this period. Sparganium fruits have been described from the Paleocene, while macrofossils of Typha have been recorded from the Eocene (Daghlian, 1981), indicating good agreement between micro- and macrofossils and suggesting a Paleocene development of the family.

Looking back on the monocotyledonous record as a whole, one can dimly discern the presence, already in the Lower Cretaceous, of an older branch represented by vaguely identifiable types which probably have been produced by ancestral Alismidae and Liliidae, while somewhat later, in the Upper Cretaceous, firmer evidence for the development of Commelinidae and Arecidae appears.

The relatively late appearance of Gramineae and Cyperaceae supports in particular the view of Stebbins (1974) that these families are highly advanced and actively evolving young branches of the monocotyledons.

It is, however, clear that a much closer study of the Cretaceous macro- and microfossil record will be necessary to confirm this tentative picture.

EVOLUTIONARY MODEL

So far, we have discussed large scale taxonomic diversification. It may be worthwhile to consider smaller scale phenomena also, because here we may have a chance to detect the evolutionary process at work. Most angiosperm pollen types appear fairly sudden in the geological record and that clearly transitional series, even in thick sedimentary sequences known to be nearly continuous, such as the Eocene Maracaïbo basin in Western Venezuela or the Neogene northwest Borneo geosyncline, with which I happen to be familiar, are scarce.

To generalize too much about evolutionary processes on the basis of a single organ, i.e., the pollen grain, is dangerous; but because pollen is involved in the critical reproductive phase of fertilization and clearly shows abundant shifts in a suitable series of sediments, some worthwhile facts may emerge. Will we find a situation reflecting Darwin's view of a myriad intermediates or a sequence of punctuated equilibria? The lack of intermediates in macropalaeobotany has recently been commented upon by Stidd (1981: 96–97), and evolution in plants is as likely to proceed via punctuated equilibria as it is in animals (Gould & Eldredge, 1977).

In theory, an equilibrium situation in pollen characters may be disturbed without the rest of the plant being affected, except that the overall efficiency and competitive power (level of adaptation) may change for better or worse, either intraspecifically leading to population shift or interspecifically causing competition followed by replacement and extinction. Three different cases will be discussed.

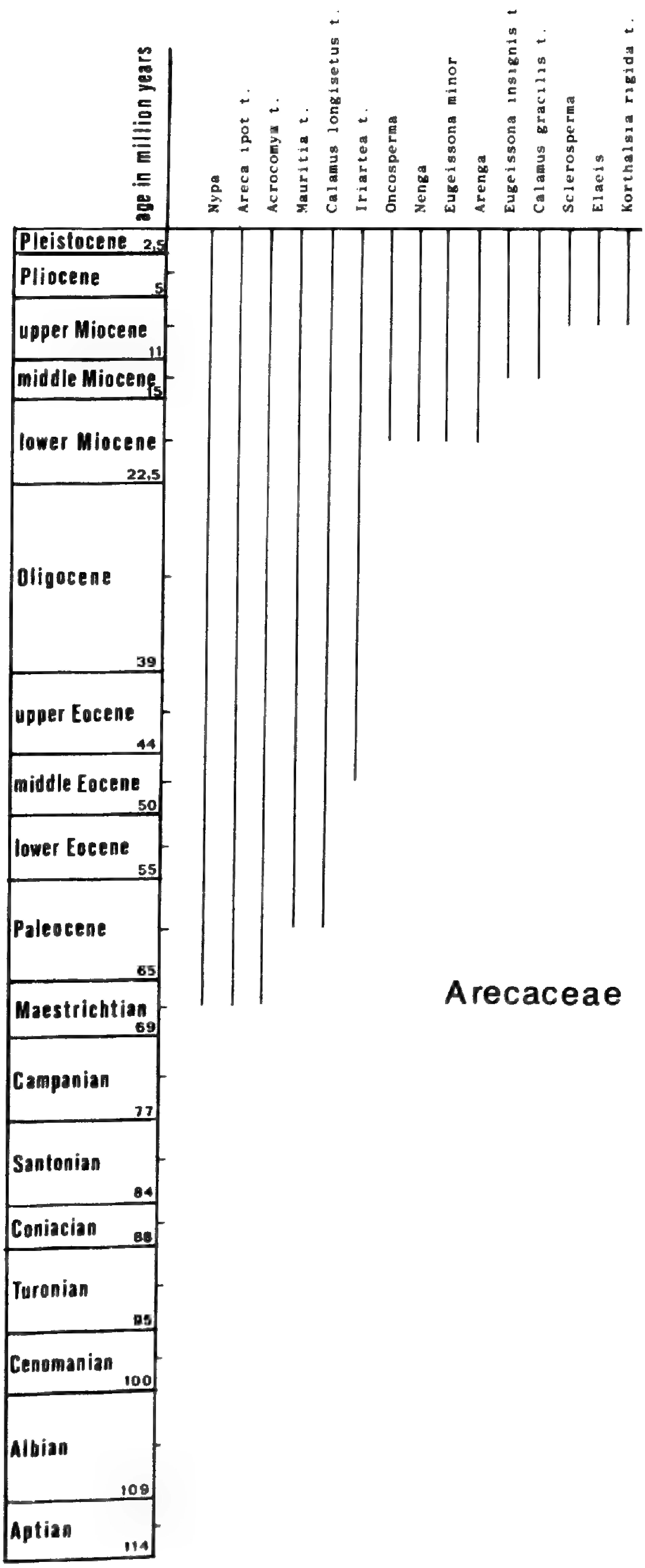

FIGURE 10. Pollen records for Arecaceae.

1. Santalales. It has been argued that the extinct group of plants that produced *Aquilapollenites* type pollen, and that was common in the upper Cretaceous of part of the northern hemisphere, was related to Santalales based on its resemblance to certain present-day loranthaceous and santalaceous pollen types (Jarzen, 1977).

By comparison with Recent harmomegathic types, the peculiar morphology of this genus can be described as a multidimensional harmomegathic stress system. The oblate, disc-shaped pollen types of certain Loranthaceae, in contrast, show a concentration of harmomegathic movement along the polar axis and could be derived from an *Aquilapollenites* ancestral type by a fairly simple structural change. This change may have been accompanied by a change in pollination mode, since the *Aquilapollenites* types were more abundant in the Upper Cretaceous than the succeeding loranthaceous types, which first occur in the Lower Eocene but remain scarce. Actually, the crucial transitional stages have not been discovered yet, suggesting that small populations were involved. Probably only a minor part of the *Aquilapollenites* complex succeeded in branching off in a new adaptive niche and most of its species die out of the top Cretaceous. An alternative interpretation of the evidence would be to assume an independent origin of Loranthaceae from a much earlier ancestral santalaceous complex that also gave rise to the *Aquilapollenites* group in mid-Cretaceous times. Wiggins (1982) suggested that *Expressipollis striatus* from the Campanian of Alaska can be assigned to Loranthaceae, and this species thus could form part of a transitional series.

This separate development is even more likely for Olacaceae and Santalaceae, because some of their genera have retained a basic tricolporate pollen type that shows no obvious relation to *Aquilapollenites*. Moreover, in Olacaceae advanced pollen types, like the *Anacolosa* type are quite different from *Aquilapollenites* and appear already in the Maestrichtian, suggesting an even earlier origin for this family.

Anacolosidites striatus from the Campanian of Alaska, claimed by Wiggins (1982) to represent Olacaceae, is more probably loranthaceous.

Thus, although the *Aquilapollenites* complex could be placed taxonomically in Santalales as an extinct family, with closest affinity to Loranthaceae, its exact phylogenetic relationship within the order remains to be discovered.

2. Juglandales. Rather more firmly established is the connection between Juglandales and the preceding Normapolles group, the morphological link between which has already been discussed in a previous paragraph. As in the preceding case, most Normapolles plants became extinct, some as late as Eocene, but a few appear to have given rise, by abandonment of the highly specialized apertural adaptations typical for the group, to a new line of evolution. Nichols (1973) has studied these early Juglandales in detail and it appears here also that the transitional populations may have been small. The subsequent evolution leading towards pollen types such as those of *Engelhardia, Carya, Platycarya,* and *Pterocarya* can, however, be followed in great detail and appears to be quite gradual, making it difficult to establish precise taxonomic separations. Structurally, these later pollen types do not diverge strongly and all remain typical wind pollinated forms. Taxonomically the Normapolles group can be recognized as an extinct family within Juglandales.

3. Sonneratia. On a much smaller scale is the origin of the genus *Sonneratia.* As shown in Figure 11, two Recent pollen types, which are restricted to two good species that hybridize but produce infertile offspring, were found to originate via a short-lived phase of small transitional populations, from an extinct ancestral type resembling certain lythraceous pollen types (Muller, 1978). This diagram clearly shows the typical branching pattern of the punctuated equilibrium model of Eldredge and Gould (1972).

The critical transition of the pollen characters involves a short period of morphological reconstruction that can be interpreted as a rearrangement of the harmomegathic stress system (Muller, 1981b). The striking subsequent increase in abundance testifies to the ecologic success of the new taxa, which presumably competed directly with the less specialized parent plant. However, what other factors have been involved remains quite unknown in the absence of macrofossils.

As far as pollen characters are concerned, the evolutionary process has still not stabilized itself, as witnessed by a large degree of morphological variability still present, and the hybridization between several species of the genus (Muller, 1969; Muller & Hou-Liu, 1966).

The early ancestors of this complex may have been plants from the Tethys shores, adapted to insect pollination, although *Sonneratia* is now adapted to pollination by fruit-eating bats, which appear in the fossil record about at the same time as the first pollen records (Muller, 1978).

The critical factor for this evolutionary development is, of course, reproductive isolation. Pollen variability, as present in the Recent species of *Sonneratia,* in itself does not promote isolation except when crosses tend to increase pollen infertility. The changes anticipated in some of the Recent populations of *S. alba* and *S. caseolaris* could conceivably lead to another new species in this way, but to be evolutionarily successful, the new species has to change its ecology also, in order to invade a new niche or to replace its parent, as probably happened in the early Miocene.

The lesson from this is that pollen development, in addition to seed and embryo development, is closely related to the coming into existence of reproductive isolation, much more probably than wood or leaf characters. After all, a cross between two leaf types almost always will result in a new leaf shape, which must be of about equal efficiency as the parent leaves, but cannot influence reproductive isolation, except very indirectly if a shift in niche results. Taxonomically, the pre-Miocene taxa appear to be intermediate between Lythraceae and Sonneratiaceae and may represent a distinct genus, ancestral to the younger species of *Sonneratia.*

When these three examples are compared, it will be clear that, for obvious reasons, the most detailed evidence has been obtained for a group of mangrove taxa; but Juglandaceae may have evolved in or close to a river floodplain and thus also have left a fairly continuous record. For the Santalales complex, evolution may have taken place far from depositional areas, however. This confirms Axelrod's (1970) claim that only in cases where evolution takes place close to the coast can the process itself be detected.

All cases agree in that they appear to follow the punctuated equilibrium model in showing evidence for small transitional populations, followed by more gradual evolutionary change. They also agree in the presence of extinct ancestral complexes that link younger descendants.

Obviously, a similar process could be postulated for the earliest evolution of the angiosperms as a whole.

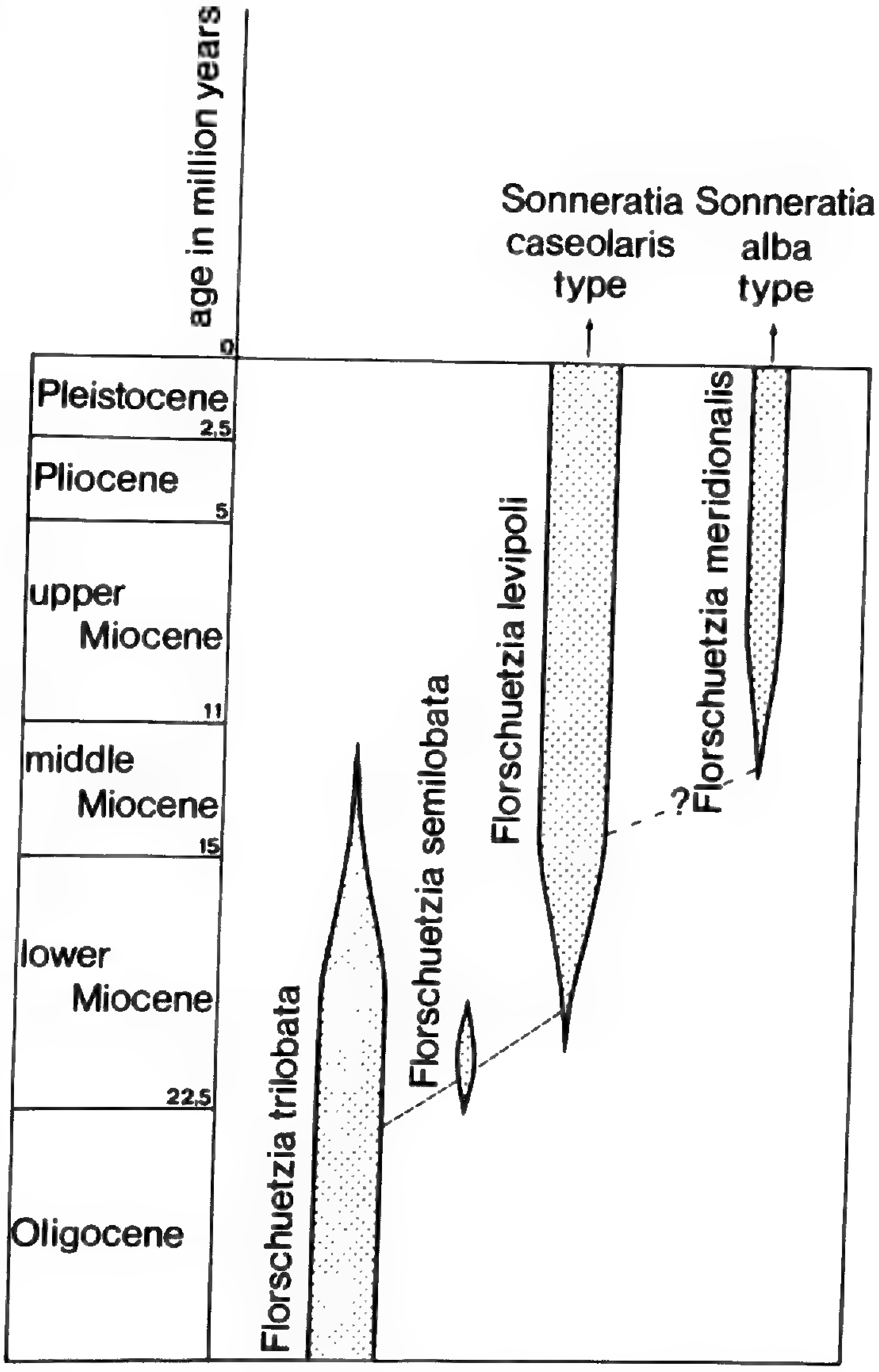

FIGURE 11. Pollen records for Sonneratiaceae in West Malesia.

AGE AND ADVANCEMENT INDEX

In the preceding discussion the fossil pollen record was compared with the taxonomic subdivision of Takhtajan (1969), but taxonomic subdivisions are subjective, especially at higher levels and many different systems exist.

A more objective approach is to compare directly with the character complexes of the taxa, and for this purpose Sporne's (1982) advancement index (A.I.) of dicotyledonous families is available, in which a low index would indicate families that have retained a high proportion of 'primitive' character states. A cardinal difficulty in Sporne's approach has always been the danger of circular reasoning and any support from fossil evidence would be decisive in testing the prediction that families with a high A.I. would appear later in the record than those with a low A.I. Sporne (1980) himself had already tested the earlier data published in 1976 and found that the prediction could be confirmed. On the basis of the present data and of Sporne's latest list of 1980, I retested the prediction and the resulting scattergram is shown in Figure 12. Obviously, a large amount of scatter is present, which is no doubt due to a number of disturbing factors: entomophilous taxa will be recorded later than anemophilous ones, coastal species tend to be recorded earlier than inland species, and families that contain both unspecialized and advanced pollen types tend to be recorded only when the latter have evolved. Nevertheless, the expected correlation, if weak ($r = -0.3$), is there and highly significant ($P > 0.95$). If we look at the averages for certain periods we can see that they are situated approximately on a straight line.

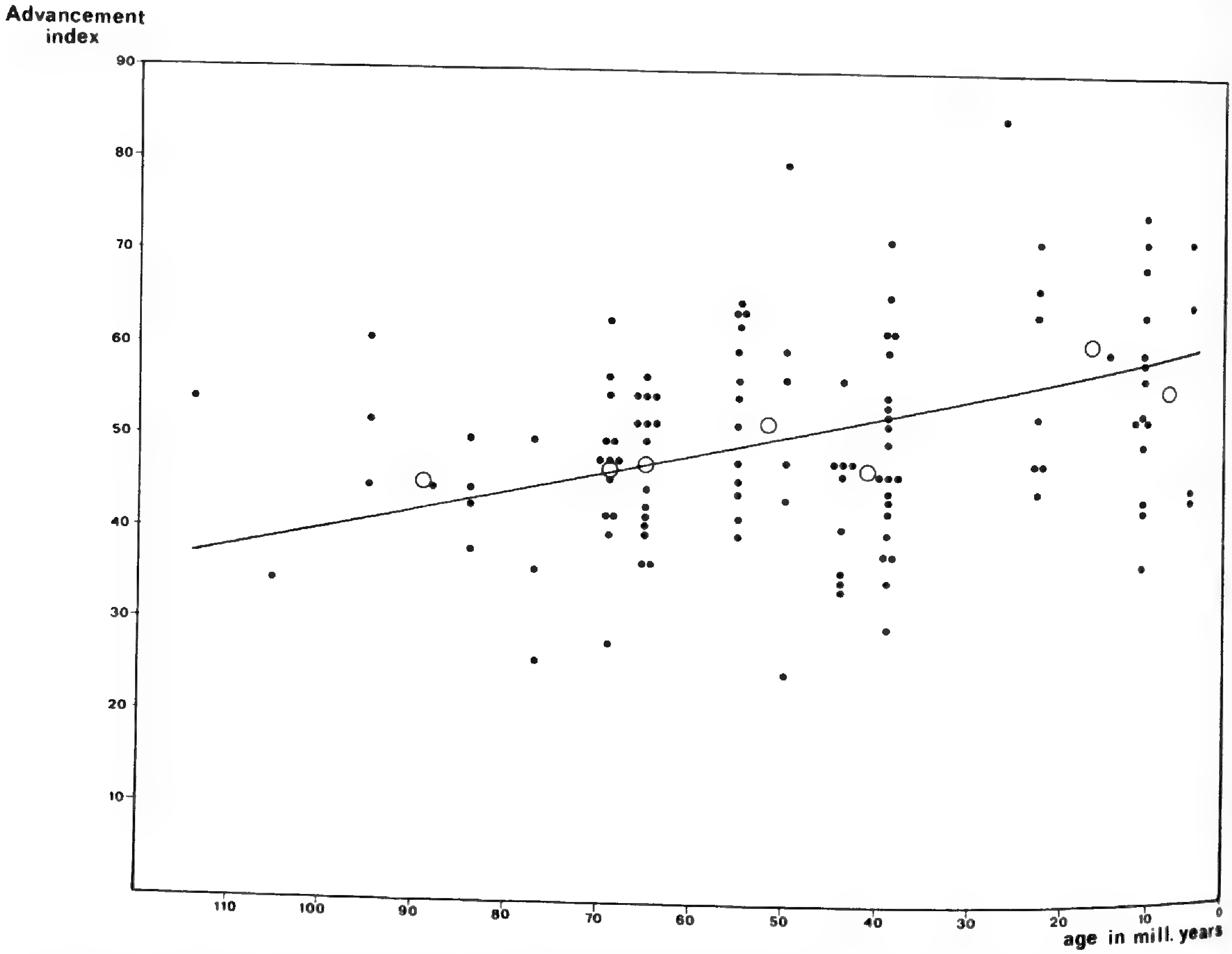

FIGURE 12. Relation between age of first pollen record and Sporne's advancement index for dicotyledonous families. Pearson's product-moment correlation $r^2 = -0.3$; $P < 0.05$, df = 116. Data based on Muller (1981) with the addition of Gentianaceae—Paleocene (Crepet & Daghlian, 1981) and a change of Winteraceae from Maestrichtian to Aptian/Albian (Walker et al., 1983).

Perhaps the results become more meaningful in Figure 13, which shows the relation between A.I. and first occurrence for about 52 selected families. For these families, the pollen record is exceptionally reliable or extensive.

It may be noted that, if Sonneratiaceae are merged with Lythraceae, the correlation improves. In fact, the difference in A.I. between these two closely related families is very much influenced by the woody character of the former and the many advanced herbs in the latter.

Most striking is the contrast between the Cretaceous plus Paleocene and the post-Paleocene families, but clearly families like Winteraceae and Schisandraceae are prime examples of families with a low A.I., which can only be detected when their specialized pollen types appear. Magnoliaceae, as stated before (Muller, 1970) are probably completely underrepresented and, were it not for the significant ancestral chloranthaceous and winteraceous grains in the lower Cretaceous, our survey would hardly have produced any significant information on the earliest phase of angiosperm development at all.

One can also test which of the character complexes used by Sporne (1980) show the closest correlation with age of first pollen record. This has been attempted by Baas (1982) for xylem characters. He comes to the conclusion that families recorded from the Cretaceous show a higher incidence of primitive vessel, fiber, and parenchyma features than those that appear in the Tertiary, thus confirming the well-known "Baileyan trends" in xylem evolution.

The apparent straight line relation between age of first occurrence and A.I., if extrapolated, strongly suggests a Jurassic 'origin' for the angiosperms as a whole. This can also be tested in a different way, by plotting the time of first appearance on the diagram, published by Stebbins (1974, fig. 11-1), based on Cronquist (1968), which includes the monocotyledons and also ar-

Advancement Index	Cretaceous	Paleocene	Eocene	Oligocene–Pliocene
71–75				Acanthaceae Compositae
66–70				Plantaginaceae
61–65	Chenopod./Amaranth. Haloragaceae		Loranthaceae Nyctaginaceae Santalaceae	
56–60	Proteaceae	Apocynaceae	Convolvulaceae Lythraceae Malpighiaceae Umbelliferae	
51–55	Onagraceae Chloranthaceae Ulmaceae	Icacinaceae Polygalaceae Anacardiaceae	Thymelaeaceae Alangiaceae	
46–50	Juglandaceae Myricaceae Sapotaceae Leguminosae Symplocaceae Olacaceae	Casuarinaceae	Lecythidaceae Malvaceae Rubiaceae	Sonneratiaceae Trapaceae
41–45	Aquifoliaceae Myrtaceae Sapindaceae Fagaceae Bombacaceae Ericac./Clethrac.	Didymelaceae Tiliaceae	Caryocaraceae Guttiferae	
36–40	Annonaceae Betulaceae Buxaceae	Euphorbiaceae Hamamelidaceae	Rhizophoraceae	
31–35	Winteraceae			
26–30	Schisandraceae			

FIGURE 13. Age of first pollen record and Sporne's advancement index for selected families.

ranges the families according to their relative advancement, estimated differently from Sporne, however. Here also, Asteridae stand out as the youngest and most advanced angiosperms. As is well known, this group also has the highest proportion of herbaceous types within the dicotyledons, supporting the notion, first formulated by Sinnott and Bailey (1914) nearly 70 years ago, that, in general, woodiness is primitive and herbaceous growth habit advanced within dicotyledons. Note, however, that within the monocotyledons the woody palms appear young and were probably derived from herbaceous or shrubby ancestors, as also postulated already by these same authors.

As in the correlation diagram shown previously, this diagram also shows the central hole of very low A.I., through which, metaphorically speaking, the earliest angiosperms have emerged undetected as yet by any pollen or macrofossil record and not having survived unchanged in the Recent flora.

CONCLUSIONS

The significance of the fossil pollen data, which I have attempted to show here, thus covers the whole spectrum, from a broad view of the development of the angiosperms as a whole with a first pollen record from the Barremian but probably originating earlier; to the early split between monocotyledons and dicotyledons; to the split within the dicotyledons between woody Ranales and a more advanced group; to the achievement of dominance in the vegetation by successful competition with gymnosperms and ferns; to the crystallization of most orders of angiosperms in the course of the Cretaceous, and of many modern families and genera in the Cretaceous and Tertiary; and finally to the origin of some modern species in the younger Tertiary.

Of course, any taxon starts as a species, and the connection with the Recent flora just represents a fleeting moment in time, frozen in our Recent taxonomy. To adopt the rules of modern taxonomy to fossil groups takes special care but is possible, as long as we always remember that a taxon is constructed by the independent evolution of character complexes. Wood and pollen evolution, as well as leaf and pollen evolution, thus, have hardly any common factors, but flower and pollen evolution are much more closely linked and it may be argued that much of what we see in the fossil pollen evolution reflects, in essence, the struggle for outbreeding by improvement of the changes for cross pollination.

The palaeobotanical data as a whole show more and more clearly the different timing of first occurrence of characters as well as the shorter or longer period of evolutionary coherence that follows. Clausen and Hiesey (1960) have shown that a genetic basis can be found for the difference between a variable and a uniform period in the life of a taxon, and Gould and Eldredge (1977) have drawn attention to the significance of periods of stasis in their interpretation of the fossil record.

Possibly the pre-magnoliid plants from the early Cretaceous ancestral to Chloranthaceae and Winteraceae have existed for an even longer time than their pollen record indicates.

In general, Chloranthaceae are considered to combine a primitive wood anatomy and pollen morphology with highly reduced and specialized reproductive structures (cf. Stebbins, 1974: 123).

Leroy (1983) has recently challenged the current interpretation of the chloranthaceous flower, which he considers to be primitive and primarily anemophilous. In particular, the strobiloid nature of the male flower of *Hedyosmum* would bring this genus close to the elusive angiosperm ancestors.

In Winteraceae, a more specialized pollen type, which had already evolved in the Aptian/Albian, is combined with primitive reproductive structures and vesselless wood.

In both cases, it would appear that reproduction has not changed much since the lower Cretaceous and was probably dependant on the same pollinating agents as today.

At the other extreme, we have seen that the 'tubiflorous' families, adapted to specialized insect visitors, and Sonneratia, adapted to bat pollination, are young groups, and that in the latter, 'stasis' in pollen characters has not been achieved yet.

More indirectly, the fossil pollen evidence indicates the younger are of the herbaceous dicotyledons and confirms the predicted correlation with advancement indices.

For the monocotyledons, the secondary development of the woody palms is clearly shown, as well as the young development of Gramineae and Cyperaceae, which may have played a role in the extinction of the Restionaceae in the northern hemisphere.

The recognition of extinct groups of angiosperms on the basis of the pollen record is paralleled by recent palaeobotanical research on macrofossils and tends to challenge further the formerly widely held idea that the middle Cretaceous angiosperm flora contained many modern taxa, some exceptions (*Platanus*) notwithstanding. But even these early extinct groups can be related to present-day taxa and thus incorporated in the body of taxonomic knowledge.

The question of external factors providing periodic impulses for accelerated angiosperm evolution concentrates on the modernization in the Maestrichtian, in which many unrelated taxa appear to be affected. One can think of climatic factors, such as a radiation maximum, decrease of grazing pressure of dinosaurs, and evolution of chemical defenses, to mention a few possibilities. Rather more firmly established is the role of changing climates in the evolution of herbaceous groups in the course of the Tertiary, and the co-evolution with specialized insect and bat groups in the mid-Tertiary.

To a certain extent, the fossil pollen data provide support for a view of angiosperm evolution as a fairly gradual additive process, proposed recently by Tiffney (1981).

Remaining is the mystery of the origin of the angiosperms. If I were bold enough to express an opinion here, I would follow Stebbins (1974) and Doyle (1978) and say that they probably lived in a semi-arid inland environment in West Gondwanaland, not that they were coastal plants, as recently proposed by Dilcher and Retallack (1981). Thus, the lack of transitional types with gymnosperms, although regrettable, becomes at least understandable.

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ANGIOSPERM ORIGINS AND EVOLUTION BASED ON DISPERSED FOSSIL POLLEN ULTRASTRUCTURE[1]

MICHAEL S. ZAVADA[2]

ABSTRACT

Wall ultrastructure of fossil-dispersed pollen has recently played an important role in increasing our understanding of the origin and early evolution of angiosperms. The criteria currently used to determine the affinities of fossil-dispersed pollen is discussed in relationship to homologies of gymnosperm and angiosperm wall layers based on biochemical, developmental, and morphological data. The bearing of these data on our present interpretation of angiosperm origins and early evolution is discussed along with new data on the wall structure of early Mesozoic dispersed pollen.

The phylogenetic significance of pollen was first recognized by Wodehouse (1928, 1936) long before palynology became a separate botanical subdiscipline. Since Wodehouse's time numerous comparative morphological pollen studies have been initiated with the intent of elucidating taxonomically significant pollen characteristics and the phylogenetic relationships of various plant groups. One of the most intensely studied groups with regard to pollen morphology and phylogeny is the ranalean complex (e.g., Walker, 1974a, 1974b, 1976). The monocots have not received the attention lavished on ranalean taxa, but there have been significant studies of monocot pollen that provide a basis for a preliminary phylogenetic overview (Kuprianova, 1948; Zavada, 1983a). One objective of paleopalynologists is to provide additional data that can either support, refine, or refute these proposed phylogenetic schemes based on studies of extant pollen. Until recently, corroborative fossil evidence has been scanty. However, this situation is being improved by the employment of new techniques that allow a wider range of morphological features to be used in elucidating the taxonomic and phylogenetic relationships of fossil-dispersed pollen [e.g., single pollen grain investigations with scanning electron microscopy (SEM) and transmission electron microscopy (TEM)]. The intent of this paper is to review data on fossil-dispersed pollen and provide new data that bear upon our current understanding of the origin and early evolution of angiosperms. A brief summary of the phylogenetic relationships believed to exist among the primitive dicotyledons and monocotyledons based on comparative palynological studies of extant angiosperms is presented before the fossil evidence is reviewed. This is followed by an examination of the criteria used to distinguish fossil angiosperm pollen from pollen of other major plant groups (e.g., gymnosperms). The establishment of good taxonomic criteria to distinguish pollen of major plant groups is necessary before the phylogenetic implications of the fossil pollen record can be fully appreciated. The value of the dispersed Mesozoic pollen record in clarifying angiosperm origins and evolution is then discussed against the background of these data.

PHYLOGENETIC RELATIONSHIPS OF EXTANT ANGIOSPERM POLLEN

Although there are numerous studies of pollen morphology and wall structure of ranalean taxa, Walker's (1974a, 1974b, 1976) studies are the most comprehensive. He has determined that monosulcate, predominantly atectate or granular walled pollen grains are the most primitive among dicotyledons. This implies that pollen with these features should be encountered in the geologic section prior to derived pollen types; i.e., multiaperturate, tectate-columellate, perforate, or imperforate pollen. Among monocotyledons, monosulcate pollen is also viewed as primitive (Kuprianova, 1948; Walker & Doyle, 1975), however, comparative morphological studies have shown that in monocotyledons the tectate-

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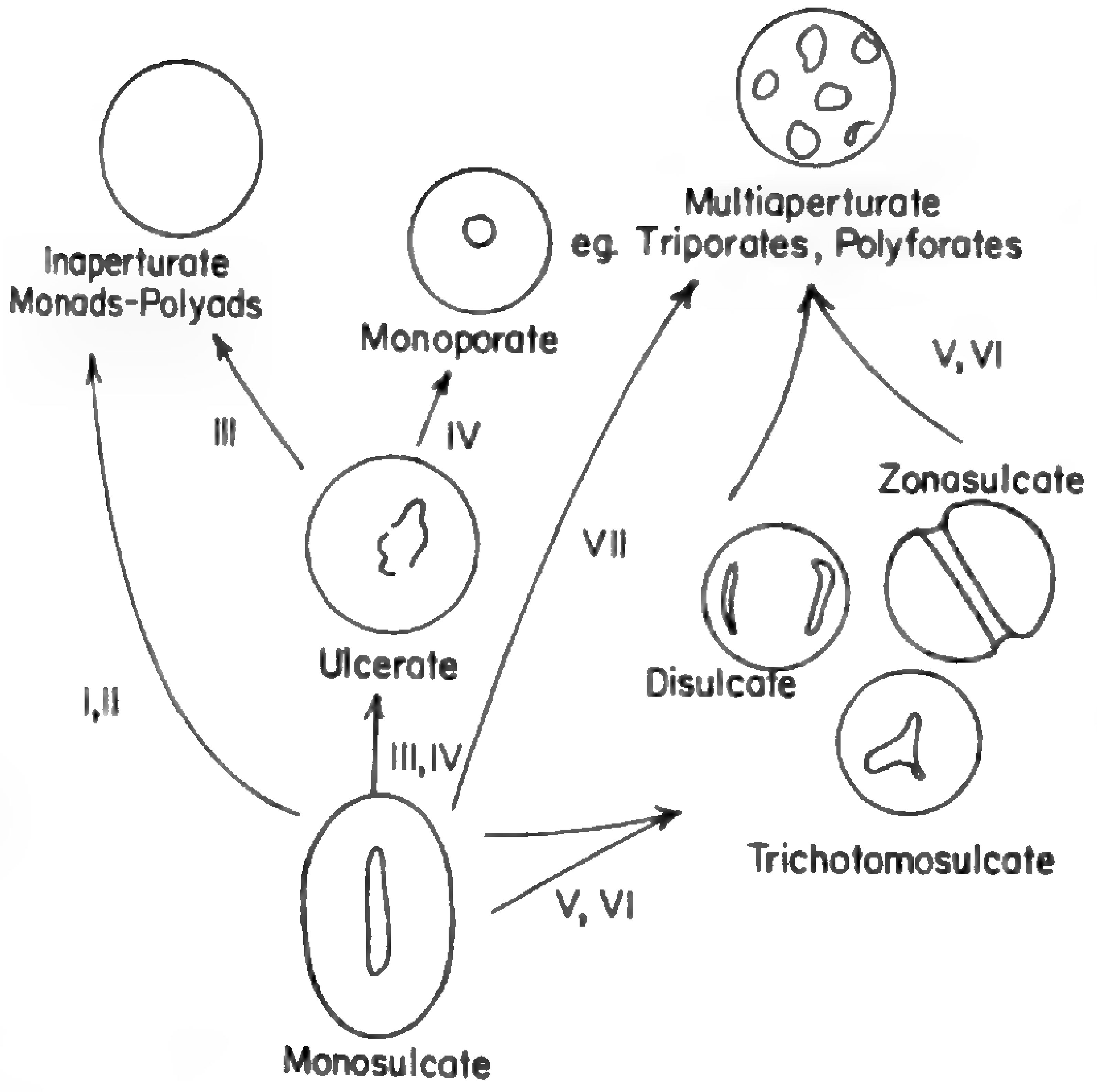
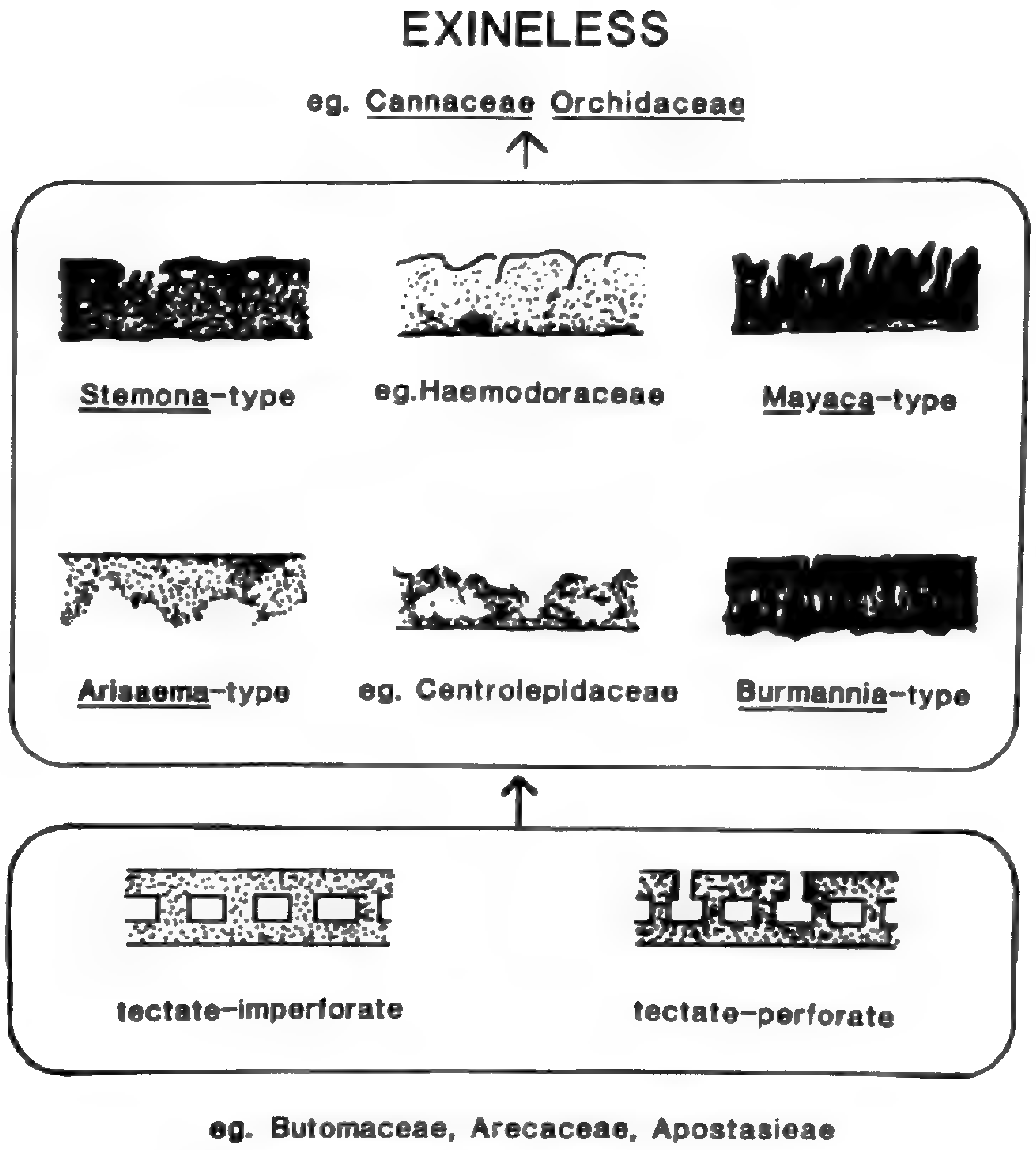


TEXT-FIGURE 1. Major evolutionary trends of apertures in monocots.

I. Alismatidean trend, monosulcate → inaperturate.
II. Zingiberidean trend, monosulcate → inaperturate.
III. Orchidacean trend, monosulcate → ulcerate → inaperturate.
IV. Commelinidean trend, monosulcate → ulcerate (irregular colpoid) → monoporate.
V. Arecidean trend, monosulcate → multiaperturate forms.
VI. Liliacean trend, monosulcate → disulcates, trichotomosulcates, zonasulcates → multiaperturate.
VII. Alismatacean trend, monosulcate → multiaperturates (polyforates).



TEXT-FIGURE 2. Major evolutionary trends of wall structure types in the monocots. The primitive tectate-columellate (perforate or imperforate) wall structure type, possibly derived from a Nymphaeacean-like ancestor with atectate or granular walls, gives rise to monocotyledonous atectate or granular walls and finally extreme reduction of the exine, in which it may be completely absent.

columellate, perforate, or imperforate wall structure is primitive (Zavada, 1983a; Text-Figs. 1, 2). The difference between the wall structure of the most primitive dicotyledons and monocotyledons, might be interpreted as contradicting a common origin of the monocotyledons and dicotyledons, and interpreted as supporting a separate origin. If the monocotyledons separated early from a nymphaeacean-like (dicotyledonous) ancestor, as morphological data seem to suggest (Cronquist, 1981), the most primitive monocotyledonous pollen might be presumed to have a granular or atectate wall structure similar to that found in the Nymphaeaceae (Ueno & Kitaguchi, 1961; Ueno, 1962; Rowley, 1967; Roland, 1965, 1968). However, comparative morphological studies of monocotyledon wall structure (Zavada, 1983a) show that the tectate-columellate wall is primitive in extant monocotyledons. It is possible that primitive tectate-columellate monocotyledons are derived from a nymphaeacean-like ancestor with atectate- or granular-walled pollen. Even among ranalean taxa, the shift from the granular or atectate to the tectate-columellate wall appears to be an early evolutionary development. Thus, a shift from the atectate- or granular-walled nymphaeacean-like ancestor to the primitive tectate-columellate type found in monocotyledons parallels the phylogenetic trend in the ranalean taxa, and places the primitive monocotyledons on the same evolutionary level as the derived ranalean taxa with monosulcate, tectate-columellate pollen; a view that seems reasonable in light of the proposed dicotyledonous origin of the monocotyledons.

Comparing evolutionary trends of aperture types and wall structure in dicotyledons and monocotyledons, we find other striking parallels. Walker (1974a, 1974b, 1976) has determined that atectate- or granular-walled pollen among some of the more advanced dicots is secondarily derived from the tectate-columellate wall structure. This is accompanied by reduction or loss of the aperture, or an increase in the number and types of apertures. The monocotyledons exhibit the same range of trends but with differing emphasis (Text-Figs. 1, 2; Zavada, 1983a). Dicotyledons more frequently exhibit a tendency toward increasing the number and types of apertures and the complexity of pollen wall structure (e.g., Compositae). Monocotyledons, in contrast, frequently exhibit a tendency toward reduction or loss of the aperture (e.g., Alismatideae, Commelinideae, Orchidaceae, Zingiberideae) and reduction in the complexity of the exine or loss of the exine altogether (e.g., Alismatideae, Orchidaceae, Zingiberideae).

We might expect to observe a progression of pollen aperture and wall structure types similar to the proposed evolutionary trends in geologic time. Before we can adequately evaluate these schemes in the context of fossil evidence, we must provide criteria to unequivocally identify angiosperm pollen in a field of superficially similar non-angiosperm palynomorphs (e.g., monosulcate gymnosperms).

POLLEN WALL HOMOLOGIES AND IDENTIFICATION OF FOSSIL-DISPERSED POLLEN

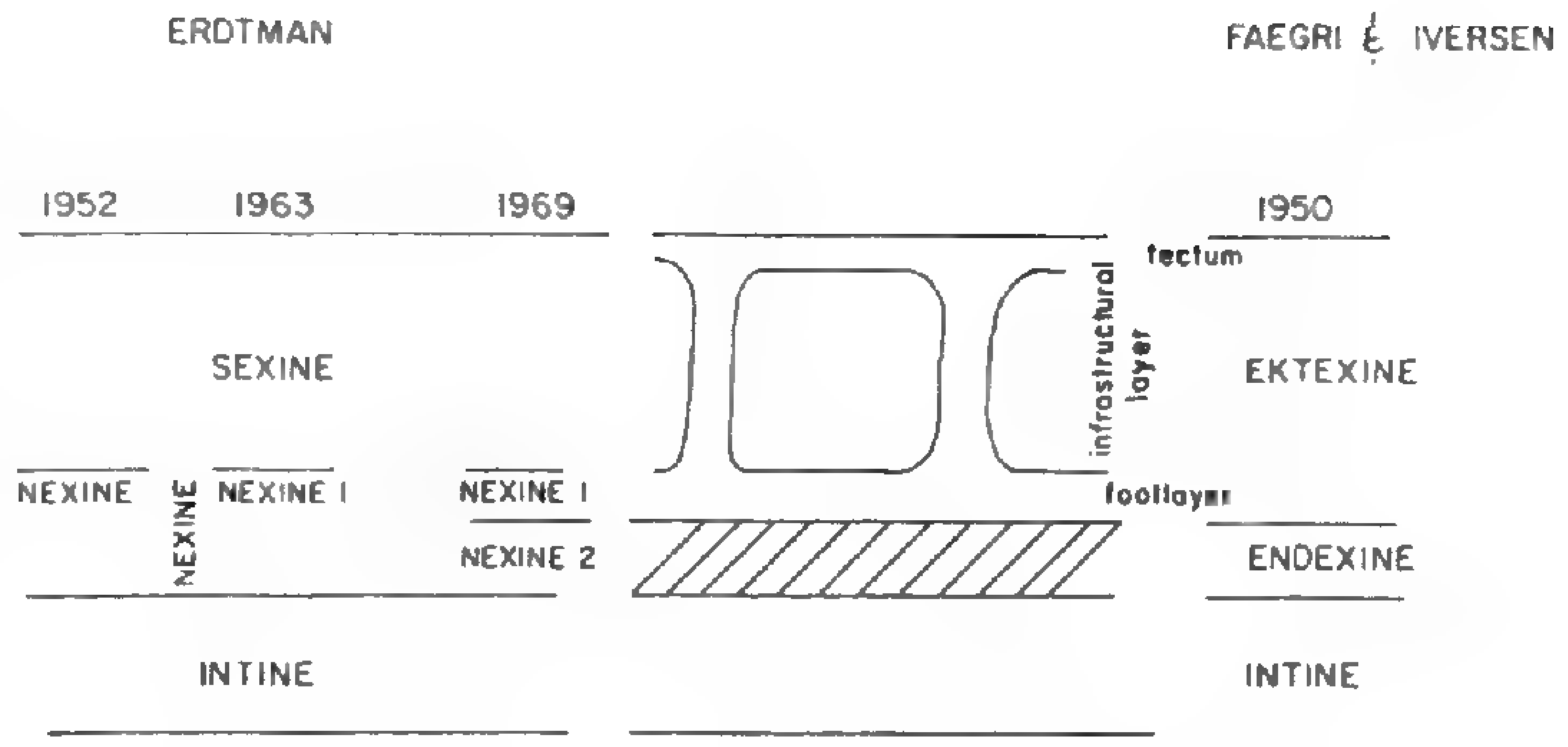
The monosulcate aperture is generally considered to be most primitive among angiosperm aperture types (Kuprianova, 1948; Walker, 1974a) and appears to be a good character in identifying early angiosperm pollen. However, monosulcate pollen is also common among gymnosperms, and its continuous stratigraphic occurrence since the Permian makes this criterion, in itself, questionable. This has long been recognized by palynologists. However, the presence of the monosulcate aperture in conjunction with pollen wall structure, may provide a basis on which angiosperm pollen can be distinguished from gymnosperm pollen. Van Campo (1971) surveyed pollen wall structure in representative gymnosperm and angiosperm taxa and proposed palynological criteria to distinguish between these groups. Doyle et al. (1975) further discussed these criteria and their application to the interpretation of the fossil record. Van Campo (1971) and Doyle et al. (1975) recognized three basic pollen wall structure types; alveolar and/or endoreticulate, tectate-granular, and tectate-columellate. The alveolar wall structure is known only in gymnosperms and the tectate-columellate wall structure is known predominantly from angiosperms. These appear to be good palynological characters for separating monosulcate pollen of these groups. The tectate-granular, however, is found in both gymnosperms and angiosperms. To further complicate matters, this is a wall structure type common among the most primitive angiosperms. To distinguish between gymnosperm and angiosperm pollen with tectate-granular walls, Doyle et al. (1975) emphasized the significance of the endexine [thought by Doyle et al. (1975) to be in part equivalent to the nexine of Erdtman (1952)]. Gymnosperms have lamellated endexines (nexines) and angiosperms have non-lamellated endexines (nexines), except in the apertural region where it is lamellated. These pollen wall criteria are presumably the basis for determining affinities of dispersed fossil palynomorphs.

Pollen wall structure terminologies are a complicated and intimidating aspect of palynology. Widely used nomenclatural schemes are, for the most part, based on structural aspects (as opposed to developmental aspects) of the various wall layers, but there has been noticeable disregard in defining the homologies for the various wall layers of the pollen of major plant groups, especially gymnosperms and angiosperms. In addition, many of the terms proposed by various authors to describe pollen wall structure are used interchangeably, implying homologies exist in contradiction to their original definitions [e.g., Faegri's endexine (in part) = Erdtman's nexine]. This has resulted in an ambiguous situation for palynologists who wish to establish taxonomic and phylogenetic relationships among various plant groups based on pollen wall structural data. To help clarify this situation it is necessary to describe in detail the two most widely used terminological systems describing pollen wall structure.

The two most widely used wall structure nomenclatural systems are those of Faegri and Iversen (1950; also Faegri, 1956) and Erdtman (1952, 1963, 1969). Faegri and Iversen (1950) distinguished three major wall layers, the outer sporopolleninous ektexine and endexine, and the inner cellulosic intine. The terms ektexine and endexine were first coined by Erdtman (1943) and correspond to Fritzsche's (1837) exine and intexine, but Erdtman (1952) later abandoned these terms. Erdtman (1952) also identified three primary wall layers, the sporopolleninous sexine and nexine, and the cellulosic intine. The intine, recognized by Faegri and Iversen (1950) and Erdtman (1952), easily corrodes in acetolyzed and fossilized pollen. It has been generally ignored in phylogenetic and taxonomic schemes and will not be discussed further.

Faegri and Iversen (1950) distinguished the outer ektexine from the inner endexine by differences in their affinity for the stain basic fuchsin. The ektexine and endexine also exhibit differences in their affinity for the transmission electron microscopic stains uranyl acetate and lead citrate, and various other cytochemical stains (e.g., Aniline blue-black, Coomasse blue; Southworth, 1973), further substantiating Faegri and Iversen's nomenclatural distinction between these wall layers. Rowley et al. (1981) have speculated that the difference in stainability between these wall layers may be due to differences in the glycocalyces associated with these wall layers, or the chemical nature of sporopollenin. In addition, Bailey (1960) and Southworth (1974) found differences in the solubility of the ektexine and endexine in fresh material treated with hot 2-aminoethanol. The ektexine is readily soluble and the endexine exhibits less solubility. This prompted Southworth (1974) to speculate that there are differences in the chemical nature of the sporopollenin between these two wall layers (cf. with one of the alternative explanations offered by Rowley et al., 1981). Regardless of the reason, Southworth's data further substantiates the terminological distinction of the ektexine and endexine (sensu Faegri & Iversen, 1950). Faegri and Iversen (1950) considered the ektexine to be a three-layered structure, based solely on morphology. The outermost tectum is the sculptured layer of the ektexine. The middle layer or infrastructural layer can be alveolar, endoreticulate, columellate, or consist of spherical or irregularly shaped granules or anastomosing rods. The innermost layer of the ektexine is the footlayer; this layer can be amorphous or lamellated (but not commonly in angiosperms), but is unsculptured.

Erdtman (1952) first identified the sexine and nexine solely by their morphology: the outer sexine referring to the variously sculptured portion of the exine, and the amorphous or lamellated nexine corresponding to the unsculptured portion of the exine. However, in 1963 Erdtman proposed the term nexine 1 for the outer portion of the nexine that is "chemically" and "physically" similar to sexine (thus = to Faegri and Iversen's footlayer) yet "topographically" part of the nexine proper. Later Erdtman (1969) proposed nexine 2 for the inner portion of the nexine that is different from nexine 1 in its response to basic fuchsin. Thus, Erdtman (1969) fully realized the significance of the differential stainability of pollen wall layers and proposed a system of terminology identical to Faegri and Iversen (1950): Erdtman's sexine plus nexine 1 are equivalent to Faegri and Iversen's ektexine, and Erdtman's nexine 2 is equivalent to Faegri and Iversen's endexine (Text-Fig. 3).



TEXT-FIGURE 3. Pollen wall homologies. Equivalent terms in the Erdtman (1969) and Faegri and Iversen (1950) terminological schemes.

There has been a quantum increase in the taxonomic and phylogenetic palynological literature since the inception of these terms, unfortunately without rigorous application of the criteria on which these terms were originally based. Thus, these terms have been confused and their use in suggesting homologies among wall layers in different taxa have been equivocal. This is often reflected in descriptive morphological studies confusing the two different nomenclatural schemes. Some workers have rejected these schemes outright and proposed their own palynological lexicon (e.g., Tsinger & Petrovskaya-Boranova, 1961; Wittmann & Walker, 1965; Reitsma, 1970), further confusing attempts to establish homologies among wall layers in different taxa. It is paramount that before any attempt is made to consider the phylogenetic significance of pollen wall structure, consistent use of terminology be established. Further, wall terminology should accurately reflect structure, histochemistry, and development so that homologies for various wall layers may be established reliably between angiosperms and gymnosperms. Although the developmental aspects of the pollen wall have been generally ignored by descriptive palynologists, the value of developmental data have long been recognized in establishing homologies (e.g., Nageli, 1842; Stebbins, 1974). A sufficient body of literature on pollen wall development has emerged over the past 25 years for providing insight into the homologies between gymnosperm pollen wall layers.

Pollen wall development in gymnosperms and angiosperms can be divided into three phases (Heslop-Harrison, 1971). The phases are: premeiotic, tetrad, and the free spore phase. The premeiotic phase encompasses the developmental interval between the initiation of the pollen mother cells and meiotic cytokinesis. The premeiotic phases in gymnosperms and angiosperms are generally similar and are not directly related to the development of the sporopolleninous exine. Thus, they need not be discussed further in the present context. However, there are significant differences in wall development between angiosperms and gymnosperms during the tetrad and free spore phases.

In cycads and conifers, for example, the sporopolleninous sexine begins development immediately after the four microspores are enclosed in the callose special wall. There is no deposition of a dense staining fibrillar primexine with embedded radially directed elements (procolumellae), as in many angiosperms. A dispersed fibrillar material is deposited between the callose wall and the microspore plasmalemma, at the same time the centripetal development of the sexine is occurring. Audran (1981), Dickinson (1971), Willemse (1971), and Vasil and Aldridge (1970) have interpreted the dispersed fibrillar material as homologous with the primexine of angiosperms. The differences in electron density between the dispersed fibrillar material in cycad and conifers, and the primexine of angiosperms, and that accretion of the sporopolleninous sexine begins immediately, without any recognizable nonsporopolleninous matrix, suggest that the fibrillar material in gymnosperms is not entirely comparable with the primexine of angiosperms.

Upon completion of the sexine, development of the nexine (footlayer) begins by accumulation of sporopollenin on unit-like membranes. These sheets of sporopollenin are successively appressed to one another but retain their lamellated appearance, even at maturity, in both apertural regions and nonapertural regions. After formation of the nexine, the callose special wall is destroyed and the microspores are free in the sporangium. In most gymnosperms no additional sporopolleninous wall layers form during the free spore phase (however, see Rohr, 1977). The *entire* sporopolleninous wall, sexine, and nexine are completed during the tetrad phase (Audran, 1981; Zavada, 1983b).

In angiosperms the tetrad phase is also marked by the sequestering of the four microspores by callose. Prior to the appearance of the sporopolleninous wall, a distinctive fibrillar wall not found in gymnosperms (see above), the primexine, is formed. Embedded in the primexine shortly after it becomes distinct are nonsporopolleninous radially directed probacules (procolumellae). Subsequently, the probacules become more electron dense as sporopollenin accumulates (Heslop-Harrison, 1971; Zavada, 1984). The tectum is then formed by the lateral accumulation of sporopollenin at the distal ends of the bacules. Finally, the footlayer (nexine 1) develops on unit-like membranes (as in gymnosperms) and at times appears lamellated in apertural and nonapertural regions at maturity (e.g., Magnoliaceae, Praglowski, 1974; Annonaceae, Le Thomas, 1981). Next the bases of the bacules become fused to the footlayer (nexine 1). Upon completion of the footlayer (nexine 1), the callose wall is destroyed and the pollen grains are free in the anther locule. During the free spore phase and in contrast to most gymnosperms, an additional sporopolleninous wall layer can develop—the endexine. Along with the footlayer, the endexine has been considered equivalent to the nexine in gymnosperms (Doyle et al., 1975). Endexine appears to have two modes of deposition in angiosperms. In one instance, endexine is the result of the accumulation of unit-like membranes with sporopollenin, similar to footlayer (nexine 1) formation. This imparts a lamellated appearance to this wall layer in apertural and, occasionally, in nonapertural endexine at maturity (e.g., Compositae, Horner & Pearson, 1978; *Ricinus, Saintpaulia,* Larson et al., 1962). The second mode of endexine formation is by the accumulation of sporopolleninous granules in nonapertural regions. Endexine formed in this manner appears homogeneous at maturity in nonapertural regions. However, apertural endexine in the same pollen is formed on unit-like membranes and has a lamellated appearance at maturity. Granular nonapertural endexine is known from a number of taxa (e.g., *Zea,* Skvarla & Larson, 1966; *Helloborus,* Echlin & Godwin, 1969; *Passiflora,* Larson, 1966; *Austrobaileya,* Zavada, 1984).

Another significant aspect of endexine formation is that, in some taxa, endexine is interbedded with intine. When these taxa are treated with acetolysis solution, the intine corrodes and fragments the endexine. This gives the false impression that endexine is scanty or absent in acetolyzed material (e.g., *Austrobaileya,* Zavada, 1984).

Although the mode of deposition of the various wall layers in angiosperms may vary, the timing of their development is consistent among the angiosperms thus far studied.

Criteria currently used to distinguish fossil gymnosperm from the most primitive angiosperm pollen (e.g., tectate-granular) depend on characteristics of the nexine of gymnosperms and the endexine of angiosperms (Doyle et al., 1975). The use of nexine and endexine synonymously implies that these wall layers are homologous. However, evidence presented above, including the chemical difference between nexine of gymnosperms (which is composed entirely of nexine 1 or footlayer) and the endexine of angiosperms, born out by their differential stainability with various cytochemical and TEM stains, by differential solubility in 2-aminoethanol, and by the different mode of deposition of the endexine in some angiosperms, suggests the nexine of gymnosperms and endexine of angiosperms are not homologous wall layers. Thus, the criteria currently used to distinguish dispersed angiosperm pollen from dispersed gymnosperm pollen, which imply the nexine and endexine are homologous, must be rejected (e.g., Doyle et al., 1975). This does not preclude the use of other pollen characteristics in identifying dispersed fossil angiosperm pollen. The columellate infrastructure is known only from extant angiosperms (cf. Van Campo, 1971). The endexine of angiosperms lamellated or homogeneous has what appears to be a developmentally and cytochemically equivalent wall layer in *Ginkgo biloba* (Rohr, 1977). In addition, the columellate infrastructure and endexine are relatively advanced features among angiosperms (Walker, 1976) and are not likely to be found in primitive fossil angiosperm pollen. To make this situation worse, wall structure characteristics of primitive angiosperms are indistinguishable from those of many gymnosperms (e.g., the granular type occurs in both gymnosperms and angiosperms). Thus, there are no reliable taxonomic features that can be used to distinguish primitive angiosperm pollen and gymnosperm pollen, and it will be difficult to elucidate the origin of the angiospermous condition on palynological data alone.

Despite these difficulties, studies of fossil pollen wall structure can still be enlightening in a few respects. First, these studies can help determine general patterns of pollen wall evolution. Second, these studies can be used to corroborate general evolutionary trends of wall structure based on neontological data, i.e., to identify primitive and derived character states. Further, first occurrences of key wall structure types can provide a temporal framework for the evolutionary trends in pollen proposed on neontological grounds. Third, studies of dispersed pollen correlated with pollen found in fossil fructifications might reveal the affinities of the dispersed pollen. Once a dispersed pollen grain can be associated with a megafossil, the morphological features of the pollen and the megafossil can then be used to evaluate their relationship to angiosperms.

In the following sections new data is presented on fossil pollen wall structure for a number of saccate and non-saccate dispersed pollen. The significance of these data to early angiosperm evolution and origins will be discussed in conjunction with data from other studies on fossil pollen wall structure.

MATERIALS AND METHODS

Pollen was recovered from sediment by treatment with HCl, HF, Schulze's solution, and KOH. After each treatment the residue was washed with distilled water until neutral (pH 7). After the final washing the residue was centrifuged in the heavy liquid $ZnCl_2$, sp. gr. 2, and the supranatant was collected, dehydrated in an alcohol series and embedded in polystyrene after Frangioni and Borgioli (1979). The suspension was smeared on a microscope slide and allowed to harden, then photographed. Pollen grains were then cut out of the hardened plastic and re-embedded in polystyrene in Beem^R capsules for transmission electron microscopy (TEM). Sectioning was done on an LKB-1 ultramicrotome and pollen was stained for 15 minutes in both uranyl acetate and lead citrate. Sections were viewed with a Philips EM-300. Pollen was prepared for scanning electron microscopy (SEM) by dissolution of the polystyrene embedded pollen in toluene until the pollen was free of all embedding material, or the pollen residue prior to embedding in polystyrene was mounted directly on SEM stubs, coated with gold-palladium, and viewed with a Coates and Welter field emission electron microscope.

The identification of pollen wall layers and determination of pollen wall homologies, as mentioned, is based on staining properties with various cytochemical and TEM stains, solubility in 2-aminoethanol, development, and morphology in extant pollen. Although it is difficult to study developmental aspects of fossil-dispersed pollen, few of the pertinent biochemical tests have been used in attempts to interpret wall structure in fossil pollen. Thus, identification of wall layers in fossil pollen depends primarily on morphology and staining properties with TEM stains. Interpretation of fossil pollen wall structure based on staining properties with TEM stains must be viewed with some reservation because their reaction to the stains are known to differ from extant pollen. Rowley et al. (1981) have proposed that staining is effectuated by the labile exine moiety (glycocalyx) and not by the relatively inert and decay-resistant sporopolleninous wall fraction. Thus, the depositional microenvironment and diagenetic processes associated with fossilization can have profound effects on the staining properties of fossil pollen walls. Southworth (1974) found that fresh pollen is readily soluble in 2-aminoethanol, but that pollen taken from old herbarium material exhibits less solubility. This suggests that even recent material undergoes biochemical changes that affect the physical and chemical properties of the exine. Stanley (1966) has demonstrated that fossil pollen from various geologic stages can exhibit differential staining with the nonspecific stain Safranin-O, further suggesting that fossilization affects the physical and biochemical aspects of the exine. Until the microenvironmental and diagenetic factors influencing staining can be more fully understood, interpretations based on these criteria are tentative.

POLLEN WALL STRUCTURE OF DISPERSED FOSSIL POLLEN

PRAECOLPATITES SINUOSUS, PERMIAN

This form genus was recovered from Permian sediments of the Olive River Basin, Cape York Peninsula, Queensland, Australia. Foster and Price (1982) examined this taxon using light, scanning electron, and transmission electron microscopy. Pollen is elongate, probably multiaperturate (2–4 sulcate) and exine sculpturing is verrucate-granulate. The pollen wall is 2–3 μm thick and is considered to have two primary layers, an inner laminated layer (possibly footlayer, intexine of Foster & Price, 1982) and an outer structured layer (exoexine of Foster & Price, 1982). The inner part of the outer layer is composed of a granular infrastructure, which is overlain by a tectum that is occasionally perforated with small channels. Foster and Price (1982) considered the wall structure of this taxon to be similar to the granular wall structure types found in extant ranalean taxa (e.g., Magnoliaceae).

MARSUPIPOLLENITES TRIRADIATUS, PERMIAN

This form genus is from the Blair Athol Basin of central Queensland, Australia. It was studied in detail using light, scanning electron, and transmission electron microscopy by Foster and Price (1982). Pollen is spherical to slightly elongate and has a distal sulcus and a proximal triradiate scar. Exine sculpturing is verrucate to granulate. The pollen wall is composed of two primary layers and an inner unsculptured layer (intexine of Foster & Price, 1982) and an outer layer that has a granular infrastructure and a tectum occasionally perforated by small channels (Foster & Price, 1982). The wall structure of this taxon also shows striking similarities to the granular infrastructure of some ranalean taxa.

MONOSULCITES SPP.,
UPPER PALEOZOIC-TERTIARY

This widespread Mesozoic form genus is monosulcate, ovoid to boat-shaped, and exine sculpturing is psilate. Trevisan (1980) investigated the wall structure of one form from the Lower Cretaceous of Italy, and, in the present study, one form was investigated from the Yorkshire Jurassic. Both are identical in every respect. Pollen wall structure consists of two layers, an inner continuous lamellated footlayer (Layer A of Trevisan) and an outer massive layer. The inner portion of the outer massive layer consists of closely packed, somewhat homogeneous granules. This imparts a spongy appearance to the inner portion of the outer massive layer. The outer portion of this wall layer appears homogeneous and may comprise the tectum. The outer massive layer thins in the region of the sulcus, however, the basal layer (footlayer) remains of constant thickness throughout. Trevisan (1980) noted a thin electron dense marginal layer of the exine, also present in my material. This is not considered a distinctive layer, but an artifact of preservation (see discussion on *Eucommidiites*). Taylor (1973) investigated pollen from the Cretaceous taxon *Cycadeiodea dacotensis*, which is similar in many respects to the dispersed pollen investigated in this study and by Trevisan (1980).

CLASSOPOLLIS SPP., TRIASSIC-LOWER CRETACEOUS

This form genus has been associated with a few gymnosperm fructifications and probably represents a diverse group of plants (e.g., *Cheirolepis muensteri,* Harris, 1957; *Pseudofrenelopsis,* Alvin et al., 1978). Pollen has a distal aperture in addition to a proximal triradiate suture and frequently occurs in tetrads. Pollen wall structure has been investigated by Pettitt and Chaloner (1964); they offered two interpretations of the complex wall structure. One interpretation viewed the pollen wall consisting of an outer tectum, a columellate infrastructure with the columellae fused to a thick three-layered footlayer. The outermost portion of the footlayer is a thick homogeneous layer. The middle of the footlayer consists of large, irregular shaped, inwardly directed columns which rest on a thick lamellated inner layer. The alternative interpretation considered the innermost lamellated layer—the footlayer, in toto, the large irregular shaped columns—the columellate infrastructure and the outermost layer—tectum. The tectum is now considered the complex three-layered structure consisting of an inner homogeneous layer fused to a supratectal layer (also see Taylor & Alvin, 1984). Regardless of what interpretation is favored, the wall structure of this taxon is unique among fossil and extant gymnosperms. It represents a gymnosperm pollen type with a columellate infrastructure, a characteristic thought only to occur in angiosperms.

EUCOMMIIDITES SPP., TRIASSIC-LOWER CRETACEOUS

This form genus occurs abundantly in Lower Mesozoic sediments. Pollen is elliptical to broadly oval and has three apertures. One aperture is a conspicuous, broad, sulcus-like aperture and the two other apertures are thin and fold-like (Figs. 1, 2). They are evenly distributed on the pollen grain, all with their long axes parallel to the long axes of the pollen grain. Pollen has been studied using TEM (Doyle et al., 1975; Trevisan, 1980; present study Figs. 1–3). Three forms are recognized based on pollen wall structure.

A Jurassic form investigated in the present study and a Lower Cretaceous form investigated by Trevisan (1980, *Eucommiidites* sp., Fig. 1) have a three-layered wall. The innermost layer (layer A of Trevisan) is unsculptured, often lamellated, and doesn't thin in the apertural region (Figs. 2, 3). Based on its position and lamellated nature it can be considered footlayer (nexine 1). The middle layer or infrastructural layer (layer B_1 of Trevisan) consists of irregular shaped columellae, often interspersed with irregularly shaped granules (Fig. 3). The columellae and granules are fused to a thick tectum (layer B_2 of Trevisan), which is homogeneous in the lower portion and comprised of compacted supratectal granules in the outer portion (Fig. 3). Trevisan considered the outer layer of granules a distinct (layer C) layer due to its differential stainability with SEM and TEM stains. She divided this C layer into a three-layered structure consisting of C_1, C_2, and C_3. Erdtman (1963) proposed the term stegine for the outer margin of the exine that stains differently from the more central region. This phenomenon may not be indicative of true biochemical differences in the exine. It may be due to differential chemical extraction of the more labile moiety (glycocalyx) of the exine during fossilization or affected by preparation of the sediment to recover fossil-dispersed pollen (cf. Rowley et al., 1981). This differential marginal staining is common in many of the fossil taxa investigated (see below), and probably doesn't represent a distinctive biochemical layer.

Trevisan (1980) described a second form of *Eucommiidites* (*E.* sp. 2). She considered its wall to consist of three layers, an A layer similar in all respects to the A layer of *E.* sp. 1 and appears to represent footlayer (nexine 1). The middle B layer is further divided into B_1, B_2, and B_3. Layers B_1 and B_2 represent a granular infrastructural layer and B_3 a homogeneous layer comprising the tectum. The outer C layer is distinguished once again on its differential staining from the inner portion of the tectum, and is a similar situation to that observed in the C layer of *E.* sp. 1.

Doyle et al. (1975) described a third form of *Eucommiidites* from the Lower Cretaceous. Its wall consists of three layers. An inner lamellated layer, which Doyle et al. (1975) term endexine, probably represents footlayer (nexine 1), in light of its position, staining characteristics and presumed gymnospermous origin. The infrastructural layer is comprised of spherical granules that are overlain by a homogeneous tectum that is traversed by small perforations.

The three taxa of *Eucommiidites* all have three-layered exines, a lamellated footlayer [nexine 1, A layer of Trevisan, endexine of Doyle et al. (1975)], an infrastructural layer consisting of spherical granules (Doyle et al., 1975), or a ho-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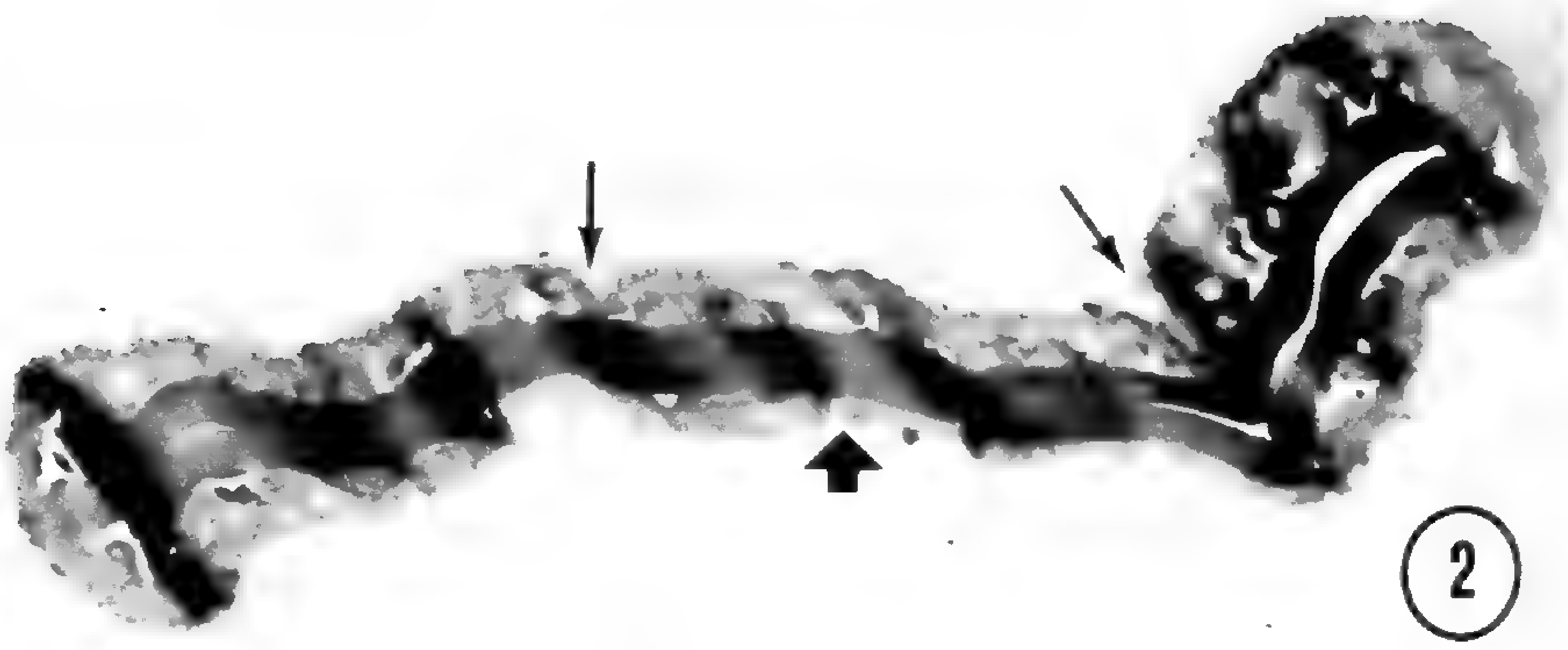
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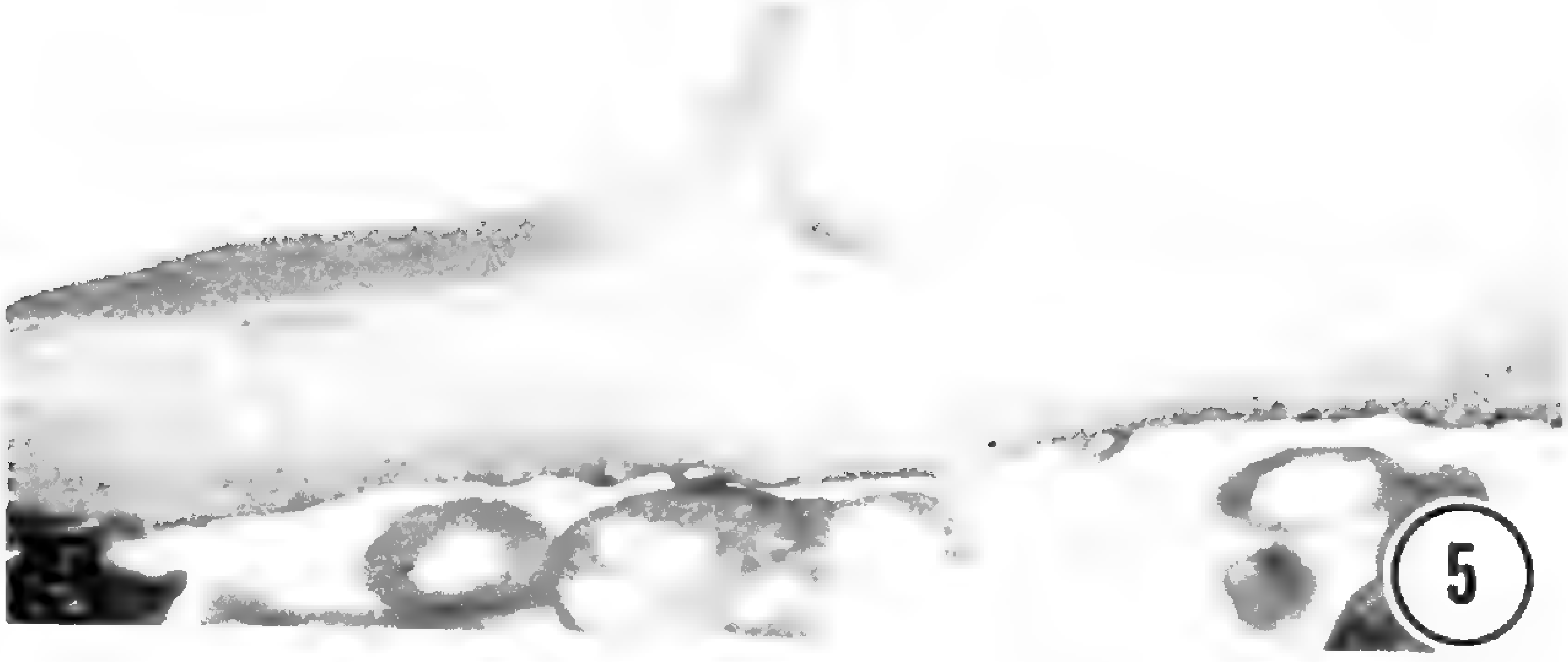
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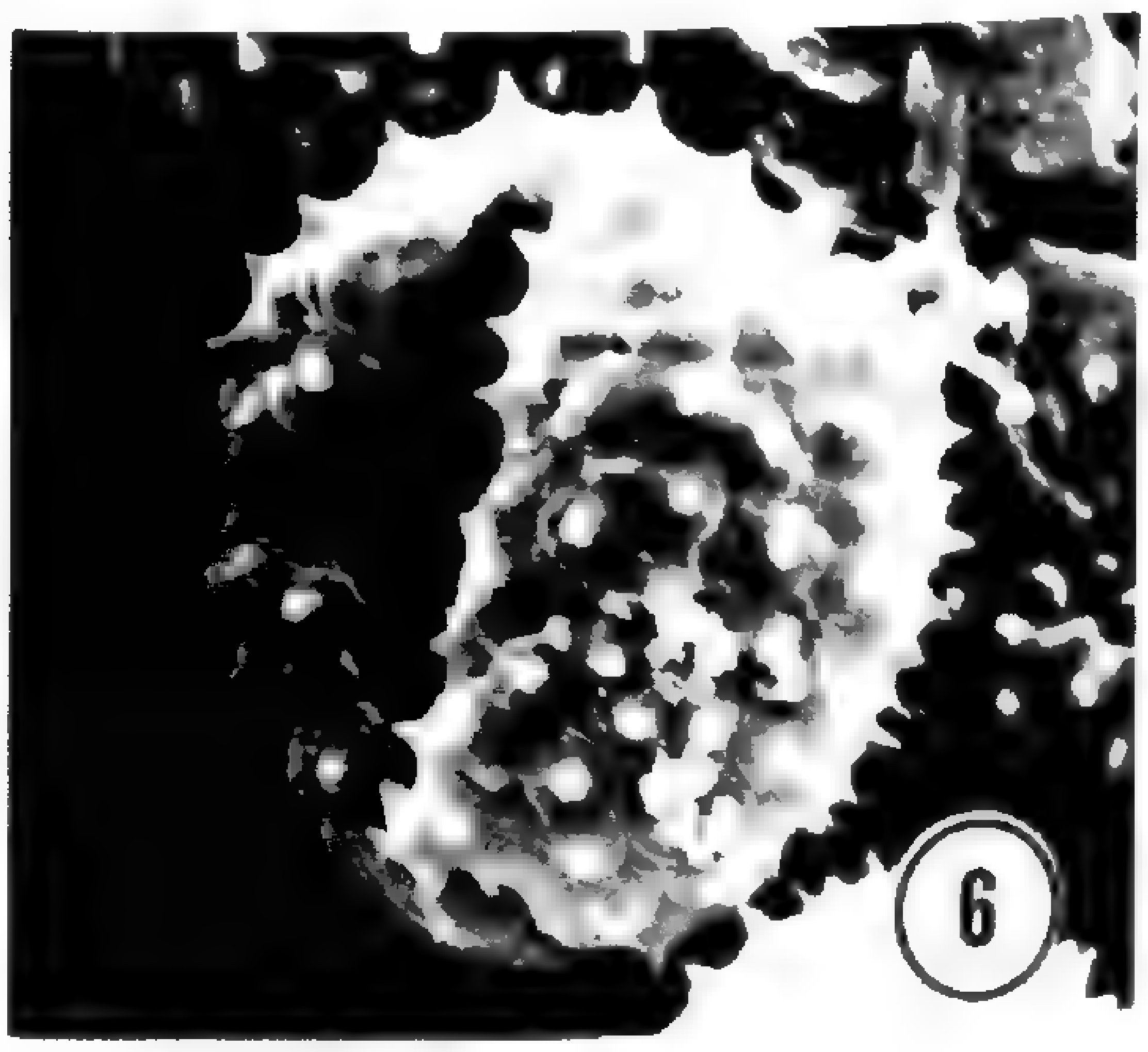
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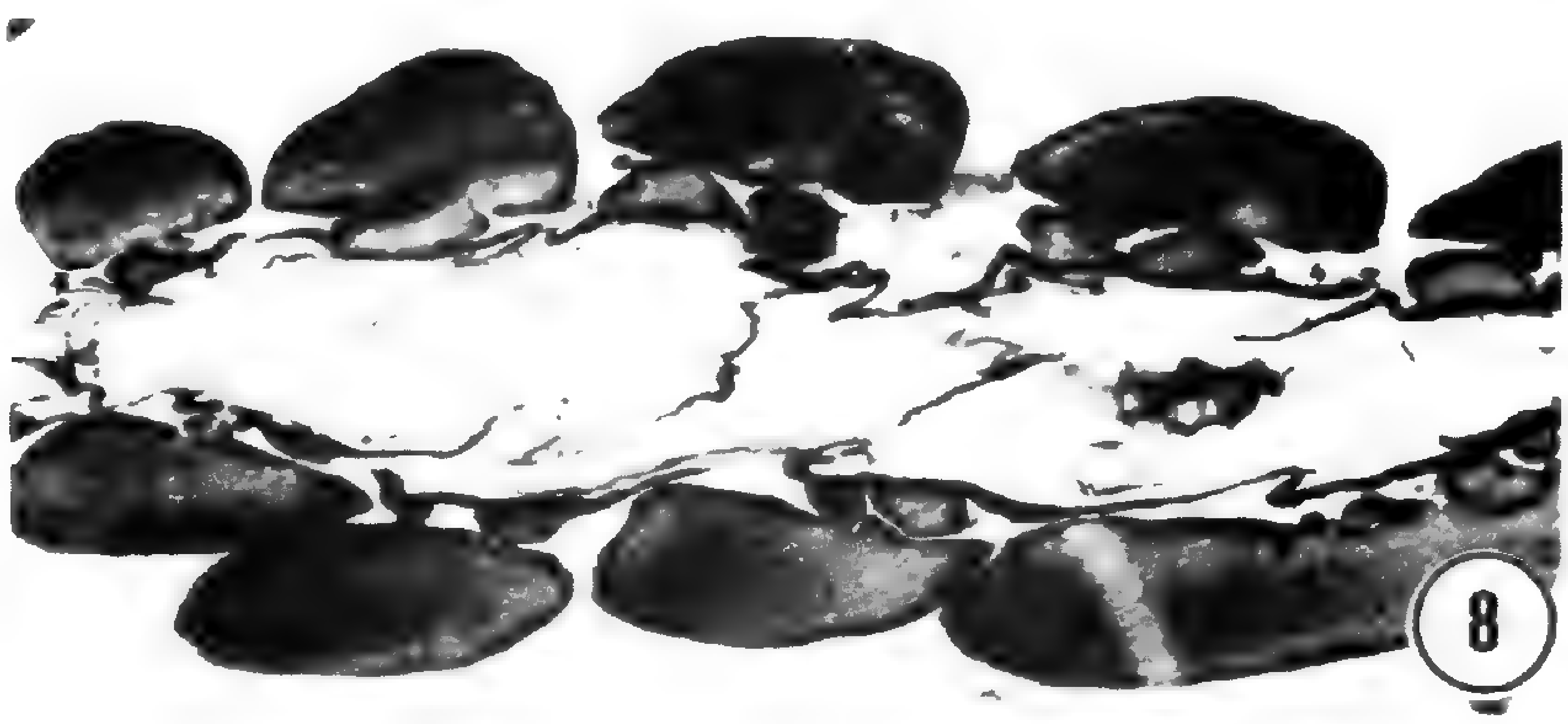
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mogeneous to granular layer (Trevisan, 1980, *E.* sp. 2) or a columellate to granular infrastructure (Trevisan, 1980, *E.* sp. 1, form investigated in the present study), and a tectum that may or may not have supratectal ornaments and can be minutely perforate.

Only four individual pollen grains of this form genus have been studied with TEM thus far. These studies have revealed that three distinctive taxa exist based on pollen wall ultrastructure, suggesting that this form genus (sensu lato) was quite diverse during the Mesozoic. Although the granular infrastructure is most common, there is a tendency toward the columellate infrastructure in *E.* sp. 1 of Trevisan and the form investigated in the present study (which are considered here to be the same taxon).

EPHEDRIPITES SPP., TRIASSIC-RECENT

This form genus, as Mchedlishvili and Shakmoundes (1973) have pointed out, does not form a natural group. Trevisan (1980) sectioned two species from the Lower Cretaceous and in the present study one species from the Triassic Chinle Formation was investigated (*Equisetoporites chinleana*).

The pollen is oval to elliptical approximately 25–60 μm long, monosulcate to inaperturate (or possibly multiaperturate) with conspicuous longitudinal ridges. It is superficially similar to pollen of the extant taxon *Ephedra* (however, compare Figs. 8, 9 with Fig. 5 of *Gnetum* and Fig. 7 of *Ephedra*). Trevisan (1980) sectioned a monosulcate form and distinguished two major wall layers; an inner continuous lamellated layer (layer A) and an outer complex layer that comprises the ridges and grooves. The inner A layer, based on its position in relationship to the outer wall layers and lamellated nature, probably is footlayer (nexine 1). The outer layer, the infrastructural layer, and tectum is further subdivided into layers B_1, B_2, B_3, C, and D by Trevisan (1980). Layer B_1 is a thin, continuous layer that underlies the B_2 layer, which is composed of fragmented and anastomosing units. The B_2 layer is similar to the granular infrastructural layer in extant *Ephedra* (Fig. 7) and *Gnetum* (Figs. 5, 6). Layer B_3 is homogeneous and thins in the regions of the grooves (as does the tectum in extant *Ephedra* pollen). The outer margin of the tectum stains differently than the inner portion, in a similar manner to that observed in other fossil taxa (see above) and is distinguished as layer C by Trevisan (1980). On the surface of the exine are scattered "globulets" 0.01–0.09 μm in diameter, which Trevisan terms the discontinuous D layer. The globulets are possibly the remains of a tapetal deposit.

The Triassic Chinle form genus *Equisetoporites chinleana* (Daugherty, 1941) also falls within the morphological circumscription of *Ephedripites* and has been reported as tectate-columellate by Cornet (1979). Pollen of this type has been found associated with the gymnospermous taxon *Masculostrobus clathratus* (Ash, 1972). My investigation of this taxon has shown the pollen to lack a conspicuous aperture (however, see below; Figs. 4, 8). The wall is a three-layered structure consisting of a thin, lamellated footlayer (Fig. 8), which is fused to short stout columellae (Figs. 8, 9) (their stout appearance may be a result of compression). The columellae are overlain by a thick homogeneous tectum, which forms the conspicuous ridges (Fig. 8). Both

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FIGURES 1–9. 1–3. *Eucommiidites* sp.—1. Yorkshire Jurassic, ×400.—2. Transmission electron micrograph of the same grain pictured in Figure 1. Note the three apertures (arrows) and the three-layered exine, ×4,040.—3. Transmission electron micrograph of the same grain pictured in Figure 1, showing three-layered exine; the inner dark staining footlayer (nexine 1), infrastructural layer with columellate-like structures and interspersed granules, and the homogeneous tectum with a supratectal granule layer. This grain is similar in all respects to the *Eucommiidites* sp. 1 of Trevisan, 1980, ×12,975.—4. *Equisetoporites chinleana,* Triassic Chinle Fm., ×400. 5–7. Pollen of the Gnetales.—5. Transmission electron micrograph of *Gnetum* showing thick footlayer (nexine 1), fine granular layer beneath the homogeneous tectum comprising a spine, ×32,200.—6. Scanning electron micrograph of *Gnetum* showing sulcus and echinate sculpturing, ×1,200.—7. Transmission electron micrograph of the polyplicate pollen of *Ephedra californica,* showing inner footlayer (lightly staining), granular infrastructural layer and thick tectum. Note tectum is continuous in the groove (arrow), ×21,000. 8–9. *Equisetoporites chinleana.*—8. Transmission electron micrograph of the same grain pictured in Figure 4, showing thin lamellated footlayer (nexine 1), stout columellae, and thick outer tectum. Note tectum is discontinuous in the grooves (compare with Fig. 7), and that the wall structure is remarkably different from the Gnetaceous taxa in Figures 5 and 7, ×11,600.—9. Transmission electron micrograph of the same grain pictured in Figure 4, tangential section of the pollen wall showing the columellate structures underlying the tectum (arrow), ×14,200.

the tectum and columellae are absent in the region of the grooves (Figs. 8, 9). The grooves might constitute structurally weak areas of the pollen wall and might have functioned as apertures (thus this form would be multiaperturate; Fig. 8). The tectate-columellate structure in this Triassic form genus represents the earliest occurrence of this wall structure type in the fossil record, a wall structure type thought to be restricted to angiosperms.

BISACCATE POLLEN WITH GRANULAR INFRASTRUCTURE, TRIASSIC-CAMPANIAN

In all extant plant groups bisaccate pollen has alveolar (more precisely endoreticulate) wall structure. Many of the Paleozoic saccate gymnosperms thus far investigated also have endoreticulate wall structures (e.g., see Millay & Taylor, 1974). Thus Mesozoic saccate pollen, although little studied, is generally considered a morphologically homogeneous group. However, my continuing studies of Triassic, Jurassic, and Cretaceous saccate pollen have confirmed the existence of the granular infrastructure among pollen of this type.

In all the forms investigated, the corpus is circular to elliptical with a distally located sulcus flanked by two relatively small sacs (Figs. 10–17). Pollen ranges from about 30 μm to greater than 50 μm in size (including sacs). The sacs may appear fully functional, as in many of the Triassic and Lower Jurassic forms (Figs. 10, 11), or may be small, apparently highly reduced, vestigial structures (Figs. 12–17). Pollen with the small, highly reduced sacs often appears to be morphologically similar (except for the sacs) to monosulcate, non-saccate pollen of the genus *Verrumonocolpites* (compare Figs. 18, 21, 22 with Figs. 12–17, 19, 20). The pollen wall in all of the taxa investigated is a three-layered structure (Figs. 23–30, including the non-saccate genus *Verrumonocolpites*). The inner layer is homogeneous or lamellated (Figs. 23–30) and, based on its position and similar staining properties to the outer wall layers, represents footlayer (nexine 1). The infrastructural layer consists of spherical to irregularly shaped granules or anastomosing rods (Figs. 23–30), and in some of the Cretaceous forms approaches the columellate condition (Figs. 24, 25). The outer layer, tectum, is thick and may (Figs. 25, 27) or may not be perforated (Figs. 29, 31). Exine sculpturing is usually scabrate (Figs. 19–22, 26, 29, 31). The sacs in many cases result from a separation of the footlayer and intrastructural layer, identical to sac formation in extant endoreticulate (alveolar) walled gymnosperm pollen (Figs. 27, 28). However, in some forms, i.e., *Punctamultivesiculites inchoatus* (Figs. 15, 30) and *Granabivesiculites inchoatus* (Figs. 13, 24), the sacci result from a build up of exinal material.

Pollen wall structure of these saccate gymnosperms is similar in many respects to granular wall structure of extant ranalean taxa.

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FIGURES 10–22. Fossil saccate pollen.—10. Bisaccate grain from the Triassic Chinle Fm. (transmission electron micrograph of the same grain is pictured in Fig. 23), ×400.—11. Bisaccate grain from the Yorkshire Jurassic, showing relatively small sacci (similar to *Bacubivesiculites inchoatus* of the Cenomanian Dakota Fm., Minnesota, Fig. 12), ×400.—12. *Bacubivesiculites inchoatus*, Cenomanian Dakota Fm., Minnesota, showing small sacci flanking the sulcus, ×400.—13. *Granabivesiculites inchoatus*, Cenomanian Dakota Fm., Minnesota, showing small, vestigial-like sacci (transmission electron micrographs of the same grain are pictured in Figs. 24 and 25), ×400.—14. *Granabivesiculites* sp., Cenomanian Dakota Fm., Minnesota, showing vestigial-like sacci flanking the sulcus (transmission electron micrographs of the same grain are pictured in Figs. 26 and 27, scanning electron micrographs of a similar grain are Figs. 19 and 20), ×400.—15. *Punctamultivesiculites inchoatus*, Cenomanian Dakota Fm., Minnesota, showing small pustule-like sacci (transmission electron micrographs of the same grain are pictured in Figs. 29 and 30), ×400.—16. Vestigial saccate pollen from the Albian Kowa Fm., Kansas (transmission electron micrograph of the same grain is pictured in Fig. 28), ×400.—17. *Clavabivesiculites pannosus*, Cenomanian Dakota Fm. of Minnesota, showing very rudimentary sacci flanking the sulcus, ×400.—18. *Verrumonocolpites conspicuus*, Cenomanian Dakota Fm., Minnesota, showing sulcus (transmission electron micrograph of the same grain is pictured in Fig. 31). This species is similar to many of the saccate forms, but lacks sacci, ×400.—19. *Granabivesiculites* sp., Cenomanian Dakota Fm. of Minnesota, scanning electron micrograph showing vestigial sacci (VW) and sulcus. Similar to the grain pictured in Figure 14, ×1,650.—20. *Granabivesiculites* sp., same grain as in Figure 19, scanning electron micrography showing details of exine sculpturing which is similar to the exine sculpturing of *Verrumonocolpites conspicuus* (Fig. 21), ×9,000.—21. *Verrumonocolpites conspicuus*, Cenomanian Dakota Fm. of Minnesota, scanning electron micrograph showing details of exine sculpturing, compare with Figure 20 of *Granabivesiculites* sp., ×9,460.—22. *V. conspicuus*, same grain as in Figure 21, scanning electron micrograph showing sulcus and exine sculpturing, ×1,800.


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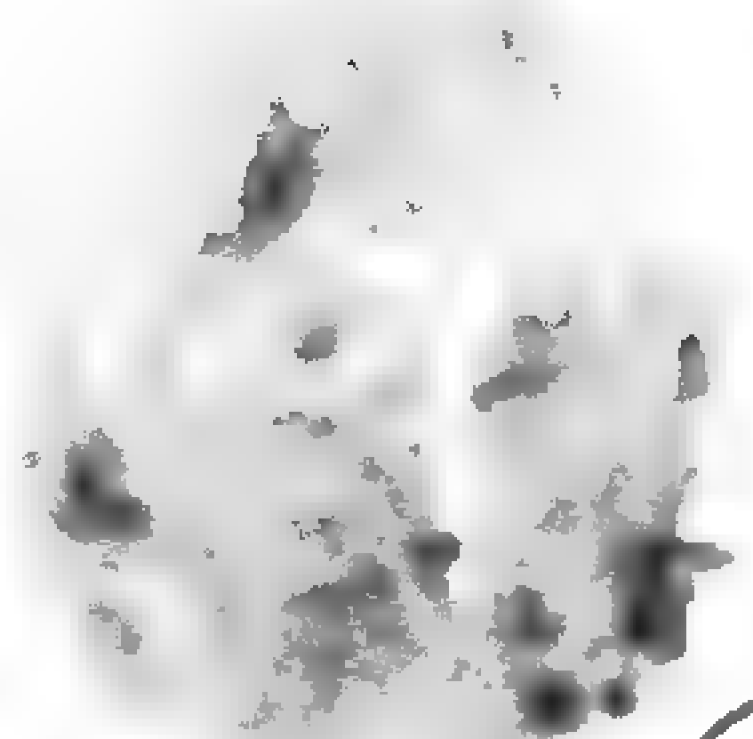
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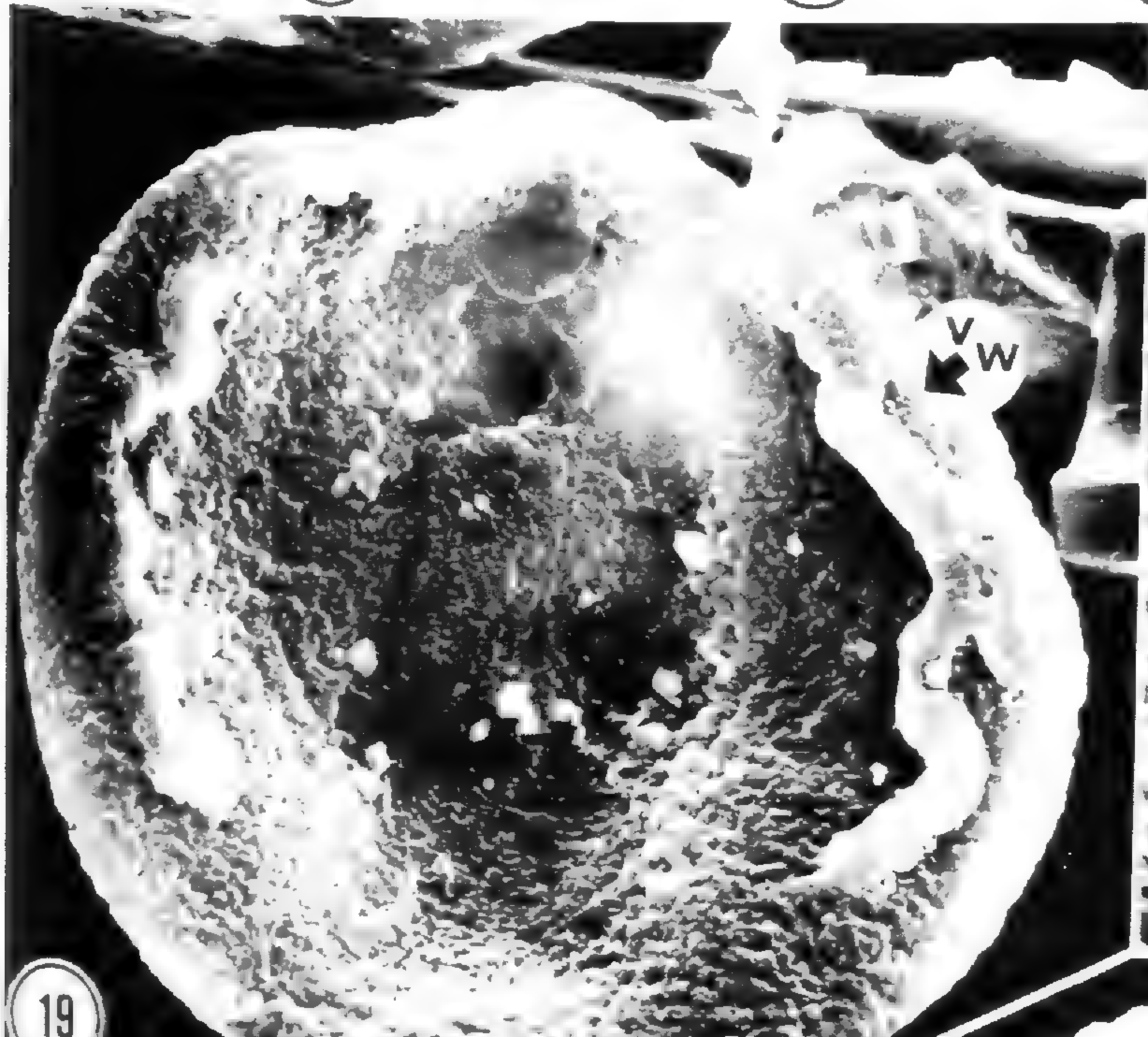

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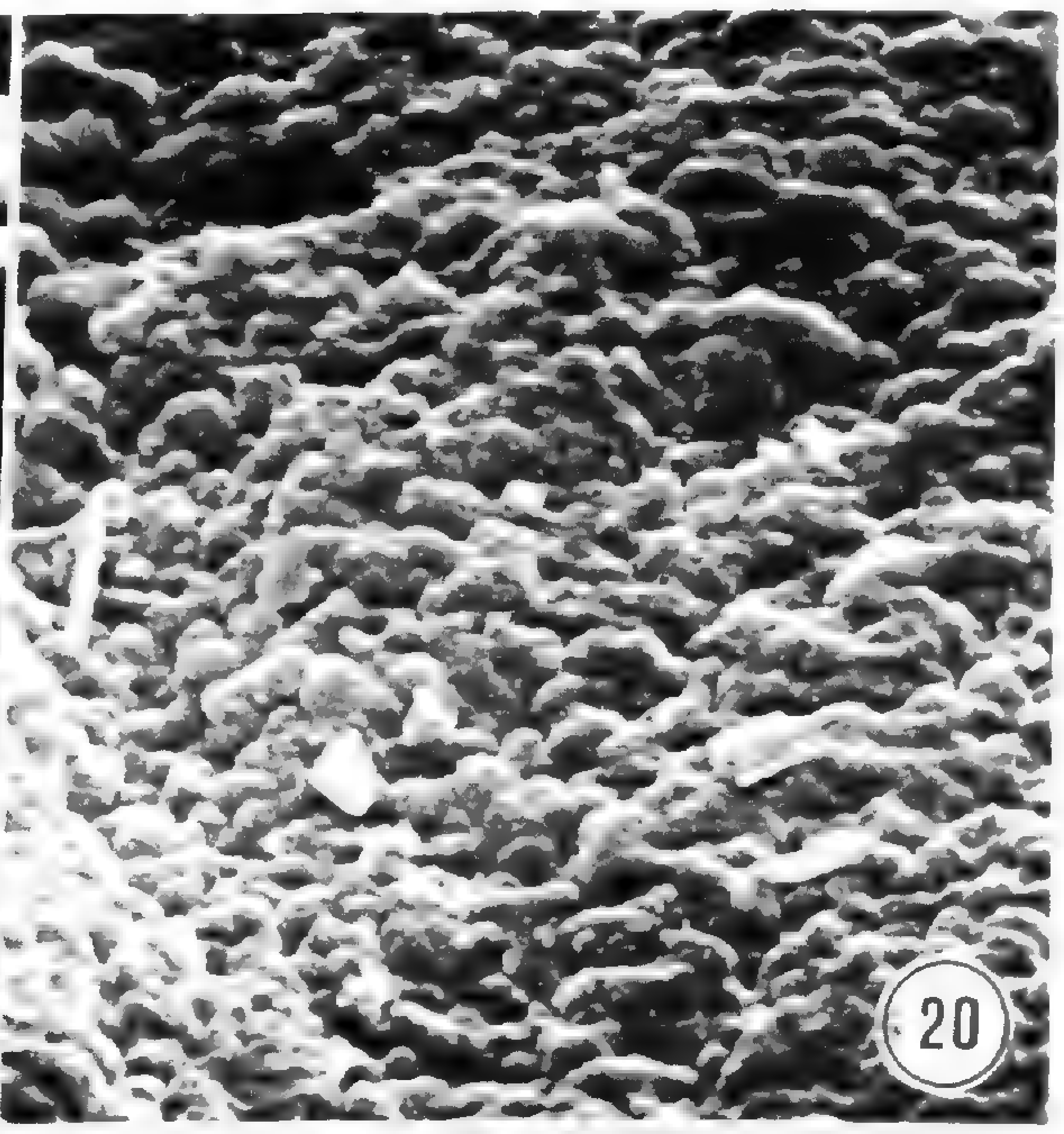
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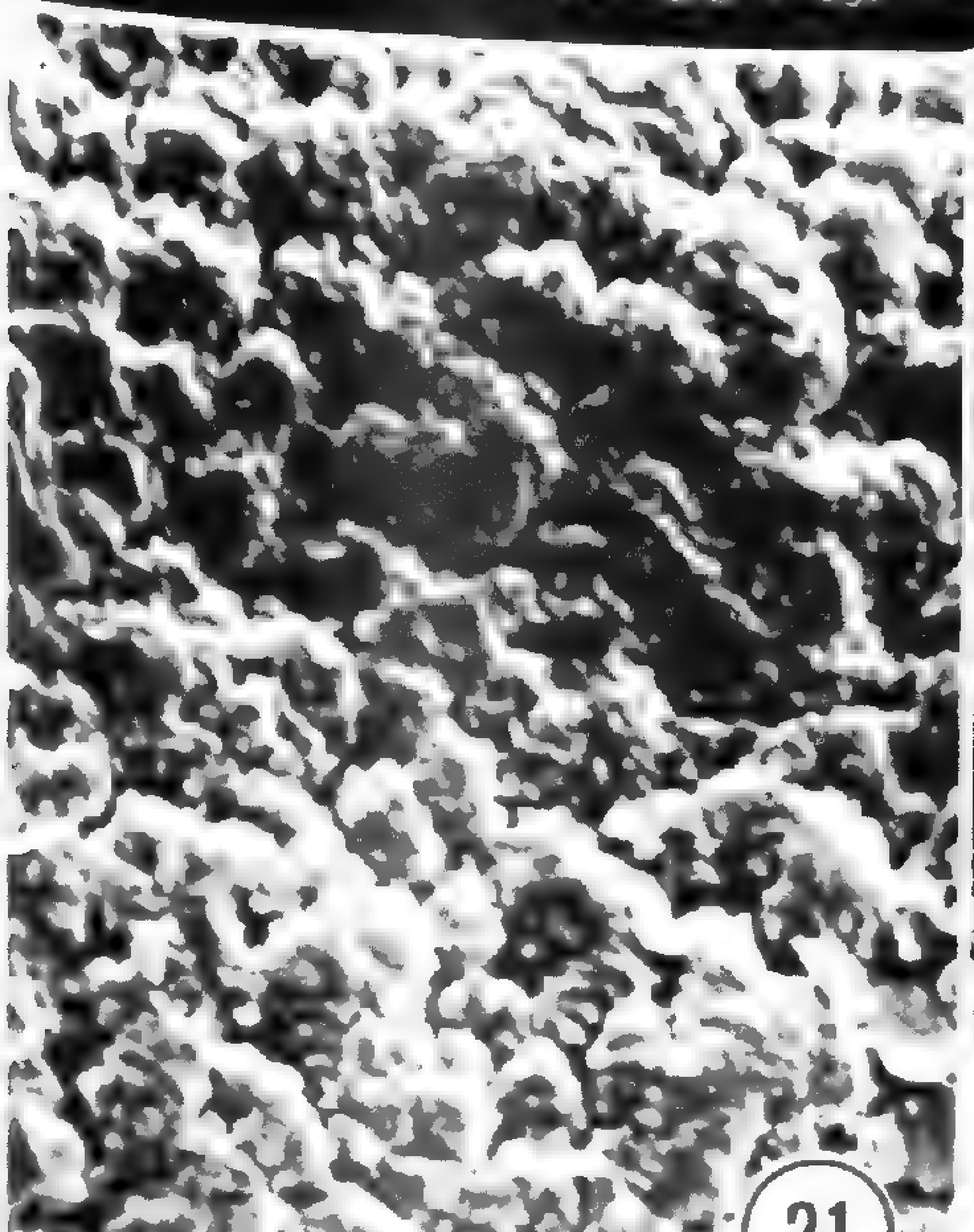
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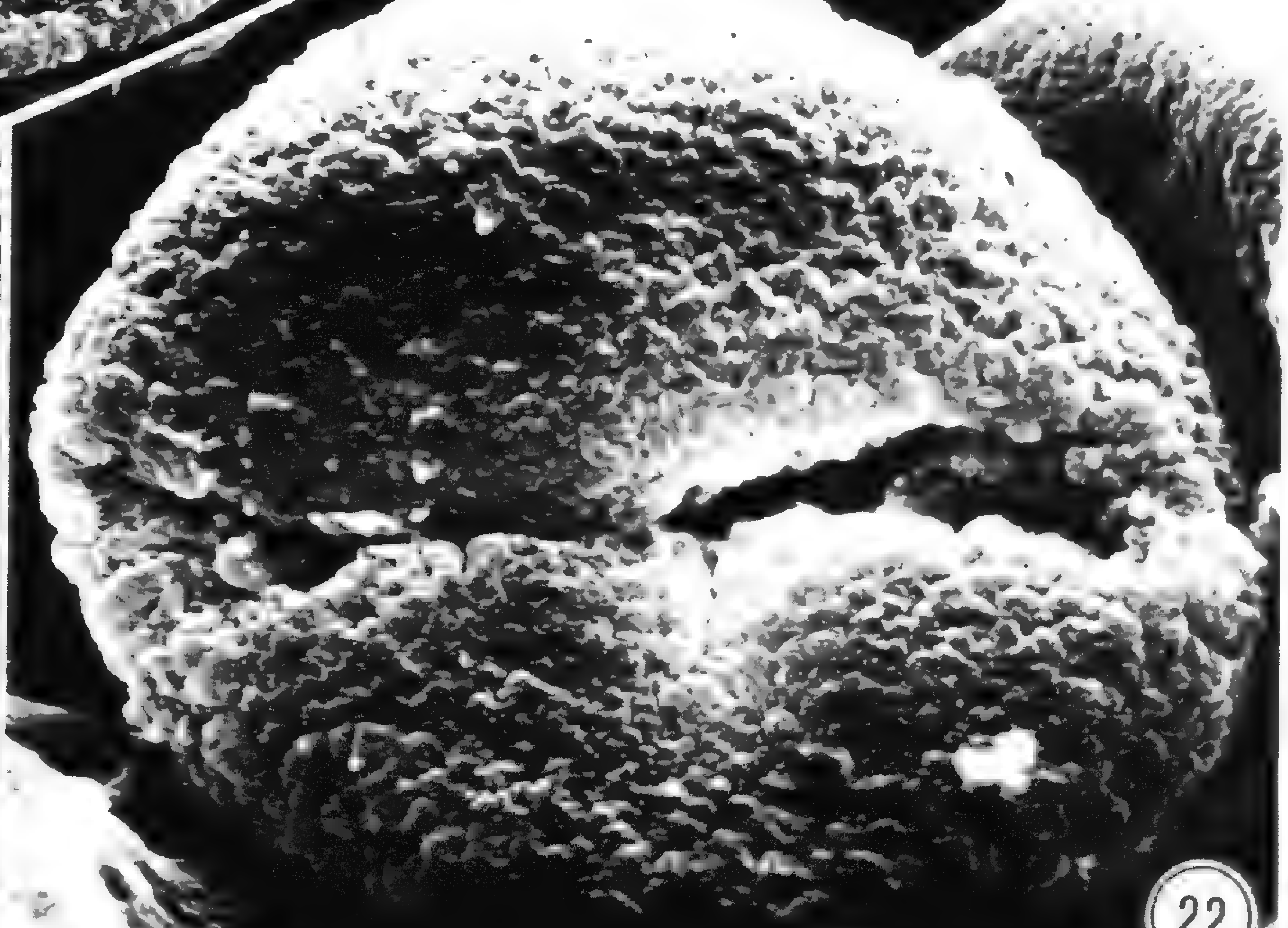
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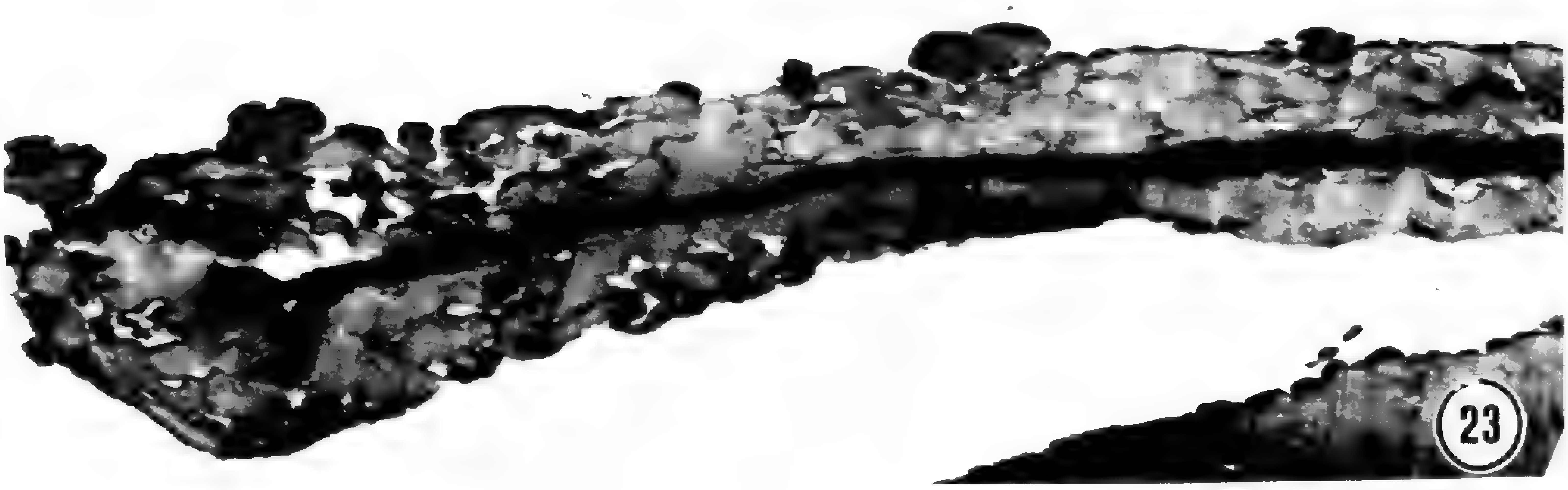
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CLAVATIPOLLENITES SPP., LOWER CRETACEOUS (BARREMIAN-CENOMANIAN)

This form genus appears to encompass a diverse array of taxa (Walker & Walker, 1984). Pollen is monosulcate to ulceroid, and ovoid to spherical. Exine sculpturing is reticulate. Pollen wall structure using SEM and TEM was investigated by Doyle et al. (1975) and Walker and Walker (1984). Pollen wall structure is tectate-columellate with a homogeneous footlayer. In the apertural region the footlayer appears lamellated and is underlain by an endexine (nexine 2) that exhibits endosculpturing. Possibly, the endosculptured endexine is due to corrosion during fossilization. Endexines of extant taxa, especially when interbedded with intine, exhibit corrosion upon treatment with acetolysis solution (e.g., *Helleborus,* Echlin & Godwin, 1969; *Austrobaileya,* Zavada, 1984). The columellate infrastructure and especially endexine (nexine 2) are features of angiosperm pollen grains. *Clavatipollenites* shares many character states with pollen of the Chloranthaceae (Kuprianova, 1981; Walker & Walker, 1984).

RETIMONOCOLPITES PERORETICULATUS, LOWER CRETACEOUS (APTIAN)

This widespread and diverse form was investigated using TEM and SEM by Doyle et al. (1975) and Walker and Walker (1984). Pollen appears monosulcate and elliptical in outline; exine sculpturing is an open reticulum. Pollen wall structure consists of a thick homogeneous inner layer, footlayer, which is underlain in the apertural region by a thin endexine (nexine 2). The sculptured outer layer of the wall forming the reticulum is attached directly to the footlayer with no apparent infrastructural layer. The presence of an endexine suggests that this form is angiospermous, however, the unusual direct attachment of the wall layer comprising the reticulum is unknown in extant angiosperms (Doyle et al., 1975; Walker & Walker, 1984).

STELLATOPOLLIS SPP., ALBIAN-CENOMANIAN

This form has been investigated using SEM and TEM by Doyle et al. (1975) and Walker and Walker (1984). Pollen is monosulcate and elliptical to subcircular; exine sculpturing is semitectate, reticulate, with the muri of the reticulum bearing supratectal projections, triangular to elliptical in surface view. Pollen wall structure consists of a thick inner footlayer (nexine 1), believed to be underlain by endexine (nexine 2) in the apertural region. The reticulum bearing the supratectal triangular to elliptical processes has a columellate infrastructure. The presence of endexine (nexine 2) and the columellate infrastructure suggests that this form is angiospermous.

LILIACIDITES SPP. (MONOCOTYLEDONOUS POLLEN TYPES), APTIAN/ALBIAN-UPPER CRETACEOUS

Forms similar to those investigated in the present study from the Cenomanian of Kansas were studied by Doyle (1973) and Walker and Walker (1984) using SEM and TEM, respectively. Pollen is predominantly monosulcate, but serial sections of single pollen grains investigated in this study have shown them to be inaperturate (Figs. 33–35). Pollen is elliptical, large, averaging 36 μm along its long axis, and is invariably folded, giving the impression that an aperture is present (Fig. 32). The exine is reticulate, and the reticulum becomes finer toward opposite ends of the

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FIGURES 23–27. Transmission electron micrograph of fossil saccate pollen.—23. Bisaccate grain from the Triassic Chinle Fm. (same grain pictured in Fig. 10). Transmission electron micrograph of the corpus showing thin footlayer (nexine 1), granular infrastructure and thin tectum, ×11,600.—24. *Granabivesiculites inchoatus,* same grain pictured in Figure 13, transmission electron micrograph showing thin non-lamellated footlayer (nexine 1), granular infrastructural layer and thick occasionally perforate tectum. Note the sacci do not result from a simple separation of the footlayer and the outer wall layers, ×6,060.—25. *G. inchoatus,* same grain pictured in Figures 13 and 24. Transmission electron micrograph showing details of the wall structure, note that some elements in the granular infrastructural layer appear columellate, ×24,150.—26. *Granabivesiculites* sp., same grain pictured in Figures 14 and 27. Transmission electron micrograph showing pollen wall structure in the nonapertural region, ×24,150.—27. *Granabivesiculites* sp., same grain pictured in Figures 14 and 26. Transmission electron micrograph showing a sac (arrow) which results from a separation of the footlayer (nexine 1) and the outer portion of the wall, and flanks the sulcus (S), ×12,500.

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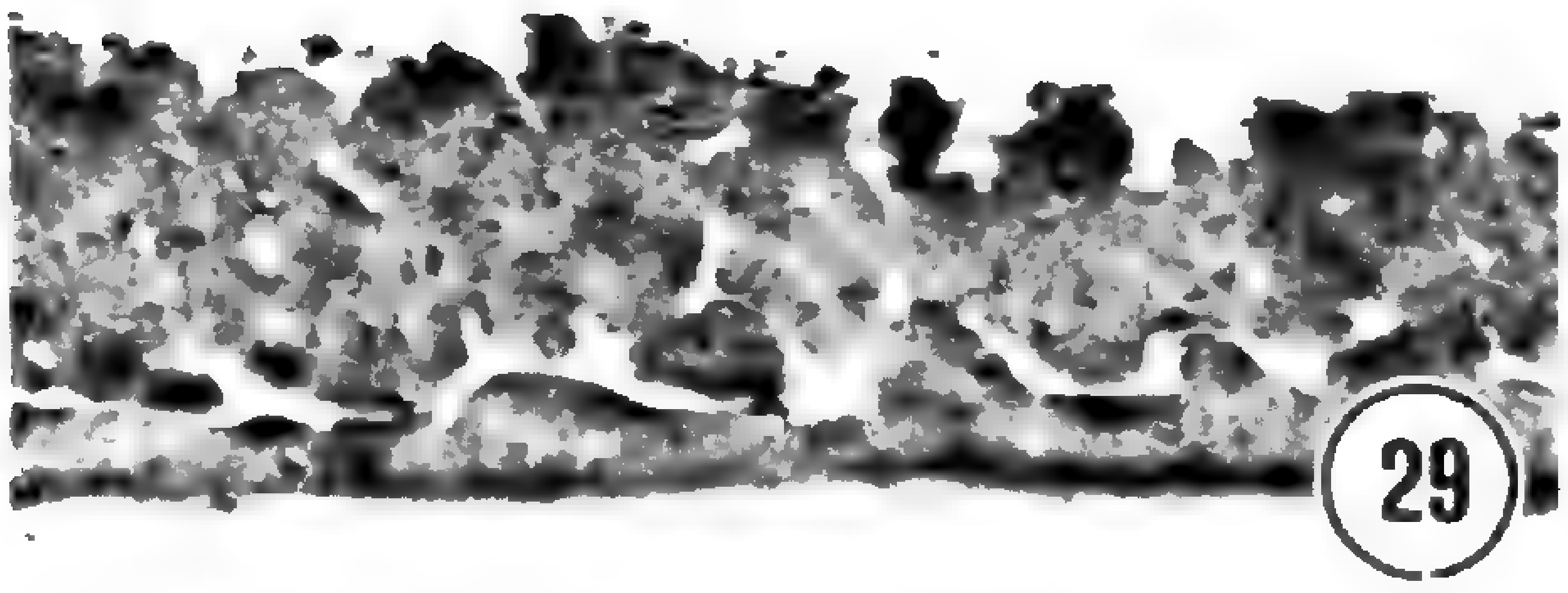

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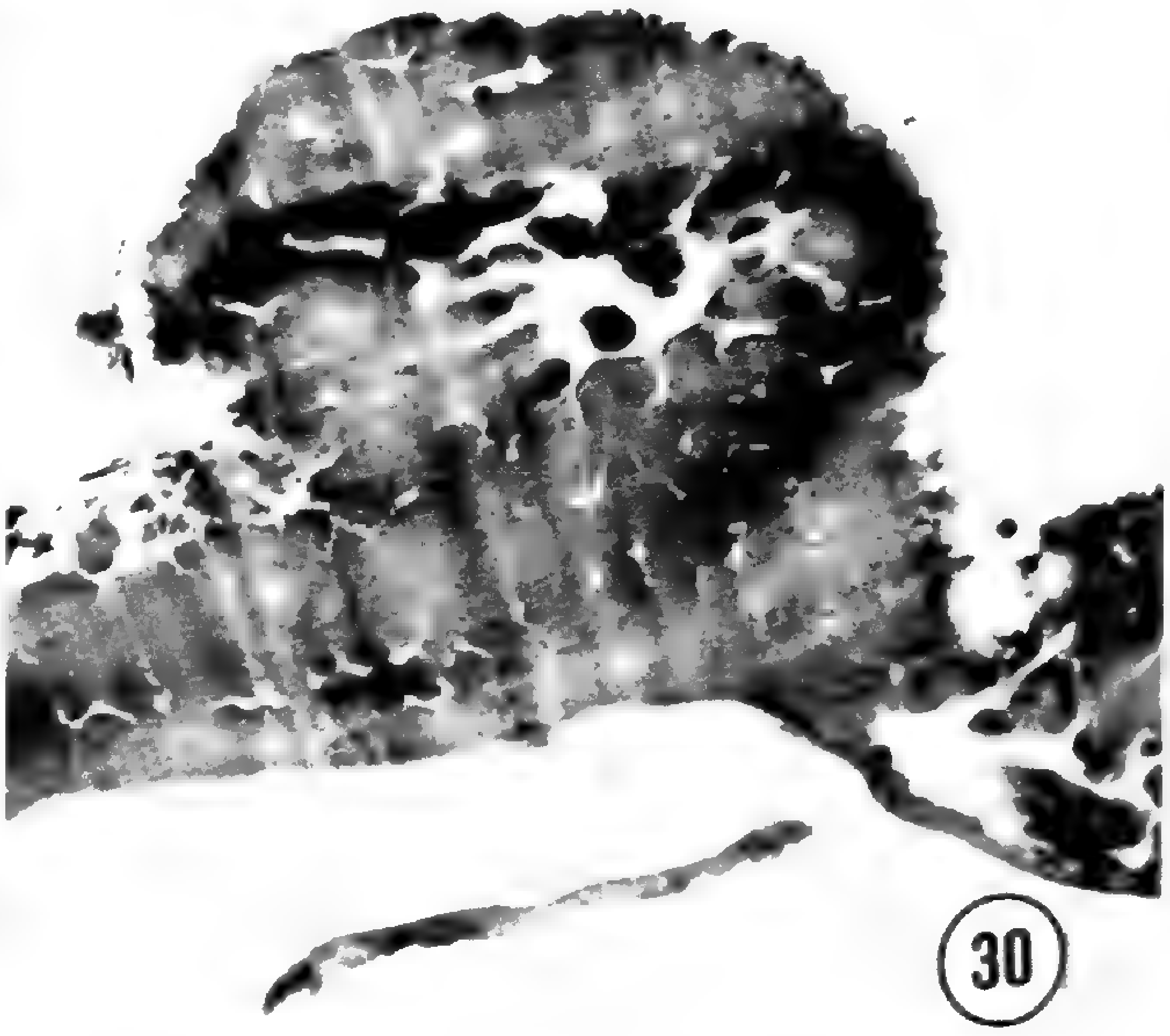

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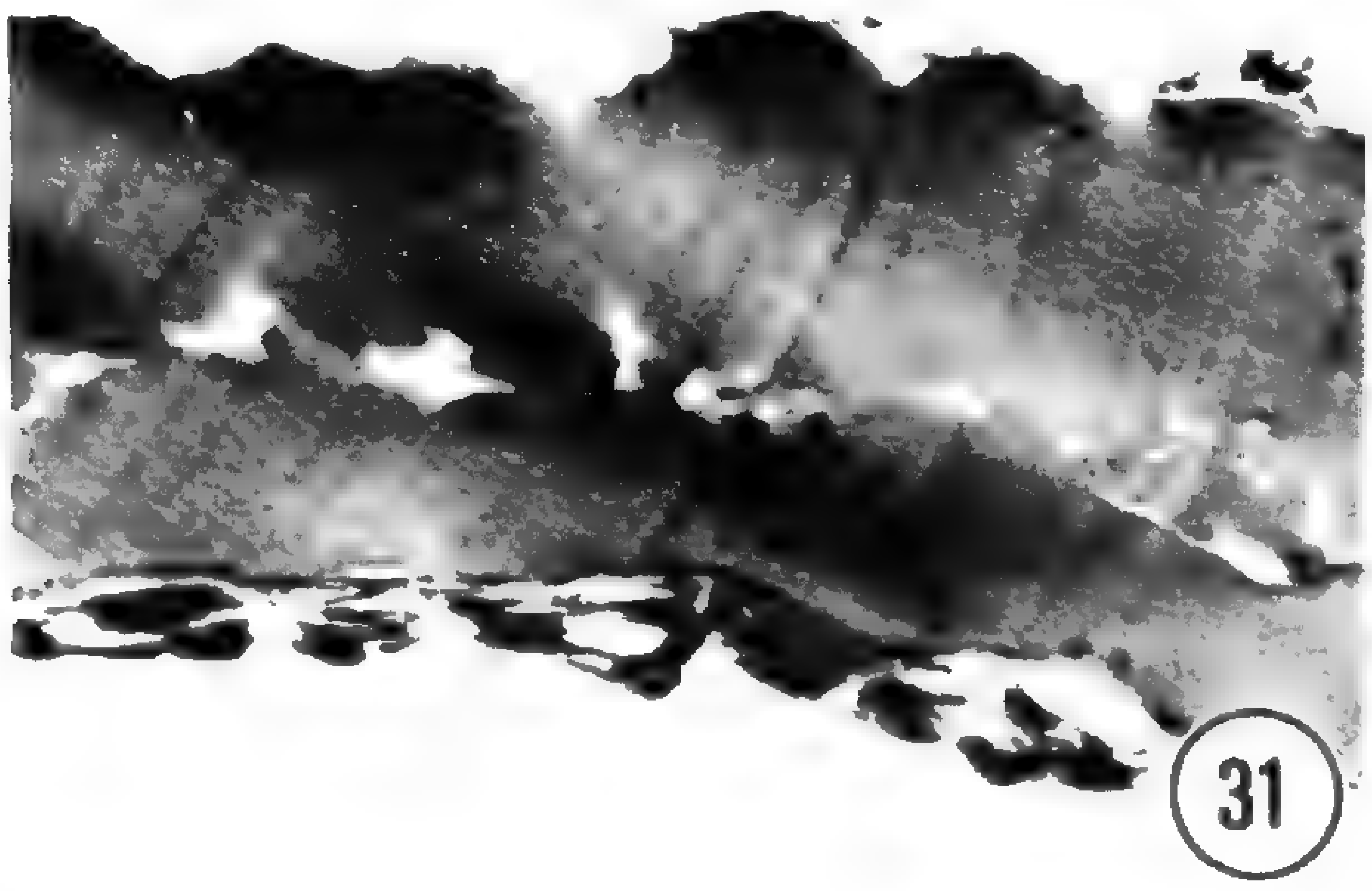

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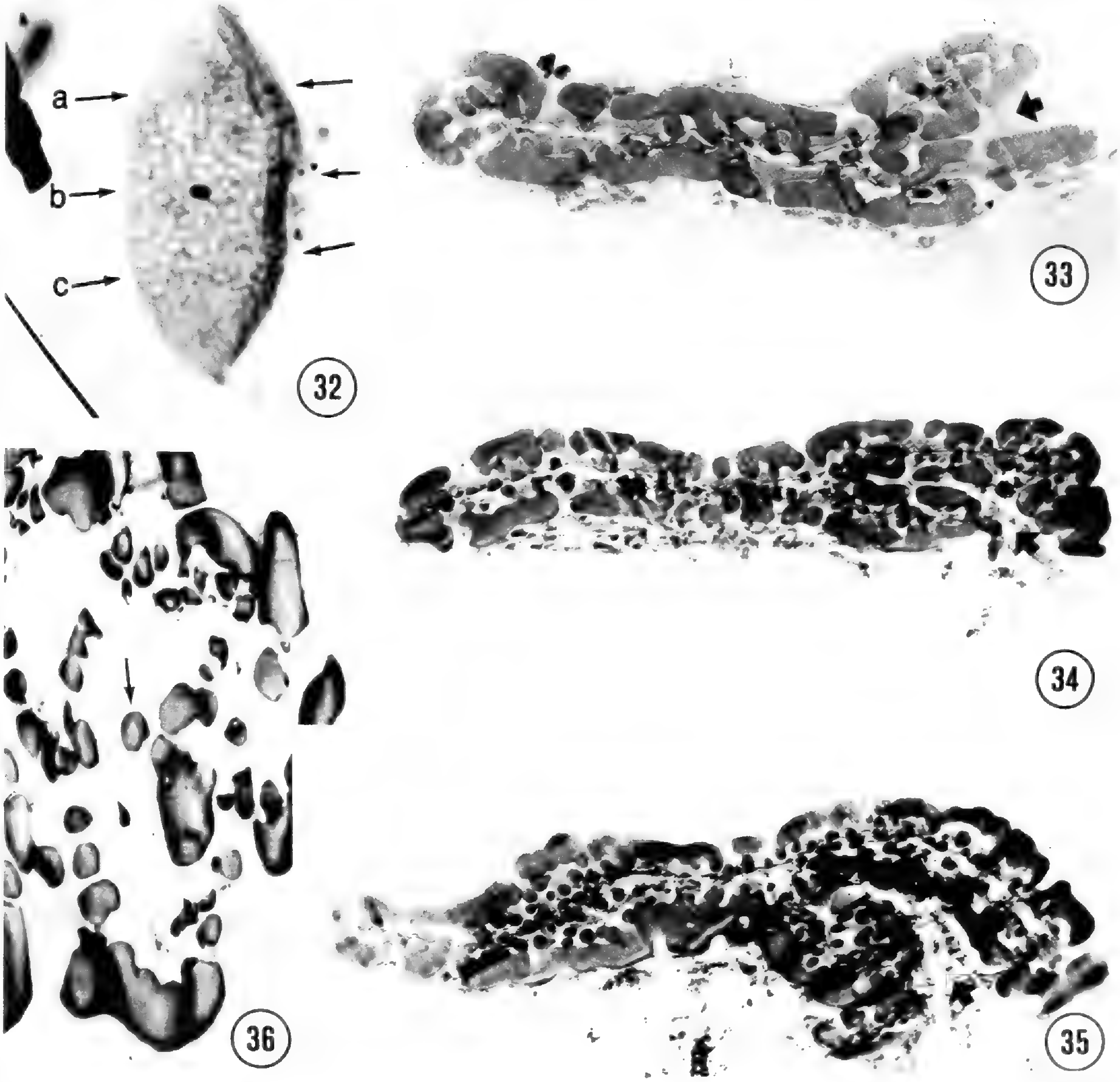
FIGURES 28–31. Transmission electron micrograph of fossil saccate pollen.—28. Transmission electron micrograph of vestigial saccate pollen grain (same grain pictured in Fig. 16), showing sulcus, separation of the footlayer (nexine 1), and outer wall layers (arrows) resulting in the sac and the granular infrastructure, ×7,000.—29. *Punctamultivesiculites inchoatus*, same grain pictured in Figure 15, transmission electron micrograph showing details of the wall structure; a thin inner non-lamellated footlayer (nexine 1), granular infrastructure, and outer tectum with supratectal scabrae, ×14,200.—30. *P. inchoatus*, same grain pictured in Figures 15 and 29, transmission electron micrograph showing wall structure of the pustule-like sacci, note it is not a simple separation of the footlayer and the outer layers of the exine, but is constructed of exinal material, ×11,600.—31. *Verrumonocolpites conspicuus*, same grain is pictured in Figure 18, transmission electron micrograph showing wall structure; thick footlayer (nexine 1), which is underlain by a thin, ragged lamellated layer (possibly endexine), granular infrastructural layer and thick tectum, ×29,000.



Figures 32–35. 32. Monocotyledonoid pollen grain from the Cenomanian Dakota Fm. of Kansas. Note the reticulum becomes finer toward the polar areas and appears to be monosulcate, ×400.—33–35. Transmission electron micrograph of serial sections of the same grain in Figure 32. The wall structure consists of a very thin footlayer, a columellate layer, and a relatively thick tectum. Note that in the area where there is presumably a sulcus (arrows) there is no modification of the exine, thus is inaperturate, ×3,600.—36. Transmission electron micrograph of the same grain pictured in Figure 32. Tangential section showing that the tectum is underlain by isolated islands of sporopollenin (arrows), columellae, ×10,600.

pollen grain (Fig. 32), a characteristic of some monocotyledonous pollen. Pollen wall structure consists of a columellate infrastructure and a tectum (Figs. 33–36). The columellae are not fused to the thin footlayer, a feature observed in some alismatidean taxa. This form exhibits many monocotyledonous features, however, the lack of a sulcus makes the combination of features observed in this taxon unique among primitive monocotyledons.

Discussion

It has already been demonstrated that, based on neontological data, the only exclusive angiosperm pollen feature is the columellate infrastructure. Wall structure of fossil-dispersed pollen, however, indicates that the clear demarcation in pollen wall structure between extant gymnosperms and angiosperms based on this criterion doesn't exist among the Mesozoic taxa.

The columellate wall structure occurs among Mesozoic dispersed pollen known to be associated with gymnosperm megafossils. For example, the Triassic form genus *Equisetoporites chinleana* clearly exhibits the angiospermous columellate infrastructure. This pollen type is associated with the gymnosperm fructification *Masculostrobus clathratus* (Ash, 1972). Two other form genera, *Classopollis* (Pettitt & Chaloner, 1964) and *Eucommiidites* (*E.* sp. 1 of Trevisan, 1980; present study) also have columellate infrastructure and both are associated with gymnospermous megafossils (e.g., *Cheirolepis muensteri,* Harris, 1957 and *Hastystrobus muirii,* Konijnenburg-van Cittert, 1971, respectively). Thus, the use of the columellate infrastructure to determine taxonomic affinities of fossil-dispersed pollen breaks down when the dimension of time is involved. Endexine (nexine 2) is thought to be an exclusive angiosperm feature. Unfortunately, it has a developmentally and cytochemically equivalent wall layer in *Ginkgo biloba* (Rohn, 1977), in addition, it is a derived feature and not likely to be found in early angiosperm pollen and has a tendency to corrode (see above).

Despite difficulties in determining the taxonomic position of fossil-dispersed pollen, there are a few significant aspects of the dispersed fossil pollen record. First, the temporal occurrences of presumably primitive pollen wall characteristics based on neontological studies, precede the first occurrences of derived wall characteristics. This lends support to the proposed phylogenetic trends of pollen wall structure based on comparative morphological studies of extant pollen (e.g., Walker, 1974a, 1974b, 1976). Secondly, the occurrences of angiosperm wall structural and apertural features prior to the alleged Lower Cretaceous origin of the angiosperms, suggests the selective pressures important to the derivation of angiospermous pollen features may also have acted on earlier Mesozoic gymnosperms.

Comparative morphological studies of extant pollen have shown the granular or atectate wall structure to be most primitive (Walker, 1976). The first occurrence of this wall structural type is in the Permian and is exemplified by the form genera *Praecolpatites* and *Marsupipollenites* (Foster & Price, 1982) and the early Mesozoic genera *Monosulcites* and *Eucommiidites* (*E.* sp. 2 of Trevisan, 1980; Doyle et al., 1975). All these genera are presumably gymnosperms or have been associated with gymnosperm fructifications (Foster & Price, 1980; Taylor, 1973; Doyle et al., 1975).

Although the granular wall structure is known from some extant nonsaccate gymnosperms, it has not been observed in extant saccate pollen. The appearance of the granular wall structure in Triassic to Cretaceous saccate pollen, contemporaneously with endoreticulate saccate pollen, is especially interesting. Among the granular-walled saccate pollen types we also note a Triassic-Cretaceous trend in the reduction of the size of the sacci. This trend may have culminated in the loss of sacci altogether in some Jurassic/Cretaceous taxa. For example, the Jurassic/Cretaceous form genus *Verrumonocolpites,* aside from lacking sacci, is similar in every respect to the granular walled saccate pollen. Its morphology and wall structure is also similar to pollen in the extant Magnoliaceae and Annonaceae (e.g., the annonaceous taxon *Miscogyne ellistianum,* Walker, 1976). Another significant aspect is that most gymnosperms that are leading contenders for angiosperm ancestors have saccate pollen (e.g., *Caytonanthus*). As a result, it is reasonable to assume that the transition to angiospermy included the reduction of the sacci. Even though little is known about the wall structure of fossil saccate gymnosperms, it is also reasonable to assume that this transition is accompanied by a change from the endoreticulate to the primitive granular or atectate angiosperm wall structure. Such a change in wall structure is assumed because all saccate gymnosperms (extant and fossil) thus far studied have endoreticulate wall structure. However, the presence of saccate granular-walled pollen in the fossil record prior to the first unequivocal angiosperm pollen makes the saccate-nonsaccate transition conceptually more palatable. Thus, by the Permo-Triassic, the granular infrastructure is well established in a number of morphologically diverse, dispersed pollen genera that persisted through the Jurassic and Lower Cretaceous.

The next major palynological event is the Upper Triassic appearance of the columellate infrastructure in the form genera *Equisetoporites* and *Classopollis* (Chaloner, 1976). The appearance of the columellate structure post-dates the first appearance of the granular types. Although the taxonomic relationship of these taxa to the earlier occurring granular-walled dispersed pollen is unknown, the latter temporal occurrence of the columellate infrastructure parallels the progression of evolutionary events proposed for pollen evolution by Walker (1976). However, the phylogenetic relationships of the granular and columellate wall structure is substantiated by the occurrence of the granular and somewhat columellate structures found in a few species of *Eucommiidites* (such structures also coincidentally occur in some extant families, e.g., Annonaceae, Le Thomas, 1981). All of these dispersed pollen taxa are associated with gymnosperm megafossils and none are considered ancestral to the angiosperms. This suggests that the selective pressures that eventually resulted in angiospermy were in operation as early, or earlier, than the Upper Triassic. The appearance of the angiosperm-like wall structure takes place during the Upper Permian (represented by granular-walled pollen), then the columellate type appears subsequently in the Upper Triassic. These palynological events appear to have occurred in a number of form genera, which may not be closely related. A shift toward more angiospermous features among gymnosperms during the early Mesozoic is also born out by the megafossil record (e.g., *Sanmiguelia, Caytonia*). However, one aspect of the pre-Cretaceous occurrences of angiospermous features in gymnosperms is that we never find an array of primitive angiosperm features occurring concomitantly. In many instances the angiospermous features appear to be isolated developments or occur with features that are considered advanced. Even the most angiosperm-like pre-Cretaceous pollen, *Equisetoporites,* is tectate-columellate with a thin footlayer, and lacks a sulcus. The grooves in this pollen could be interpreted as apertures, in which case it would be called multiaperturate, but in either case these characteristics are thought to be indicative of the more advanced columellate angiosperm pollen and would not be expected to occur in the first tectate-columellate fossil pollen. The pre-Cretaceous taxon *Classopollis* also exhibits a columellate infrastructure but has an unusual apertural arrangement and other exinal elaborations not known in extant angiosperm pollen. It is not until we encounter the Lower Cretaceous forms, i.e., *Retimonocolpites, Clavatipollenites,* and *Liliacidites,* that we see the greatest number of coincident angiosperm features occurring in combinations expected of angiosperm pollen. But, even among these earliest angiosperm pollen grains, there are notable differences between their morphology and our concept of the morphologically primitive angiosperm pollen as based on comparative morphological studies of extant pollen. *Retimonocolpites peroreticulatus,* for example, is similar to many reticulate, monosulcate angiosperm pollen types but lacks a columellate infrastructure, a combination of characteristics unknown in extant angiosperms (Doyle et al., 1975). *Liliacidites* (present study), thought to represent an early monocotyledon, exhibits some monocotyledonous features but lacks a sulcus, a situation not expected to occur in primitive monocots. Aside from double fertilization (an impractical paleobotanical criterion), there is no one exclusively angiosperm morphological feature, and the scattered occurrences of pre-Cretaceous angiosperm features (and in some cases features that are presumably advanced among angiosperms) in a few apparently unrelated form genera makes is difficult to speculate on the role these plant groups played in the origin of the angiosperms. Our recognition of an angiosperm depends on the concomitant occurrence of many "angiospermous" features in a number of plant organs. This is the basis on which the Lower Cretaceous origin of angiosperms is widely accepted. The occurrence of angiospermous pollen and leaves, and their subsequent persistence, tends to support the Lower Cretaceous origin (Doyle & Hickey, 1976). The acceptance of pre-Cretaceous occurrences of plant organs with angiospermous features (e.g., *Sanmiguelia, Equisetoporites*) awaits their association with other plant organs exhibiting angiospermous features, thus, mutually validating their identification as an angiosperm.

The broad definition of angiospermy that is currently adhered to involves characteristics of different plant organs that undoubtedly were subject to a diverse array of selective pressures. These selective pressures, however, were not necessarily contemporaneous in effect, or interrelated. Thus the simultaneous (in terms of geologic time) acquisition of the wide range of features we use to define angiospermy seems unlikely. It is more likely that angiospermy was achieved by the cumulative acquisition of angiospermous features over an extended period of time (cf. Faegri, 1980), culminating in a combination of characteristics we currently use to define angiospermy. As Stebbins (1981) has suggested, the initial radiation and continuing success of angiosperms is due to the cumulative effect of a number of independently derived advantageous angiosperm features that involve pollination biology; seed development, morphology and dispersal; vegetative anatomy and morphology; and biochemistry. Thus, our reluctance to seriously consider pre-Cretaceous plants with angiosperm features, as angiosperms, seems more related to our broad definition of angiospermy and in some respects to our deep-seated hypothetical notions that have prevailed in past years, than to major inadequacies of the fossil record. Undoubtedly, further palynological investigations of dispersed pollen will lead us to the most likely angiosperm ancestor(s) and possibly into pre-Cretaceous sediments, but our own definition of angiospermy seems to relegate the further elucidation of angiosperm origins to a concerted effort by paleobotanists and palynologists.

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ULTRASTRUCTURE OF LOWER CRETACEOUS ANGIOSPERM POLLEN AND THE ORIGIN AND EARLY EVOLUTION OF FLOWERING PLANTS[1]

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Abstract

In the last decade significant new information has been gained about the early evolution of flowering plants through studies of Early Cretaceous angiosperm pollen and the pollen of living primitive flowering plants. Although most recent palynological studies of extant primitive angiosperms have used both scanning and transmission electron microscopy, few ultrastructural studies of early fossil angiosperm pollen grains exist. This paper represents an attempt to remedy this situation. Thirteen different types of Lower Cretaceous angiosperm pollen grains from the Potomac Group of eastern North America and the Fredericksburgian of Oklahoma were examined ultrastructurally, including *Clavatipollenites hughesii*, two aff. *Clavatipollenites* species, *Asteropollis asteroides*, *Stephanocolpites fredericksburgensis*, *Retimonocolpites dividuus*, *R. peroreticulatus*, two aff. *Retimonocolpites* species, *Stellatopollis barghoornii*, and three species of *Liliacidites*. These grains were investigated using a technique that we have developed for working with single fossil pollen grains by which we are able to undertake combined light, scanning electron, and transmission electron microscopy of the same pollen grain. This technique is invaluable for the evolutionary study of small, light-microscopically similar, dispersed fossil pollen grains, such as those that constitute the bulk of the earliest known part of the fossil record of the flowering plants, and provides a much improved means of delimiting Early Cretaceous angiosperm pollen form genera such as *Clavatipollenites*, *Retimonocolpites*, and *Liliacidites*. Our study also reveals that a close similarity exists between some Early Cretaceous angiosperm pollen and pollen produced by certain living primitive angiosperms. *Clavatipollenites hughesii*, *Asteropollis asteroides*, and *Stephanocolpites fredericksburgensis* exhibit varying degrees of similarity at the ultrastructural level respectively to pollen of the extant angiosperm genera *Ascarina*, *Hedyosmum*, and *Chloranthus*, all three of which belong to the modern family Chloranthaceae. Pollen described under the form genus *Liliacidites* possesses many features that are restricted to pollen of living monocotyledons, while *Retimonocolpites* possesses certain monocotyledonous palynological features, but to a lesser extent. Large monosulcate pollen grains with distinctive crotonoid sculpturing described as *Stellatopollis barghoornii* have no counterpart among the pollen of extant angiosperms.

The question of the origin and early evolution of the angiosperms is dealt with in the second part of the paper, and the fossil pollen record of early flowering plants is considered in light of what is known about pollen evolution in living primitive angiosperms. Analysis of the taxonomic distribution of characters of living primitive angiosperms suggests that angiosperm pollen is primitively monosulcate, boat-shaped, large- to medium-sized, psilate or at best only weakly sculptured, noninterstitiate to interstitiate-granular, atectate, and without endexine. This type of pollen is found today only in the otherwise primitive angiosperm families Magnoliaceae, Degeneriaceae, and Annonaceae. It is concluded that *Clavatipollenites* and other currently known types of Early Cretaceous angiosperm pollen grains represent relatively advanced primitive angiosperm pollen that is already too specialized to reveal anything about the earliest evolution (or the origin) of the flowering plants. Finally, what can be deduced about the origin and early evolution of flowering plants from fossil and living primitive angiosperms is considered. The conclusion is drawn that the ancestory of the angiosperms must be sought in the pteridosperms or in a derivative group. A 5-stage model of early angiosperm evolution is proposed, based on the early (Barremian to Middle Cenomanian) fossil pollen record of the flowering plants and the inferred phylogenetic relationships of living primitive angiosperms. From an original, pre-Barremian basal complex of entomophilous flowering plants, whose living descendants include such angiosperms as the Magnoliales, Laurales, and Winterales, we envision evolution of a major line of anemophilous and apetalous angiosperms in the Barremian-Aptian, the descendants of which include advanced magnoliid angiosperms, such as the Chloranthaceae, as well as related primitive hamamelidid angiosperms, such as the Trochodendrales, Cercidiphyllales, and Hamamelidales. The evolution of

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wind-pollination so early within the angiosperms may have been connected with the increasing aridity (and possible decline in insect pollinators) that occurred soon after the earliest appearance of *Clavatipollenites*-type pollen in the Barremian of Africa and South America, when major splitting of West Gondwana was taking place. The majority of dicots, including the subclasses Dilleniidae, Rosidae, and Asteridae, appear to be derived from this early group of entomophilous-derived anemophilous angiosperms, and, thus, most of the dicots probably represent flowering plants that have secondarily returned to entomophily.

Palynology has rapidly become an important source of taxonomic and phylogenetic information for angiosperm systematics, and, indeed, few other fields of botanical inquiry provide so much systematic data from so little material (cf. Walker & Doyle, 1975). In the last decade, for example, significant new insight has been gained into the early evolution of flowering plants through investigations of early fossil angiosperm pollen (Brenner, 1967, 1976; Doyle, 1969, 1970, 1973, 1977a, 1977b, 1978a, 1978b; Doyle et al., 1977; Doyle & Hickey, 1976; Doyle et al., 1982; Doyle & Robbins, 1977; Doyle et al., 1975; Hickey & Doyle, 1977; Hughes, 1976, 1977; Hughes et al., 1979; Kemp, 1968; Laing, 1976; Muller, 1970, 1981; Walker et al., 1983), as well as from studies of the pollen of extant primitive flowering plants (Le Thomas, 1980, 1981; Le Thomas & Lugardon, 1974, 1976a, 1976b; Lugardon & Le Thomas, 1974; Praglowski, 1974a, 1974b, 1976, 1979; Walker, 1971a, 1971b, 1971c, 1972a, 1972b, 1974a, 1974b, 1976a, 1976b, 1979; Walker & Doyle, 1975; Walker & Skvarla, 1975; Walker & Walker, 1979, 1980, 1981, 1983).

Although most recent palynological investigations of living primitive angiosperms have used both scanning electron and transmission electron microscopy, few ultrastructural studies of Early Cretaceous angiosperm pollen grains exist (e.g., Davies & Norris, 1976; Doyle et al., 1975; Hughes et al., 1979). Moreover, most workers have employed scanning electron microscopy (SEM) alone, and few (e.g., Doyle et al., 1975) have used transmission electron microscopy (TEM) as well. This is no doubt due to the difficulties inherent in examining dispersed fossil pollen grains with electron microscopy, and by TEM in particular. For this reason we have begun an ultrastructural investigation of Early Cretaceous angiosperm pollen, using a technique that we have developed for working with single fossil pollen grains by which we are able to undertake light, scanning electron, and transmission electron microscopy of the same pollen grain. The purpose of this paper is to discuss the results and evolutionary implications of a preliminary study of Lower Cretaceous angiosperm pollen from the Potomac Group of eastern North America and the Fredericksburgian of Oklahoma, using this technique.

ULTRASTRUCTURAL STUDY OF LOWER CRETACEOUS ANGIOSPERM POLLEN

Our initial study of Early Cretaceous angiosperm pollen has centered mainly on the Potomac Group of the Atlantic Coastal Plain of eastern North America. We chose the Potomac Group for a detailed investigation for several reasons. First, much of the important light-microscope-based evolutionary studies of early fossil angiosperm pollen (e.g., Brenner, 1967; Doyle, 1969, 1970, 1977a, 1977b; Doyle & Hickey, 1976; Doyle & Robbins, 1977; Hickey & Doyle, 1977) are based on the pollen of the Potomac Group. Second, Potomac Group pollen is especially well preserved, not only at the light microscope level (cf. Brenner, 1963), but also ultrastructurally. Third, we have been able to acquire numerous Potomac Group rock samples, the most important of which are more than 50 closely spaced core samples from two shallow wells drilled through the Potomac Group near Delaware City, Delaware, which were kindly provided by Dr. Robert R. Jordan, Director of the Delaware Geological Survey (see Doyle & Robbins, 1977, for a detailed light microscope study of angiosperm pollen from these two Delaware wells). In addition to Potomac Group pollen, we have also examined pollen grains isolated from prepared samples taken from the Fredericksburgian (Albian) of Oklahoma. These samples, which were kindly provided by Dr. R. W. Hedlund, are important because they are the same samples from which the type specimens of both *Asteropollis* Hedlund & Norris and *Stephanocolpites fredericksburgensis* Hedlund & Norris were obtained.

The Potomac Group (Table 1) dates from about the Late Barremian-Early Aptian through the Early Cenomanian according to Doyle and Robbins (1977), and consists of four formations—the Patuxent, Arundel Clay, Patapsco, and Elk Neck Beds (or "Maryland Raritan"). The Late

TABLE 1. Stratigraphy of the Potomac Group, based on Doyle and Robbins (1977). (Boundaries between stages in Ma, after van Eysinga, 1978.)

SERIES	STAGE	SUBSTAGE		FORMATION	ZONE	SUBZONE	
Upper Cretaceous	Cenomanian (100 m.y.)	Lower	upper	Elk Neck Beds ("Maryland Raritan")	III	Upper	
			lower			Lower	
Lower Cretaceous	Albian (109 m.y.)	Upper	upper		II	C	
			lower	Patapsco Formation		B	upper
		Middle	upper				middle
			middle				lower
			lower			A	
		Lower		Arundel Clay	I	Upper	
	Aptian (114 m.y.)	Upper					
		Lower		Patuxent Formation		Lower	
	Barremian (118 m.y.)						

Barremian to Early Cenomanian represents a time span of approximately 18 Ma from about 116–98 Ma, following van Eysinga (1978). The Potomac Group has been divided into three major zones based on pollen and spore types (Brenner, 1963; Doyle, 1970, 1977a; Doyle & Robbins, 1977). Zone I (from ? Upper Barremian through Lower Albian) is characterized by monosulcate angiosperm pollen, Zone II (Middle and Upper Albian) is characterized by tricolpate to tricolporoidate angiosperm pollen, and Zone III (Lower Cenomanian) is characterized by tricolporate angiosperm pollen that is frequently triangular in equatorial outline. Triporate Normapolles enter above Zone III in the Middle Cenomanian. The most detailed palyno-zonation of the Potomac Group is that of Doyle and Robbins (1977), who recognized subzones as well, dividing Zones I and III into lower and upper subzones, and Zone II into subzones IIA, IIB, and IIC. For discussion of the geological setting of the Potomac Group from a paleopalynological perspective the reader is referred to the papers of Brenner (1963), Doyle (1977a), Doyle and Hickey (1976), Doyle and Robbins (1977), Hickey and Doyle (1977), and Wolfe and Pakiser (1971).

We initially have restricted ourselves to examination of monosulcate and monosulcate-derived early fossil angiosperm pollen before we attempt investigation of the more advanced tricolpate and tricolpate-derived pollen types. The pollen grains we have studied fall into six different currently recognized form genera: *Clavatipollenites, Asteropollis, Stephanocolpites, Retimonocolpites, Stellatopollis,* and *Liliacidites.*

MATERIALS

Lower Cretaceous pollen grains examined in this study were obtained from outcrop and core samples (Potomac Group zonation follows Doyle & Robbins, 1977):

(1) Cleaves 27: E. T. Cleaves (1968) sample no. 27, outcrop sample from the undifferentiated Potomac Formation, Maryland; Lower Zone I of the Potomac Group fide Doyle et al. (1975), Barremian-Lower Aptian (ca. 115 Ma old).

(2) Brenner 10: G. J. Brenner (1963) station no. 10, outcrop sample from the Arundel Clay, Maryland; Upper Zone I of the Potomac Group, Upper Aptian-Lower Albian (ca. 110 Ma old).

(3) Cornet Beltway: B. Cornet outcrop sample from Rt. 495 (Beltway), Exit 25, Maryland; Zone IIB of the Potomac Group fide Cornet, Middle-Upper Albian (ca. 105 Ma old).

(4) Hedlund 3916: R. W. Hedlund collection 3916 cited in Hedlund and Norris (1968), outcrop sample from the Fredericksburgian of Oklahoma; correlative with Middle Zone IIB of the Potomac Group fide Doyle and Robbins (1977), upper Middle Albian (ca. 105 Ma old).

(5) D12-515: Tidewater Oil Company well D12 (Delaware Geological Survey no. Dc53-7), near Delaware City, Delaware, core sample from 515 feet (Delaware Geological Survey sample no. 20083); Middle Zone IIB of the Potomac Group fide Doyle and Robbins (1977), upper Middle Albian (ca. 105 Ma old).

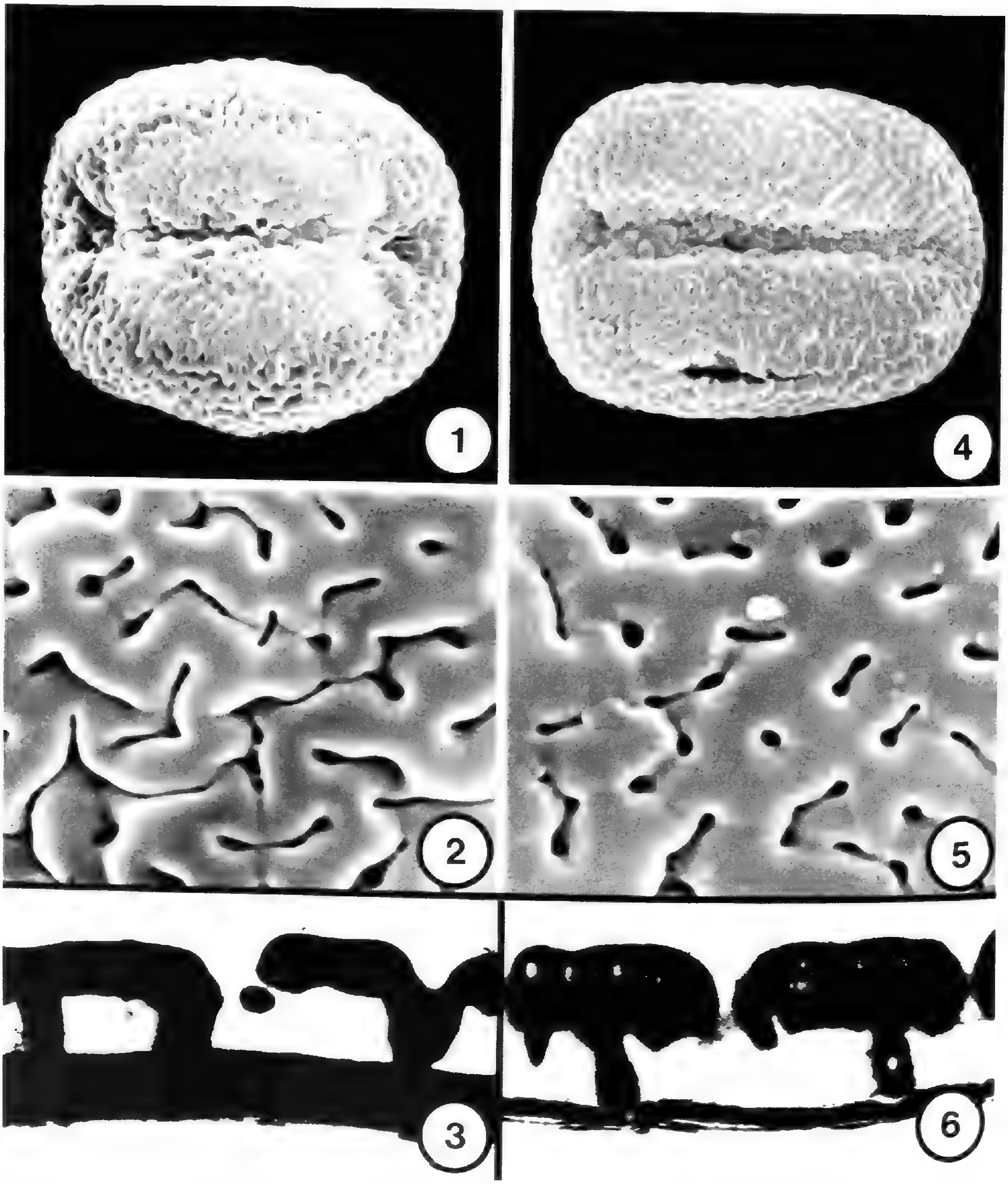
(6) D13-535: Tidewater Oil Company well D13 (Delaware Geological Survey no. Ec14-1), near Delaware City, Delaware, core sample from 535 feet (Delaware Geological Survey sample no. 20235); Upper Zone IIB of the Potomac Group fide Doyle and Robbins (1977), lower Upper Albian (ca. 103 Ma old).

"P" numbers in text and figure legends are palynological accession numbers given to each plant collection from which modern pollen was obtained. "FP" numbers represent fossil palynomorph accession numbers given to every individual fossil palynomorph isolated.

METHODS

When we initially began this investigation of early fossil angiosperm pollen our sole interest was in studying the ultrastructure of the pollen grains we examined. However, since most of the literature and almost all the nomenclature of dispersed fossil pollen and spores is based on light microscope studies alone, it was soon apparent that it would also be highly desirable to have photomicrographs of the same pollen grains that we examined with electron microscopy. Moreover, during our palynological studies of extant Myristicaceae (Walker & Walker, 1979), a family whose pollen is similar at the light microscope level to some types of Lower Cretaceous angiosperm pollen grains, we discovered that closely related genera could produce pollen virtually identical with regard to exine sculpturing as seen with the scanning electron microscope that, nevertheless, was always distinguishable by exine structure when examined with the transmission electron microscope (cf. Figs. 1–6). Thus, when investigating dispersed fossil pollen grains for taxonomic and evolutionary (as opposed to stratigraphic) purposes, we felt that it was highly advantageous to be able to undertake combined light, scanning electron, and transmission electron microscopy of the same pollen grain to establish unequivocally that one was actually dealing with pollen produced by one and the same biological entity. To this end we developed a technique that allows us to obtain photomicrographs (PMG), scanning electron micrographs (SEMG), and transmission electron micrographs (TEMG) of the same individual pollen grain. We believe that this technique is a virtual necessity for the evolutionary study of small, light-microscopically similar, dispersed fossil pollen grains such as those that constitute most of the earliest known part of the fossil record of the flowering plants.

Our technique for working with single fossil pollen grains is as follows. Fossil pollen was extracted from Potomac Group outcrop and core samples using a slightly modified version of the sample preparation outlined by Brenner (1963). Rock samples are first crushed in distilled water with a mortar and pestle. The disaggregated material is then centrifuged and ZnCl heavy liquid solution (specific gravity 2) is used to separate organic from inorganic matter by flotation. The float is pipetted off, and a few drops of 10% HCl are added to prevent zinc hydroxide precipitation. The sample is then washed twice with distilled water, and, after centrifugation, HF is added to remove clay particles. After washing and further centrifugation, the sample is oxidized briefly (2–3 minutes) with a 5.25% solution of sodium



FIGURES 1–6. Myristicaceae. 1–3. *Compsoneura*. 4–6. *Virola*.—1. Whole grain SEMG, ×2,520.—2. Exine surface SEMG, ×12,000.—3. Nonapertural exine section TEMG, ×15,100.—4. Whole grain SEMG, ×2,360.—5. Exine surface SEMG, ×16,000.—6. Nonapertural exine section TEMG, ×18,200. Although pollen grains of some species of *Compsoneura* and *Virola* are virtually identical externally, even in SEMG (cf. Figs. 1 & 4, 2 & 5), pollen of the two closely related genera can be distinguished consistently by features of exine structure evident in TEMG (cf. Figs. 3 & 6). Pollen of *Compsoneura* (Fig. 3) has a relatively thick, non-lamellate nexine, while pollen of *Virola* (Fig. 6) is characterized by a very thin, finely lamellate nexine. In addition, pollen grains of *Virola* (Fig. 6) have conspicuous, spherical, intra-exinous cavities within the sexine that are lacking in the pollen of *Compsoneura* (Fig. 3).

hypochlorite. This is followed by another wash cycle and treatment with 10% NH_4OH for three minutes. Finally, the material is washed again, and the pollen/spore samples are stored in glycerin-water. We found that a shorter period of oxidation than the 20 minutes used by Brenner gave excellent results, and have adopted this modification since we consider it highly desirable for ultrastructural studies to have as gentle a preparatory process as possible.

In order to get single angiosperm pollen grains for study, open glycerin spreads are made on microscope slides from outcrop and core samples that have had their pollen extracted and prepared as outlined above. These slides are then carefully scanned under low power (160–200×) of a light microscope and individual pollen grains are picked out with an eyelash attached to a wooden applicator stick (or with a micropipette). Single pollen grain slides are prepared, and each grain is given its own "FP" (fossil palynomorph) accession number. Isolation of angiosperm pollen grains from gymnosperm pollen as well as spores may take considerable time since in some Potomac Group samples angiosperm pollen makes up less than 1% of the total pollen grains and spores present.

Each grain is then photographed under a Leitz NPL Fluotar 100× oil immersion objective with a Leitz Dialux 20 brightfield light microscope and a Leitz Vario Orthomat camera, using Kodak High Contrast Copy Film or Kodak Technical Pan Film 2415. Following photomicroscopy, the cover slip is removed from the original slide and the pollen grain is transferred to a clean microscope slide and washed with 70% ethanol several times using a micropipette to remove the glycerin. The washed pollen grain is then placed on an SEM specimen holder and sputter-coated with gold-palladium for about three minutes. After scanning electron micrographs of one side of the grain are taken with a JEOL JSM-35 SEM using Polaroid Type 665 positive/negative film (with 0° tilt and an accelerating voltage of 30 kV), 70% ethanol is used to loosen the grain, and it is turned over with an eyelash under a light microscope. The grain is then re-coated in the sputter coater and its other side is photographed with the SEM.

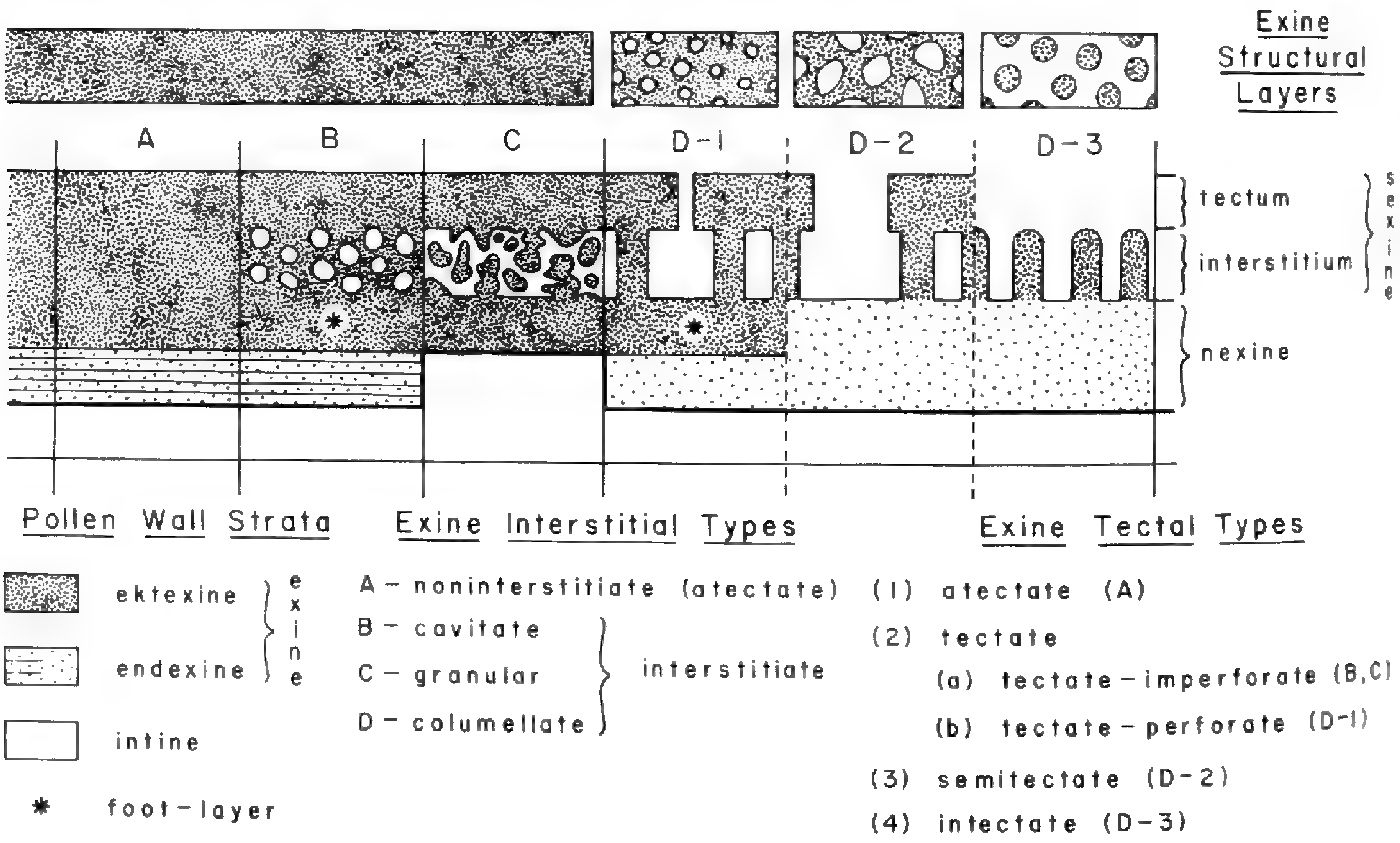
After scanning electron microscopy has been completed, the grain is treated with dilute aqua regia to remove the heavy metal coating. This is followed by preparation for transmission electron microscopy. First, the grain is placed in agar and fixed in a 1% aqueous solution of OsO_4 for two hours at room temperature. Then, it is washed four times with distilled water and enbloc stained in a saturated aqueous solution of uranyl acetate for two hours at room temperature. After washing four times with distilled water, the grain is dehydrated in an acetone series and embedded in Spurr's low viscosity embedding medium, which is cured in an oven at 70°C for 12 hours. The block containing the single pollen grain is trimmed down to the grain itself (one of the most difficult parts of the entire procedure) and the grain is then sectioned with a Reichert ultramicrotome using a Dupont diamond knife. The sections are picked up on formvar-coated, single-slot grids, and then stained in 1% $KMnO_4$ followed by Reynold's lead citrate. The sections are then examined and photographed with a Zeiss 9A transmission electron microscope, using Kodak Electron Image Film 4463. Prints were made on Agfa Brovira paper with Omega Pro-Lab 4 × 5 standard and point-source enlargers equipped with Schneider Componon-S lenses.

POLLEN WALL ARCHITECTURE AND STRATIFICATION

While palynological characters such as aperture type, pollen shape, and pollen size can be readily determined by light or photomicroscopy (LM) alone, scanning electron microscopy (SEM) and transmission electron microscopy (TEM) are required to obtain a thorough understanding of the morphology of the pollen wall itself. Since concepts and terminology dealing with the pollen wall are considerably varied, basic features of pollen wall morphology will be briefly outlined at this point to provide a general background for our ultrastructural study of Lower Cretaceous angiosperm pollen.

As with plant cells in general, the living protoplast of each pollen grain is surrounded by a predominantly cellulosic cell wall layer, which in pollen is known as the intine. Pollen grains, however, have an additional wall layer external to the intine that is known as the exine. The exine, unlike the cellulosic intine, is made-up of sporopollenin, which is a highly chemically and biologically resistant material consisting of carotenoid polymers (Shaw, 1971). The exine represents the taxonomically and evolutionarily most important part of the pollen wall since the intine is generally not preserved in fossil pollen and is usually destroyed as well during the commonly employed preparatory treatment used for modern pollen known as acetolysis. Moreover, the exine is generally a complex layer, both externally (sculpturally) and internally (structurally), whereas the intine with a few notable exceptions is usually simple morphologically. For these reasons the following discussion will be restricted to consideration of the exine alone. Exine morphology will be discussed under the following four headings: nonapertural exine sculpturing, nonapertural exine structure, exine stratification, and aperture ultrastructure. Certain aspects of pollen wall architecture and stratification in gen-

TABLE 2. Composite nonapertural pollen wall section with exine surface views at top, showing basic pollen wall stratification and exine structure (including major exine interstitial and tectal types).



eral are summarized in Table 2, which will be referred to throughout the following discussion.

Nonapertural exine sculpturing. Nonapertural exine sculpturing refers to all external surface features of the nonapertural exine, and usually is taken to include only features of the outer exine surface, although sometimes the inner surface of the exine may have important sculptural details as well (cf. Van Campo, 1978). Although it can be studied by light microscopy alone, nonapertural exine sculpturing, particularly in small pollen grains, is best observed with scanning electron microscopy (cf. Walker, 1972a). Pollen grains that are (1) psilate (smooth), (2) foveolate (pitted), (3) fossulate (grooved), (4) scabrate (with fine surface features), (5) verrucate (warty), (6) baculate (with rod-like elements), (7) pilate or clavate (with rod-like elements that have swollen heads), and (8) echinate (spiny) include the most commonly encountered types of nonapertural exine sculpturing.

Pollen that is reticulate, i.e., has an open network or reticulum on the surface of its exine (Table 2, D-2), represents another common type of nonapertural exine sculpturing, and, indeed, reticulate sculpturing is characteristic of all Lower Cretaceous angiosperm pollen grains examined in this study. The reticulum in reticulate pollen consists of walls known as muri with spaces between the muri, which are designated as the lumina. In the Lower Cretaceous angiosperm pollen grains examined the muri may be smooth, i.e., psilate (Fig. 89), covered with small spines, i.e., spinulose (Fig. 46), covered with granules, i.e., granulose (Fig. 24), divided into discrete, bead-like subunits, i.e., beaded (Fig. 21), or covered with fine, band-like lines, i.e., banded (Fig. 66). In one pollen type the muri are covered with triangular elements, resulting in a "crotonoid" sculpturing pattern (Fig. 83), named after a similar type of sculpturing found in the pollen of the euphorbiaceous genus *Croton*. Most of the fossil pollen types investigated have an irregular reticulum with a variety of lumina sizes and shapes (Fig. 9), but in a few instances the reticulum is regular with either circular (Figs. 83, 95) or polygonal (Fig. 101) lumina. Sometimes the same pollen grain has both coarsely and finely reticulate areas on its exine surface (Figs. 88–90), and some pollen types exhibit strongly dimorphic lumina with minute lumina interspersed among much larger ones (Figs. 89, 95, 101). Finally, in a few instances the muri are nodose, i.e., swollen at the points where the underlying columellae meet them (Fig. 34).

Nonapertural exine structure. Nonapertural exine structure refers to all internal morphological features of the nonapertural exine. Although light microscopy can give some idea of exine structure, internal exine features are best observed in scanning electron and transmission electron micrographs of exine sections. In some pollen grains the nonapertural exine is morphologically uniform (Table 2, A). We designate such pollen as noninterstitiate (or atectate). The nonapertural exine of most pollen grains, however, is interstitiate (Table 2, B–D-2), and has an inner structural layer or zone that we have termed the interstitium (Walker & Walker, 1981). There are several exine interstitial types, including cavitate interstitia with a series of structural cavities (Table 2, B), granular interstitia composed of granules (Table 2, C), and columellate interstitia that consist of a series of upright, rod-like structural elements known as columellae (Table 2, D-1, D-2). It is the presence of an interstitium that allows recognition of a basal exine layer, the nexine, and a roof-like layer, the tectum, in the typical pollen grain (cf. Table 2). The interstitium plus the tectum constitutes the so-called sexine. The thickness of the nexine, interstitium, and tectum as a percentage of total nonapertural exine thickness is often a taxonomically important character. For this reason the various exine layers thickness classes used in this paper have been defined in Table 3. If, for example, the nexine constitutes 60% of the total thickness of the nonapertural exine in a particular pollen grain, and the columellae account for 30% while the tectum makes up only 10% of the exine thickness, the pollen grain would be described as having a very thick nexine, an average interstitium, and an extremely to very thin tectum.

Several different exine tectal types are possible in interstitiate pollen grains. In tectate pollen, i.e., in pollen that has a roof or tectum as part of its exine, the tectum may be solid, resulting in a tectate-imperforate exine (Table 2, B, C), or small holes, i.e., tectal perforations, may be present in the tectum, resulting in tectate-perforate pollen (Table 2, D-1). If the tectal perforations are as large or larger than the remaining solid areas of the tectum that lie between them, the pollen is semitectate (Table 2, D-2). While semitectate pollen is invariably reticulately sculptured as well, tectate-perforate pollen grains may be reticulately sculptured or not. In some pollen the nonapertural exine is represented simply by a solid basal layer and overlying sculptural elements; such pollen may be described as intectate (Table 2, D-3), but this condition is rare.

TABLE 3. Pollen exine layers (nexine, interstitium, and tectum) thickness classes.

Percent of Total Nonapertural Exine Thickness	Thickness Class
>75%	extremely thick
50–75%	very thick
41–49%	moderately thick
25–40%	average
15–24%	moderately thin
10–14%	very thin
<10%	extremely thin

Exine stratification. Exine stratification refers to chemical differences that may be evident in various layers or strata of the exine. Exine stratification is best observed in exine section transmission electron micrographs as layers of differing electron opaqueness, although basic fuchsin staining and light microscopy can also be used to reveal chemical differences in exine layers, even in fossil pollen grains (cf. Leffingwell et al., 1970). Using the methods outlined above, it is apparent that the exine in many pollen grains consists of two chemically different layers—an outer, generally denser layer designated the ektexine, and an inner, generally less dense layer known as the endexine (cf. Table 2, A, B, D). As a rule, chemically uniform exine appears to be wholly ektexinous and without endexine (Table 2, C). In fossil pollen ektexine-endexine polarity is frequently reversed, with the inner endexine appearing denser than the outer ektexine (cf. Trevisan, 1980).

Endexine may be found throughout the exine or it may occur only as part of the apertures. In gymnosperms, the endexine is generally laminated (Van Campo, 1971) with a series of parallel laminations that are continuous throughout both the apertural and nonapertural regions of the endexine (cf. Table 2, A, B). In angiosperms, on the other hand, endexine is either absent entirely (Table 2, C) or present but non-laminated (Table 2, D) (cf. Doyle et al., 1975). Sometimes, however, the nexine of a wholly ektexinous, nonstratified exine may be lamellate. This, for example, is common in such primitive angiosperm families as the Annonaceae (Le Thomas, 1980,

1981) and Myristicaceae (Fig. 6) (Walker & Walker, 1979, 1980, 1981, 1983). In other instances, the endexine under apertures in angiosperm pollen may be lamellate, but this type of lamellate endexine is generally composed of discontinuous lamellae that apparently are fundamentally different from the truly laminated endexine of gymnosperms. When endexine is present in nonapertural regions of the exine, it most commonly comprises only part of the nexine, i.e., the morphologically defined basal layer of an interstitiate exine, and, when this is the case, the upper ektexinous part of the nexine is termed the foot-layer (Table 2, B, D-1). Rarely, is the nexine wholly endexinous, and a foot-layer absent (Table 2, D-2, D-3).

Aperture ultrastructure. Generally, pollen apertures represent sculpturally (i.e., externally) as well as structurally (internally) distinct areas of the exine. Externally, apertures usually appear as differently sculptured areas of the exine (Figs. 8, 13, 39, 52), while internally they commonly represent disorganized regions of the sexine underlaid by thinner nexine, relative to the nexine in nonapertural regions of the exine (Fig. 85). Sometimes, however, an aperture may be represented internally only by a thinning of the nexine, and by little or no discernible disorganization of the overlying sexine (Fig. 91). In pollen grains with endexine, frequently the endexine is thicker under the apertures (cf. Figs. 48, 49), or as previously indicated, endexine may be restricted to apertural areas and absent entirely in the nonapertural exine (cf. Figs. 16, 17). Although the endexine in angiosperms is usually homogeneous (Fig. 11), sometimes it is heterogeneous and stratified (Figs. 17, 43), and in some instances the foot-layer and endexine may be conspicuously interbedded (Fig. 49).

RESULTS

CLAVATIPOLLENITES COUPER

The most widely discussed type of Early Cretaceous angiosperm pollen consists of medium-sized, slightly boat-shaped to globose, monosulcate pollen grains referred to under the form genus *Clavatipollenites* Couper. Couper's diagnosis of the genus (Couper, 1958) was based on the type species, *Clavatipollenites hughesii* Couper. The holotype of *C. hughesii* comes from the Wealden of England and, according to Kemp (1968), is probably Upper Barremian in age. Couper described *Clavatipollenites* as "monosulcate, sulcus broad and long; grains broadly elliptical to almost spherical in equatorial contour; exine clearly stratified, consisting of an inner unsculptured layer (nexine) arising from which is a sculptured layer (sexine) made up of clavate projections, tending to expand and fuse together at their tips to form a tectate exine."

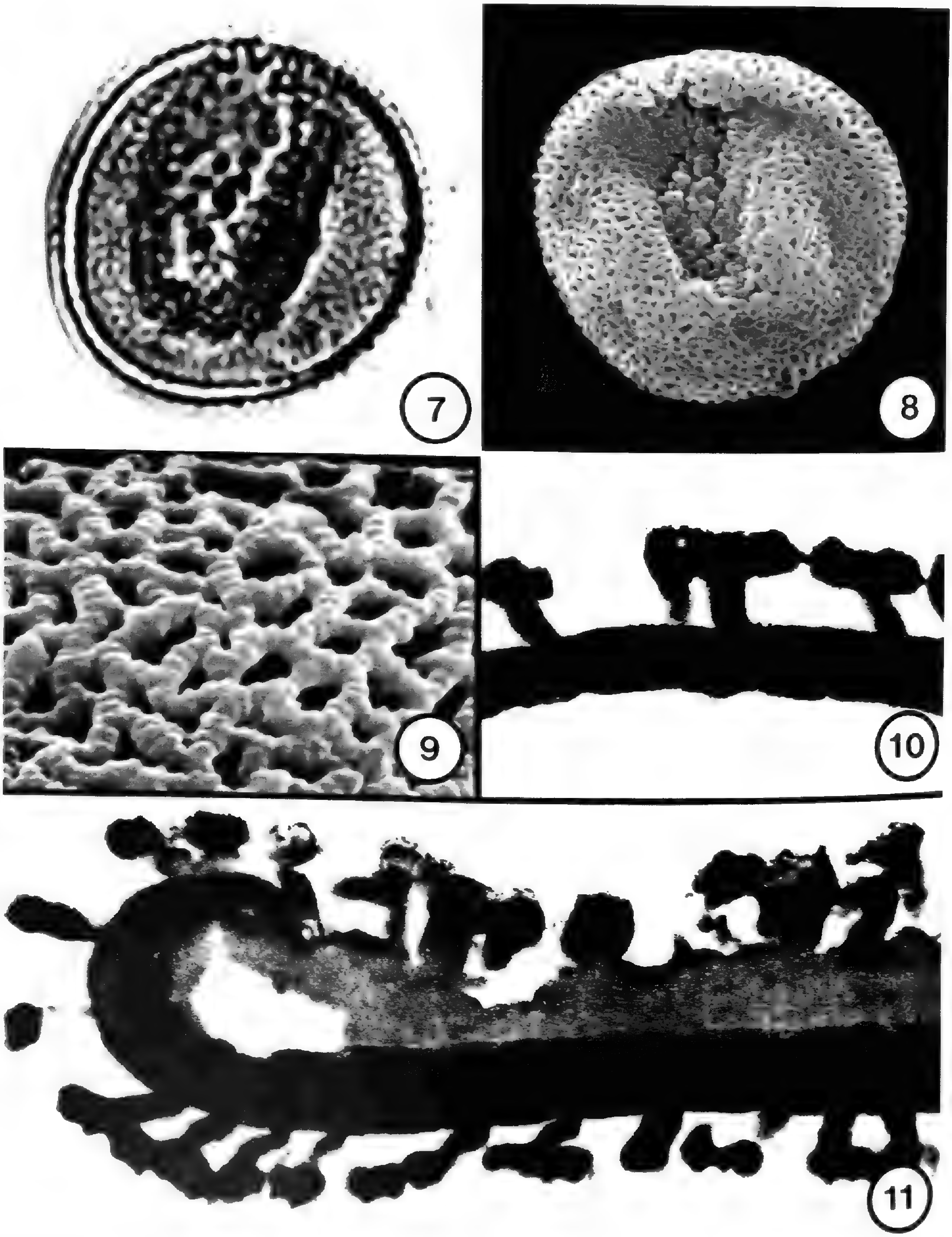
In 1968, Kemp redescribed *Clavatipollenites hughesii* and published photomicrographs of additional pollen grains of this species, some of which were obtained from the same core sample that originally provided the holotype of *C. hughesii.* Although *Clavatipollenites* as originally described by Couper (1958) and redescribed by Kemp (1968) encompassed only monosulcate pollen, some workers, e.g., Doyle and Robbins (1977), have broadened the circumscription of the genus to include trichotomosulcate pollen grains as well. Pollen of the *Clavatipollenites* type (at least as judged by light microscopy) is geographically widespread in the middle and late Early Cretaceous, occurring according to Doyle (1969) in the Barremian through Albian of West Africa, the Aptian and Albian of Central America, the presumed pre-Albian of southern Argentina, the Albian of Australia, the Aptian and Albian of Portugal, the Barremian through Albian of England, the probable late Barremian through Albian of central Atlantic North America, and the Middle through Late Albian of the Canadian Plains.

Pollen grains from the Potomac Group that would be described as *Clavatipollenites* from light microscope study alone fall into two different groups when examined ultrastructurally. Pollen in the first group is the same we believe as the type species of the genus, *C. hughesii.* The second group contains a diversity of pollen types that at this time we will refer to simply as the aff. (= affinity) *Clavatipollenites* group.

Clavatipollenites hughesii. Preliminary studies suggest that *Clavatipollenites hughesii* Couper, i.e., pollen strictly referable to the type of the genus *Clavatipollenites* from the Wealden of England, also occurs in the Potomac Group, at least in Lower Zone I, which is probably Barremian to Lower Aptian in age. A pollen grain that we consider to belong to *C. hughesii* is shown in Figures 7–11. The photomicrographs (PMG), scanning electron micrographs (SEMG), and transmission electron micrographs (TEMG), as is the case with all Lower Cretaceous angiosperm pollen included in this study, were all obtained from the same pollen grain. For this reason there can be no doubt whatsoever that all palynological features observed in Figures 7–11 belong to one and the same biological entity, irrespective of whether these characters were observed by means of light (Fig. 7), scanning electron (Figs. 8, 9), or transmission electron (Figs. 10, 11) microscopy. The conspicuous columellae, which have frequently been described as clavae by those working with light microscopy alone, and which are responsible for the name *Clavatipollenites* itself, can be clearly seen at the top right in Figure 7. Scanning electron microscopy, however, shows that *C. hughesii* is not intectate with clavate sculpturing, as originally supposed by Couper (1958) when he described *Clavatipollenites* as "made up of clavate projections, tending to expand and fuse together at their tips to form a tectate exine." It is clear from SEM and TEM examination that *C. hughesii* is tectate-perforate to semitectate (Figs. 9, 10), and not intectate. SEM also reveals that *C. hughesii* is characterized by an irregular reticulum composed of beaded to spinulose muri (Fig. 9). TEM further demonstrates that *C. hughesii* has a moderately to very thick nexine, well-developed columellae, and a distinct tectum (Fig. 10). Moreover, TEM reveals that a thick endexine is present under the aperture of *C. hughesii* (Fig. 11), while in nonapertural regions endexine is absent (Fig. 10).

The aperture of *C. hughesii* is externally verrucate (Fig. 8), while internally it consists of a very thick, apparently homogeneous endexine and a thin, occasionally lamellate foot-layer overlaid by a thick sexine organized into verrucae (Fig. 11). Doyle et al. (1975), however, contended that *C. hughesii* has only low verrucate apertural sculpturing, and that the prominent apertural details observed with light microscopy (cf. Fig. 7) are at least partly internal. This conclusion is based on SEM and TEM study of pollen grains designated as *Clavatipollenites* cf. *hughesii*, which were isolated from the same Potomac Group outcrop sample (Cleaves 27) from which we obtained the pollen grain illustrated in Figures 7–11. Furthermore, they described endexine under the aperture of *C. hughesii* as "endosculptured," and suggested that this internal sculpturing is "responsible for much of the granular appearance of the sulcus membrane as seen with light microscopy." Our whole grain SEMG of *C. hughesii*, in which the aperture is more or less fully expanded, clearly shows that the aperture is conspicuously verrucate (Fig. 8). Moreover, TEMG of this grain (Fig. 11) demonstrate that the endexine under the aperture is not "endosculptured," even though light microscopy of the same grain (Fig. 7) reveals a highly "granular" aperture. We believe that the so-called endosculpturing of the apertural endexine described by Doyle et al. (1975) was probably just a preservational artifact due to selective degradation of part of the endexine, and that the granular appearance of the aperture of *C. hughesii* observed in photomicrographs is due to an externally verrucate surface, and not to any internal sculpturing. In this connection, it is interesting to note that a similar condition, presumably also representing differential preservation with the endexine uniform in some grains and ragged in others, was encountered in *Stephanocolpites fredericksburgensis* (cf. below).

Aff. Clavatipollenites group. We have discovered that many Potomac Group pollen grains that appear to be essentially the same as *C. hughesii* in the light microscope, are actually quite different from *C. hughesii* when examined ultrastructurally. For the present, we have chosen to refer to these pollen types simply as the "aff. *Clavatipollenites* group." Two examples of this type of pollen, which we have designated as aff. *Clavatipollenites* Couper spp. 1 and 2, are shown in Figures 18–22 and Figures 23–26, respectively. Aff. *Clavatipollenites* sp. 1 (Figs. 18–22) is trichotomosulcate, while aff. *Clavatipollenites* sp. 2 (Figs. 23–26) is monosulcate. Both types of pollen are medium-sized and more or less globose, although sometimes aff. *Clavatipollenites* sp. 2 is slightly boat-shaped. In contrast to *C. hughesii*, which has a truly spinulose reticulum, muri of the aff. *Clavatipollenites* group are fundamentally beaded (Figs. 20, 21), although in aff. *Clavatipollenites* sp. 2 it appears that the bead-like subunits of the muri have broken-up into coarse, double-rowed granules (Fig. 24). In addition, pollen of the aff. *Clavatipollenites* group on the whole seems to have somewhat larger tectal perforations than *C. hughesii*, and, therefore, is basically semitectate (Figs. 18, 19, 23) rather than tectate-perforate (Fig. 8). While well-developed columellae are present in both pollen types, the nonapertural nexine is only average in thickness in pollen grains of the aff. *Clavatipollenites* group (Figs. 22, 26), while in *C. hughesii* it is moderately to very thick (Fig. 10). The most distinctive feature of the aff. *Clavatipollenites* group, however, is a lack of endexine, even under the aperture (Figs. 22, 25), which is markedly different from *C. hughesii*, with its well-devel-

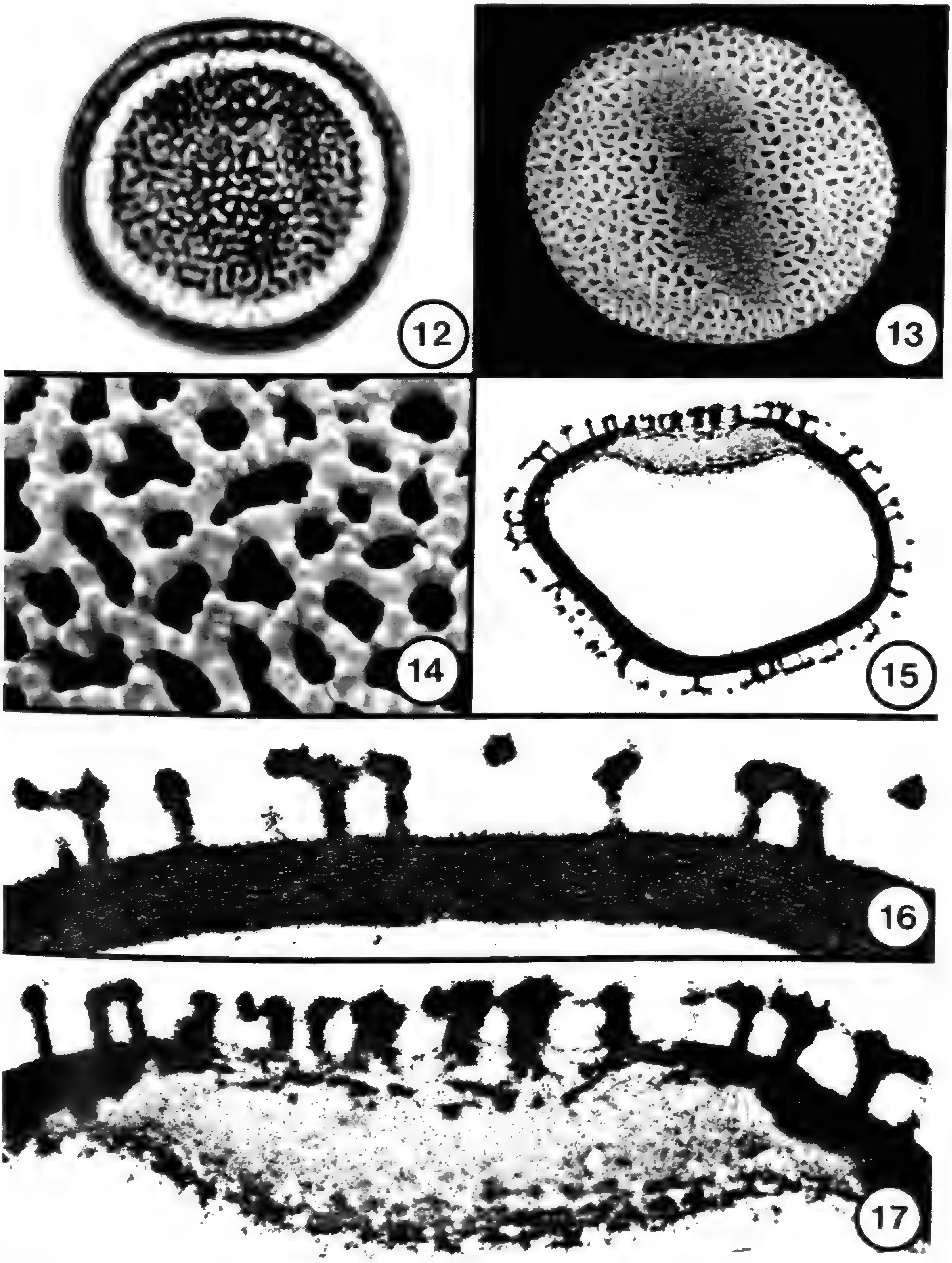


FIGURES 7–11. *Clavatipollenites hughesii* Couper (FP-364; *Cleaves 27*) from Lower Zone I of the Potomac Group, Barremian-Lower Aptian (ca. 115 Ma).—7. Whole grain PMG, ×2,190.—8. Whole grain SEMG, ×2,380.—9. Exine surface SEMG, ×12,000.—10. Nonapertural exine section TEMG, ×17,700.—11. Part of whole grain exine section TEMG, with aperture on top and appressed non-apertural side below, ×18,200.

oped apertural endexine (Fig. 11). In both aff. *Clavatipollenites* sp. 1 and 2, the aperture is evident internally, simply by a thinning of the nexine and disorganization of the overlying sexine.

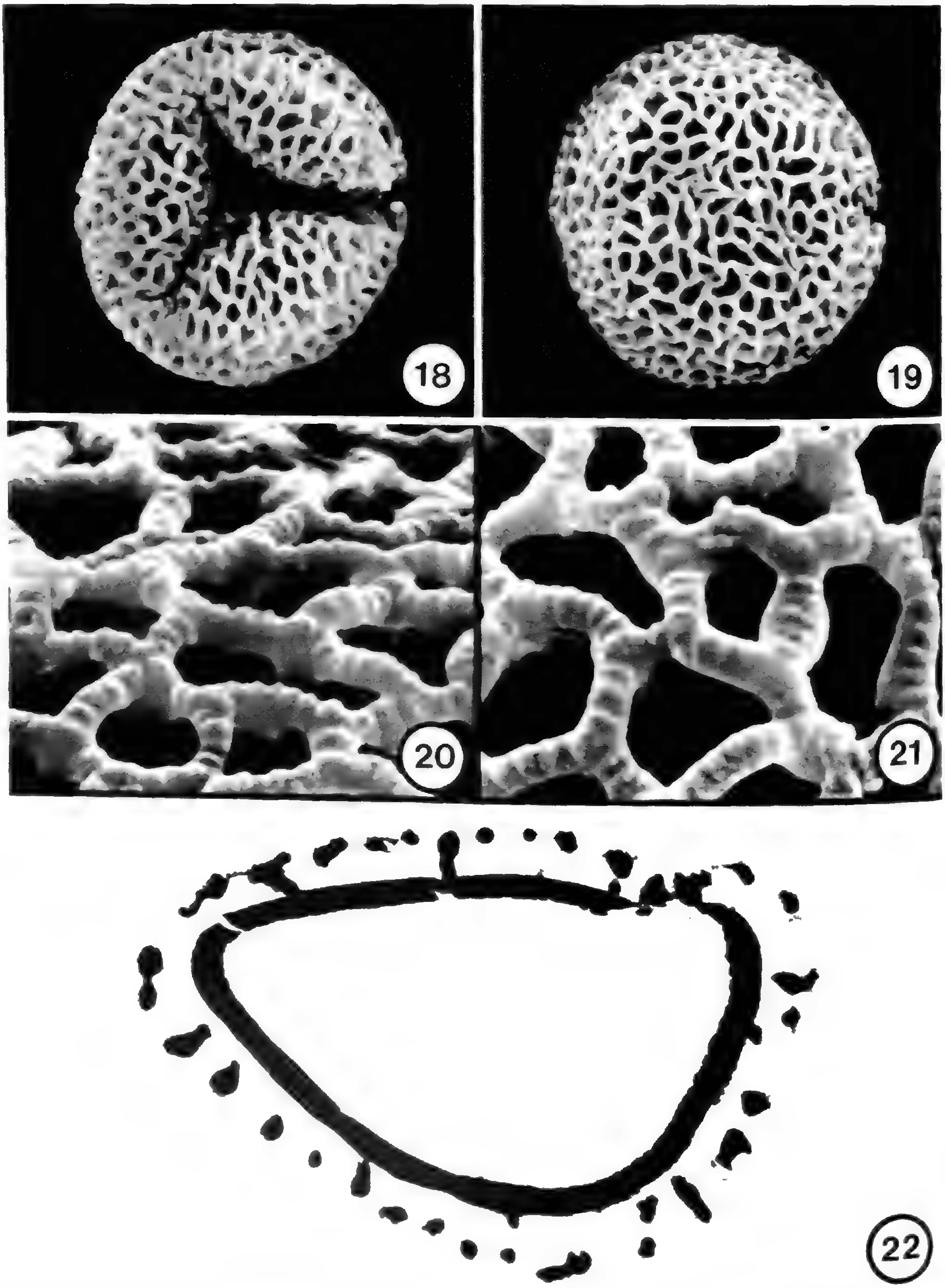
ASTEROPOLLIS HEDLUND & NORRIS

In 1968, Hedlund and Norris described the genus *Asteropollis* from the Fredericksburgian (Albian) of Oklahoma. They diagnosed the pol-



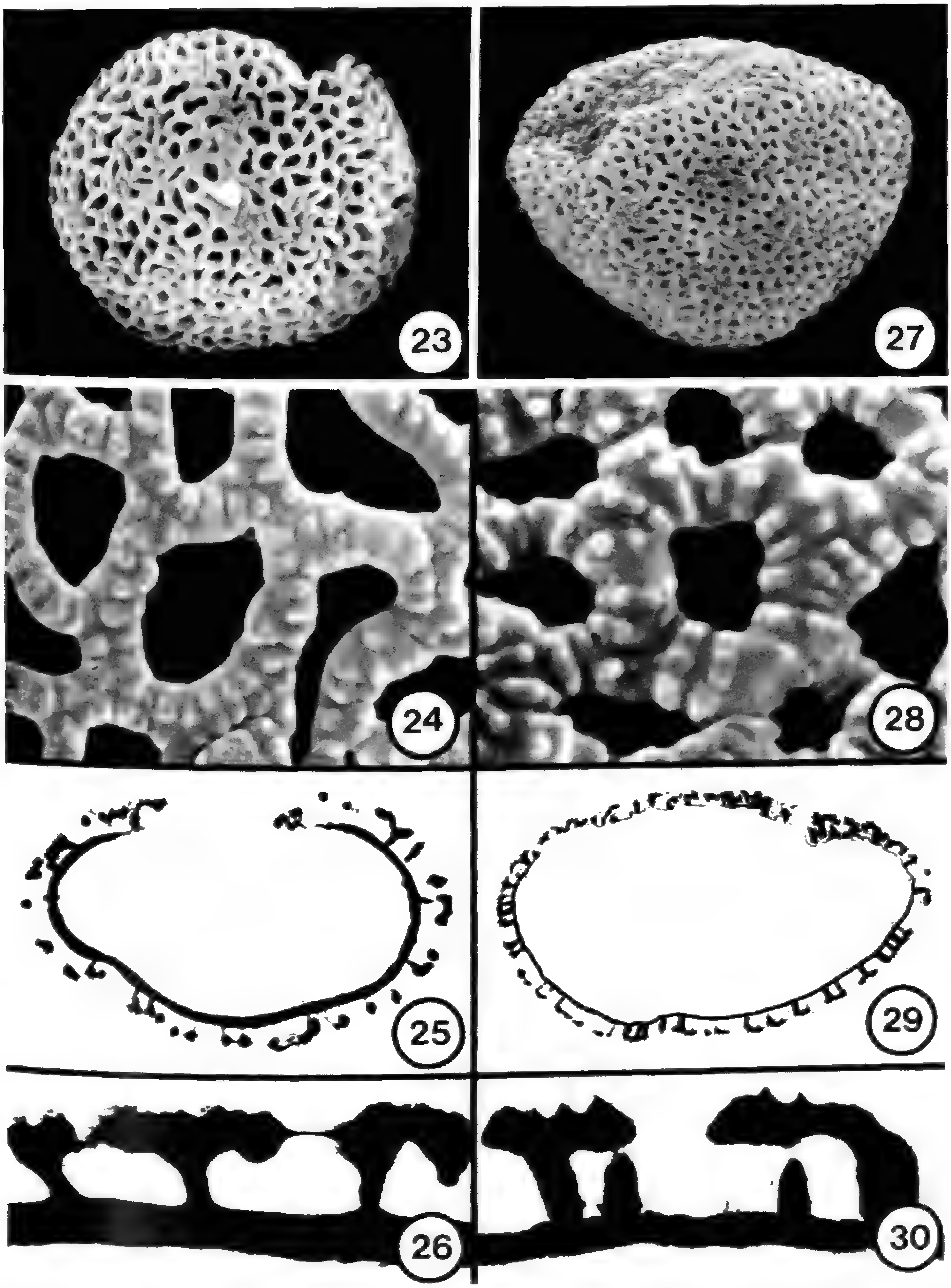
FIGURES 12–17. *Ascarina diffusa* A. C. Smith of the Chloranthaceae (P-1091; *Kajewski 863,* Arnold Arboretum).—12. Whole grain PMG, ×1,880.—13. Whole grain SEMG, ×2,150.—14. Exine surface SEMG, ×12,000.—15. Whole grain exine section TEMG, with aperture at top, ×2,680.—16. Nonapertural exine section TEMG, ×15,000.—17. Apertural exine section TEMG, ×11,800.

len of their monotypic new genus as "radiosymmetric, oblate, with circular amb; tetra- or pentachotomosulcate; heteropolar." In their description of the type species, *Asteropollis asteroides,* they noted that the pollen has a "sulcus with four or five equally developed branches almost reaching the equator" and that it is columellate and uniformly microreticulate. From a



FIGURES 18–22. Aff. *Clavatipollenites* Couper sp. 1 (FP-43; Cornet Beltway) from Zone IIB of the Potomac Group, Middle-Upper Albian (ca. 105 Ma).—18. Whole grain SEMG, showing apertural side, ×2,000.—19. Whole grain SEMG, showing nonapertural side, ×2,000.—20. Exine surface SEMG on apertural side, ×12,000.—21. Exine surface SEMG on nonapertural side, ×12,000.—22. Whole grain exine section TEMG, with aperture at top right, ×4,820.

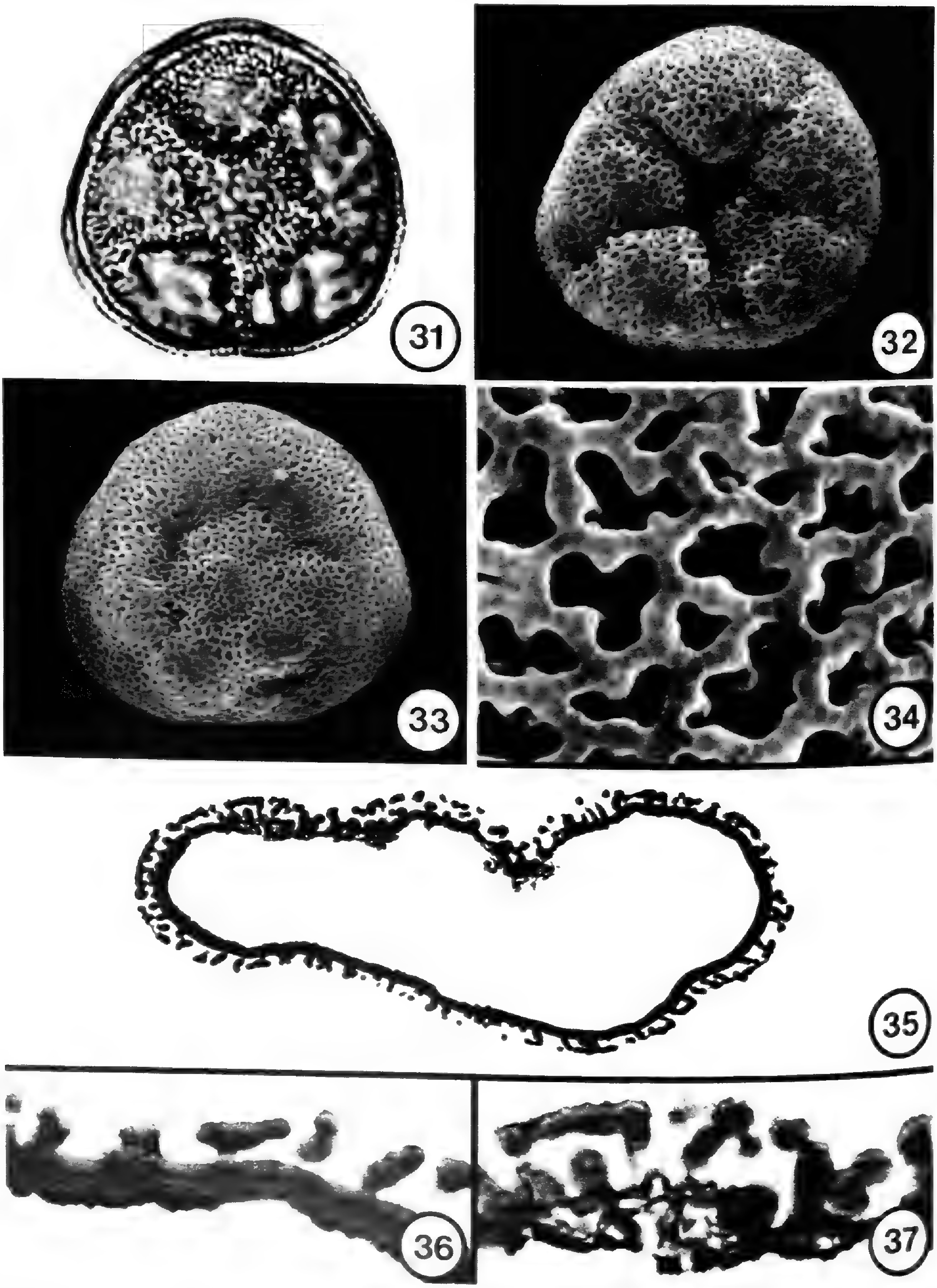
survey of 38 grains of *Asteropollis,* Davies and Norris (1976) found that approximately 30% were tetrachotomosulcate, 50% were pentachotomosulcate, and 20% were hexachotomosulcate, the latter condition not having been reported by Hedlund and Norris (1968) in their original description of the genus. Thus, *Asteropollis* is basically pentachotomosulcate. In addition to the Fredericksburgian, pollen of *Asteropollis* has been found in the Potomac Group of eastern North



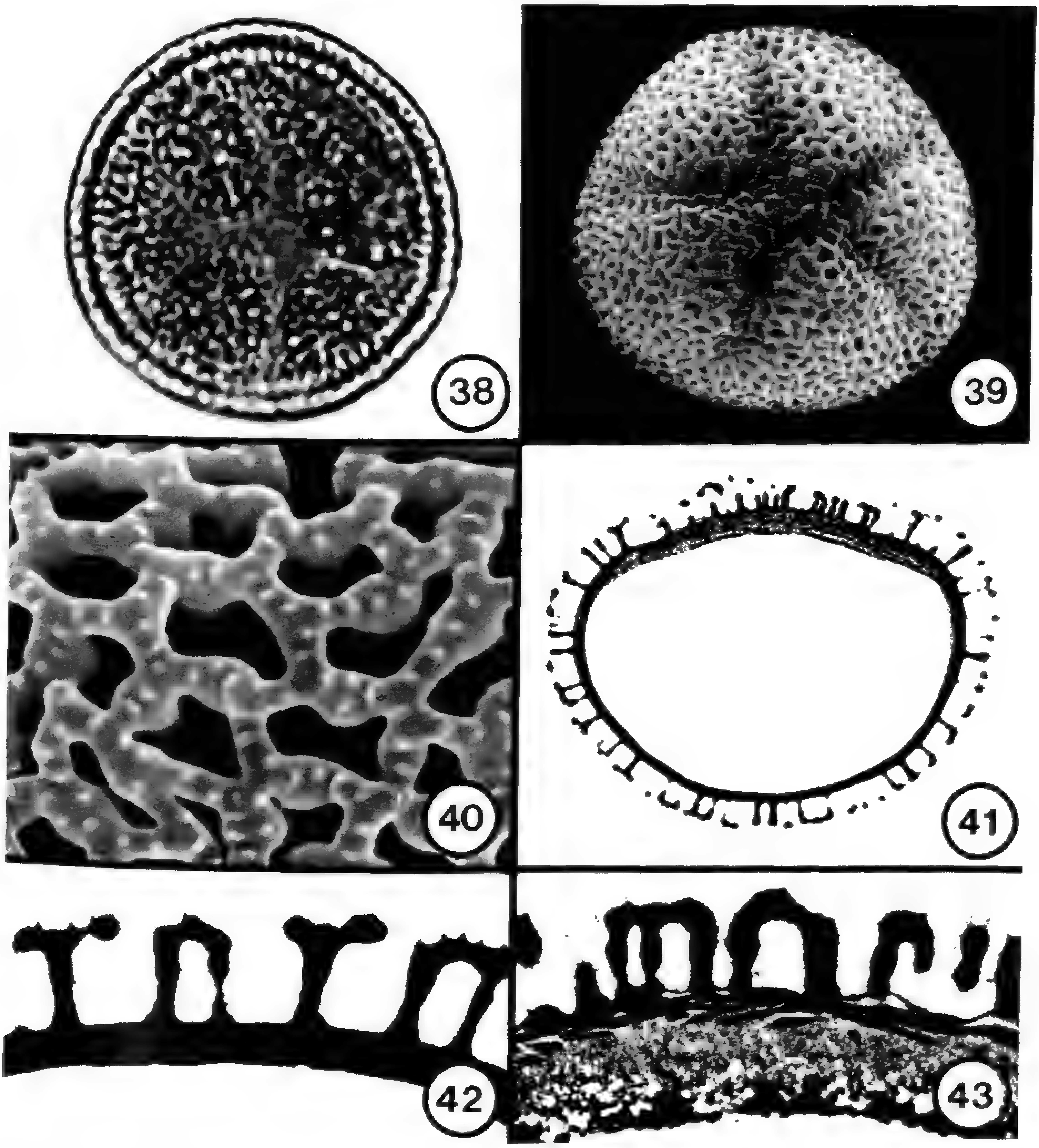
FIGURES 23–30. Aff. *Clavatipollenites* Couper sp. 2 (FP-41; Cornet Beltway) from Zone IIB of the Potomac Group, Middle-Upper Albian (ca. 105 Ma) (23–26) and *Virola weberbaueri* Markgraf (P-2734; *Tessmann 4339*, Stockholm) of the Myristicaceae (27–30).—23. Whole grain SEMG, ×1,810.—24. Exine surface SEMG, ×12,000.—25. Whole grain exine section TEMG, with aperture at top, ×2,530.—26. Nonapertural exine section TEMG, ×11,200.—27. Whole grain SEMG, ×2,440.—28. Exine surface SEMG, ×24,000.—29. Whole grain exine section TEMG, with aperture at top, ×2,510.—30. Nonapertural exine section TEMG, ×17,900.

America (Doyle & Robbins, 1977), and, according to Dettmann (1973), it also occurs in the Albian of eastern Australia.

A pollen grain of *Asteropollis* that was isolated from the same outcrop sample (Hedlund 3916) as the holotype of the genus is shown in Figures 31–37. According to Doyle (1977a), the Fredericksburgian Antlers-"Walnut" sequence of



FIGURES 31–37. *Asteropollis asteroides* Hedlund & Norris (FP-338; *Hedlund 3916*) from the Fredericksburgian of Oklahoma, correlative with Middle Zone IIB of the Potomac Group, upper Middle Albian (ca. 105 Ma).—31. Whole grain PMG, ×1,440.—32. Whole grain SEMG, showing apertural side, ×1,450.—33. Whole grain SEMG, showing nonapertural side, ×1,450.—34. Exine surface SEMG, ×12,000.—35. Whole grain exine section TEMG, with apertural regions on top, ×3,060.—36. Nonapertural exine section TEMG, ×11,100.—37. Apertural exine section TEMG, ×11,100.



FIGURES 38–43. *Hedyosmum orientale* Merr. & Chun of the Chloranthaceae (P-1102; *Poilane 32871,* Paris).—38. Whole grain PMG, ×1,480.—39. Whole grain SEMG, ×1,810.—40. Exine surface SEMG, ×12,000.—41. Whole grain exine section TEMG, with aperture at top, ×1,950.—42. Nonapertural exine section TEMG, ×8,360.—43. Apertural exine section TEMG, ×9,350.

Oklahoma that this grain was obtained from is correlated with Middle Zone IIB of the Potomac Group, and, hence, is upper Middle Albian in age. The grain shown in Figures 31–37 is pentachotomosulcate (Figs. 31, 32), although, as previously indicated, *Asteropollis* may also be tetra- or hexachotomosulcate. SEMG of both the apertural (Fig. 32) and nonapertural (Fig. 33) sides confirm that *Asteropollis* has a modified sulcate aperture (being tetra-, penta-, or hexa-chotomosulcate as the case may be) and is not colpate as suggested by Srivastava (1975). SEM reveals that *Asteropollis* has an irregular reticulum, with weakly beaded to spinulose muri that are conspicuously nodose (Fig. 34). Structurally, *Asteropollis* is tectate-perforate to semitectate (Figs. 32–34). TEM demonstrates that *Asteropollis* has an average to moderately thick nonapertural nexine (Fig. 36), while SEM and TEM together give the impression that columellae in this genus are composed of granule-like subunits (Figs. 34, 36). A thin, somewhat patchy (real or ? artifact) endexine is present in both the nonapertural (Fig. 36) and apertural (Fig. 37) exine. The aperture itself is evident internally as a lamellate zone in the nexine that consists of a thin endexine and a somewhat thicker foot-layer overlaid by a disorganized region of sexine (Figs. 35, 37).

STEPHANOCOLPITES FREDERICKSBURGENSIS HEDLUND & NORRIS

From the same outcrop sample of the Fredericksburgian of Oklahoma from which they isolated *Asteropollis*, Hedlund and Norris (1968) described another Early Cretaceous pollen type under the name *Stephanocolpites fredericksburgensis*. Unfortunately, according to Jansonius and Hills (1976), the form genus name *Stephanocolpites*, which was proposed for any pollen with more than three meridional colpi, is illegitimate because the holotype of the type species is a Recent pollen grain of *Lycopus europaeus* of the Labiatae. Nevertheless, for the present we will continue to refer to this pollen type as *Stephanocolpites fredericksburgensis*. Hedlund and Norris (1968) noted that the radiosymmetric, prolate to spheroidal, isopolar pollen of *S. fredericksburgensis* has four or five brevicolpi that are less than half the polar diameter in length, and that it is baculate (i.e., columellate) and uniformly microreticulate. Out of 62 grains examined, Davies and Norris (1976) found that about 70% were tetracolpoidate and 30% were pentacolpoidate. Doyle and Robbins (1977) have reported that *S. fredericksburgensis* also occurs in the Middle-Upper Albian of the Potomac Group.

Material of *S. fredericksburgensis* that we studied (Figs. 44–50) was isolated from the same outcrop sample (Hedlund 3916) that provided the holotype of the species. Figures 44–49 were all obtained from the same grain of *S. fredericksburgensis*, while the whole grain exine section TEMG shown in Figure 50 is from another grain. A pentacolpoidate grain is shown in Figures 44 and 45. SEM reveals that the pollen is irregularly reticulate with spinulose muri (Fig. 46), and that it has small tectal perforations, and consequently is tectate-perforate (Figs. 45, 46). TEM shows that the nonapertural nexine is moderately to very thick and that columellae are present (Fig. 48), and also reveals that well-developed endexine is present throughout the exine, in nonapertural (Fig. 48) as well as apertural (Fig. 49) regions. While some grains of *S. fredericksburgensis* have a relatively uniform endexine (Fig. 48), in others the endexine is ragged (Fig. 50). Although grains of the latter type have been described as internally sculptured by Davies and Norris (1976), we believe that this ragged endexine may be simply a preservation artifact. It will be recalled that a similar occurrence of uniform and ragged endexine in different grains of the same pollen was also encountered in the case of *Clavatipollenites hughesii*. Ultrastructurally, the apertures of *S. fredericksburgensis* are represented by areas of thick endexine conspicuously lamellate at the top and interbedded with the foot-layer, that in turn are overlaid by somewhat reduced sexine composed of laterally thickened elements (Fig. 49), the last being especially evident in exine section SEMG that show the transitional region between apertural and nonapertural exine (Fig. 47).

RETIMONOCOLPITES PIERCE

The form genus *Retimonocolpites* was described by Pierce (1961) for "reticulate, monocolpate pollen." Several different pollen types have been included in this form genus, and there has been some question about what it should encompass. During the present study we examined four different pollen types that, at the light microscope level at least, are referable to *Retimonocolpites*, including *R. dividuus* and *R. peroreticulatus*. Two undescribed types of pollen that we have studied are simply referred to for now as aff. *Retimonocolpites* spp. 1 and 2.

Retimonocolpites dividuus. Since there have been a number of divergent opinions concerning the circumscription of the form genus *Retimonocolpites*, we thought it was particularly important to study the type species of the genus, *Retimonocolpites dividuus* Pierce. A grain of *R. dividuus* is pictured in Figures 57–62. This particular grain was isolated from the D13-535 core sample of the Potomac Group, which, according to Doyle and Robbins (1977), is Late Zone IIB or early Late Albian in age. The characteristic light microscope appearance of *R. dividuus* is shown at high (Fig. 57) and low (Fig. 58) focus. Frequently the coarse reticulum becomes locally detached from the rest of the grain, and sometimes one even finds completely psilate "nexines" of *R. dividuus* from which the reticulum is entirely detached (cf. Brenner, 1963, under discussion of *Liliacidites dividuus*; Kemp, 1968, under discussion of *Clavatipollenites rotundus*). One of the most distinctive light microscope features of the monosulcate pollen of *R. dividuus* is its conspicuously bordered aperture (Figs. 57, 58). SEM

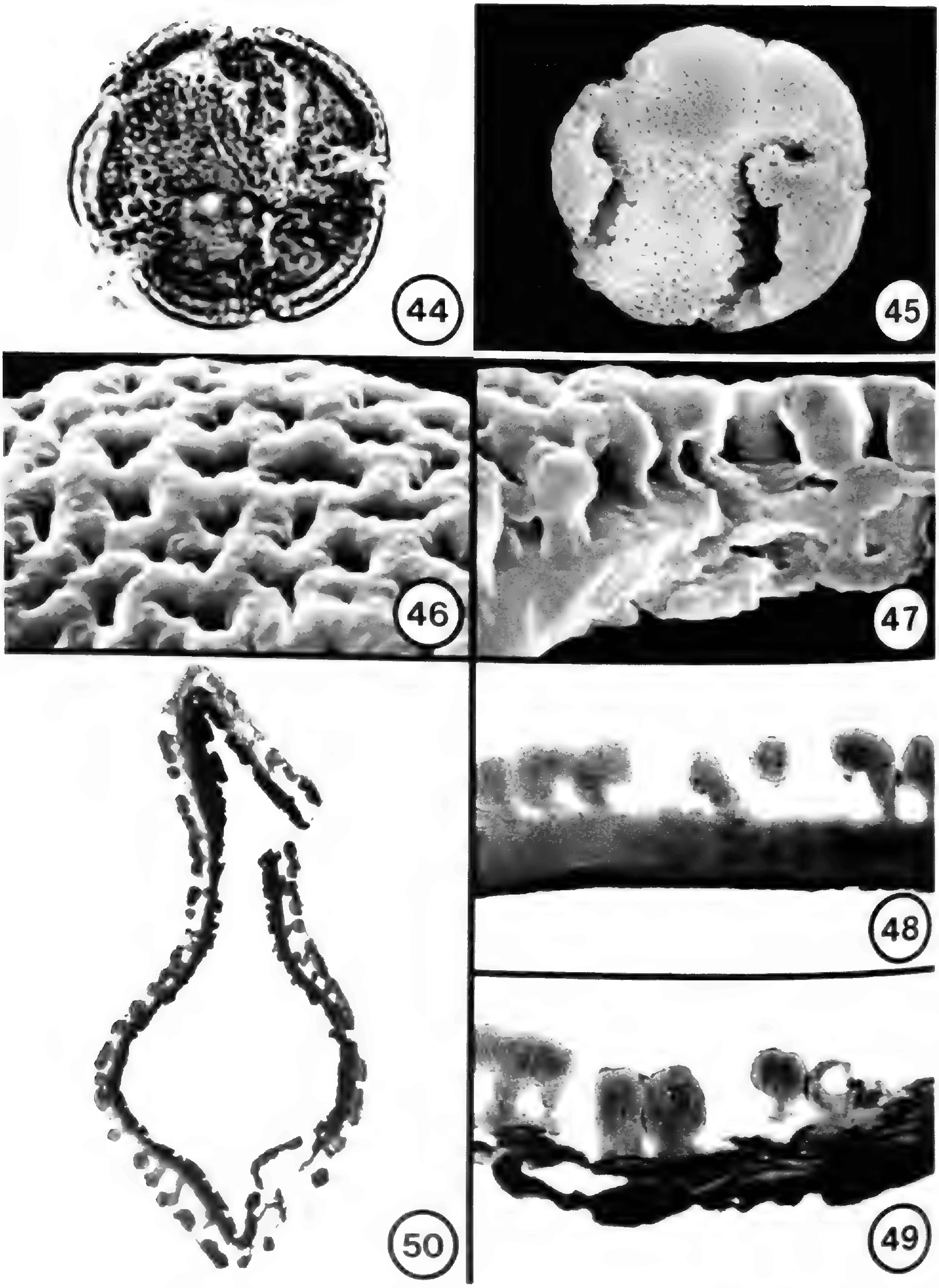
(Fig. 59) and TEM (Fig. 61) indicate that this border is not due to thickening of the nexine, but apparently results from infolding of the thin-walled exine itself (cf. Kemp, 1968, under discussion of *Clavatipollenites rotundus*). SEM further shows that the pollen, which is decidedly semitectate (Fig. 59), has an irregular reticulum with muri covered by fine bands that are frequently discontinuous (Fig. 60). TEM reveals that the exine is composed of an extremely to very thin nexine, short columellae, and a thick tectum (Figs. 61, 62). Endexine was not observed. Externally, the aperture is represented by a definite interruption in the reticulum (Fig. 59), while internally it is scarcely evident (Figs. 61, 62).

Aff. Retimonocolpites sp. 1. During our ultrastructural study of Potomac Group angiosperm pollen we encountered a pollen type that clearly illustrates the advantage of combined light, SEM, and TEM examination of the same pollen grain. This pollen type, which we have designated aff. *Retimonocolpites* sp. 1, is shown in Figures 63–68. Although this pollen type looks somewhat different from *R. dividuus* at the light microscope level (Fig. 63), scanning electron microscopy (Figs. 64–66) reveals a pollen type that greatly resembles *R. dividuus,* even down to its finely banded reticulum (Fig. 66). Transmission electron microscopy, however, indicates that aff. *Retimonocolpites* sp. 1 has a very thick nexine and much stouter columellae (Figs. 67, 68) compared to *R. dividuus* (Figs. 61, 62). This particular example demonstrates some of the problems inherent in studying early fossil angiosperm pollen by direct SEM search of "strew mounts" as was done by Hughes et al. (1979). Grains that look rather similar in the scanning electron microscope may be vastly different when examined with transmission electron microscopy.

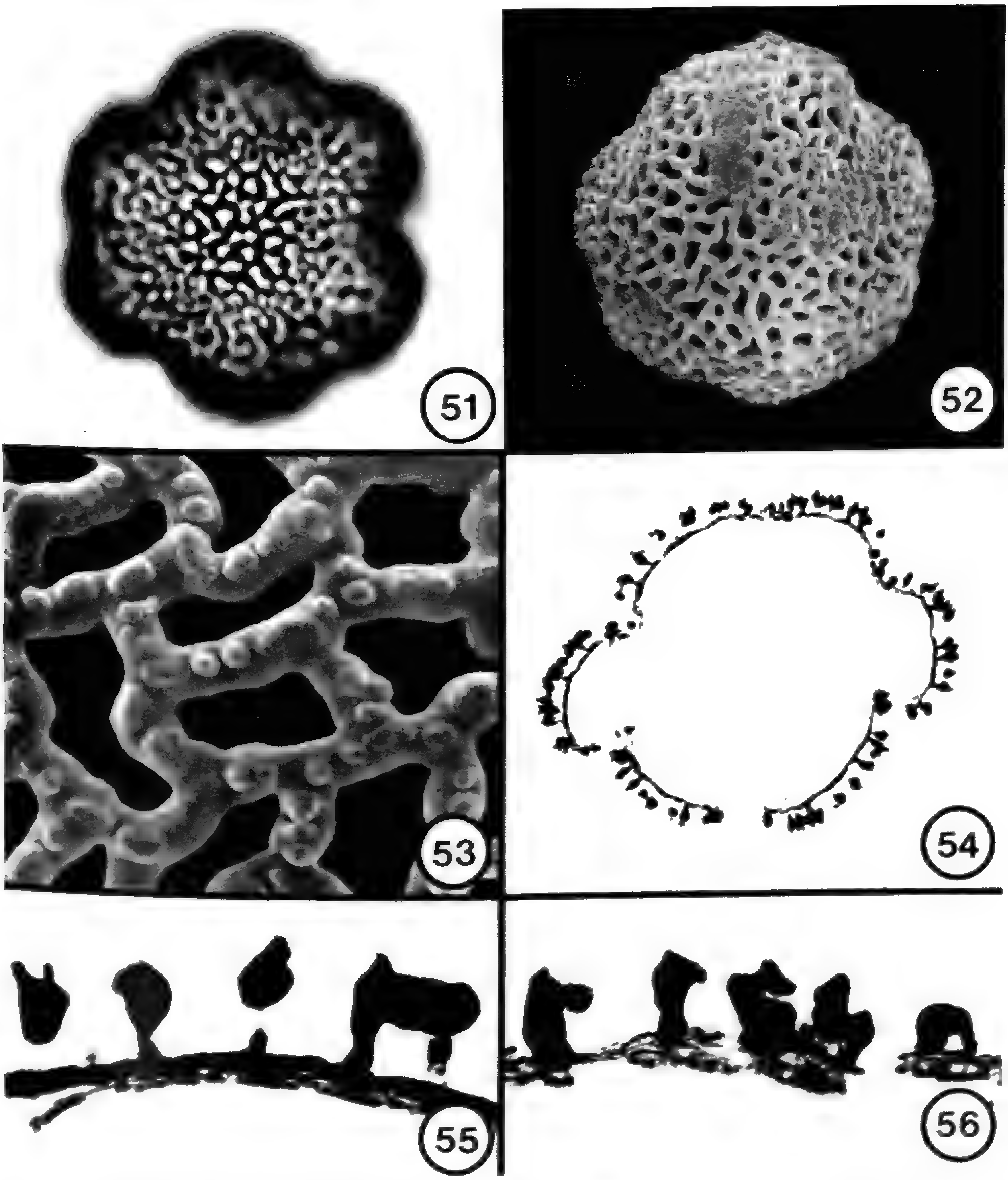
Retimonocolpites peroreticulatus. Another type of Early Cretaceous angiosperm pollen that has been included under the form genus *Retimonocolpites* is represented by pollen grains known as *Retimonocolpites peroreticulatus* (Brenner) Doyle. This species was first described by Brenner (1963) under *Peromonolites,* which is a form genus proposed by Couper (1953) for perinate, monolete spores. Doyle in Doyle et al. (1975) transferred the species to *Retimonocolpites* and gave a number of reasons for considering it an angiosperm pollen grain rather than a fern spore, including the different nature of its detached reticulum from a true perisporium, its non-reniform shape, its apparent true aperture rather than tetrad scar, and its similarities to certain undoubted angiosperm pollen types, including members of the form genera *Clavatipollenites* and *Retimonocolpites.* Doyle et al. (1975), who examined *R. peroreticulatus* and a possibly related pollen type, *R. reticulatus* (Brenner) Doyle, which is somewhat larger and has a less coarsely developed reticulum, noted that in addition to the Potomac Group, pollen of this general type occurs in the Albian of Oklahoma, western Canada, and Peru, as well as in the Barremian of England and the probable Barremian-Aptian of central Africa.

Although we have also studied *R. peroreticulatus* from the Potomac Group, the particular grain illustrated in Figures 69–73 is from the upper Middle Albian of Oklahoma (Hedlund sample 3916), which according to Doyle and Robbins (1977) is correlative with Middle Zone IIB of the Potomac Group. The coarse, detached reticulum so evident at the light microscope level can be seen in the whole grain PMG shown in Figure 69. Whole grain SEMG of the apertural (Fig. 70) and nonapertural (Fig. 71) sides of the grain show no evidence of any columellae, and this is confirmed by whole grain exine section TEMG (Fig. 73). The grain has a well-developed aperture, which consists of a sharply defined, bordered slit in the reticulum itself (Fig. 70) and a definite thinning of the underlying nexine (Fig. 73). Exine surface SEMG reveal that the reticulum is covered by distinctive recurved spines (Fig. 72). TEMG sections of the whole grain (Fig. 73) show that the smooth central body, i.e., the nexine proper, is moderately to very thick, as is the reticulum itself. The impression is given that the reticulum is directly united with the underlying nexine at only a few points (? possibly only at the aperture), and this may be why the reticulum so frequently appears for all intents to be free of the central body. Although we found no evidence of endexine in the grain of *R. peroreticulatus* shown in Figures 69–73, Doyle et al. (1975) encountered endexine under the aperture of a grain that they considered was probably the related *R. reticulatus.*

Aff. Retimonocolpites sp. 2. A pollen type (Figs. 74–80) that was isolated from an Upper Zone I Potomac Group outcrop sample (Brenner 10) is virtually identical with *R. peroreticulatus* except that it has well-developed columellae (Fig. 77) and a somewhat tighter reticulum (Figs. 75, 76). We have designated this pollen type as aff. *Retimonocolpites* sp. 2. Although aff. *Retimono-*

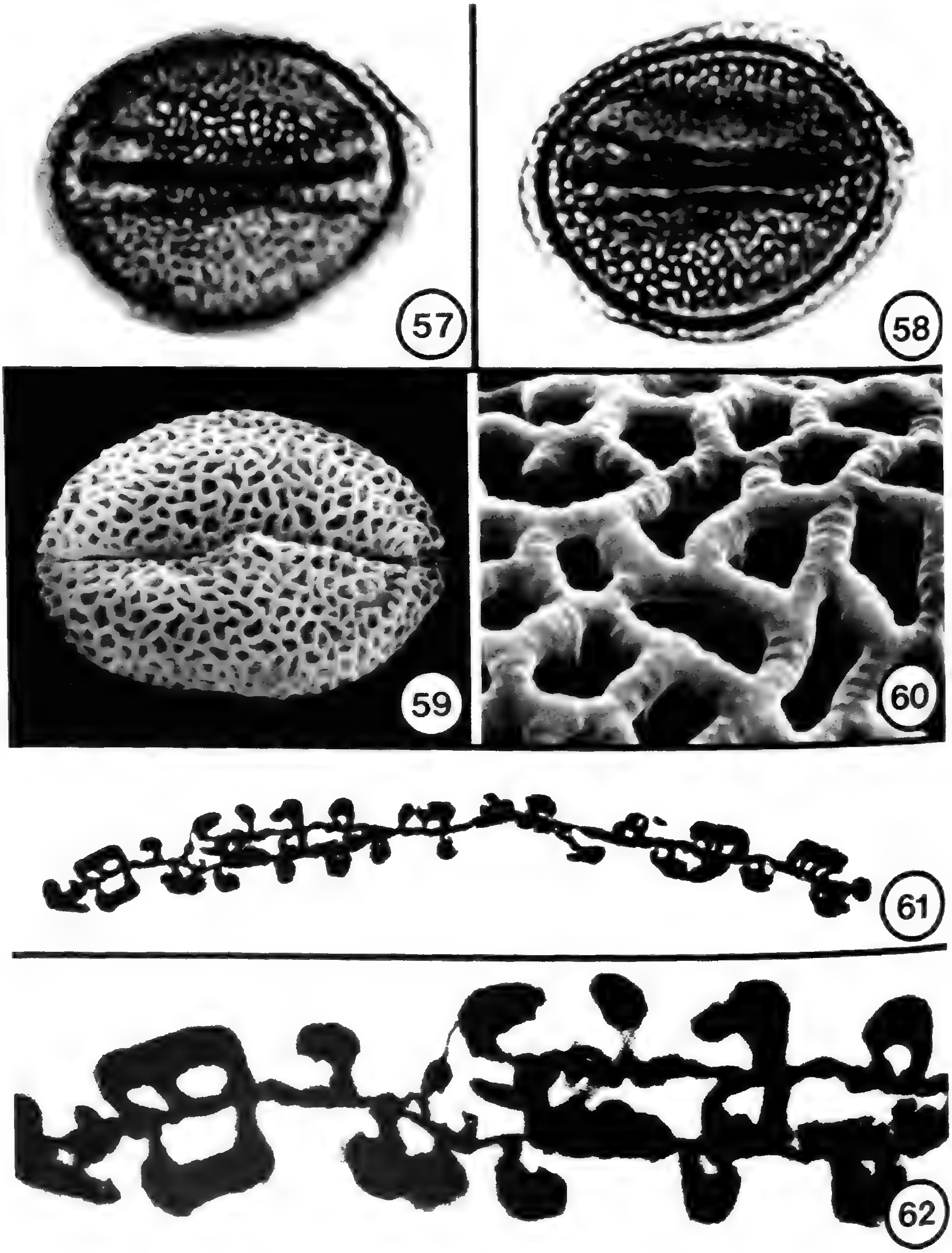


FIGURES 44–50. *Stephanocolpites fredericksburgensis* Hedlund & Norris (44–49, FP-292, 50, FP-306; *Hedlund 3916*) from the Fredericksburgian of Oklahoma, correlative with Middle Zone IIB of the Potomac Group, upper Middle Albian (ca. 105 Ma).—44. Whole grain PMG, ×1,500.—45. Whole grain SEMG, ×1,540.—46. Exine surface SEMG, ×12,000.—47. Exine section SEMG, showing non-apertural (to the left) and apertural (to the right) exine, ×12,000.—48. Nonapertural exine section TEMG, ×10,800.—49. Apertural exine section TEMG, ×10,700.—50. Whole grain exine section TEMG, ×4,240.



FIGURES 51–56. *Chloranthus japonicus* Sieb. of the Chloranthaceae (P-2791; *Furuse s.n.*, Stockholm).—51. Whole grain PMG, ×1,770.—52. Whole grain SEMG, ×2,170.—53. Exine surface SEMG, ×12,000.—54. Whole grain exine section TEMG, ×1,700.—55. Nonapertural exine section TEMG, ×10,600.—56. Apertural exine section TEMG, ×10,600.

colpites sp. 2 looks quite different from *R. peroreticulatus* in the light microscope (cf. Figs. 69, 74), SEM and TEM reveal a remarkable resemblance between these two pollen types, including a similar reticulum with distinctive, recurved spines (cf. Figs. 72, 77) and a similarly thick nexine (cf. Figs. 73, 78, 79). Although aff. *Retimonocolpites* sp. 2 has a weakly developed endexine under the apertural (Fig. 80) and nonapertural (Fig. 79) exine, and no endexine was found in *R. peroreticulatus* shown in Figures 69–73, we suspect that further studies will discover that *R. peroreticulatus* has a thin endexine. The major difference between aff. *Retimonocolpites* sp. 2 and *R. peroreticulatus* is that the former has well-developed columellae (Fig. 77) and the latter has none (Figs. 71, 72). Pollen of the aff. *Retimonocolpites* sp. 2 type, which may actually be a more primitive pollen type that is closely related to *R. peroreticulatus*, is significant, at the least, in that

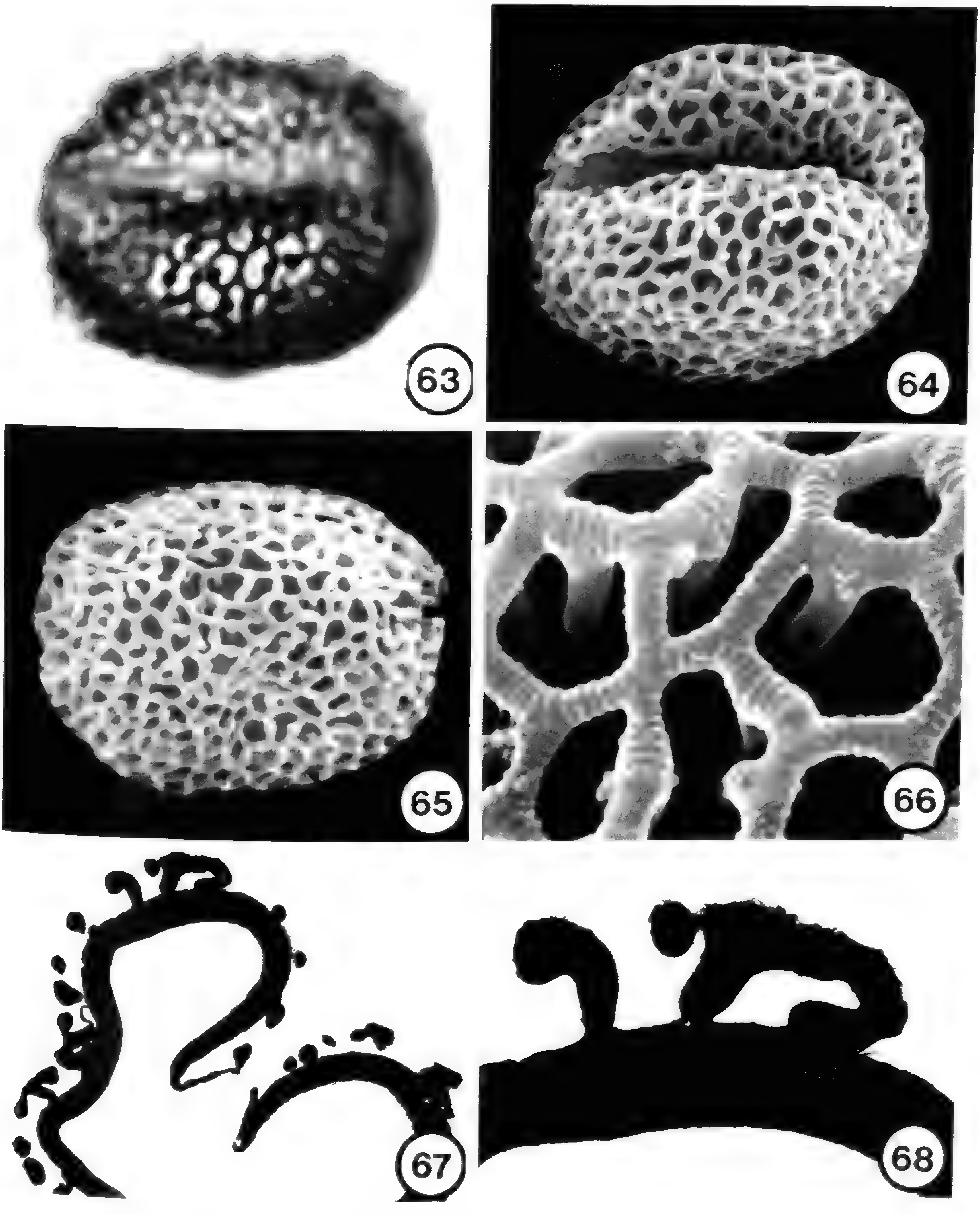


FIGURES 57–62. *Retimonocolpites dividuus* Pierce (FP-372; D13-535) from Upper Zone IIB of the Potomac Group, lower Upper Albian (ca. 103 Ma).—57. Whole grain PMG at high focus, × 1,780.—58. Whole grain PMG at low focus, × 1,780.—59. Whole grain SEMG, × 1,940.—60. Exine surface SEMG, × 12,000.—61. Whole grain exine section TEMG, × 5,900.—62. Part of whole grain exine section TEMG, showing infolded, presumptive apertural region, × 17,200.

it represents a model of a more normal columellate pollen type from which the bizarre, noncolumellate *R. peroreticulatus* could have evolved.

STELLATOPOLLIS DOYLE

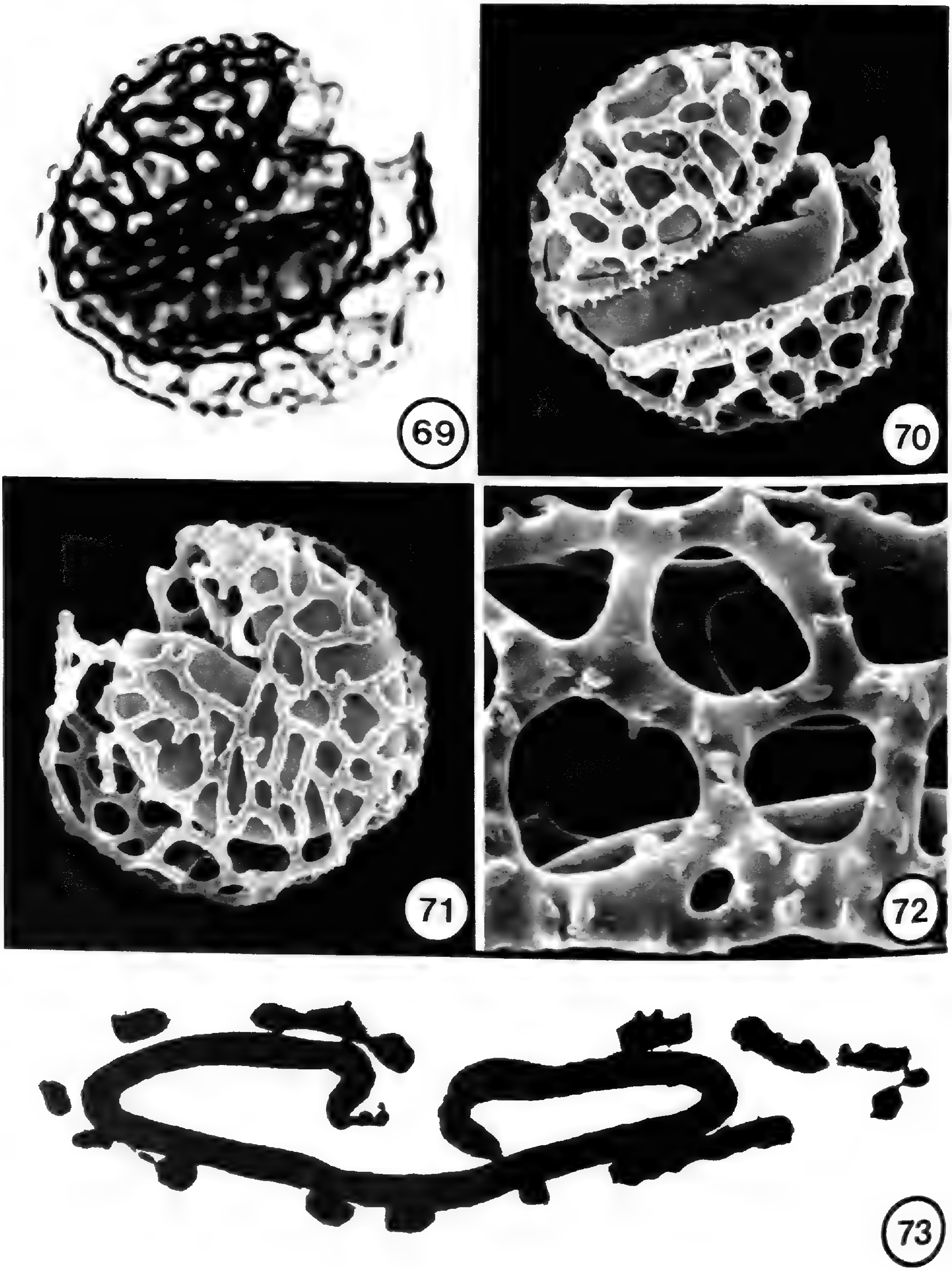
One of the most distinctive types of Early Cretaceous angiosperm pollen is represented by large monosulcate pollen grains that have a remark-



FIGURES 63–68. Aff. *Retimonocolpites* Pierce sp. 1 (FP-190; Cornet Beltway), from Zone IIB of the Potomac Group, Middle-Upper Albian (ca. 105 Ma).—63. Whole grain PMG, ×2,080.—64. Whole grain SEMG, showing apertural side, ×2,080.—65. Whole grain SEMG, showing nonapertural side, ×2,080.—66. Exine surface SEMG, ×12,000.—67. Whole grain exine section TEMG, showing aperture, ×3,530.—68. Nonapertural exine section TEMG, ×12,200.

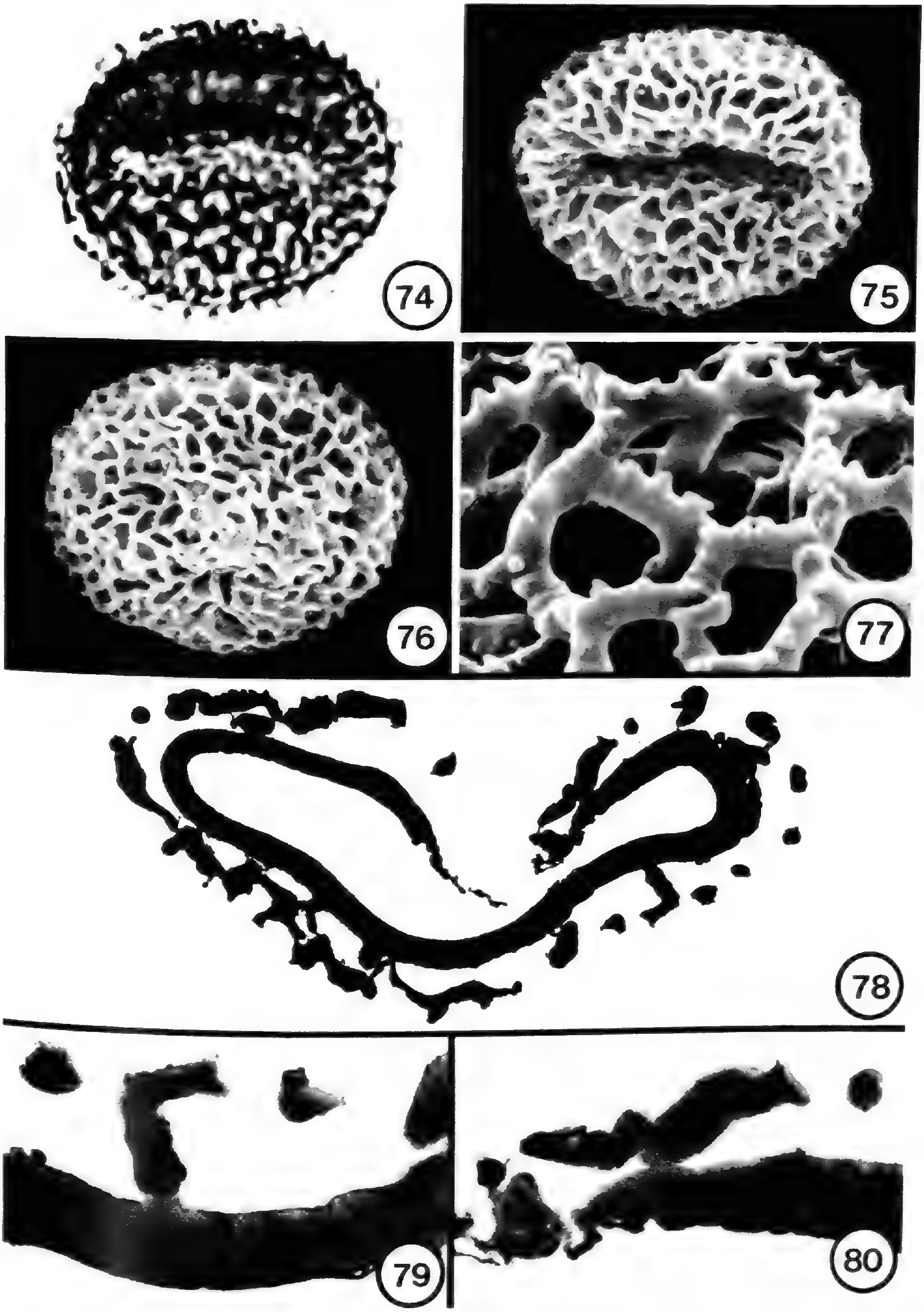
ably well-developed "crotonoid" sculpturing. Pollen of this type, with a semitectate-reticulate exine composed of muri bearing triangular to elliptical supratectate elements, has been described by Doyle in Doyle et al. (1975) under the name *Stellatopollis* Doyle. According to Doyle et al. (1975), *Stellatopollis* is known, in addition to the Potomac Group, from the Middle Albian of Oklahoma and Brazil, the Barremian of England, and the presumed Barremian-Aptian of equatorial Africa.

We have studied pollen of the type species of the form genus, *Stellatopollis barghoornii* Doyle, taken from the D12-515 core sample of the Po-

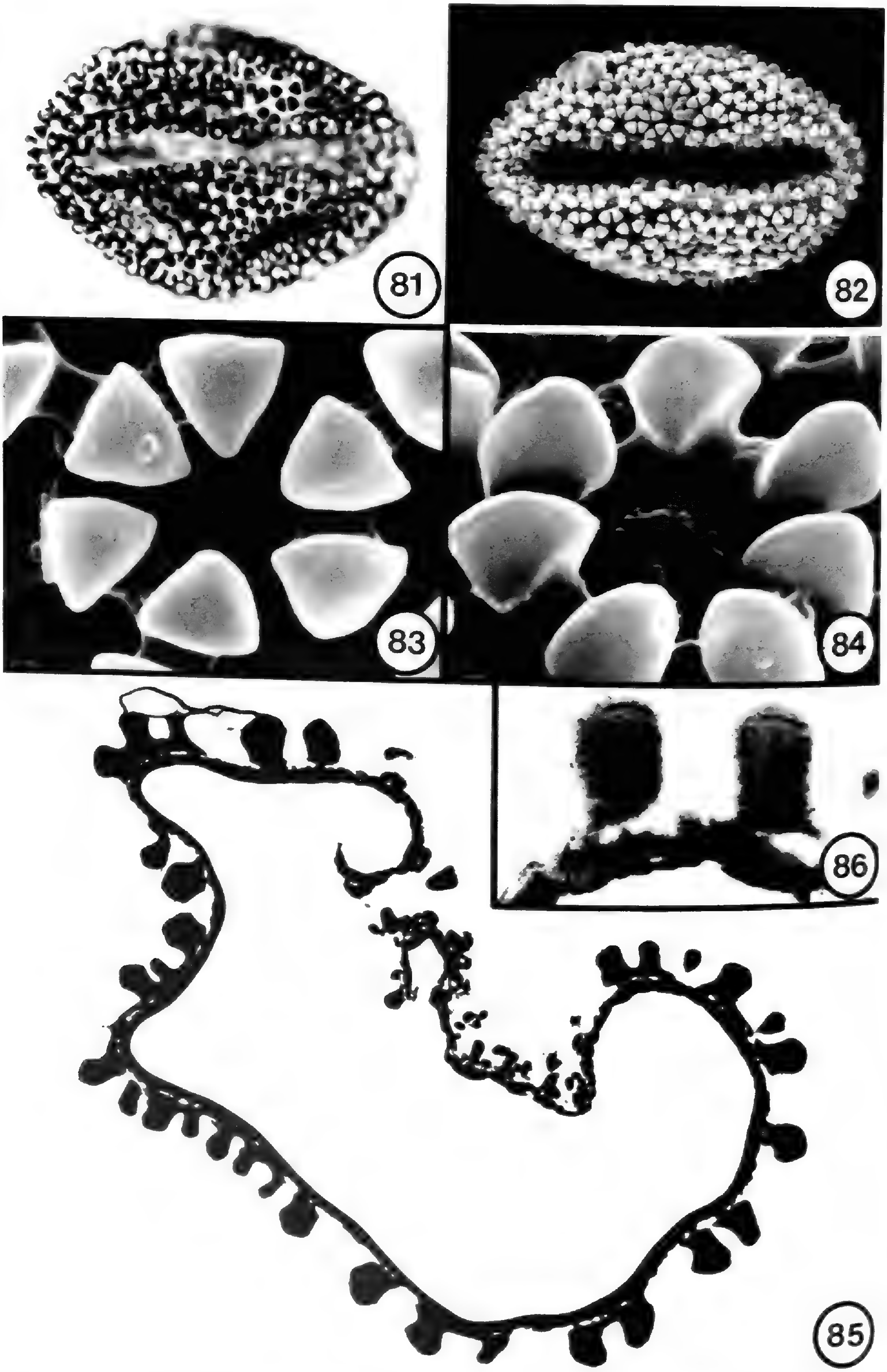


FIGURES 69–73. *Retimonocolpites peroreticulatus* (Brenner) Doyle (FP-341; *Hedlund 3916*), from the Fredericksburgian of Oklahoma, correlative with Middle Zone IIB of the Potomac Group, upper Middle Albian (ca. 105 Ma).—69. Whole grain PMG, ×2,610.—70. Whole grain SEMG, showing apertural side, ×2,610.—71. Whole grain SEMG, showing nonapertural side, ×2,610.—72. Exine surface SEMG, ×11,500.—73. Whole grain exine section TEMG, with aperture at top middle, ×8,640.

tomac Group (Figs. 81–86), which is the same core sample from which the holotype of the species was obtained. In their ultrastructural investigation of early fossil angiosperm pollen, Doyle et al. (1975) also examined material of *S. barghoornii* that was isolated from this core sample, and our observations agree with theirs. Whole grains of *S. barghoornii* are so large (to 70



FIGURES 74–80. Aff. *Retimonocolpites* Pierce sp. 2 (FP-102; *Brenner 10*), from Upper Zone I of the Potomac Group, Upper Aptian-Lower Albian (ca. 110 Ma).—74. Whole grain PMG, ×1,920.—75. Whole grain SEMG, showing apertural side, ×2,040.—76. Whole grain SEMG, showing nonapertural side, ×2,040.—77. Exine surface SEMG, ×11,800.—78. Whole grain exine section TEMG, with aperture at top middle, ×6,430.—79. Nonapertural exine section TEMG, ×18,500.—80. Apertural exine section TEMG, ×18,500.



FIGURES 81–86. *Stellatopollis barghoornii* Doyle (FP-377; D12-515), from Middle Zone IIB of the Potomac Group, upper Middle Albian (ca. 105 Ma).—81. Whole grain PMG, ×1,030.—82. Whole grain SEMG, ×1,140.—83–84. Exine surface SEMG, ×12,000.—85. Whole grain exine section TEMG, with aperture at top center, ×4,300.—86. Nonapertural exine section TEMG, ×11,900.

μm) that the "crotonoid" sculpturing, which appears so beautiful in SEMG (Fig. 82), is clearly evident in PMG as well (Fig. 81). Exine surface SEMG show that the triangular projections that form the "crotonoid" sculpturing pattern are attached to an underlying reticulum that is formed by muri that are distinctly circular (Figs. 83, 84). TEM sections further reveal that short columellae occur below the reticulum itself (Fig. 85). The moderately thin nexine in the nonapertural exine is composed of a thick foot-layer and a relatively thin endexine (Fig. 86). In the apertural region the sexine is highly disorganized (Fig. 85), and, as Doyle et al. (1975) have indicated, endexine probably occurs under the aperture, although we were not able to confirm this with the material we have examined so far.

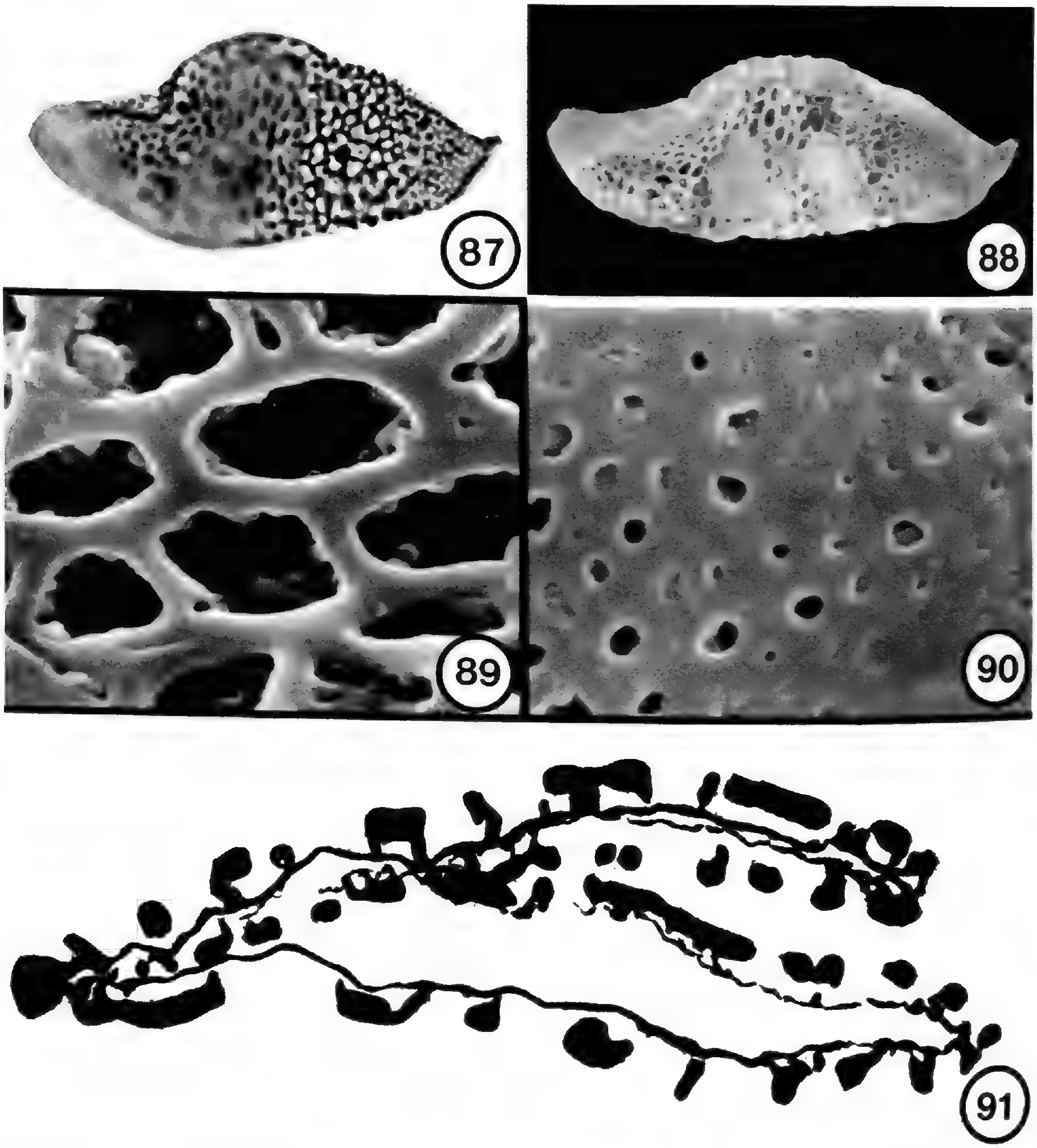
LILIACIDITES COUPER

In 1953, Couper described the form genus *Liliacidites* Couper from the Upper Cretaceous-Eocene of New Zealand. His diagnosis of the genus was pollen "free, anisopolar, bilateral, monosulcate, occasionally trichotomosulcate; sulcus long, broad; grain usually elongate; exine clearly reticulate, lumina of reticulum variable in size; clavate, baculate in optical section (muri composed of baculi or clavae)." Although there has been considerable disagreement concerning the circumscription of *Liliacidites,* we believe that three Potomac Group pollen types that we have investigated fall under this form genus sensu lato.

Liliacidites sp. 1. One type of *Liliacidites* that we have studied, which we have designated as *Liliacidites* sp. 1 (Figs. 87–91), is the same as *Liliacidites* sp. F of Doyle and Robbins (1977). The most distinctive feature of this large, strongly boat-shaped, monosulcate pollen is the differentiation of its irregularly reticulate sculpturing into coarse (Fig. 89) and fine (Fig. 90) areas, with the fine areas occurring at the ends of the boat-shaped grain (Figs. 87, 88). In addition, the muri themselves are psilate, and within the coarse reticulum the lumina are strongly dimorphic (Fig. 89). TEMG of the whole grain (Fig. 91) reveal that the nexine is extremely to very thin, and that it is overlaid by a thick tectum supported by short columellae. Endexine was not observed. The aperture appears to be very broad and consists of a thinner nexine relative to the nonapertural nexine overlaid by a relatively unreduced sexine (the infolded aperture can be seen on the right side in Fig. 91).

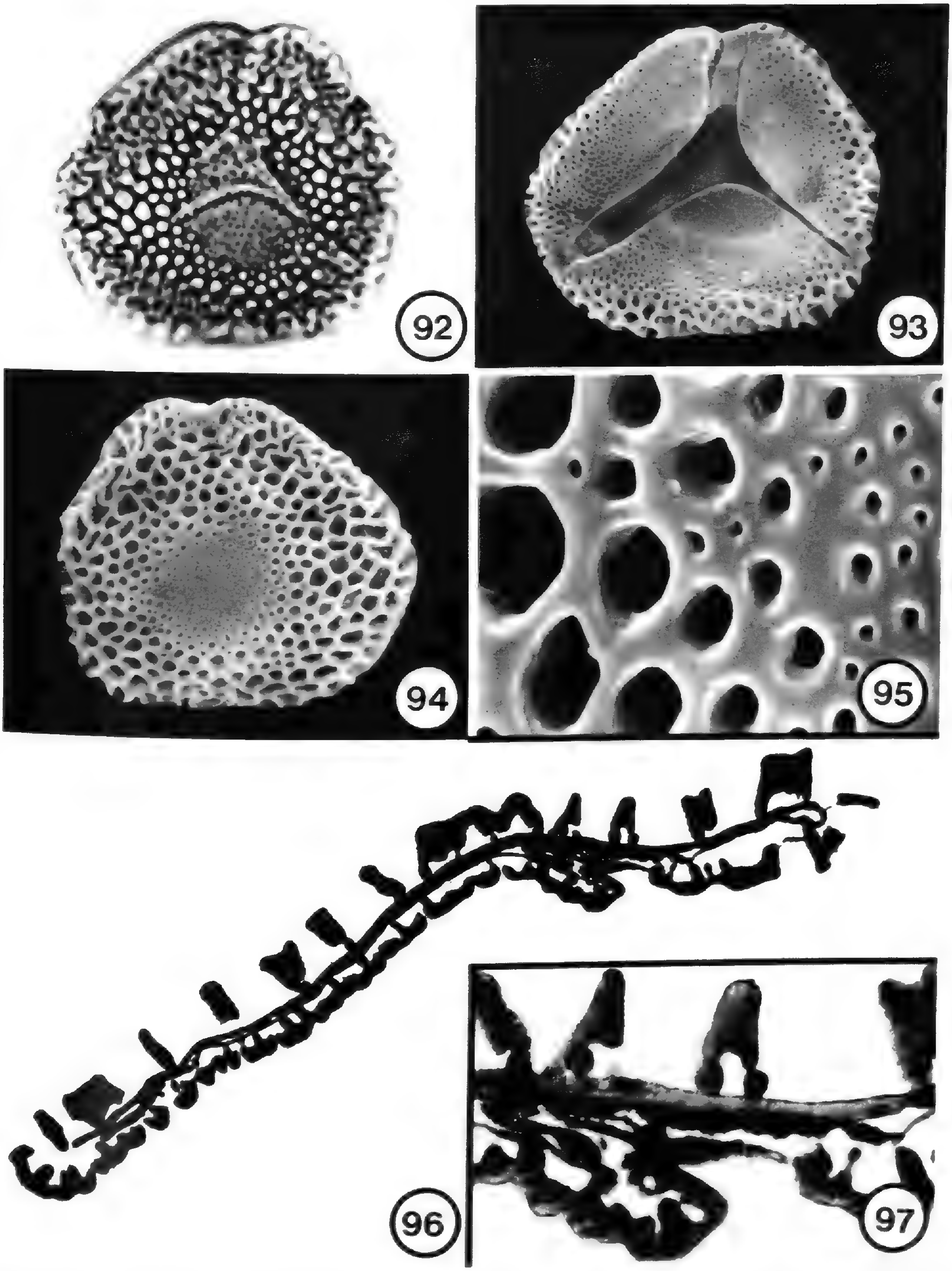
Liliacidites sp. 2. A second type of *Liliacidites,* which we have designated *Liliacidites* sp. 2, is shown in Figures 92–97. This species is the same as *Liliacidites* sp. E of Doyle and Robbins (1977) and was obtained from the same Potomac Group core sample (D13-535) as the grain pictured by them. Unlike *Liliacidites* sp. 1, which is boat-shaped and monosulcate, *Liliacidites* sp. 2 is globose and trichotomosulcate (Figs. 92, 93). In the grain shown in Figures 92–97 one arm of the trichotomosulcus is notably smaller than the other two (Fig. 93). This is common in other types of trichotomosulcate pollen (cf. Wilson, 1964), and may be indicative of an evolutionary stage that is intermediate between monosulcate pollen and pollen that has a fully developed, equal-armed, trichotomosulcus. *Liliacidites* sp. 2 is similar to *Liliacidites* sp. 1 in that it also possesses reticulate sculpturing differentiated into coarse and fine areas (Fig. 95), although instead of having the fine reticulum at the ends of a boat-shaped grain, as in *Liliacidites* sp. 1, in *Liliacidites* sp. 2 the fine reticulum is around the aperture (Fig. 93) and in the middle of the nonapertural face (Figs. 92, 94). Although the muri are psilate, as in *Liliacidites* sp. 1, in *Liliacidites* sp. 2 they are more or less circular (Figs. 94, 95) rather than irregular. Strongly dimorphic lumina can occasionally be seen within the coarse reticulum (Fig. 95). TEM sections of *Liliacidites* sp. 2 reveal that, as in *Liliacidites* sp. 1, the nexine is thin and the columellae are short (Fig. 96). In the grain shown in Figure 96, the two sides are tightly appressed, with the nonapertural face on top and the apertural side on the bottom. A section through part of the finely reticulate spot on the nonapertural side of the grain is present at the top right of Figure 96 just below the line dividing Figures 94 and 95, while a section through part of the trichotomosulcus can be seen below and slightly to the right of this. It is interesting to note that the exine is considerably thicker on the nonapertural face because the tectum is thicker on this side. TEMG in the apertural region (Fig. 97) reveal the presence of endexine in *Liliacidites* sp. 2, at least under the aperture itself. Externally, the aperture is apparent as a broad, more or less psilate area (Fig. 93), while internally it appears as a thinner region of the exine that seems to consist largely of endexine.

"*Liliacidites*" *minutus.* The third type of Early Cretaceous angiosperm pollen that for the present at least is included under the form genus

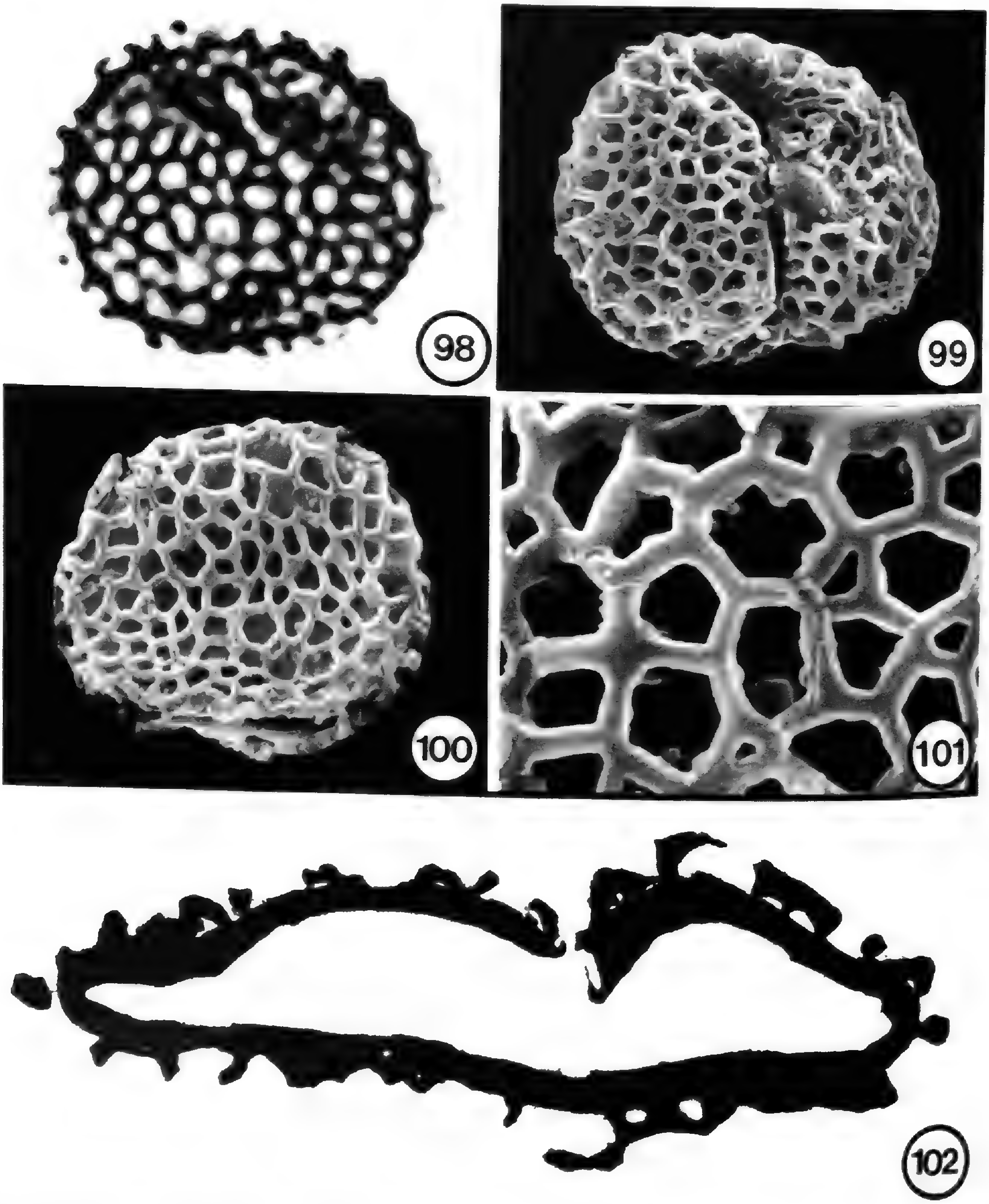


FIGURES 87–91. *Liliacidites* Couper sp. 1 (FP-392; D13-535), from Upper Zone IIB of the Potomac Group, lower Upper Albian (ca. 103 Ma).—87. Whole grain PMG, ×1,340.—88. Whole grain SEMG, ×1,340.—89. Exine surface SEMG, showing coarse reticulum, ×12,000.—90. Exine surface SEMG, showing fine reticulum, ×12,000.—91. Whole grain exine section TEMG, with infolded aperture at right, ×8,130.

Liliacidites is apparently the same as pollen described by Brenner (1963) as *Clavatipollenites minutus* Brenner and pictured in Doyle and Robbins (1977). Although this pollen type is probably best treated as a distinct genus, for the time being we will refer to it as "*Liliacidites*" *minutus*. "*Liliacidites*" *minutus* (Figs. 98–102) is characterized by its small size (generally about 15 μm long) and psilate reticulum (Figs. 99–101). The relatively coarse reticulum of "*L.*" *minutus*, which is clearly evident even in PMG (Fig. 98), gives this pollen an appearance that is considerably different from that of *Clavatipollenites*. Moreover, "*L.*" *minutus* resembles *Liliacidites* spp. 1 and 2 in having a psilate reticulum with dimorphic lumina (Fig. 101), although it differs from them in that its reticulum is frequently strongly polygonal. TEM sections (Fig. 102) reveal that "*L.*" *minutus* has a moderately thick nexine, however, that is different from the thin nexine of *Liliacidites* spp. 1 and 2. This thick nexine is overlaid by short columellae and a thick



FIGURES 92–97. *Liliacidites* Couper sp. 2 (FP-366; D13-535), from Upper Zone IIB of the Potomac Group, lower Upper Albian (ca. 103 Ma).—92. Whole grain PMG, ×1,350.—93. Whole grain SEMG, showing apertural side, ×1,620.—94. Whole grain SEMG, showing nonapertural side, ×1,620.—95. Exine surface SEMG, ×12,000.—96. Whole grain exine section TEMG, with aperture at bottom right, ×5,680.—97. Apertural exine section TEMG, with apertural region at bottom and appressed non-apertural side above, ×14,300.



FIGURES 98–102. "*Liliacidites*" *minutus* (= *Clavatipollenites minutus* Brenner) (FP-194; Cornet Beltway), from Zone IIB of the Potomac Group, Middle-Upper Albian (ca. 105 Ma).—98. Whole grain PMG, ×2,800.—99. Whole grain SEMG, showing apertural side, ×3,100.—100. Whole grain SEMG, showing nonapertural side, ×3,100.—101. Exine surface SEMG, ×12,000.—102. Whole grain exine section TEMG, with aperture at top and slightly right of center, ×9,270.

tectum. Endexine was not observed. Although "*Liliacidites*" *minutus* does not agree with typical *Liliacidites* pollen, such as *Liliacidites* spp. 1 and 2, in all respects, this pollen type appears to have a greater overall similarity with *Liliacidites* than with *Clavatipollenites*, and for this reason we have chosen to include it under our discussion of the pollen of *Liliacidites*.

MAJOR FEATURES OF LOWER CRETACEOUS ANGIOSPERM POLLEN

The major features of the 13 types of Lower Cretaceous angiosperm pollen grains that we have investigated with combined light, scanning electron, and transmission electron microscopy are summarized in Table 4. Characters of these Early

Cretaceous pollen grains are considered under the following seven headings: aperture type, pollen shape, pollen size, nonapertural exine sculpturing, nonapertural exine structure, exine stratification, and aperture ultrastructure.

Aperture type. The majority of pollen grain types included in this study (nine out of 13) have a monosulcate aperture, e.g., *Clavatipollenites hughesii* (Figs. 7, 8), *Retimonocolpites peroreticulatus* (Fig. 70), *Stellatopollis barghoornii* (Figs. 81, 82), and "*Liliacidites*" *minutus* (Fig. 99). Two pollen types, aff. *Clavatipollenites* sp. 1 (Fig. 18) and *Liliacidites* sp. 2 (Fig. 93) have trichotomosulcate apertures, while pollen grains of *Asteropollis asteroides* are basically pentachotomosulcate (Figs. 31, 32), although sometimes they may be tetra- or hexachotomosulcate. *Stephanocolpites fredericksburgensis* is the only type of pollen included in our investigation that has several equatorial apertures instead of a single polar aperture. According to Davies and Norris (1976), *S. fredericksburgensis* is basically tetracolpoidate, less commonly pentacolpoidate as pictured in Figures 44 and 45.

Pollen shape. Shape of the pollen grains studied varies from strongly boat-shaped in *Liliacidites* sp. 1 (Figs. 87, 88, 103) and moderately boat-shaped in aff. *Retimonocolpites* spp. 1 (Figs. 63–65) and 2 (Figs. 74–76) to globose in *Asteropollis asteroides* (Figs. 31–33), *Stephanocolpites fredericksburgensis* (Figs. 44, 45), aff. *Clavatipollenites* sp. 1 (Figs. 18, 19), and *Liliacidites* sp. 2 (Figs. 92–94). *Retimonocolpites peroreticulatus* (Figs. 69–71), *R. dividuus* (Figs. 57–59), and *Stellatopollis barghoornii* (Figs. 81, 82) all vary from boat-shaped to globose, while *Clavatipollenites hughesii* (Figs. 7, 8), aff. *Clavatipollenites* sp. 2 (Fig. 23), and "*Liliacidites*" *minutus* (Figs. 98–100) vary from slightly boat-shaped to globose.

Pollen size. Most of the grains examined are medium-sized with a range of about 20–30 μm, although *Liliacidites* sp. 2 (Figs. 92–97) and to some extent *Retimonocolpites dividuus* (Figs. 57–62) average a little above this size range. *Retimonocolpites peroreticulatus* (Figs. 69–73), which is usually somewhat below 20 μm, is basically small- to medium-sized. Pollen of *Liliacidites* sp. 1 (Figs. 87–91) and *Stellatopollis barghoornii* (Figs. 81–86) is mostly large (usually over 50 μm), while pollen grains of "*Liliacidites*" *minutus* (Figs. 98–102) are small (usually around 15 μm).

Nonapertural exine sculpturing. Most of the pollen types studied are irregularly reticulate, e.g., *Clavatipollenites hughesii* (Fig. 9), *Asteropollis asteroides* (Fig. 34), *Stephanocolpites fredericksburgensis* (Fig. 46), although *Stellatopollis barghoornii* is regularly reticulate with circular muri (Figs. 82–84) and *Liliacidites* sp. 2 is more or less regularly reticulate with muri that are almost circular (Figs. 94, 95). "*Liliacidites*" *minutus*, which is irregularly to more or less regularly reticulate (Figs. 99, 100), is distinctive in that its muri are mostly decidedly polygonal (Fig. 101). *Liliacidites* spp. 1 and 2 are characterized by differentiation of their reticulate sculpturing into coarse and fine areas (Figs. 89, 90, 95). In *Liliacidites* sp. 1 the finer reticulum is at the ends of the boat-shaped pollen (Figs. 87, 88, 103), while in *Liliacidites* sp. 2 the area around the aperture (Fig. 93) and the middle of the nonapertural side of the grain (Fig. 94) are both surrounded by a finer reticulum.

The nature of the muri or walls of the reticulum varies considerably. In *Clavatipollenites hughesii*, the muri are beaded to spinulose (Fig. 9), while they are weakly beaded to spinulose in *Asteropollis asteroides* (Fig. 34), and spinulose in *Stephanocolpites fredericksburgensis* (Fig. 46). Muri with recurved spines are found in both *Retimonocolpites peroreticulatus* (Fig. 72) and aff. *Retimonocolpites* sp. 2 (Fig. 77). Banded muri occur in aff. *Retimonocolpites* sp. 1 (Figs. 63–68) and in *Retimonocolpites dividuus* (Figs. 57–62), being distinctly banded in the former (Fig. 66) while finely and discontinuously banded in the latter (Fig. 60). Beaded muri characterize aff. *Clavatipollenites* sp. 1 (Figs. 20, 21), while aff. *Clavatipollenites* sp. 2 has beaded-granulose muri (Fig. 24). *Stellatopollis barghoornii* has muri covered by psilate, triangular supratectal elements, which form a "crotonoid" sculpturing pattern (Figs. 83, 84). In all three species of *Liliacidites* the muri are psilate and the lumina are generally strongly dimorphic, with small lumina mixed in with much larger ones (Figs. 89, 95, 101). Nodose muri with node-like, swollen areas at points where columellae and muri meet occur in *Asteropollis asteroides* (Fig. 34) and aff. *Retimonocolpites* sp. 1 (Figs. 63–66).

Nonapertural exine structure. Most of the pollen types investigated are semitectate, except *Stephanocolpites fredericksburgensis*, which is tectate-perforate (Figs. 45, 46), and *Clavatipollenites hughesii* (Figs. 8, 9) and *Asteropollis asteroides* (Figs. 32–34), which are tectate-perforate to semitectate. The coarse and finely reticulate *Liliacidites* spp. 1 and 2 are basically

TABLE 4. Major features of Lower Cretaceous angiosperm pollen.

Pollen Type	Aperture Type, Pollen Shape, and Pollen Size	Nonapertural Exine Sculpturing
(1) *Clavatipollenites hughesii*	Monosulcate; slightly boat-shaped to globose; medium-sized	Irregularly reticulate, muri beaded to spinulose
(2) *Asteropollis asteroides*	(4–)5(–6)-chotomosulcate; globose; medium-sized	Irregularly reticulate, muri weakly beaded to spinulose, nodose
(3) *Stephanocolpites fredericksburgensis*	4(–5)-colpoidate; globose; medium-sized	Irregularly reticulate, muri spinulose
(4) *Retimonocolpites peroreticulatus*	Monosulcate; boat-shaped to globose; small- to medium-sized	Irregularly reticulate, muri with recurved spines, reticulum ± free from nexine
(5) aff. *Retimonocolpites* sp. 2	Monosulcate; boat-shaped; medium-sized	Irregularly reticulate, muri with recurved spines
(6) aff. *Retimonocolpites* sp. 1	Monosulcate; boat-shaped; medium-sized	Irregularly reticulate, muri distinctly banded, nodose
(7) aff. *Clavatipollenites* sp. 1	Trichotomosulcate; globose; medium-sized	Irregularly reticulate, muri beaded
(8) aff. *Clavatipollenites* sp. 2	Monosulcate; slightly boat-shaped to globose; medium-sized	Irregularly reticulate, muri beaded-granulose
(9) *Stellatopollis barghoornii*	Monosulcate; boat-shaped to ± globose; large	Regularly reticulate, muri circular, with psilate, triangular supratectal elements, i.e., "crotonoid"
(10) *Liliacidites* sp. 1	Monosulcate; strongly boat-shaped; large	Irregularly coarsely and finely reticulate, muri psilate, lumina within coarse reticulum strongly dimorphic
(11) *Liliacidites* sp. 2	Trichotomosulcate; globose; a little above medium-sized	± regularly coarsely and finely reticulate, muri psilate, ± circular, lumina within coarse reticulum occasionally strongly dimorphic
(12) "*Liliacidites*" *minutus*	Monosulcate; slightly boat-shaped to globose; small	Irregularly to ± regularly reticulate, muri psilate, mostly decidedly polygonal, lumina dimorphic
(13) *Retimonocolpites dividuus*	Monosulcate; boat-shaped to globose; ± medium-sized	Irregularly reticulate, muri finely and discontinuously banded

TABLE 4. *(Continued).*

Nonapertural Exine Structure	Exine Stratification	Aperture Ultrastructure
(1) Tectate-perforate to semitectate; nexine moderately to very thick, columellae well-developed	Thick endexine under aperture only	Aperture externally verrucate, internally with a very thick, apparently homogeneous endexine and a thin, occasionally lamellate foot-layer overlaid by a thick sexine organized into verrucae
(2) Tectate-perforate to semitectate; nexine average to moderately thick, columellae seemingly composed of granules	Thin endexine throughout	Aperture evident internally as a lamellate nexine consisting of a thin endexine and a somewhat thicker foot-layer overlaid by a disorganized sexine
(3) Tectate-perforate; nexine moderately to very thick, columellae present	Well-developed endexine throughout, conspicuously interbedded with foot-layer under aperture	Apertures internally with a thick endexine conspicuously lamellate at top and interbedded with foot-layer, sexine somewhat reduced, composed of laterally thickened elements
(4) Semitectate; nexine moderately to very thick, columellae absent	Thin endexine possibly present	Aperture represented externally by a definite, distinctly bordered slit in the reticulum, evident internally by a definite thinning of the nexine
(5) Semitectate; nexine average to moderately thick, well-developed columellae present	Thin endexine throughout	Aperture evident internally by a definite thinning of the nexine and a disorganization of the sexine
(6) Semitectate; nexine moderately thick, well-developed columellae present	Endexine not observed	Aperture appearing externally as an interruption in the reticulum, evident internally by a marked thinning of the nexine
(7) Semitectate; nexine average, well-developed columellae present	Endexine not observed	Aperture evident internally by a thinning of the nexine and a disorganization of the sexine
(8) Semitectate; nexine average, well-developed columellae present	Endexine not observed	Aperture evident internally by a thinning of the nexine and a disorganization of the sexine
(9) Semitectate; nexine moderately thin, columellae very short, tectum and overlying elements thick	Thin endexine probably throughout	Aperture probably appearing externally as a differently organized, non-"crotonoid" region of the exine, evident internally by a thinning of the nexine, which becomes lamellate, and a marked disorganization and reduction of the sexine
(10) Semitectate to tectate-perforate at ends of grain; nexine extremely to very thin, columellae short, tectum thick	Endexine not observed	Aperture evident internally as a broad, infolded region of the exine with a thinner nexine but apparently unreduced sexine

TABLE 4. (Continued).

Nonapertural Exine Structure	Exine Stratification	Aperture Ultrastructure
(11) Semitectate to tectate-perforate around aperture and in middle of non-apertural side; nexine very to moderately thin, columellae short, tectum thick (especially on non-apertural side)	Well-developed endexine, at least under aperture	Aperture appearing externally as a broad, ± psilate area, evident internally as a thinner region of the exine that appears to consist largely of endexine
(12) Semitectate; nexine moderately thick, columellae short, tectum thick	Endexine not observed	Aperture appearing externally as an interruption in the reticulum, evident internally by a thinning of the nexine
(13) Semitectate; nexine extremely to very thin, columellae short, tectum thick	Endexine not observed	Aperture represented externally by a definite interruption in the reticulum that in the light microscope appears characteristically folded on either side, scarcely evident internally, "border" observed in PMG presumably due to infolding of the exine

semitectate, with tectate-perforate areas at the ends of the boat-shaped pollen of *Liliacidites* sp. 1 (Figs. 87, 88, 90) and around the aperture and in the middle of the nonapertural side of *Liliacidites* sp. 2 (Figs. 93, 94).

Nexine thickness in the nonapertural exine (cf. Table 3) ranges from very thick to extremely thin. *Clavatipollenites hughesii* (Fig. 10), *Stephanocolpites fredericksburgensis* (Fig. 48), and *Retimonocolpites peroreticulatus* (Fig. 73) have a moderately to very thick nexine, aff. *Retimonocolpites* sp. 1 (Fig. 68) and "*Liliacidites*" *minutus* (Fig. 102) have a moderately thick nexine, and *Asteropollis asteroides* (Fig. 36) and aff. *Retimonocolpites* sp. 2 (Fig. 78) have an average to moderately thick nexine. An average nexine characterizes the pollen of aff. *Clavatipollenites* spp. 1 and 2 (Figs. 22, 26). By contrast, the nexine is moderately thin in *Stellatopollis barghoornii* (Figs. 85, 86), very to moderately thin in *Liliacidites* sp. 2 (Fig. 96), and extremely to very thin in *Retimonocolpites dividuus* (Figs. 61, 62) and *Liliacidites* sp. 1 (Fig. 91).

Most of the pollen types have well-developed columellae, although the columellae are short (and the tectum is thick) in *Stellatopollis barghoornii* (Figs. 85, 86), *Retimonocolpites dividuus* (Figs. 61, 62), and in all species of *Liliacidites* (Figs. 91, 96, 102). *Liliacidites* sp. 2 is noteworthy in that the tectum is considerably thicker on the nonapertural side of the pollen grain (Fig. 96). *Retimonocolpites peroreticulatus* is unusual in that columellae are absent and the reticulum is more or less free from the underlying nexine (Figs. 69–73). The columellae are seemingly composed of granules in *Asteropollis asteroides* (Figs. 34, 36).

Exine stratification. Endexine was not observed in the pollen of aff. *Clavatipollenites* spp. 1 (Fig. 22) and 2 (Figs. 25, 26), aff. *Retimonocolpites* sp. 1 (Figs. 67, 68), *Retimonocolpites dividuus* (Figs. 61, 62), *Liliacidites* sp. 1 (Fig. 91), and "*Liliacidites*" *minutus* (Fig. 102). A thin endexine is possibly present in *Retimonocolpites peroreticulatus*, although it cannot be seen in the TEMG shown in Figure 73. Thick endexine only under the aperture occurs in *Clavatipollenites hughesii* (Fig. 11) and well-developed endexine, at least under the aperture, was found in *Liliacidites* sp. 2 (Fig. 97). A thin endexine throughout the grain (in both apertural and nonapertural regions) characterizes *Asteropollis asteroides* (Figs. 36, 37) and aff. *Retimonocolpites* sp. 2 (Figs. 79, 80), and is probably present in *Stellatopollis* *barghoornii* as well (cf. Fig. 86, in which definite endexine can be seen in sections of the nonapertural exine). In *Stephanocolpites fredericksburgensis,* a well-developed endexine is present throughout the grain (Figs. 48, 50), and the endexine is conspicuously interbedded with the foot-layer under the aperture (Fig. 49).

Aperture ultrastructure. Considerable variation exists in the pollen grains examined with regard to aperture ultrastructure, with reference both to external sculpturing and internal structure. Externally apertures may appear either as differentially sculptured areas of the exine or as definite interruptions in the reticulum itself. In *Clavatipollenites hughesii* the aperture is conspicuously verrucate (Fig. 8), while in *Liliacidites* sp. 2 the aperture appears as a broad, more or less psilate area (Fig. 93). The aperture is marked by an interruption in the reticulum itself in aff. *Retimonocolpites* sp. 1 (Fig. 64), "*Liliacidites*" *minutus* (Fig. 99), and *Retimonocolpites dividuus* (Fig. 59), while in *Retimonocolpites peroreticulatus* the aperture is represented externally by a definite, distinctly bordered slit in the reticulum (Fig. 70). The aperture probably appears externally as a differently organized, non-"crotonoid" region of the exine in *Stellatopollis barghoornii* (cf. Fig. 85).

Apertures are just as varied internally or structurally. In many instances the aperture is marked by a thinning of the nexine and a disorganization of the sexine relative to the nonapertural exine, e.g., aff. *Clavatipollenites* sp. 1 (Fig. 22) and *Stellatopollis barghoornii* (Fig. 85). If endexine is present in the pollen grain, it may be restricted to the aperture, as in *Clavatipollenites hughesii,* which has a particularly thick apertural endexine (Fig. 11), and in *Liliacidites* sp. 2 (Fig. 97), or it may be thicker under the aperture, as in *Stephanocolpites fredericksburgensis* (cf. Figs. 48, 49). In *Asteropollis asteroides* (cf. Figs. 36, 37) and in aff. *Retimonocolpites* sp. 2 (cf. Figs. 79, 80) endexine is apparently about equally developed in apertural and nonapertural areas. The nexine under the aperture is lamellate in *Asteropollis asteroides* (Fig. 37) and *Stellatopollis barghoornii* (Fig. 85), while in *Clavatipollenites hughesii* occasionally the foot-layer appears lamellate (Fig. 11). In *Stephanocolpites fredericksburgensis* the apertural endexine is conspicuously lamellate at the top and interbedded with the foot-layer (Fig. 49). In some pollen types the apertural sexine is relatively unreduced but differently organized as compared with the nonapertural sexine, e.g., the apertural sexine is organized into verrucae in *Clavatipollenites hughesii* (Figs. 8, 11) and into laterally thickened elements in *Stephanocolpites fredericksburgensis* (Figs. 47, 49). The broad aperture in *Liliacidites* sp. 1, which we have not observed expanded, and which can be seen infolded on the right side of the grain pictured in Figure 91, consists of an extremely to very thin nexine overlaid by a conspicuously well-developed and little reduced sexine. By contrast, the aperture of *Liliacidites* sp. 2 shows considerable reduction of its sexine (Figs. 93, 96, 97). The bordered aperture that is so conspicuous in PMG of *Retimonocolpites dividuus* (Figs. 57, 58) is scarcely evident in TEMG (Figs. 61, 62), and is apparently the result of infolding of the thin-walled exine itself.

DELIMITATION OF LOWER CRETACEOUS ANGIOSPERM POLLEN

Asteropollis, Stephanocolpites fredericksburgensis, and *Stellatopollis,* even at the light microscope level, are reasonably distinct taxa of Lower Cretaceous angiosperm pollen because of their characteristic apertures (4–6-chotomosulcate in *Asteropollis,* 4–5-colpoidate in *S. fredericksburgensis*) and sculpturing (monosulcate and "crotonoid" in *Stellatopollis*). In contrast, delimitation of *Clavatipollenites, Retimonocolpites,* and *Liliacidites* based on light microscope studies alone has proved to be extremely difficult. This is evident by the fact that the type species of the genus *Retimonocolpites, R. dividuus,* has been formally transferred to *Liliacidites* by Brenner (1963), as *Liliacidites dividuus* (Pierce) Brenner, while pollen that appears to be identical with *R. dividuus* has been described by Kemp (1968) as *Clavatipollenites rotundus* Kemp. Some authors, by contrast, have at times referred to pollen of the *Liliacidites* type under the name *Retimonocolpites* (cf. Doyle, 1973).

As might be expected, our same grain combined light and electron microscope study of Lower Cretaceous angiosperm pollen grains has revealed a number of differences that can be used to delimit *Clavatipollenites, Retimonocolpites,* and *Liliacidites. Clavatipollenites,* at least in the restricted sense of *C. hughesii,* has a beaded to spinulose reticulum that is tectate-perforate to semitectate (Fig. 9), a thick nexine (Fig. 10), well-developed columellae (Fig. 10), and a thick plug of endexine under the aperture (Fig. 11), while *Retimonocolpites,* at least in the sense of its type

TABLE 5. Systematic affinities of Lower Cretaceous angiosperm pollen.

I. CHLORANTHACEOUS POLLEN TYPES
- (1) *Clavatipollenites hughesii* (chloranthaceous, extremely similar to *Ascarina*)
- (2) *Asteropollis asteroides* (chloranthaceous, with a large number of similarities to *Hedyosmum*)
- (3) *Stephanocolpites fredericksburgensis* (chloranthaceous, with certain similarities to *Chloranthus*)

II. MYRISTICACEOUS-LIKE POLLEN TYPES
- (1) aff. *Clavatipollenites* sp. 2 (similar to some myristicaceous pollen)
- (2) aff. *Clavatipollenites* sp. 1 (certain similarities to myristicaceous pollen)

III. MONOCOTYLEDONOUS POLLEN TYPES
- (1) *Liliacidites* sp. 1 (monocotyledonous)
- (2) *Liliacidites* sp. 2 (monocotyledonous)
- (3) "*Liliacidites*" *minutus* (possibly monocotyledonous)
- (4) *Retimonocolpites dividuus* (probably monocotyledonous)

IV. POLLEN TYPES OF UNCERTAIN OR UNKNOWN AFFINITY
- (1) *Retimonocolpites peroreticulatus*
- (2) aff. *Retimonocolpites* sp. 2
- (3) aff. *Retimonocolpites* sp. 1
- (4) *Stellatopollis barghoornii*

species, *R. dividuus,* differs considerably in its banded, semitectate reticulum (Fig. 60), thin nexine (Fig. 61), short columellae (Fig. 61), and apparent lack of endexine (Fig. 62). Some authors, e.g., Doyle et al. (1975), have suggested restricting *Liliacidites* to monosulcate pollen grains that exhibit a differentiation into coarsely and finely reticulate areas such as observed in *Liliacidites* spp. 1 (Figs. 87, 88, 103) and 2 (Figs. 93, 94). However, unless one wishes to create a separate genus for "*Liliacidites*" *minutus* (Figs. 98–102), which is probably warranted, the most important features of *Liliacidites* as presently delimited would appear to be its psilate, semitectate reticulum and strongly dimorphic lumina (cf. Figs. 89, 95, 101).

Although for the present we prefer to keep the 13 taxa of Lower Cretaceous angiosperm pollen grains that we have investigated in six form genera delimited largely on the basis of light microscopy, we believe that the majority of these 13 taxa probably represent good genera in a biological sense. For example, *Retimonocolpites peroreticulatus* is certainly sufficiently distinct from *R. dividuus* to warrant its recognition as a separate genus. However, until more examples of Lower Cretaceous angiosperm pollen grains have been investigated ultrastructurally, especially using same grain combined light, scanning electron, and transmission electron microscopy, we believe that for now it is prudent simply to refer to the pollen grains that we have studied under established form genera such as *Clavatipollenites, Retimonocolpites,* and *Liliacidites.*

SYSTEMATIC AFFINITIES OF LOWER CRETACEOUS ANGIOSPERM POLLEN

The Lower Cretaceous angiosperm pollen that we have examined can be placed into four different groups based on systematic affinity. One group of pollen grains is clearly related to the primitive dicotyledon family Chloranthaceae, while a second group exhibits certain resemblances at least to pollen of the family Myristicaceae. A third group consists of pollen grains with features that are characteristic of monocotyledon pollen. Finally, there is a fourth group of pollen types that are of uncertain or unknown systematic affinity. Table 5 summarizes the possible systematic affinities of the Lower Cretaceous angiosperm pollen included in this study.

CHLORANTHACEOUS POLLEN TYPES

A number of workers, including Couper (1960), Kuprianova (1967, 1981), Kemp (1968), Doyle (1969), and Muller (1981), have noted certain resemblances between some Early Cretaceous angiosperm pollen types and pollen of the extant primitive dicot family Chloranthaceae. Since these suggested relationships have virtually all been based on light microscope comparisons

TABLE 6. Major features of pollen of the family Chloranthaceae.

Pollen Feature	*Ascarina*[a]	*Hedyosmum*[b]	*Chloranthus*[c]
Aperture Type, Pollen Shape, and Pollen Size	Monosulcate; slightly boat-shaped to globose; medium-sized	5(–6)-chotomosulcate; globose; ± medium-sized	(4–5–)6-colpoidate; globose; medium-sized
Nonapertural Exine Sculpturing	Irregularly reticulate, muri beaded to spinulose	Irregularly reticulate, muri conspicuously spinulose, nodose	Irregularly reticulate, muri bluntly spinulose to ± granulose
Nonapertural Exine Structure	Tectate-perforate to semitectate; nexine moderately to very thick, columellae well-developed	Tectate-perforate to semitectate; nexine average, columellae well-developed	Semitectate; nexine moderately thin to average; columellae present
Exine Stratification	Thick endexine under aperture only	Thick endexine under aperture only; foot-layer under aperture conspicuously coarsely lamellate	Endexine throughout, finely lamellate, especially under aperture
Aperture Ultrastructure	Aperture externally finely verrucate, internally with a very thick, somewhat heterogeneously stratified endexine and a disorganized foot-layer overlaid by a thick sexine organized into verrucae	Aperture represented externally as more tightly organized regions of the reticulum, evident internally as a very thick, somewhat heterogeneously stratified endexine and a conspicuously lamellate foot-layer overlaid by a thick, hardly reduced sexine that is scarcely disorganized relative to the non-apertural sexine	Apertures represented externally as solid, ± scabrate areas in the reticulum, evident internally by development of a finely lamellate endexine, extreme thinning of the foot-layer, and reduction and disorganization of the sexine

[a] Ultrastructure based on *Ascarina diffusa* A. C. Smith.
[b] Ultrastructure based on *Hedyosmum orientale* Merr. & Chun.
[c] Ultrastructure based on *Chloranthus japonicus* Sieb.

alone, we decided to examine pollen of the Chloranthaceae with SEM and TEM to see if there were ultrastructural similarities as well.

The Chloranthaceae is a very small family of five genera and approximately 70 species. The largest genus, *Hedyosmum*, with some 40 species, is restricted to the American tropics except for one species, *H. orientale*, which is found only in southeast Asia. *Ascarina*, with 11 species (Smith, 1976), is basically Australasian, while the monotypic *Ascarinopsis* is endemic to Madagascar. *Chloranthus* (15 species) and *Sarcandra* (three species) are Indomalaysian. Major features of pollen of the three main genera of Chloranthaceae (*Ascarina*, *Hedyosmum*, and *Chloranthus*) are summarized in Table 6. Three taxa of Lower Cretaceous angiosperm pollen grains, *Clavatipollenites*, *Asteropollis*, and *Stephanocolpites fredericksburgensis*, exhibit various degrees of similarity to particular genera of Chloranthaceae.

Clavatipollenites and Ascarina. Many people have noted a similarity between *Clavatipollenites* and pollen produced specifically by the chloranthaceous genus *Ascarina*. From light microscopy alone it is apparent that pollen grains of both *Clavatipollenites* (Figs. 7–11) and *Ascarina* (Figs. 12–17) are monosulcate, slightly boat-shaped to globose, and medium-sized. Moreover, both types of pollen have well-developed columellae, which in optical section appear more as sculptural clavae (cf. Figs. 7, 12) than as internal structural elements. SEM and TEM examination, however, reveals an even more remarkable similarity between *Ascarina* and *Clavatipollenites* in the strict sense of *C. hughesii*. *Clavatipollenites hughesii* and *Ascarina* are identical in all the following ultrastructural features; an irregular reticulum with beaded to spinulose muri (cf. Figs. 9, 14), a tectate-perforate to semitectate exine (cf. Figs. 8, 9, 13, 14), a moderately to very thick nonapertural nexine with well-developed columellae and a thin tectum (cf. Figs. 10, 16), thick endexine present under the aperture only (cf. Figs. 11, 15, 17), and a somewhat verrucate aperture composed of tightly organized sexinous elements (cf. Figs. 8, 11, 13, 17). Thus, in ultrastructural as well as light microscope observable characters, *Clavatipollenites hughesii* is for all intents identical to the pollen of *Ascarina*. Pollen of the two genera differs only in minor details, and not in any substantive morphological features. We agree with Muller (1981) that *Clavatipollenites* has little in common with pollen of *Austrobaileya,* which was suggested by Endress and Honegger (1980).

Asteropollis and Hedyosmum. Since the distinctive, fundamentally pentachotomosulcate aperture of *Asteropollis* (Figs. 31–37) is particularly suggestive of the aperture in the pollen of the extant chloranthaceous genus *Hedyosmum,* we thought that it would be interesting to examine pollen of *Hedyosmum* (Figs. 38–43) ultrastructurally. Although *Hedyosmum* pollen appears to be basically pentachotomosulcate (Fig. 39), sometimes, just like *Asteropollis,* it exhibits variation in the number of apertural arms present (cf. Fig. 38, which shows a PMG of a pollen grain of *Hedyosmum* that has a six-armed aperture). In addition, in both genera the pollen is globose and medium-sized. Ultrastructurally, *Asteropollis* exhibits a number of similarities to *Hedyosmum* pollen, including an irregular, nodose reticulum with somewhat spinulose muri (cf. Figs. 34, 40), a tectate-perforate to semitectate exine (cf. Figs. 32–34, 39, 40), a nonapertural nexine that is more or less average in thickness (cf. Figs. 36, 42), and a conspicuously lamellate apertural foot-layer (cf. Figs. 37, 43). Although both *Asteropollis* and *Hedyosmum* have a spinulose reticulum, the spinules are better developed in *Hedyosmum* (at least in the species shown in Fig. 40). Also, columellae are not as well-developed in *Asteropollis* (Fig. 36) as they are in *Hedyosmum* (Fig. 42). Finally, *Hedyosmum* (again at least in the species examined) has endexine only under the aperture (Figs. 41–43), while in *Asteropollis* traces of endexine are evident in both the apertural (Fig. 37) and nonapertural (Fig. 36) exine. Thus, while not agreeing in every morphological feature, *Asteropollis,* nevertheless, does exhibit a number of ultrastructural resemblances to pollen of *Hedyosmum,* in addition to its strikingly similar aperture type.

Stephanocolpites fredericksburgensis and Chloranthus. Stephanocolpites fredericksburgensis has been compared to the pollen of the genus *Chloranthus* because both pollen types are polycolpoidate. In light of this we decided to study pollen of *Chloranthus japonicus* with SEM and TEM in order to determine how *S. fredericksburgensis* (Figs. 44–50) compares ultrastructurally with the pollen of *Chloranthus* (Figs. 51–56). *Chloranthus* pollen appears to be mostly 6-aperturate (Figs. 51, 52), although sometimes it is 4–5-aperturate as well. Davies and Norris (1976) found that *S. fredericksburgensis* was most commonly 4-aperturate. The pollen of *Chloranthus japonicus* is semitectate (Figs. 52, 53) rather than tectate-perforate, as in *S. fredericksburgensis* (Figs. 45, 46), and the spinules on its reticulum are much coarser (cf. Figs. 46, 53). Moreover, the nonapertural nexine is moderately thin to average in *C. japonicus* (Figs. 54, 55), while it is moderately to very thick in *S. fredericksburgensis* (Fig. 48). *Chloranthus japonicus,* just as *S. fredericksburgensis,* has endexine throughout the grain, under both the apertural (cf. Figs. 49, 56) and nonapertural (cf. Figs. 48, 55) regions. Although *S. fredericksburgensis* resembles pollen of *Chloranthus* in its aperture type, its ultrastructure is somewhat different (at least as judged by *C. japonicus*). Moreover, *S. fredericksburgensis* exhibits some general chloranthaceous attributes, including a spinulose reticulum (Fig. 46), a thick nonapertural nexine (Fig. 48), which is reminiscent of *Ascarina* (Fig. 16) and *Clavatipollenites hughesii* (Fig. 10), and a conspicuously lamellate apertural foot-layer (Fig. 49), which is similar to the foot-layer that occurs in the apertural region of the pollen of *Hedyosmum* (Fig. 43). The definite presence of endexine in the pollen of *S. fredericksburgensis* may also be taken to support the idea of a general chloranthaceous relationship. Thus, while *Stephanocolpites fredericksburgensis* shows some resemblance to the pollen of *Chloranthus,* it has a number of features that can only be described as generalized chloranthaceous palynological attributes.

MYRISTICACEOUS-LIKE POLLEN TYPES

Unlike *Clavatipollenites hughesii,* which, as we have seen, strikingly resembles pollen of the Chloranthaceae, particularly of the genus *Ascarina,* pollen grains of what we have termed the aff. *Clavatipollenites* group exhibit more similarity to pollen of the primitive dicot family Myristicaceae (cf. Walker & Walker, 1979, 1980, 1981, 1983) than to the Chloranthaceae. Both aff. *Clavatipollenites* spp. 1 (Figs. 18–22) and 2 (Figs. 23–26) appear more myristicaceous than chloranthaceous in their beaded (Figs. 21, 24) rather than spinulose reticulum, average (Figs. 22, 26) rather than thick nonapertural nexine, and apparent total lack of endexine (Figs. 22, 25, 26). Aff. *Clavatipollenites* sp. 2 (Figs. 23–26), for example, is very similar to pollen of *Virola weberbaueri* Markgraf (Figs. 27–30) of the Myristicaceae, both having the same distinctive type of beaded-granulose reticulum with granules in rows (cf. Figs. 24, 28). We have designated pollen of the aff. *Clavatipollenites* group as "myristicaceous-like" instead of "myristicaceous" to emphasize our belief that this type of early angiosperm pollen was not necessarily produced by members of the family Myristicaceae as such. The reason for suggesting this is that myristicaceous pollen is not as ultrastructurally distinctive as chloranthaceous pollen, and, moreover, the Myristicaceae, unlike the Chloranthaceae, produces exceedingly small amounts of pollen, so that it is rather unlikely that myristicaceous pollen grains would occur in such relative abundance as does pollen of the aff. *Clavatipollenites* group in Lower Cretaceous rocks.

MONOCOTYLEDONOUS POLLEN TYPES

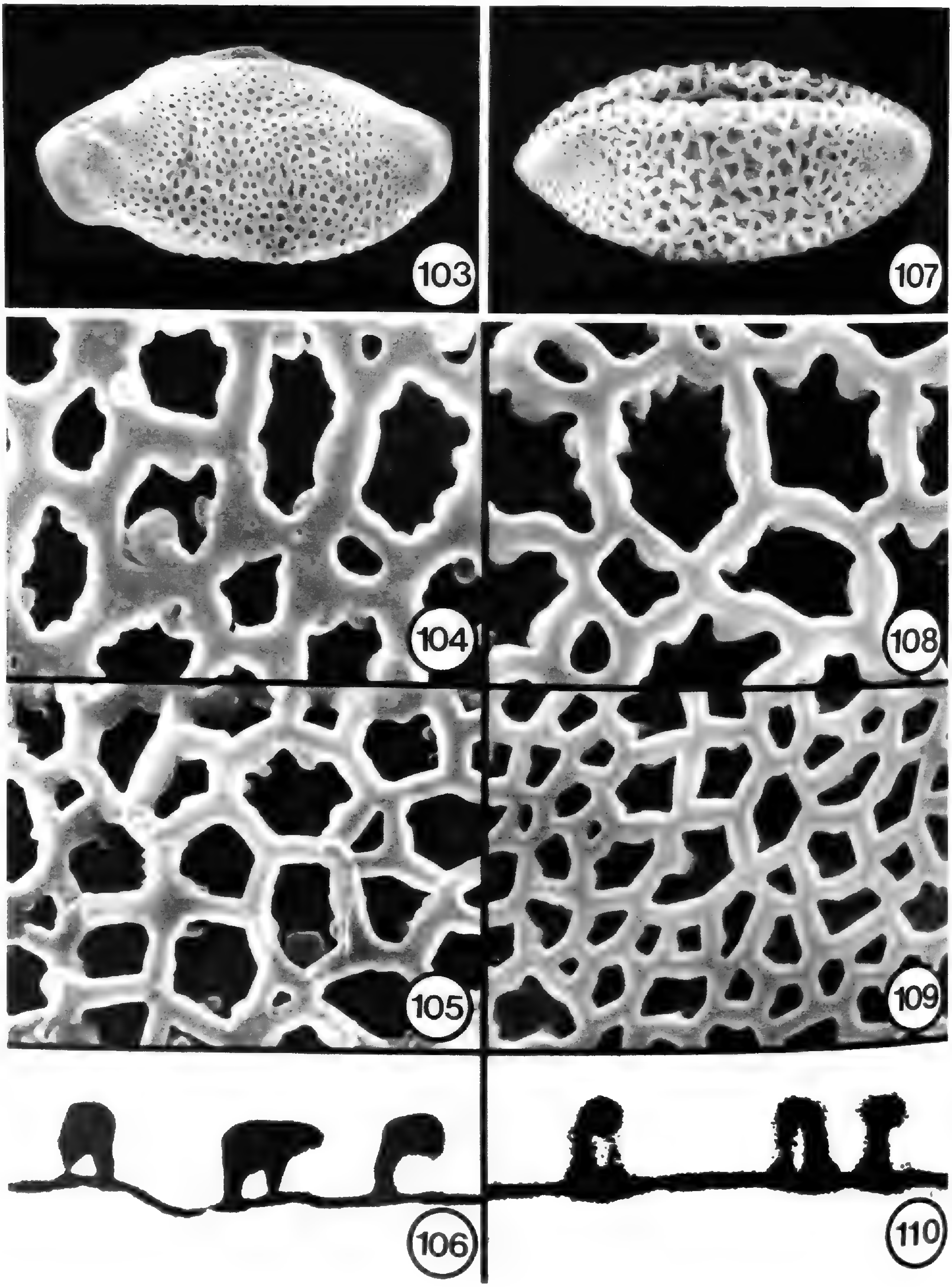
Several types of Lower Cretaceous angiosperm pollen grains that we have examined have features characteristic of monocot pollen. While none of these fossil pollen grains can be compared directly with the pollen of any particular extant monocotyledon, they do seem to represent monocotyledonous rather than dicotyledonous pollen types. In Figures 103–110 various Lower Cretaceous angiosperm pollen grains (Figs. 103–106) are compared with similar pollen produced by different living monocots (Figs. 107–110). Monocotyledonous features observed in these Lower Cretaceous angiosperm pollen grains include (1) reticulate sculpturing differentiated into coarse and fine areas (cf. Figs. 103, 107); (2) psilate muri (cf. Figs. 104, 105, 108, 109); (3) dimorphic lumina (cf. Figs. 104, 105, 108, 109); (4) "frilled" muri due to lateral extension of underlying columellae (cf. Figs. 104, 108); (5) more or less regular, decidedly polygonal lumina (cf. Figs. 105, 109); (6) a thin pollen wall in general, especially relative to pollen grain size, combined with a very thin nonapertural nexine in particular relative to the rest of the exine (cf. Figs. 106, 110); and (7) a total lack of endexine (cf. Figs. 106, 110).

Differentiation of reticulate sculpturing into coarse and fine areas, as stressed by Doyle (1973), appears to be a characteristic monocotyledonous pollen feature. We have never encountered this character in any monosulcate dicot pollen, and, moreover, it is very common in monocots as a whole, occurring often in the pollen of families such as the Liliaceae, Amaryllidaceae, Bromeliaceae, Butomaceae, and Araceae among others. Psilate muri, "frilled" muri, and dimorphic lumina are also rather frequently encountered in the pollen of monocots, as is a thin exine with a very thin nonapertural nexine. While not particularly common in monocot pollen as a whole, polygonal reticula do occur in some monocotyledonous pollen grains, and, moreover, are rarely encountered in monosulcate dicot pollen. Finally, a total lack of endexine seems to be characteristic of monocot pollen in general, and is certainly true of various primitive monocot pollen types that we have studied (Walker & Walker, unpubl. data).

Two fossil pollen types that we have investigated (*Liliacidites* spp. 1 and 2) appear to be definitely monocotyledonous, while two other types are probably (*Retimonocolpites dividuus*) or possibly ("*Liliacidites*" *minutus*) monocotyledonous.

Liliacidites spp. 1 and 2. *Liliacidites* sp. 1 (Figs. 87–91) has the following monocotyledonous features: (1) reticulate sculpturing differentiated into coarse (Fig. 89) and fine (Fig. 90) areas, with the finer reticulum at the ends of the strongly boat-shaped grain (Figs. 87, 88); (2) psilate and "frilled" muri (Fig. 89); (3) lumina that are strongly dimorphic within the coarse reticulum (Fig. 89); (4) a thin exine with a particularly thin nonapertural nexine (Fig. 91); and (5) no endexine (Fig. 91). The trichotomosulcate *Liliacidites* sp. 2 (Figs. 92–97) also has many monocotyledonous features, including a coarse and fine reticulum, which in this instance is finer around the aperture (Fig. 93) and in the center of the nonapertural side (Fig. 94). In *Liliacidites* sp. 2 the muri are also psilate (Figs. 94, 95), but they are not "frilled" as in *Liliacidites* sp. 1. Furthermore, *Liliacidites* sp. 2 also has dimorphic lumina within its coarse reticulum (Fig. 95) and a thin exine with a very thin nonapertural nexine (Fig. 96). Surprisingly, however, endexine appears to be present in *Liliacidites* sp. 2, at least under the aperture (Fig. 97).

Retimonocolpites dividuus. Another Lower Cretaceous angiosperm pollen type, *Retimono-*



FIGURES 103–110. *Liliacidites* Couper from Zone IIB of the Potomac Group, Middle-Upper Albian (ca. 103–105 Ma) (103–106) and extant monocot pollen (107–110).—103. Whole grain SEMG of *Liliacidites* Couper sp. 1 (FP-388; D13-535), ×1,390.—104. Exine surface SEMG of *Liliacidites* Couper sp. 1 (FP-368; D13-535), ×12,000.—105. Exine surface SEMG of "*Liliacidites*" *minutus* (= *Clavatipollenites minutus* Brenner) (FP-194, Cornet Beltway), ×12,000.—106. Nonapertural exine section TEMG of *Liliacidites* Couper sp. 1 (FP-392; D13-535), ×16,500.—107. Whole grain SEMG of *Hemerocallis* of the Liliaceae (P-1538), ×675.—108. Exine surface SEMG of *Butomus* of the Butomaceae (P-3117), ×12,000.—109. Exine surface SEMG of *Xerophyllum* of the Liliaceae (P-3819), ×12,000.—110. Nonapertural exine section TEMG of *Hechtia* of the Bromeliaceae (P-3114), ×16,500.

colpites dividuus (Figs. 57–62), probably has monocotyledonous affinities as well, although it lacks some of the monocot pollen features previously enumerated. The chief argument for a probable monocotyledonous relationship of *Retimonocolpites dividuus* is its extremely to very thin nonapertural nexine combined with short columellae, a thick tectum, and an apparent lack of endexine, all of which give it a striking resemblance to the pollen of *Liliacidites* spp. 1 and 2 (cf. Figs. 61, 62 of *R. dividuus* with Figs. 91, 96 of *Liliacidites* spp. 1 and 2). Moreover, Doyle and Robbins (1977) have reported a Potomac Group pollen type ("*Retimonocolpites* sp. A") that looks just like *R. dividuus* except that it has a finely reticulate patch of sculpturing on its nonapertural side reminiscent of *Liliacidites* sp. 2 (Figs. 92, 94). Thus, *Retimonocolpites dividuus* is probably a monocotyledonous rather than a dicotyledonous pollen type, even though it clearly represents a genus that is distinct from *Liliacidites* itself.

"*Liliacidites*" *minutus*. While possibly monocotyledonous, "*Liliacidites*" *minutus* (Figs. 98–102) has fewer monocotyledonous features than *Liliacidites* spp. 1 and 2 and *Retimonocolpites dividuus*. Its chief monocotyledonous features are its psilate muri and dimorphic lumina (Figs. 99–101). The reticulum of "*L.*" *minutus*, however, is not differentiated into coarse and fine areas, as in *Liliacidites* spp. 1 and 2, and, moreover, the reticulum is decidedly polygonal in outline. Although no endexine was observed, the moderately thick nonapertural nexine of "*L.*" *minutus* (Fig. 102) is very different from the nonapertural nexine of *Liliacidites* spp. 1 and 2 (Figs. 91, 96) and *Retimonocolpites dividuus* (Figs. 61, 62). Another feature, however, that links the three species together is their colorless, transparent exine that does not take up stains such as safranin or basic fuchsin long after other pollen and spore types have become heavily stained.

POLLEN TYPES OF UNCERTAIN OR UNKNOWN AFFINITY

Four Lower Cretaceous angiosperm pollen types that we have studied (*Retimonocolpites peroreticulatus*, aff. *Retimonocolpites* sp. 2, aff. *Retimonocolpites* sp. 1, and *Stellatopollis barghoornii*) have no close counterparts among the pollen of living primitive angiosperms. *Retimonocolpites peroreticulatus* (Figs. 69–73) is especially difficult to place with its loose, non-columellate, spine-covered reticulum, although its thick nexine and spinose reticulum suggest a possible chloranthaceous affinity. If it is, indeed, related to *R. peroreticulatus*, aff. *Retimonocolpites* sp. 2 (Figs. 74–80) may have a similar affinity. Aff. *Retimonocolpites* sp. 1 (Figs. 63–68) may also be part of this same complex. Its moderately thick nonapertural nexine (Figs. 67, 68) is similar to that of *R. peroreticulatus* (Fig. 73) and aff. *Retimonocolpites* sp. 2 (Fig. 78), although its banded reticulum (Fig. 66) is somewhat reminiscent of *Retimonocolpites dividuus* (Fig. 60). Finally, *Stellatopollis barghoornii* (Figs. 81–86) is particularly difficult to place, and could have either dicotyledonous or monocotyledonous affinities.

PRIMITIVE ANGIOSPERM POLLEN AND THE ORIGIN AND EARLY EVOLUTION OF FLOWERING PLANTS

Scanning electron and transmission electron microscopy, particularly when used together to examine the same fossil pollen grain, reveal a whole new dimension in the morphology of Early Cretaceous angiosperm pollen. The evolutionary implications of what we have learned in this ultrastructural study of Lower Cretaceous angiosperm pollen will now be discussed. First, we will review major evolutionary trends in the pollen of living primitive angiosperms. Then, we will evaluate the fossil pollen record of early flowering plants in light of what is known about pollen evolution in living primitive angiosperms in order to obtain a better understanding of the evolution of early fossil angiosperm pollen. Finally, we will discuss a model for the early evolution of flowering plants based on a synthesis of our knowledge of both extant and fossil primitive angiosperm pollen.

POLLEN EVOLUTION IN LIVING PRIMITIVE ANGIOSPERMS

Since the trends in pollen evolution in living primitive angiosperms that we recognize are based on the putative phylogenetic relationships of primitive angiosperms, we shall first discuss our concept of evolutionary relationships among the families of primitive angiosperms themselves before reviewing the major evolutionary trends in the pollen of living primitive angiosperms. The putative phylogenetic relationships of the 26 families that we delimit as the subclass Magnoliidae are shown in Figure 111. These families

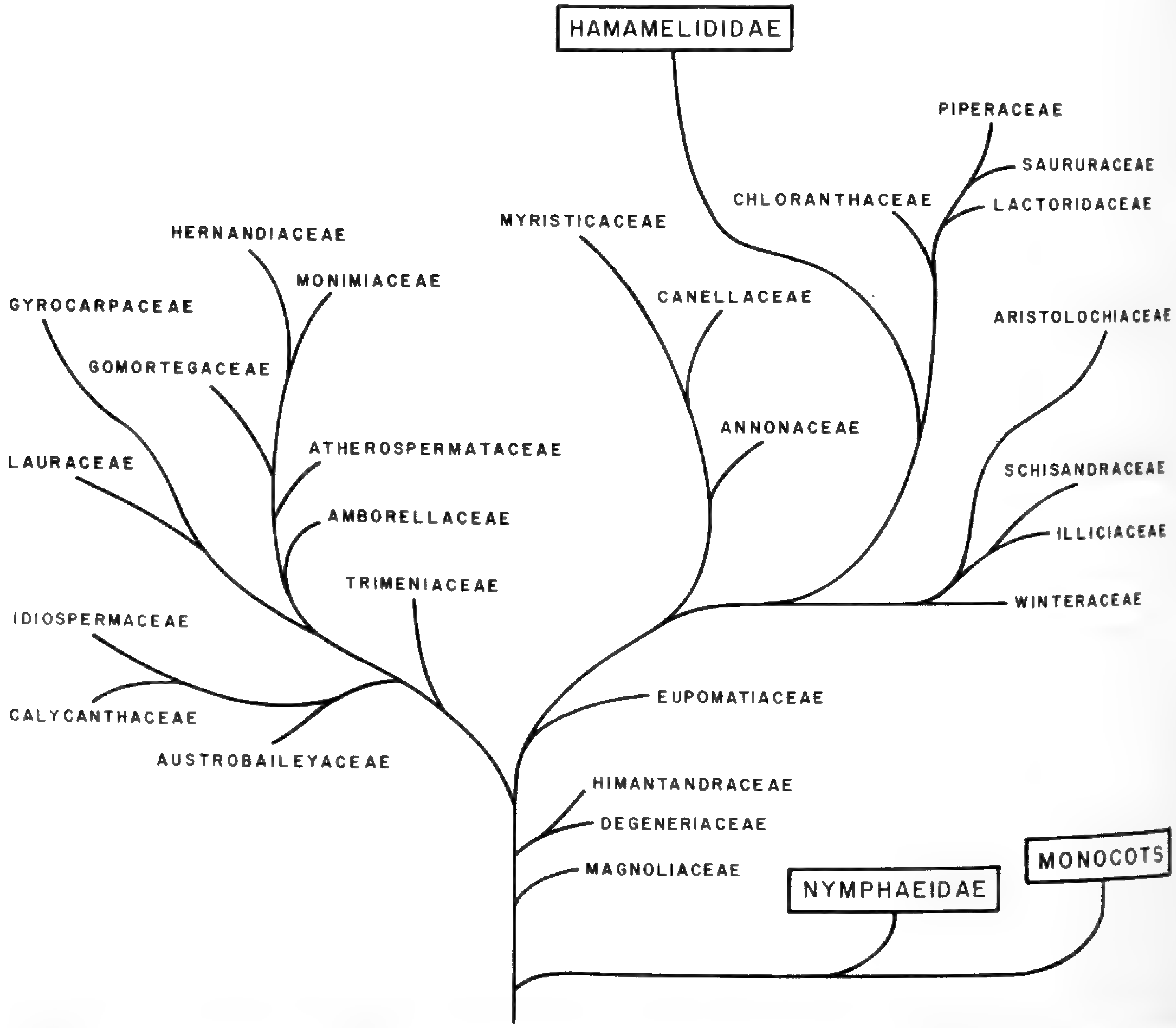


FIGURE 111. Putative phylogenetic relationships of the families of primitive angiosperms (subclass Magnoliidae).

of dicotyledonous angiosperms, which are classified in Table 7, have been designated in whole or part by various taxonomists as the Ranales, Polycarpicae, Apocarpicae, Monochlamydeae, Magnoliales, Magnoliiflorae, Magnoliidae, Magnolianae, or Annoniflorae, and are generally regarded by the majority of modern phylogenists as the most primitive group of living flowering plants (cf. Cronquist, 1968, 1981; Dahlgren, 1975, 1980; Hutchinson, 1973; Takhtajan, 1969, 1973, 1980; Thorne, 1974, 1976). As a group these families possess many features that are usually considered to be primitive angiosperm characters—vesselless wood, monosulcate pollen, laminar, 3-trace stamens, apocarpous gynoecia, unsealed carpels, and free, spirally arranged floral parts indefinite in number. In fact, it appears that no other living flowering plants have any characters more primitive than those possessed by at least some members of the subclass Magnoliidae.

As delimited by us (Table 7), the subclass Magnoliidae consists of 26 families grouped into three infraclasses (the Magnoliiflorae, Aristolochiiflorae, and Piperiflorae), five superorders, and nine orders. Our concept of the evolutionary relationships of the families of primitive angiosperms (the subclass Magnoliidae) may be summarized as follows. The order Magnoliales is the central and most primitive order in the subclass. It is divisible into two groups. One, the suborder Magnoliineae, contains the exceedingly primitive families Magnoliaceae, Degeneriaceae, Himantandraceae, and Eupomatiaceae. The other, the suborder Annonineae, consists of the more advanced families Annonaceae, Canellaceae, and Myristicaceae. The superorder Lauranae, which shows definite connections with the Magnoliales, particularly through its most primitive family Austrobaileyaceae, represents a terminal evolutionary line that has given rise to no other groups of living angiosperms. The family Winteraceae has been removed from the order Magnoliales sensu stricto and made the type of an order Winterales, to which the families Illiciaceae and Schisandraceae have also been added, although in a suborder of their own. Finally, the family Aristolochiaceae has been made the type of its own infraclass, the Aristolochiiflorae, while the families Chloranthaceae and Lactoridaceae have both been taken out of the order Laurales sensu lato, where they have frequently been placed, and have been included with the families Saururaceae and Piperaceae in the infraclass Piperiflorae, each in its own monotypic order.

Unlike the terminal Lauranae, the Winterales (which are phenetically closest to the Magnoliales but cladistically closer to the Aristolochiiflorae and Piperiflorae), Aristolochiiflorae, and Piperiflorae exhibit definite connections with families in other subclasses of dicotyledons. The Winterales and Aristolochiiflorae have ties with the subclasses Ranunculidae and Caryophyllidae, while the Piperiflorae, and especially the family Chloranthaceae, are linked to the subclass Hamamelididae, and through it to the bulk of the dicots, including the subclasses Dilleniidae, Rosidae, and Asteridae (cf. Walker, 1976b, fig. 4). In fact, the Piperiflorae appears to be the sister-group of the subclass Hamamelididae. Characters of the family Chloranthaceae that indicate a relationship with the subclass Hamamelididae include apetaly, anemophily, frequent catkin-like inflorescences, and often unisexual flowers. Moreover, the two most primitive families in the Hamamelididae, the Trochodendraceae and Tetracentraceae, are both primitively vesselless just like the chloranthaceous genus *Sarcandra*, and they both have the same distinctive tooth type on their leaf margins as does the Chloranthaceae (the so-called Chloranthoid tooth of Hickey & Wolfe, 1975). Finally, there are striking similarities between the pollen of chloranthaceous genera such as *Ascarina* and *Hedyosmum* and pollen of primitive hamamelidid families such as the Trochodendraceae, Cercidiphyllaceae, and Eupteleaceae, including similar reticulate sculpturing with the same type of spinulose muri, well-de-

TABLE 7. Classification of the families of primitive angiosperms (subclass Magnoliidae).

- Subclass Magnoliidae
  - Infraclass 1. Magnoliiflorae
    - Superorder 1. Magnolianae
      - Order 1. Magnoliales
        - Suborder 1. Magnoliineae
          - 1. Magnoliaceae
          - 2. Degeneriaceae
          - 3. Himantandraceae
          - 4. Eupomatiaceae
        - Suborder 2. Annonineae
          - 5. Annonaceae
          - 6. Canellaceae
          - 7. Myristicaceae
      - Order 2. Winterales
        - Suborder 1. Winterineae
          - 8. Winteraceae
        - Suborder 2. Illiciineae
          - 9. Illiciaceae
          - 10. Schisandraceae
    - Superorder 2. Lauranae
      - Order 1. Austrobaileyales
        - Suborder 1. Austrobaileyineae
          - 11. Austrobaileyaceae
        - Suborder 2. Calycanthineae
          - 12. Calycanthaceae
          - 13. Idiospermaceae
      - Order 2. Trimeniales
        - 14. Trimeniaceae
      - Order 3. Laurales
        - Suborder 1. Monimiineae
          - 15. Amborellaceae
          - 16. Atherospermataceae
          - 17. Monimiaceae
          - 18. Gomortegaceae
          - 19. Hernandiaceae
        - Suborder 2. Laurineae
          - 20. Lauraceae
          - 21. Gyrocarpaceae
  - Infraclass 2. Aristolochiiflorae
    - Order 1. Aristolochiales
      - 22. Aristolochiaceae
  - Infraclass 3. Piperiflorae
    - Superorder 1. Chloranthanae
      - Order 1. Chloranthales
        - 23. Chloranthaceae
    - Superorder 2. Piperanae
      - Order 1. Lactoridales
        - 24. Lactoridaceae
      - Order. 2. Piperales
        - 25. Saururaceae
        - 26. Piperaceae

veloped columellae, and the presence of endexine (cf. Walker, 1976b).

The putative phylogeny of primitive angiosperms outlined above is based on an analysis of the taxonomic distribution of characters both within and without the subclass Magnoliidae, i.e., on both in-group and out-group analysis. Taxonomic characters from many fields, including floral morphology, vegetative morphology, vegetative anatomy, palynology, and cytology, were examined, and using the principle of reciprocal illumination (Hennig, 1966), the putative phylogeny of the Magnoliidae shown in Figure 111 was established. We intend to discuss the basis for our classification and phylogeny of primitive angiosperm families at a later date. Based on our proposed phylogeny, which, again, we would like to emphasize is based on character analysis from many different fields, we shall now consider the taxonomic distribution of individual palynological characters in order to determine the most probable direction or polarity of major evolutionary trends in the pollen of living primitive angiosperms. Our discussion will be organized under seven different categories of pollen characters, including aperture type, pollen shape, pollen size, nonapertural exine sculpturing, exine interstitial type, exine tectal type, and exine stratification.

Aperture type. Although some other miscellaneous aperture types characterize a few primitive angiosperms (cf. Walker, 1974b, 1976a; Sampson, 1975), most members of the subclass Magnoliidae have pollen with one of the following aperture types: (1) monosulcate pollen (with a single, furrow-like aperture), (2) zonasulculate pollen (with a ring-like aperture), (3) ulcerate pollen (with a pore-like aperture), (4) inaperturate pollen (without any apertures), (5) disulculate pollen (with two furrow-like apertures), (6) tricolpate pollen (with three furrow-like apertures), or (7) polycolpate pollen (with more than three furrow-like apertures).

Monosulcate pollen occurs in some or all members of every family of the Magnoliales except the Eupomatiaceae, which has zonasulculate pollen grains. Monosulcate pollen is the only type in the families Magnoliaceae, Degeneriaceae, and Himantandraceae, and is also clearly the basic type in the Canellaceae and Myristicaceae as well, although occasionally pollen in the Canellaceae may be trichotomosulcate (with a three-armed aperture), and sometimes pollen of the Myristicaceae is ulcerate. Although the Annonaceae, the largest family of primitive angiosperms with some 130 genera and 2,300 species, has a few other aperture types, most of its pollen is either monosulcate or inaperturate. Detailed character analysis within the family indicates that monosulcate pollen is the primitive type (Walker, 1971b; Le Thomas, 1980, 1981). Outside the Magnoliales, monosulcate pollen is found in the Austrobaileyaceae in the Lauranae, rarely in the Aristolochiiflorae (in the primitive genus *Saruma*), and in at least some members of every family of the Piperiflorae. In contrast to the Magnoliales, most members of the Lauranae have inaperturate pollen, although the Calycanthineae is characterized by disulculate pollen and the Austrobaileyaceae, as previously mentioned, has monosulcate pollen. An ulcerate aperture type is a constant feature of the Winteraceae. Tricolpate pollen occurs in the Illiciaceae and in a few Schisandraceae, while polycolpate pollen is found in many Schisandraceae and in some Aristolochiaceae and Chloranthaceae.

The overwhelming presence of monosulcate pollen in the primitive order Magnoliales, along with its occurrence in such primitive elements as the Austrobaileyaceae in the Lauranae and *Saruma* in the Aristolochiiflorae, strongly suggests that monosulcate pollen represents the primitive aperture type for the Magnoliidae. Outgroup comparison further confirms this in as much as monosulcate pollen is clearly the primitive type in monocotyledonous angiosperms and gymnosperms as well.

Pollen shape. With regard to shape, pollen grains in general are either boat-shaped or globose (globe-shaped). In the Magnoliidae boat-shaped pollen grains are characteristic only of the Magnoliaceae, Degeneriaceae, and many Annonaceae. Pollen may be weakly boat-shaped in some Myristicaceae, as well as in a few Chloranthaceae and in some Piperales; elsewhere in the Magnoliidae pollen grains are basically globose. The restriction of boat-shaped pollen entirely to the order Magnoliales, as well as its presence in primitive monocots, such as the Liliaceae, Butomaceae, Araceae, and Palmae, and in many types of gymnosperms strongly suggest that boat-shaped pollen grains represent a primitive feature of angiosperm pollen.

Pollen size. With regard to overall size, pollen grains may be categorized as minute (<10 μm), small (10–24 μm), medium-sized (25–49 μm), large (50–99 μm), very large (100–199 μm), or gigantic (200 μm or larger). Large or large- to medium-sized pollen characterizes a number of primitive families within the Magnoliidae, including the Magnoliaceae and Degeneriaceae within the Magnoliineae, the Annonaceae within the Annonineae, and the Austrobaileyaceae and Calycanthaceae within the Lauranae. On the other hand, the somewhat more advanced Winterales have medium-sized pollen, the highly advanced Chloranthaceae and Myristicaceae have medium-sized to small pollen, and the exceedingly advanced Piperales have minute pollen. Thus, character distribution suggests that the most primitive angiosperm pollen was large or large-to medium-sized.

Nonapertural exine sculpturing. Many of the most primitive members of the subclass Magnoliidae have pollen grains that are remarkably psilate, even when examined with scanning electron microscopy. Psilate pollen of this extreme type occurs in at least some members of virtually every family of the order Magnoliales. Other exine sculpturing types, represented by verrucate or echinate pollen, for example, occur sporadically in several families of the Magnoliidae, including advanced members of the Annonaceae and Myristicaceae. Reticulate pollen, by contrast, is rare within the Magnoliales, occurring only in a few Annonaceae and in some Myristicaceae. On the other hand, reticulate pollen is basically the only pollen type in the Winterales and in the Chloranthaceae. The strong concentration of psilate or at most foveolate (pitted) to fossulate (grooved) pollen in the primitive order Magnoliales, and the occurrence of other sculpturing types in more advanced members of the Magnoliidae suggests that angiosperm pollen was primitively psilate, or at most only weakly sculptured, e.g., foveolate, fossulate, or scabrate.

Exine interstitial type. Noninterstitiate to interstitiate-granular pollen characterizes many members of the primitive order Magnoliales. For example, the Degeneriaceae and Eupomatiaceae have noninterstitiate pollen grains, while most members of the Magnoliaceae have pollen with a granular interstitium. Within the family Annonaceae many primitive genera have a granular interstitium, while a few are almost noninterstitiate. Both the Canellaceae and Myristicaceae have some primitive members with interstitiate-granular pollen. Pollen with well-developed columellae, by contrast, characterizes advanced members of the Annonaceae, Canellaceae, and Myristicaceae, as well as most members of the more advanced orders Winterales and Chloranthales. Thus, the taxonomic distribution of exine interstitial types strongly suggests that columellate pollen is advanced within the Magnoliidae, and that primitive angiosperm pollen is noninterstitiate to interstitiate-granular.

Pollen of living primitive angiosperms, however, exhibits several different types of granular interstitia, e.g., in the Magnoliaceae the granular interstitium occurs more or less in the middle of the exine, in the Annonaceae the interstitium develops in the lowermost part of the exine, and in the Myristicaceae the interstitium is found as a series of granules that in their most primitive evolutionary state appear to be pendent from the inner face of the incipient tectum, and not at all or only weakly attached to the basal nexine. Thus, the morphological diversity of interstitial types within the Magnoliidae indicates that noninterstitiate pollen probably represents the basic primitive type from which the various kinds of interstitiate-granular pollen grains have been derived. Columellate pollen, in turn, has apparently evolved independently a number of times from granular pollen types.

Exine tectal type. Atectate to tectate-imperforate pollen characterizes many members of the order Magnoliales, including most Magnoliaceae, the Degeneriaceae, the Himantandraceae, the Eupomatiaceae, many primitive Annonaceae, and some primitive Canellaceae and Myristicaceae. By contrast, pollen grains in advanced members of the Annonaceae, Canellaceae, and Myristicaceae are tectate-perforate. Finally, pollen in the order Winterales is almost always semitectate, while in the family Chloranthaceae pollen varies from tectate-perforate to semitectate. The heavy concentration of atectate to tectate-imperforate pollen grains in primitive members of the highly primitive order Magnoliales suggests that atectate to tectate-imperforate pollen represents the primitive exine tectal type in the Magnoliidae, and, hence, probably in the angiosperms as a whole.

Exine stratification. Except for the Canellaceae, which may have pollen with endexine under the aperture, pollen of the order Magnoliales is totally without endexine, and consequently has a wholly ektexinous exine. By contrast, at least some endexine is present throughout the pollen of many Lauranae, well-developed endexine occurs throughout the pollen of the Winterales, and endexine is present either only in the apertural region or throughout the pollen in the Chloranthaceae. Thus, the taxonomic distribution of endexine within the Magnoliidae, along with the fact that endexine appears to be absent in almost all monocots, strongly suggests that endexine is primitively absent in angiosperms. Furthermore, one gets the impression that endexine in the Magnoliidae initially evolved in the apertural areas (e.g., as in the Canellaceae and in primitive Chloranthaceae such as *Ascarina*) and subsequently developed in nonapertural regions as well (e.g., as in the Winterales and in advanced Chloranthaceae such as *Chloranthus*).

The presence of a distinctive, laminated type of endexine in both extant and fossil gymnosperms (cf. Doyle et al., 1975) suggests either that angiosperms arose from some group of gymnosperms that had not yet evolved endexine or that endexine was secondarily lost in the group of gymnosperms that gave rise to the flowering plants. In any case, clearly the endexine present in gymnosperm and angiosperm pollen is not homologous.

Nature of primitive angiosperm pollen. Major evolutionary trends in the pollen of living primitive angiosperms of the subclass Magnoliidae, many of which have been previously discussed by the senior author in past contributions (Walker, 1974a, 1974b, 1976a, 1976b; Walker & Skvarla, 1975), are summarized in Table 8.

Analysis of the taxonomic distribution of palynological and non-palynological characters within living primitive angiosperms strongly suggests that primitive angiosperm pollen is monosulcate, boat-shaped, large- to medium-sized, psilate (or at best only weakly sculptured), noninterstitiate (or at best only weakly granular), basically atectate, and without endexine. This type of pollen is found today only in the otherwise primitive angiosperm families Magnoliaceae, Degeneriaceae, and Annonaceae. At a somewhat higher level is the pollen of the families Canellaceae and Myristicaceae, which, although monosulcate and sometimes psilate, is at best only weakly boat-shaped, and at the same time is medium-sized to small. Moreover, pollen of these two advanced magnolialean families is never noninterstitiate as in some of the more primitive Magnoliales, and in the Canellaceae at least endexine is present, although only under the pollen aperture itself.

Pollen of the family Winteraceae, by contrast, is uniformly advanced in being ulcerate, globose, medium-sized, reticulate, in permanent tetrads, interstitiate-columellate, semitectate, and in having well-developed endexine throughout. All of these features (along with certain other non-palynological attributes, such as complicated, basically cymose inflorescences, medium-sized to small flowers, a perianth that is differentiated into a distinct calyx and corolla, 1-trace (rather than 3-trace) stamens, basically whorled carpels, a short receptacle, baccate fruits, and estipulate leaves) emphasize the taxonomic distinctness and relative advancement of the Winteraceae compared to the order Magnoliales sensu stricto. In a similar fashion, pollen of the family Chloranthaceae is also quite advanced. For example, it may be polychotomosulcate (*Hedyosmum*), polycolpoidate (*Chloranthus*), or inaperturate (*Sarcandra*). Furthermore, chloranthaceous pollen is at best only weakly boat-shaped, being more commonly globose, while at the same time it is medium-sized to small, has reticulate sculpturing and well-developed columellae, is tectate-perforate to semitectate, and has well-developed endexine either only under the aperture or throughout the grain.

FOSSIL POLLEN RECORD OF EARLY FLOWERING PLANTS

The major characteristics of the Lower Cretaceous angiosperm pollen grains that we have examined ultrastructurally are summarized in Table 9. A comparison of Table 8, which lists the major evolutionary trends evident in the pollen of living primitive angiosperms of the subclass Magnoliidae, with Table 9 reveals that in almost every respect these early fossil pollen grains represent advanced rather than primitive angiosperm pollen types. Lower Cretaceous angiosperm pollen grains, for example, are rarely strongly boat-shaped (notable exceptions being the clearly specialized *Stellatopollis barghoornii* and the monocotyledonous *Liliacidites* sp. 1); instead, they are mostly weakly boat-shaped to globose or even wholly globose. Again, except for the two species named above, most monosulcate Lower Cretaceous angiosperm pollen is medium-sized to small, rather than large- to medium-sized, as in the most primitive members of the subclass Magnoliidae. Without exception all early fossil angiosperm pollen that we have examined is reticulately sculptured, and none is psilate or otherwise weakly sculptured. All except the obviously specialized *Retimonocolpites peroreticulatus* have columellae, and none have a truly granular interstitium. Moreover, none of the monosulcate pollen grains investigated are tectate-imperforate; instead, they are tectate-per-

TABLE 8. Major evolutionary trends in the pollen of living primitive angiosperms of the subclass Magnoliidae.

Character	Primitive State(s)	Advanced State(s)
Aperture Type	Monosulcate	Other aperture types, including trichotomosulcate, ulcerate, and inaperturate
Pollen Shape	Boat-shaped	Globose
Pollen Size	Large- to medium-sized	Medium-sized to small or very large
Nonapertural Exine Sculpturing	Psilate, foveolate, fossulate, or scabrate	Other sculpturing types, including verrucate, echinate, and reticulate
Exine Interstitial Type	Noninterstitiate to interstitiate-granular	Interstitiate-columellate
Exine Tectal Type	Atectate to tectate-imperforate	Tectate-perforate to semitectate
Exine Stratification	Endexine absent	Endexine present only under aperture to present throughout grain

forate to more commonly semitectate. Finally, many of the fossil angiosperm grains examined have a well-developed endexine that in some cases is present not only under the aperture but throughout the nonapertural exine as well.

Detailed examination of monosulcate Lower Cretaceous angiosperm pollen independent of any consideration of palynological trends observed in extant primitive angiosperms also indicates that the earliest currently known angiosperm pollen grains represent advanced rather than primitive types of monosulcate angiosperm pollen. Our present study, for example, has shown that Lower Cretaceous angiosperm pollen grains that may appear at the light microscope level as "several partially intergrading morphologic complexes assignable to the form genera *Clavatipollenites* Couper (1958), *Retimonocolpites* Pierce (1961), and *Liliacidites* Couper (1953)" (cf. Doyle & Hickey, 1976) are in reality not an inter-related evolutionary series but a mixed collection of distinctive pollen types that are easily discernible when observed at the ultrastructural level. Moreover, some of these Early Cretaceous angiosperm pollen grains, including one of the oldest known, *Clavatipollenites hughesii*, are clearly related to the magnoliid dicot family Chloranthaceae, which is one of the most advanced families of the subclass Magnoliidae.

The reason that the more primitive "magnoliaceous" types of angiosperm pollen grains have not yet been discovered in Barremian-Albian or even older rocks is probably the result of a number of factors. First, as Muller (1970) suggested, the *Magnolia*-type of pollen may fossilize badly or not at all. Second, *Magnolia*-type pollen may be present in the Lower Cretaceous but in such low amounts that it has not been discovered yet. This was, for example, true of the highly distinctive pollen of the primitive angiosperm family Winteraceae, which was only recently discovered in the Lower Cretaceous of Israel (Walker et al., 1983). Furthermore, Muller (1963) has shown that only 39% of the genera and 58% of the families of angiosperms known to be in Sarawak could be detected in a palynological examination of a peat swamp near Marudi, Sarawak. Moreover, even easily recognizable columellate angiosperm pollen types, such as *Clavatipollenites hughesii,* sometimes comprise less than 1% of the total pollen grains and spores present in a particular Lower Cretaceous rock sample. Third, and most importantly, *Magnolia*-type angiosperm pollen would have either a granular interstitium or none at all (i.e., it would be noninterstitiate), and, hence, it would be virtually impossible to distinguish it at the light microscope level from similar psilate, boat-shaped, monosulcate pollen produced by a variety of gymnosperms.

Finally, while the marked absence of tricolpate angiosperm pollen from pre-Aptian rocks throughout the world (Doyle et al., 1977), the stratigraphically controlled sequence of tricolpate–tricolporoidate–tricolporate–triporate pollen types observed in the Potomac Group (Doyle & Robbins, 1977), and the marked poleward migration of tricolpate and tricolpate-derived angiosperm pollen types (cf. Hickey & Doyle, 1977, fig. 64) all strongly suggest a true evolutionary origin and progression, it must be stressed that this is an evolutionary origin and progression of

TABLE 9. Major characteristics of Lower Cretaceous angiosperm pollen.

Character	Character State(s)
Aperture Types	Mostly monosulcate, sometimes trichotomosulcate, polychotomosulcate, or polycolpoidate
Pollen Shapes	Boat-shaped to frequently globose
Pollen Sizes	Mostly medium-sized to small, occasionally large
Nonapertural Exine Sculpturing	Variously reticulate
Exine Interstitial Types	Interstitiate-columellate[a]
Exine Tectal Types	Tectate-perforate to more commonly semitectate
Exine Stratification	Endexine not observed or commonly with endexine, either only under aperture or throughout grain

[a] Columellae absent in *Retimonocolpites peroreticulatus.*

tricolpate and tricolpate-derived pollen-bearing angiosperms, and as such has nothing to do with the evolution of the more primitive monosulcate pollen-bearing flowering plants, i.e., virtually all of the magnoliid dicots, the nymphaealean dicots, and the monocotyledons. That an earlier stage of monosulcate pollen-bearing angiosperms is yet to be discovered is indicated by the fact that closely comparable monosulcate angiosperm pollen grains representing the earliest known types of angiosperm pollen occur in pre-Aptian palynofloras (presumably Barremian in age) of such widely separated areas as the Lower Cocobeach System of equatorial Africa, the Upper Wealden of Europe, and the basal Potomac Group of eastern North America (Doyle et al., 1977).

ORIGIN AND EARLY EVOLUTION OF FLOWERING PLANTS

In the following section we shall develop a model for the early evolution of flowering plants, based on a synthesis of what is known about early angiosperms from studies of both living primitive angiosperms and of the early fossil record of flowering plants. First, however, the question of the origin of the angiosperms will be discussed.

ORIGIN OF THE ANGIOSPERMS

Probably more papers have been written on the subject of the origin of the angiosperms than on any other major aspect of angiosperm evolution. In the past many authors have stressed the supposedly rapid rise of the flowering plants. But, as Hickey and Doyle have shown, this idea was based on gross misidentification of early fossil angiosperm leaves (Doyle & Hickey, 1976; Hickey & Doyle, 1977). Furthermore, Doyle (1969), Doyle and Hickey (1976), and Hickey and Doyle (1977) have provided convincing paleopalynological, as well as fossil leaf evidence, for the progressive evolution of tricolpate and tricolpate-derived pollen-producing flowering plants starting in the Aptian. Unfortunately, as we have stressed in the previous section of this paper, there is no comparable evolutionary series known for the more primitive monosulcate pollen-producing angiosperms, and in fact no *Magnolia*-type fossil pollen has yet been found in the Lower Cretaceous for reasons that we have discussed. Thus, until fossil evidence is discovered that relates to the earliest stage of angiosperm evolution, we are forced to rely solely on extrapolation backwards from living primitive angiosperms that do produce monosulcate pollen, i.e., the subclass Magnoliidae, and on extrapolation upwards from gymnosperms that exhibit various angiospermous features, to provide more insight about the origin of the flowering plants.

With Beck's (1960a, 1960b) discovery of the organic connection between *Archaeopteris* and *Callixylon* and the subsequent recognition of a previously unknown group of vascular plants, the progymnosperms, which combined pteridophytic reproduction with gymnospermous anatomy, a new chapter was opened in our understanding of gymnosperm evolution. Consideration of what is now known about the progymnosperms as well as about living and fossil gymnosperms suggests the following scenario about gymnosperm evolution.

The gymnosperms themselves appear to be diphyletic, and it seems evident (cf. Bierhorst, 1971) that the seed arose independently in the two different lines of gymnospermous seed-plants, both of which, the coniferophyte line and the cycadophyte line, were already recognized, although on a somewhat different basis, in Chamberlain's (1935) classic work on gymnosperms.

The two lines of gymnosperms may be delimited as follows. The coniferophyte line is characterized by simple leaves that are frequently small by reduction, dense pycnoxylic wood with generally low, uniseriate rays, cauline (i.e., stem-related) reproductive organs (microsporangia and ovules) that are usually in cone-like, compound strobili, and bilateral seeds with a two-parted integument that are basically unitegmic and never cupulate. By contrast, members of the cycadophyte line of gymnosperms have basically compound leaves (although leaves may be secondarily simple in certain advanced representatives), loose manoxylic wood with generally high multiseriate rays (as well as uniseriate rays), phylline (i.e., leaf-related) reproductive organs that are basically non-strobilate except in certain advanced members (and then the strobili are always simple and never compound), and radiosymmetric seeds with a multi-parted integument that are basically cupulate and often, in more advanced members, bitegmic due to cupule reduction. The coniferophyte line consists of basically tall, often much branched, monopodial trees, while the cycadophyte line, at least in its most primitive representatives, is represented by fundamentally weakly to unbranched, slender trees and shrubs. Microsporangia are frequently synangiate in the cycadophyte line, and not so in the coniferophyte line, while saccate or winged pollen is common in the coniferophyte line, and less so in the cycadophyte line. Finally, the coniferophyte line appears to be derived from the archaeopterid progymnosperms, while the cycadophyte line seems to be connected to the aneurophyte progymnosperms. Members of the coniferophyte line include the ginkgophytes, the cordaites and conifers, and the gnetophytes. The cycadophyte line contains the pteridosperms or seed-ferns (including lyginopteran, callistophytalean, and medullosan pteridosperms, as well as the peltasperms, corystosperms, and caytonialean pteridosperms), the glossopterids, the cycads, and the cycadeoids.

With reference to the origin of the angiosperms, there seems little doubt that the flowering plants were derived from the cycadophytic rather than the coniferophytic line of gymnosperms. Angiosperm features that suggest this include manoxylic wood, phylline reproductive organs that are in simple rather than compound strobili, bitegmic ovules, and microsporangia that are more or less synangiate. Moreover, many advanced groups of cycadophytic gymnosperms exhibit angiospermous characteristics, including simple leaves in the glossopterids and some cycadeoids (e.g., *Williamsoniella*), tetrasporangiate pollen-producing organs in the caytonialean pteridosperms, megasporophyll-infolded ovules in the glossopterids, and bisexual strobili in certain cycadeoids, e.g., *Williamsoniella* and *Cycadeoidea*. Thus, there is no great mystery concerning the origin of the angiosperms, as has often been invoked by writers in the past. The angiosperms are no more isolated than many other groups of vascular plants. In fact, there are a number of problematic Mesozoic gymnosperms, such as the Czekanowskiales and Vojnovskyales, whose relationships are much more conjectural than those of the angiosperms.

Some of the best prospects for resolving the remaining uncertainty concerning angiosperm origins lie in expanded studies of Mesozoic cycadophytic gymnosperms in general, particularly with ultrastructural examination of in situ pollen grains from known pollen-producing organs of groups such as the peltasperms and other pteridosperms, as well as in continued ultrastructural investigation of Lower Cretaceous monosulcate angiosperm pollen, especially from Barremian and even older rocks. For now, however, the most that can be reasonably concluded is that the ancestry of the angiosperms must be sought in the pteridosperms sensu lato or in some as yet unknown derivative of this group of cycadophytic gymnosperms.

EARLY EVOLUTION OF THE FLOWERING PLANTS

The early evolution of the flowering plants can be divided into five different major stages (Fig. 112), based on the early (Barremian to Middle Cenomanian) fossil pollen record of the angiosperms and the phylogenetic relationships evident among living primitive angiosperms. Stage 1 is represented by the evolution of angiosperms with primitive monosulcate pollen of the *Magnolia*-type. Since more advanced monosulcate angiosperm pollen of the *Clavatipollenites-Ascarina*-type occurs in the Barremian, it is fair to assume that this initial phase of angiosperm evolution began in the pre-Barremian. Stage 1 was characterized by the evolution of the "Lower Magnoliidae," i.e., by the evolution of dicots whose descendants include such living primitive angiosperms as the Magnoliaceae and Degeneriaceae. That both advanced monosulcate dicotyledonous and monocotyledonous pollen occurs together in the earliest known angiosperm palynofloras of the Barremian suggests that the mon-

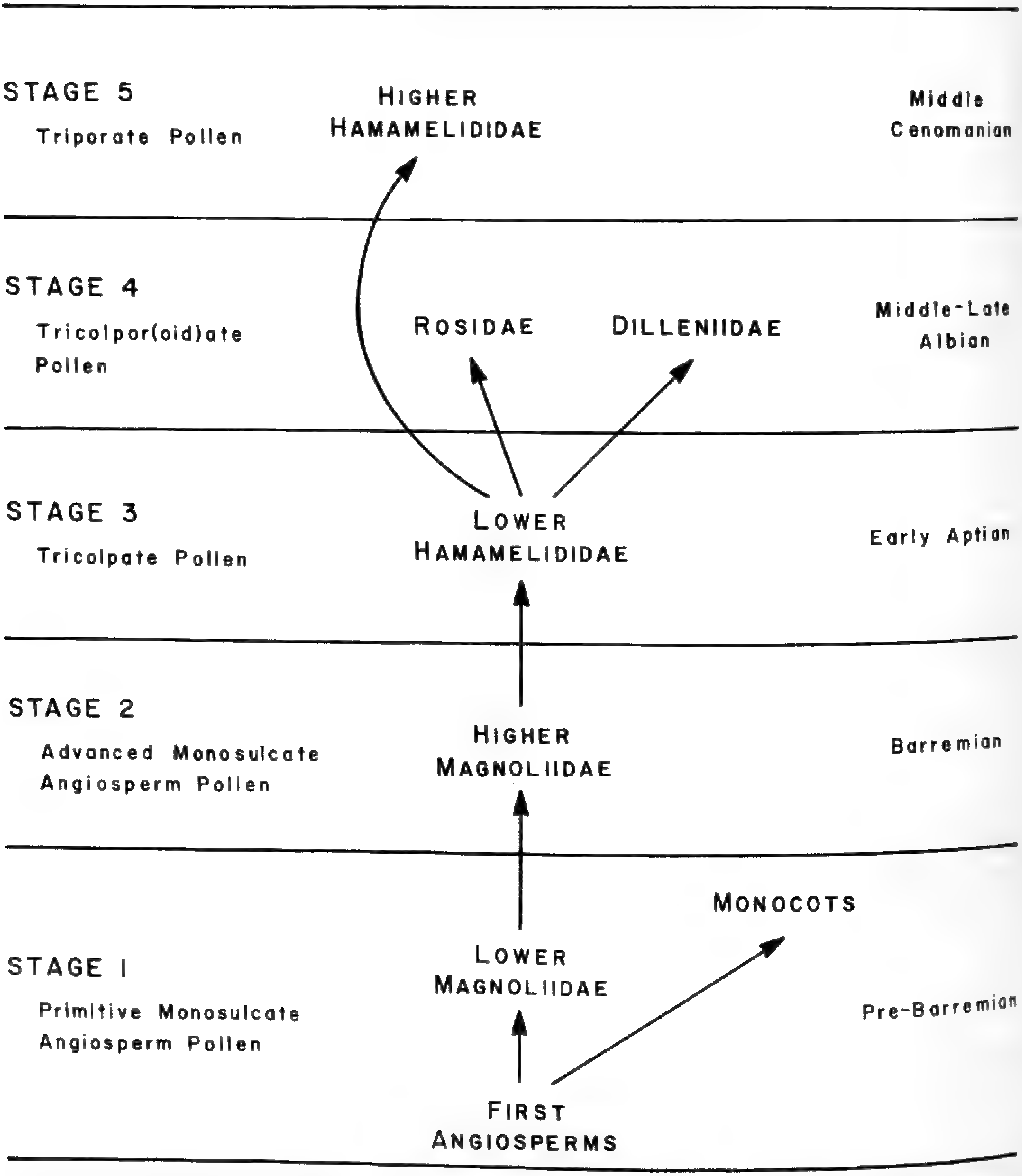


FIGURE 112. Outline of the early evolution of flowering plants based on the early (Barremian–Middle Cenomanian) fossil angiosperm pollen record and putative phylogenetic relationships of major groups of living angiosperms.

ocots had already separated from the dicots by Barremian time.

Stage 2 of early angiosperm evolution, which begins in Africa and South America, as well as in England and eastern North America, in the Barremian (cf. Hickey & Doyle, 1977), is represented by the evolution of flowering plants with advanced monosulcate pollen, and includes both dicotyledonous pollen types, such as *Clavatipollenites,* and monocotyledonous pollen types, such as *Liliacidites.* This stage was characterized by the evolution of the "Higher Magnoliidae," including the evolution of the advanced magnoliid family Chloranthaceae.

The development of tricolpate pollen constitutes Stage 3 and probably is indicative of the origin of the "Lower Hamamelididae," i.e., the Trochodendraceae, Tetracentraceae, Cercidiphyllaceae, Eupteleaceae, Hamamelidaceae, and Platanaceae. Stage 3, i.e., the evolution of tricolpate pollen-producing dicots, begins in the Early Aptian of Africa-South America (i.e., West Gondwana), and somewhat later in Europe-North America (i.e., West Laurasia), where tricolpate pollen first appears in the Early Albian (cf. Hickey & Doyle, 1977; Doyle et al., 1977).

The appearance of tricolpor(oid)ate (i.e., tricolporoidate to tricolporate) pollen in the Middle-Late Albian suggests that this may represent the beginning of the differentiation of the subclass Rosidae and possibly Dilleniidae as well, since both are characterized basically by tricolporate pollen. The evolution of tricolpor(oid)ate pollen, and with it the initial differentiation of the Rosidae (and possibly Dilleniidae) constitutes Stage 4 in the early evolution of the flowering plants.

The final phase of early angiosperm evolution, Stage 5, begins in the Middle Cenomanian with the appearance of triporate pollen, especially of the Normapolles type, in Europe and North America. Stage 5 probably represents the initial differentiation of the "Higher Hamamelididae," i.e., the Betulaceae, Casuarinaceae, Myricaceae, and Juglandaceae. That pollen of certain relatively primitive rosid families, such as the Aquifoliaceae, Gunneraceae, and Sapindaceae, occurs earlier in the Turonian-Coniacian, while pollen of such "higher" hamamelidid families as the Fagaceae, Betulaceae, and Myricaceae first appears later in the Santonian (cf. Muller, 1981) also suggests that the initial differentiation of the Rosidae began sometime before that of the "Higher Hamamelididae."

A MODEL FOR THE EARLY ADAPTIVE EVOLUTION OF THE ANGIOSPERMS

The picture of early angiosperm evolution outlined in Fig. 112 suggests the following model of the early adaptive evolution of the flowering plants. As Stebbins (1976) has stressed, the characters that most strongly set the flowering plants apart from gymnosperms are all features of the reproductive rather than vegetative part of the angiosperm life-cycle. Although it will probably never be possible to know with certainty the exact sequence by which the gymnospermous forebearers of the flowering plants acquired their angiospermous features, it is likely that entomophily was one of the earliest characteristics of the proto-angiosperms since so many basic angiosperm features, such as the perianth, carpel closure, and bisexuality of sporophytic reproductive structures (i.e., flowers), can best be explained as responses to the evolution of insect pollination. Evolution of the perianth in flowering plants in particular provides further evidence in support of the evolutionary scheme outlined in Figure 112. The taxonomic distribution of perianth types among primitive dicots of the Magnoliidae (Fig. 111), as well as throughout the major groups of dicots in general (Fig. 112), provides strong evidence that perianth evolution, which undoubtedly reflects basic changes in angiosperm pollination biology, has gone through at least six different major evolutionary stages (grades), as pictured in Figure 113.

Grade I in the evolution of the angiosperm perianth is represented, we suggest, by flowers whose sterile floral parts consisted simply of floral bracts, i.e., the flowers were composed of leaf-like elements associated with fertile floral parts, the stamens and carpels, but these sterile floral parts could only be distinguished arbitrarily as bracts versus tepals. The primitive magnoliid families Austrobaileyaceae (Endress, 1980) and Trimeniaceae (Money et al., 1950) may possibly be living representatives of this earliest stage in the evolution of the angiosperm perianth.

Grade II is typified by the evolution of a distinct perianth that initially was undifferentiated, and consisted wholly of tepals that were either entirely sepaloid or completely petaloid. With the development of this tepalar perianth into a differentiated perianth that consisted of a distinct calyx of sepals and a distinct corolla of tepalar petals, i.e., petals derived evolutionarily from an undifferentiated tepalar perianth, Grade III was reached. Most of the living primitive angiosperms of the subclass Magnoliidae have a Grade II or III perianth. Undifferentiated tepalar perianths of the Grade II type, for example, occur in some of the Magnoliaceae, most of the Lauranae, the Illiciaceae, and the Schisandraceae, while a Grade III perianth that is differentiated into tepalar petals and distinct sepals characterizes Magnoliidae such as the Degeneriaceae, Annonaceae, Canellaceae, and Winteraceae.

Flowering plants with Grade I–III perianths constitute what we shall term the "basic entomophilous angiosperms." In addition to most members of the Magnoliidae, this group includes the Nymphaeales, most of the monocotyledons,

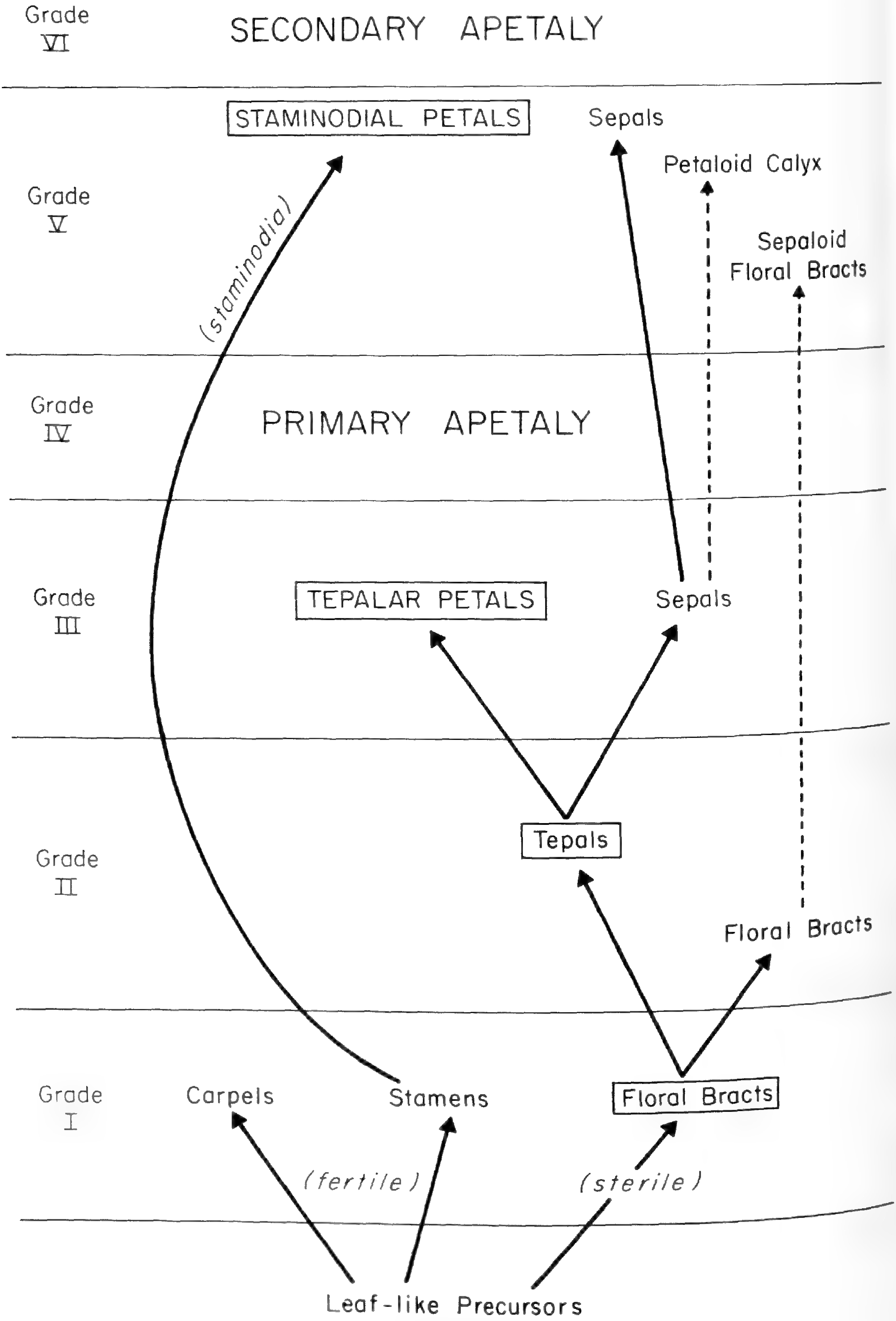


FIGURE 113. Evolution of the perianth in flowering plants.

and probably a few members of the dicot subclasses Ranunculidae and Caryophyllidae, e.g., the Paeoniaceae and Polygonaceae. Following the evolution of "basic entomophily" and the development of tepalar petals in the earliest flowering plants, it appears that the main line of angiosperm evolution (at least in the dicots) lost these original tepalar petals and reverted back to the wind pollination that characterized their gymnospermous ancestors. These early anemophilous-apetalous Grade IV flowering plants, which we designate the "primary anemophilous angiosperms" to distinguish them from later, separately derived anemophilous angiosperms, include advanced Magnoliidae, such as the Chloranthaceae, and almost all the Hamamelididae. The reason for this initial early return to anemophily may well have been tied in with the increasing aridity (and subsequent possible decline in insect pollinators) that apparently occurred soon after the earliest appearance of angiosperm pollen of the *Clavatipollenites*-type in the Barremian (cf. Hickey & Doyle, 1977; Doyle et al., 1977).

Although Dilcher (1979) has suggested that the flowers of such angiosperms as the Trochodendrales, Cercidiphyllales, Eupteleales, Hamamelidales, and Piperales may be primitively anemophilous (as well as primitively unisexual), comparative morphological studies of living primitive angiosperms as a whole, and the resultant phylogeny of the Magnoliidae-Hamamelididae as a group, do not support this contention. The Trochodendrales and Eupteleales, as well as some Hamamelidales and Piperales, all have bisexual rather than unisexual flowers as implied by Dilcher (1979) anyway. In order to accept Dilcher's hypothesis that the angiosperms enumerated above are primitively anemophilous and apetalous, one must be able to demonstrate that they are characterized by a number of other primitive features, and especially that they have some features that are even more primitive than those that occur in entomophilous, perianth-possessing magnoliid angiosperms such as the Magnoliales. Consideration of all the characters of the extant Magnoliidae-Hamamelididae, however, does not provide any evidence for the idea that the Chloranthaceae—"Lower Hamamelididae" represent a separate branch of angiosperms that evolved independent of the "Lower Magnoliidae."

The Chloranthaceae, which, unlike the "Lower Hamamelididae," at least has some members with monosulcate rather than tricolpate pollen, is characterized by a suite of advanced features, including a unicarpellate gynoecium, solitary ovules with apical placentation, drupaceous fruits, and opposite leaves. Moreover, the small scales ("tepals") that are sometimes present at the top of the chloranthaceous ovary seem to indicate that the flowers are fundamentally epigynous, which is hardly a primitive attribute.

The fossil record of angiosperm leaves also suggests that the Chloranthaceae—"Lower Hamamelididae" are advanced rather than primitive angiosperms. As Hickey and Doyle (1977) have shown, most of the earliest fossil angiosperm leaves (as well as those of most living members of the Magnoliidae) are brochidodromous and have entire margins. The leaves of the Chloranthaceae, on the other hand, are basically semicraspedodromous and have distinctive marginal teeth that have been named Chloranthoid Teeth by Hickey and Wolfe (1975). The Chloranthaceae share these Chloranthoid Teeth with the relatively advanced magnoliid families Illiciaceae and Schisandraceae, the Ranunculidae, and certain "Lower Hamamelididae," such as the Trochodendraceae, Tetracentraceae, and possibly the Cercidiphyllaceae. Reference to Figure 111 shows that our phylogenetic placement of the Chloranthaceae positions it in close proximity to all angiosperms that have Chloranthoid Teeth.

Thus, the preponderance of evidence from both living and fossil primitive angiosperms supports the conclusion that the Chloranthaceae—"Lower Hamamelididae" are secondarily apetalous-anemophilous, and that they are derived from the "Lower Magnoliidae," and not from some separate line of proto-angiosperms.

The early reversion of flowering plants back to wind-pollination in the Barremian–Early Aptian provides some understanding of why pollen of the *Clavatipollenites*-type is so abundant in the Middle Lower Cretaceous. Plants that produced pollen of the *Clavatipollenites*-type were in all probability *the earliest angiosperms that produced pollen with well-developed columellae that at the same time were wind-pollinated* (cf. Walker, 1976b). Although, in general, we agree with Hickey and Doyle (1977) that the "well-developed reticulate exine sculpture of *Clavatipollenites, Retimonocolpites, Liliacidites,* and *Stellatopollis*" provides "strong evidence that the flowering plants which produced them were insect-pollinated," for *Clavatipollenites-Ascarina,* at least, this is probably not true. Van der Hammen and González (1960), for example, have shown that the chloranthaceous genus *Hedyosmum,* which also has pollen with well-developed reticulate sculpturing, is wind-pollinated; and in addition they have indicated that the genus has a high pollen production, and that its pollen fossilizes well. That reticulate sculpturing is not always an indication of entomophily, and conversely that psilate pollen is not always indicative of anemophily, is also suggested by the fact that members of such primitive angiosperm families as the Magnoliaceae, Degeneriaceae, Eupomatiaceae, and Annonaceae frequently have perfectly psilate pollen grains and yet are entomophilous. Moreover, pollen of *Ascarina lucida,* a common coastal plant, occurs as up to 12% of the total pollen and spores present in coastal Pliocene-Pleistocene sediments of New Zealand (Mildenhall, 1978). As Muller (1981) has indicated, this "throws an interesting light on the lower Cretaceous abundance of *Clavatipollenites.*" Thus, *Clavatipollenites* was not the pollen of the earliest angiosperms, instead, it was probably the pollen of the first anemophilous angiosperms.

Neither comparative morphology of living primitive angiosperms nor the early fossil pollen and leaf record of the flowering plants provides evidence for Stebbins's (1965, 1974) idea that the first angiosperms were weedy shrubs that arose in a semiarid rather than mesic environment, as suggested by Hickey and Doyle (1977). Semixerophytic Magnoliidae are rare, and more importantly they are obviously advanced within the subclass as a whole. Moreover, the Potomac Group pollen and leaf sequence so eloquently correlated by Doyle and Hickey (1976) has nothing to do with the earliest phase of angiosperm evolution since it represents Stages 2 and 3, and not Stage 1, in the early evolution of the flowering plants (cf. Fig. 112).

Hickey and Doyle (1977: 62ff.) admit as much when they say that "it must be realized that they [these data] apply directly to only one subgroup of the angiosperms, the tricolpate dicots, and cannot automatically be extended to the angiosperms as a whole." What the Potomac Group pollen and leaf sequence does provide is data concerning the adaptive radiation of the "Higher Magnoliidae" and the "Lower Hamamelididae," and this of course has nothing to do with either the evolution of the "Lower Magnoliidae" or with the origin of the angiosperms themselves.

Apparently, soon after the origin of the wind-pollinated Chloranthaceae—"Lower Hamamelididae" in the Barremian-Early Aptian, conditions changed so that insect pollination was again favored, and the result was a secondary return to entomophily among the dicotyledonous angiosperms. The majority of the dicotyledons, including the subclass Rosidae (and its derivative the Asteridae) as well as the subclass Dilleniidae, have probably evolved as part of this secondary reversion to entomophily.

Petals evolved again in these "secondary entomophilous angiosperms," but this time they developed from stamens (Fig. 113, Grade V) rather than from tepals, as they had in the original "basic entomophilous angiosperms." Thus, the staminodial petals of the Rosidae-Dilleniidae-Asteridae are apparently not homologous with the more primitive tepalar petals of the "Lower Magnoliidae," Nymphaeales, and monocots. Although most secondarily petaliferous dicots presumably regained their petals through sterilization of stamens, in a few instances petal-like floral parts were formed from petaloid calyces, e.g., *Aristolochia,* and in a few angiosperms, such as *Mirabilis* (Nyctaginaceae), transference of function even went so far that floral bracts assumed the appearance of a calyx, while the calyx itself took over the function of a corolla. Finally, a few advanced members of the Dilleniidae-Rosidae-Asteridae, such as the Salicaceae, the Garryaceae, and *Fraxinus* of the Oleaceae, again became anemophilous-apetalous, representing yet another level (cf. Fig. 113, Grade VI) in the evolution of the angiosperm perianth.

Thus, consideration of neontological as well as paleobotanical evidence suggests that there are no living flowering plants that are primitively anemophilous. Furthermore, it is apparent that a major line of anemophilous angiosperms, including the magnoliid family Chloranthaceae and the related "Lower Hamamelididae," evolved in the Barremian-Early Aptian from more primitive "basic entomophilous angiosperms" of the "Lower Magnoliidae." It was from these "primary anemophilous angiosperms," and from the "Lower Hamamelididae" in particular, that the majority of living dicots, i.e., the subclasses Dilleniidae, Rosidae, and Asteridae, apparently evolved in the Middle-Late Albian. The major stimulus for the adaptive radiation of these higher dicots was probably their secondary return to entomophily concomitant with the evolution of staminodial petals that replaced the original tepalar petals of their distant entomophilous ancestors in the "Lower Magnoliidae," these original tepalar petals having been lost when certain "Higher Magnoliidae," including the Chloranthaceae, reverted to wind-pollination in the Barremian.

SUMMARY AND CONCLUSIONS

In the last decade significant new information has been gained about the early evolution of flowering plants through studies of Early Cretaceous angiosperm pollen and the pollen of living primitive flowering plants. Although most recent palynological studies of extant primitive angiosperms have used both scanning electron and transmission electron microscopy, few ultrastructural studies of early fossil angiosperm pollen grains exist. This paper represents an attempt to remedy this situation. Thirteen different types of Lower Cretaceous angiosperm pollen grains from the Potomac Group of the Atlantic Coastal Plain of eastern North America and the Fredericksburgian of Oklahoma were investigated ultrastructurally, using a technique that we have developed for studying single dispersed fossil pollen grains by combined light, scanning electron, and transmission electron microscopy. This technique is invaluable for the evolutionary study of small, light-microscopically similar dispersed fossil pollen grains, such as those that constitute the bulk of the earliest known microfossil record of the flowering plants.

After discussion of materials and methods and a brief review of concepts and terminology dealing with pollen wall morphology, results are presented, based on our examination of the following Lower Cretaceous angiosperm pollen types: *Clavatipollenites hughesii,* two aff. *Clavatipollenites* spp., *Asteropollis asteroides, Stephanocolpites fredericksburgensis, Retimonocolpites dividuus, Retimonocolpites peroreticulatus,* two aff. *Retimonocolpites* spp., *Stellatopollis barghoornii,* and three species of *Liliacidites.* Use of same grain combined light, scanning electron, and transmission electron microscopy provides a much improved means of delimiting Early Cretaceous angiosperm pollen form genera such as *Clavatipollenites, Retimonocolpites,* and *Liliacidites. Clavatipollenites,* in the restricted sense of its type species, *C. hughesii,* has a beaded to spinulose reticulum that is tectate-perforate to semitectate, a thick nexine, well-developed columellae, and a thick plug of endexine under the aperture, while *Retimonocolpites,* based on its type species, *R. dividuus,* has a banded, semitectate reticulum, a thin nexine, short columellae, and apparently no endexine. The most important features of *Liliacidites* sensu lato are a psilate, semitectate reticulum and strongly dimorphic lumina, while *Liliacidites* sensu stricto is probably best restricted to pollen that has reticulate sculpturing differentiated into coarse and fine areas. Other features frequently observed in pollen of the *Liliacidites*-type include "frilled" muri due to lateral extension of underlying columellae, a thin pollen wall, especially relative to grain size, a very thin nonapertural nexine relative to the rest of the exine, and a general lack of endexine.

This study further reveals that a close similarity exists between some Early Cretaceous angiosperm pollen types and pollen produced by certain living primitive angiosperms. *Clavatipollenites hughesii, Asteropollis asteroides,* and *Stephanocolpites fredericksburgensis* exhibit varying degrees of similarity at the ultrastructural level respectively to pollen of the extant angiosperm genera *Ascarina, Hedyosmum,* and *Chloranthus,* all three of which belong to the family Chloranthaceae. Pollen described under the form genus *Liliacidites* possesses many features that are presently restricted to the pollen of living monocotyledons. *Retimonocolpites dividuus* probably also has monocotyledonous affinities. Other Lower Cretaceous pollen types, including *Stellatopollis barghoornii* and *Retimonocolpites peroreticulatus,* have no counterparts among the pollen of extant angiosperms.

In the last part of the paper the question of the origin and early evolution of the flowering plants is examined. First, the phylogeny and classification of the families of the primitive angiosperm subclass Magnoliidae is discussed, and the following major taxa are recognized within the Magnoliidae: infraclasses Magnoliiflorae, Aristolochiiflorae, and Piperiflorae; superorders Magnolianae, Lauranae, Aristolochianae, Chloranthanae, and Piperanae; and orders Magnoliales, Winterales, Austrobaileyales, Trimeniales, Laurales, Aristolochiales, Chloranthales, Lactoridales, and Piperales.

Next, major evolutionary trends in the pollen of living primitive angiosperms are considered. Taxonomic distribution of characters of living primitive angiosperms suggests that angiosperm pollen is primitively monosulcate, boat-shaped, large- to medium-sized, psilate, or at best only weakly sculptured, noninterstitiate to possibly interstitiate-granular, atectate, and without endexine. This type of pollen is found today only in the otherwise primitive angiosperm families Magnoliaceae, Degeneriaceae, and Annonaceae. The fossil pollen record of early flowering plants is then considered in light of what is known about pollen evolution in living primitive angiosperms, and the point is stressed that *Clavatipollenites* and other currently known types of Early Cretaceous angiosperm pollen grains represent relatively advanced primitive (i.e., monosulcate) angiosperm pollen that is already too specialized to be able to reveal anything about the origin (or even the earliest evolution) of the flowering plants.

Finally, what can be deduced about the origin and early evolution of the flowering plants from fossil and living primitive angiosperms is considered. It is concluded that the ancestry of the angiosperms must be sought in the pteridosperms sensu lato, or more probably in some as yet unknown derivative of this group of cycadophytic gymnosperms. Following this, a 5-stage model of early angiosperm evolution is proposed, based on the early (Barremian to Middle Cenomanian) fossil pollen record of the flowering plants and the inferred phylogenetic relationships of living primitive angiosperms and their immediate derivatives.

Stage 1 of this model constitutes the yet undiscovered pre-Barremian evolution of angiosperms with primitive monosulcate pollen of the *Magnolia*-type, and represents the evolution of the "Lower Magnoliidae," i.e., dicotyledonous angiosperms whose descendants include such living primitive flowering plants as the Magnoliaceae and Degeneriaceae. The fact that monocotyledonous pollen and advanced monosulcate dicot pollen occur together in the Barremian suggests that monocots had already separated from dicots by then. Stage 2, which begins in the Barremian, is represented by the evolution of angiosperms with advanced monosulcate pollen, and includes both dicotyledonous pollen types, such as *Clavatipollenites,* and monocotyledonous pollen types, such as *Liliacidites.* This stage is characterized by the evolution of the "Higher Magnoliidae," including the family Chloranthaceae. The development of tricolpate pollen in the Early Aptian of Africa-South America, i.e., West Gondwana, constitutes Stage 3 of early angiosperm evolution, and is probably indicative of the origin of the "Lower Hamamelididae" (i.e., angiosperms whose descendants include such families as the Trochodendraceae, Tetracentraceae, Cercidiphyllaceae, Eupteleaceae, Hamamelidaceae, and Platanaceae) from the "Higher Magnoliidae." The evolution of tricolpor(oid)ate pollen in the Middle-Late Albian constitutes Stage 4, which probably represents the beginning of the differentiation of the angiosperm subclasses Rosidae and Dilleniidae from the "Lower Hamamelididae" since both of these dicot subclasses are characterized by tricolporate pollen. The final phase of early angiosperm evolution, Stage 5, begins in the Middle Cenomanian with the first appearance of triporate pollen (especially of the Normapolles type in Europe and North America, i.e., West Laurasia). This stage probably represents the initial differentiation of the "Higher Hamamelididae," whose descendants include such angiosperm families as the Betulaceae, Casuarinaceae, Myricaceae, and Juglandaceae.

The picture of early angiosperm evolution outlined above suggests the following model for the early adaptive evolution of the flowering plants. From an original complex of "basic entomophilous angiosperms" that had "tepalar" petals, and whose living descendants are today included in such orders as the Magnoliales, Laurales, and Winterales, the early evolution is envisioned of a major line of secondarily anemophilous-apetalous angiosperms, whose descendants include advanced magnoliid angiosperms, such as the Chloranthaceae, as well as related "Lower Hamamelididae," such as the Trochodendrales, Cercidiphyllales, and Hamamelidales. The reason for this early reversion back to the wind pollination that characterized the gymnospermous ancestors of the flowering plants may have been connected with the increasing aridity (and possible decline in insect pollinators) that apparently occurred soon after the earliest appearance of angiosperm pollen of the *Clavatipollenites*-type in the Barremian of Africa and South America at the time that major splitting of West Gondwana was taking place. The majority of living dicots, including the subclass Rosidae (and eventually its derivative the Asteridae) and probably the subclass Dilleniidae as well, apparently arose in the Middle-Late Albian from these early anemophilous angiosperms. This marked the beginning of the first major adaptive radiation of tricolpate (as opposed to monosulcate) pollen-producing dicotyledonous angiosperms. The major stimulus for this momentous event in the history of flowering plants may have been the secondary return of the main line of dicotyledonous flowering plants back to entomophily.

This secondary return to entomophily appears to be correlated with the evolution of new "staminodial" petals that replaced the more primitive, "tepalar" petals of the original "basic entomophilous angiosperms," i.e., the "Lower Magnoliidae," these original tepalar petals having been lost at the time when certain "Higher Magnoliidae," such as the Chloranthaceae, changed from entomophily to anemophily.

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CUTICLE EVOLUTION IN EARLY CRETACEOUS ANGIOSPERMS FROM THE POTOMAC GROUP OF VIRGINIA AND MARYLAND[1]

GARLAND R. UPCHURCH, JR.[2]

ABSTRACT

Studies of angiosperm leaf cuticles from the Lower Cretaceous Potomac Group reinforce previous evidence for a Cretaceous adaptive radiation of the flowering plants and suggest unsuspected trends in the evolution of stomata and trichomes. Early Potomac Group angiosperm leaf cuticles (Zone I of Brenner or Aptian?) show little interspecific structural diversity, particularly in stomatal organization. All species conform to the same highly plastic pattern of variation in subsidiary cell arrangement, in which the stomata on a single leaf conform to several types, including paracytic, hemiparacytic, anomocytic, laterocytic, and weakly cyclocytic. Several species resemble extant Chloranthaceae and Illiciales, but none represents a modern family. Later leaves (Subzone II-B of Brenner, or Albian) exhibit greater interspecific structural diversity, particularly in stomatal organization. Three new patterns of variation in subsidiary cell arrangement are present in addition to the older one and each has a subset of the variation present in the older pattern. Cuticular anatomy is consistent with proposed leaf affinities to Platanaceae and Rosidae. The stratigraphic trend in cuticle types supports the concept that the subclass Magnoliidae includes the most primitive living angiosperms. However, it also suggests that the uniformly paracytic stomatal pattern characteristic of Magnoliales, generally considered primitive for the flowering plants, may actually be derived from the variable condition found in Zone I leaves.

Within the past 15 years there has been a major reevaluation of the Cretaceous flowering plant record and the role of fossils in angiosperm phylogeny. Formerly, it was thought that fossils could provide little evidence on the course of angiosperm evolution, since even the earliest known remains were believed to represent modern families and genera (Axelrod, 1952, 1970). This view, based on older studies of leaf remains such as those by Fontaine (1889), Ward (1905), and Berry (1911) for the Potomac Group, has been strongly contradicted by more recent analyses of Cretaceous pollen and leaf architecture (Doyle, 1969; Muller, 1970, 1981; Wolfe et al., 1975; Doyle & Hickey, 1976; Hickey & Doyle, 1977; Hickey, 1978). These newer studies show that practically all of the older leaf identifications are incorrect and that successively younger Cretaceous angiosperm floras show the progressively higher levels of advancement predicted by many modern systems of classification (cf. Cronquist, 1968, 1981; Takhtajan, 1969, 1980; Thorne, 1976). These results indicate that the Cretaceous was a period of major angiosperm diversification and that paleobotanical studies should continue to yield new evidence on the course and timing of flowering plant evolution.

One largely untouched source of data is cuticular anatomy. Despite the fact that cuticles have long provided important characters for the systematic placement of Mesozoic gymnosperms and Tertiary angiosperm leaves (e.g., Harris, 1932, 1964; Kräusel & Weyland, 1950, 1954; Dilcher, 1974), most work on Cretaceous flowering plant leaves has neglected cuticular anatomy and relied solely on leaf architecture (e.g., venation, shape). I began a study of angiosperm leaf cuticles from the Lower Cretaceous Potomac Group of Virginia and Maryland to test previous ideas on early flowering plant evolution. At first, cuticular leaves were known only from the upper part of the Potomac Group (Palynosubzone II-B of Brenner, or probably middle to late Albian), but, later on, organically preserved leaves were collected from the lower part as well (Palynozone I of Brenner, or probably Aptian). This provided

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the opportunity to compare the stratigraphic changes seen in the systematic affinities and structural diversity of angiosperm leaf cuticles with those observed for leaf architecture and pollen morphology. This report summarizes the results of this investigation and their possible significance for flowering plant evolution: included are a comparison of the diversity of cuticular and leaf architectural features, an assessment of modern affinities based on cuticular anatomy, and two major evolutionary trends suggested by the morphological relationships of cuticular features in conjunction with their stratigraphic distribution.

Materials and Methods

All organically preserved leaf types known from Zone I and Subzone II-B were prepared using a combination of standard methods (cf. Dilcher, 1974). For light microscopy, cuticles were demineralized in HF, macerated in Schulze's solution followed by dilute alkali, stained in an aqueous solution of Safranin O, and mounted on slides in glycerine jelly. Preparations for scanning electron microscopy (SEM) varied according to the surface studied. External features were observed on unmacerated, demineralized leaf fragments. Internal features were observed on macerated cuticle that was dried down to SEM stubs coated with Duco cement in a chamber saturated with acetone vapor. All specimens were coated with gold and observed at 15 kV.

Plant debris from Zone I was analyzed to determine how much of the diversity of cuticle types was missing from the one known organically preserved leaf assemblage. Samples were obtained by disaggregating the rock in HF or Na_2CO_3, then sieving the slurry through 100 mesh screen. Unoxidized plant fragments were prepared as above, using a centrifuge, and mounted in glycerine jelly on slides or in glycerine between pairs of paraffin-sealed cover slips. Naturally macerated cuticle was mounted in glycerine in paraffin-sealed slides pending further study.

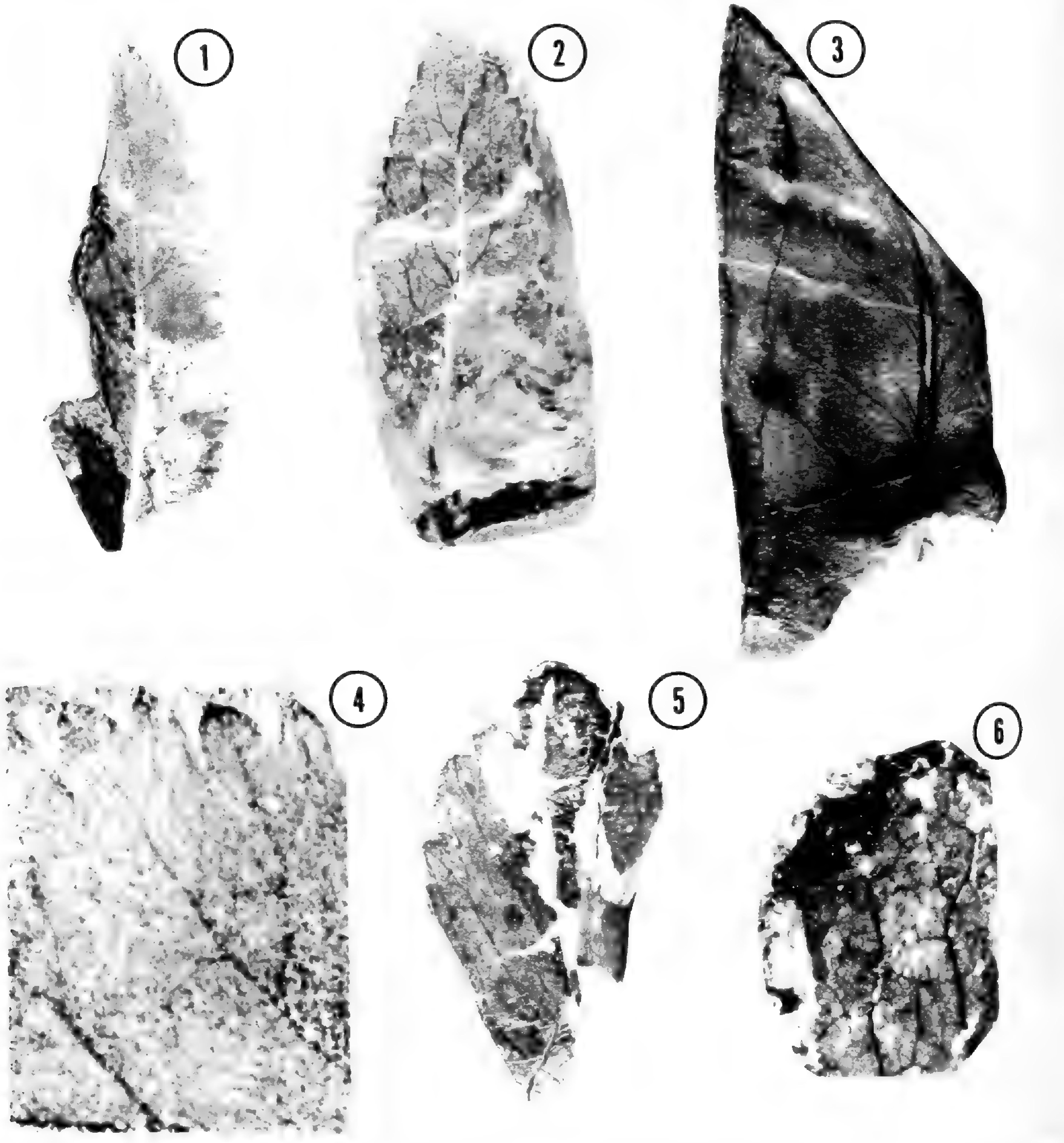
Extant angiosperm leaf cuticles were examined to test ideas on the relationships of Potomac Group leaves to modern forms. Taxa were selected for study based on two criteria: 1. their relative primitiveness according to the phylogenetic schemes of Cronquist (1968, 1981), Takhtajan (1969, 1980), and Thorne (1976), and 2. their similarity to Potomac Group angiosperms in leaf venation and pollen morphology. Observations were made on cuticle slides in the Indiana University paleobotanical collections, cleared leaves at the United States National Museum, and cuticles prepared by myself for light and scanning electron microscopy. Light microscope preparations were made from leaf fragments that were macerated in modified Jeffrey's solution (Stace, 1965), stained in Safranin O, then mounted in glycerine jelly or Piccolyte. SEM preparations were made in a manner similar to that for the fossils, except that unmacerated leaves were either boiled or shaken ultrasonically in ethanol for 30 minutes to remove the waxes and adhering debris. All specimens were coated with carbon, then gold/palladium, and observed at 20 kV.

Results

zone i angiosperm leaves

Zone I angiosperm leaves exhibit low diversity in their venation, shape, and marginal configuration compared to later Cretaceous and modern flowering plants. All Zone I leaves are simple and have pinnate venation, although in some groups the secondary veins are clustered or strengthened near the base of the leaf (also reported by Hickey & Doyle, 1977). Most leaf types possess festooned brochidodromous secondary venation (or secondaries that form several orders of loops within the margin) (e.g., Fig. 2), but *Vitiphyllum multifidum* and a new serrate form have simple craspedodromous secondary venation (or secondaries that run directly into lobes or teeth) (Fig. 1). The teeth of at least some leaf groups are a variant of the Chloranthoid type of Hickey and Wolfe (1975), with a biconvex shape, a large gland, and a pair of lateral veins that follow the margin and fuse with the gland (Fig. 4). Zone I leaves also show a low systematic diversity compared to later Potomac Group angiosperms: only 12 leaf types are recognized from Zone I, as opposed to over 30 from Subzone II-B (Hickey & Doyle, 1977).

The most distinctive feature of Zone I leaf architecture is the low degree of organization in the vein network. Secondary veins are irregularly spaced, enclose areas of variable size and shape, and often branch decurrently (e.g., Fig. 2). Tertiary and higher order veins are poorly differentiated from the secondaries and have a random course. This "first rank" pattern of venation occurs today in such primitive families as Winteraceae and Canellaceae and is considered primi-



FIGURES 1–6. Organically preserved Zone I leaf types.—1. Drewrys Bluff Leaf Type #1 (DBLT #1). University of Michigan Museum of Paleontology (UMMP) 64887, ×1.5.—2. *Celastrophyllum* sp. with associated stem fragment. UMMP 64892, ×1.5.—3. *Eucalyptophyllum oblongifolium,* specimen photographed in infrared light. Note the 2-stranded midrib and the intramarginal vein. UMMP 64859, ×1.5.—4. DBLT #1, close-up showing simple craspedodromous secondaries and chloranthoid teeth. UMMP 64887, ×8.—5. Cf. *Celastrophyllum obovatum,* UMMP 64865, ×3.—6. Cf. *Ficophyllum.* UMMP 65101, ×3.

tive for the dicots by Hickey (1971, 1977). Some authors (Wolfe et al., 1975) have suggested that several Zone I leaf types actually may be more primitive than anything extant, because they show even less vein regularity than any modern angiosperm.

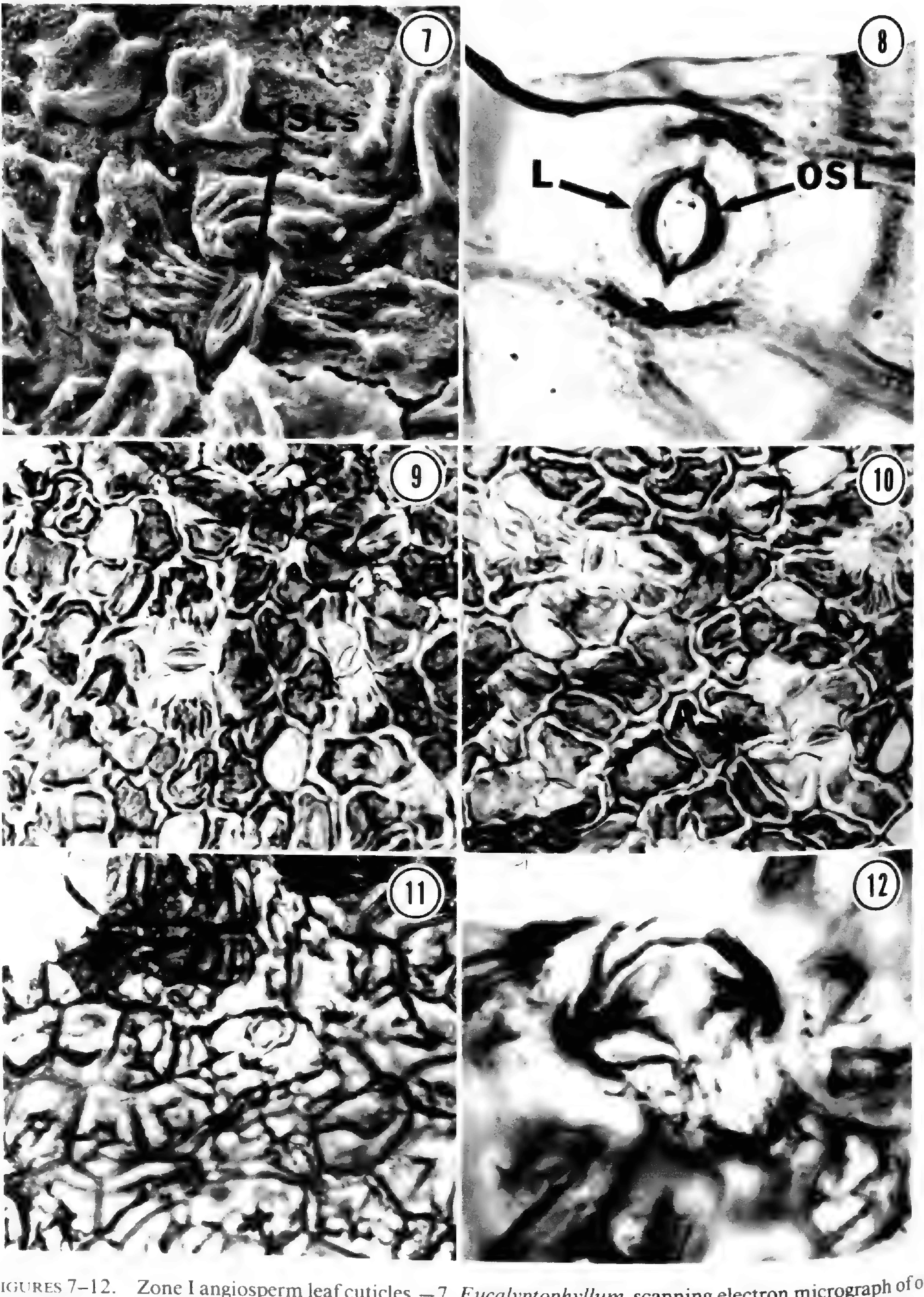
All Zone I leaves with cuticle come from a new locality at the north end of Drewrys Bluff, on the James River near Richmond, Virginia. These leaves are dated palynologically as upper Zone I of Brenner, or probably Aptian (Doyle, pers. comm.), and thus are similar in age to angiosperm leaves reported from the southern end of the exposure (Hickey & Doyle, 1977). Five leaf types are present at this locality, two of which are serrate. The most abundant form is an undescribed species referred to in this paper as Drewrys Bluff Leaf Type #1 (DBLT #1), which has simple craspedodromous secondary venation and Chloranthoid teeth (Figs. 1, 4). The other serrate leaf type has festooned brochidodromous venation, as in other Potomac Group species of *Celastrophyllum,* but differs in its low number of secondary veins and lack of a distinct petiole (*Celastrophyllum* sp., Fig. 2). Of the three entire-margined forms, *Eucalyptophyllum oblongifolium* has a midrib composed of two fusing vascular strands, numerous irregularly spaced secondary veins that connect with a prominent intramarginal vein, and only three orders of venation (Fig. 3). This suite of features in combination with the leaf's elongate areolation, is unknown in extant flowering plants (Wolfe et al., 1975; Hickey & Doyle, 1977). The other two groups are less unusual. One has an obovate shape, closely spaced, brochidodromous secondary veins, and random reticulate tertiary venation: it resembles the *Celastrophyllum obovatum* complex from Baltimore but differs by its much smaller size (cf. *C. obovatum,* Fig. 5). The other consists of fragments comparable to some specimens of *Ficophyllum* Font. in their reticulate pattern of tertiary and higher order venation (cf. *Ficophyllum,* Fig. 6). Certain characteristic Zone I leaf types, such as pinnately lobate forms (*Vitiphyllum* Font.), elongate obovate leaves (*Rogersia* Font.), and reniform leaves with basally congested secondary veins (*Proteaphyllum reniforme* Font.), are absent. Roughly one-third of the leaf types from Zone I are known with cuticle, since about 12 have been previously recognized for this interval (Hickey & Doyle, 1977).

Dispersed angiosperm cuticle is known from two Zone I localities on the James River: 1, the Drewrys Bluff angiosperm leaf bed, palynologically dated as upper Zone I, and 2, Dutch Gap Canal, palynologically dated as lower Zone I (Hickey & Doyle, 1977; Upchurch & Doyle, 1981). At least six cuticle types not known from whole leaves are present in these assemblages. This brings the total number of cuticle types up to 11, which suggests that much of the systematic diversity of Zone I leaves may be represented in the cuticles sampled for this study.

Zone I angiosperms show a limited range of cuticular variation compared to Subzone II-B and modern flower plants. As a rule these leaves are least variable in traits that often have high systematic value in extant angiosperms, while they are most variable in traits that tend to have little systematic significance (cf. Metcalfe & Chalk, 1950; Stace, 1965; Van Staveren & Baas, 1973; Jansen & Baas, 1973). In particular, Zone I leaf cuticles are relatively uniform in plan of stomatal construction, hair base structure, and types of secretory cells. More variation is present in patterns of cuticular sculpture, particularly on the outer cuticle surface. Traits such as cuticle thickness and cell contour are highly variable and of little value except in the identification of species; hence they are not discussed in the following paragraphs.

The stomatal complex shows a typically angiospermous plan of construction. In the guard cells of all species the stomatal poles are level with the stomatal pore, rather than raised, as in most gymnosperms (Harris, 1932). The stomata of most forms are level with the epidermis, but are distinctly sunken in *Eucalyptophyllum* (Fig. 7). The guard cells often bear cuticular ridges on their outer walls, or outer stomatal ledges (Fig. 7, OSL), and in many groups there are lamellar thickenings (Fig. 8, L), which are typical of primitive extant Magnoliidae (Baranova, 1972; Upchurch, unpubl. data). These lamellar thickenings are commonly associated with outer stomatal ledges, or else tend to intergrade with them. In addition, Dispersed Cuticles #1 and #3 bear strongly developed, T-shaped thickenings at the stomatal poles, or T-pieces (Figs. 8, 12). Such thickenings are present in diverse angiosperms, including the primitive family Illiciaceae (Bailey & Nast, 1948).

The arrangement of the subsidiary cells in all investigated species of Zone I angiosperms exhibits unusually high variation compared to that in extant flowering plants. Most extant angiosperm leaves possess stomata that fit into one or two standard types, defined by the presence or absence of subsidiary (or specialized) cells and their arrangement relative to the guard cells. In contrast, the stomata on a single Zone I angiosperm leaf fit into several of the conventionally recognized types as well as intermediates. This situation makes it necessary to analyze stomatal structure in a new way. In brief, a population of about 50 to 100 stomata is examined for ten features that contribute to the variation in stomatal structure for at least one species of Zone I angiosperm leaf. The range of variation in each is then recorded and the data are displayed in tabular form to facilitate comparisons between species (e.g., Tables 1–4). The ten major components of stomatal variation fall into three major categories: 1. the number and position of the contact cells (or those cells abutting on the guard cells), 2. the position of specialized contact cells, and 3. the position of specialized non-contact



FIGURES 7–12. Zone I angiosperm leaf cuticles.—7. *Eucalyptophyllum*, scanning electron micrograph of outer surface, lower cuticle. Note sunken stoma and two types of striations. UMMP 64862, ×1,000.—8. Dispersed Cuticle #1, stoma showing lamellar thickenings, outer stomatal ledges, and T-pieces. UMMP 65125-G153. ×800.—9. *Eucalyptophyllum*, paracytic stomata. UMMP 64862, ×400.—10. *Eucalyptophyllum*, anomocytic and other stomatal types. UMMP 64862, ×400.—11. Dispersed Cuticle #3, paracytic stoma. Also note partially solid papillae with radiating striations. UMMP 65126-56, ×400.—12. Same, close-up of another stoma showing concentric striations and T-pieces. UMMP 65126-56, ×1,000.

TABLE 1. Stomatal features of selected Zone I angiosperms.

	Eucalyptophyllum	cf. *Ficophyllum*	Dispersed Cuticle #1	Dispersed Cuticle #3
Number of contact cells	4–6	4–5	4–5	4–7
Number of lateral contact cells (LCCs)	2–4	2–3	2–3	2–4
Stomata with specialized LCCs?	sometimes	sometimes	sometimes	always
LCC specialization pattern within stoma	one or both guard cells	one or both guard cells	one or both guard cells	one or both guard cells
LCC specialization pattern along length of guard cells	either full or partial length	either full or partial length	mostly full length	either full or partial length
Number of polar contact cells (PCCs)	2–3	2	2–3	2–3
Stomata with specialized PCCs?	sometimes	sometimes	sometimes	sometimes
PCC specialization pattern	one or both poles	one or both poles	one or both poles	one or both poles
Other specialized cells?	sometimes	never	sometimes	sometimes
Position of other specialized cells	variable	—	mostly lateral	lateral
Number of variable features	10	7	10	8
Stomatal types[a]	P, Lc, C, and intermediates (common); H and A (rare)	P, H, A, and intermediates (common); weakly C (rare)	P, Lc, and H, all intergrading with A	P (common); H and transitional between Lc and C (rare)

[a] Key: P = paracytic; Lc = laterocytic; C = cyclocytic; H = hemiparacytic; A = anomocytic.

cells. The stomata of Zone I angiosperms are variable for at least seven of these features, with *Eucalyptophyllum* showing variation in all ten. Some of these features are variable in a number of extant angiosperms; these include the total number of contact cells, the presence or absence of specialized polar contact cells, and the presence or absence of specialized non-contact cells. Three, however, rarely vary within extant species; these are all components of lateral contact cell (or LCC) specialization. First, modified LCCs are found in many stomata, yet in others on the same leaf they are lacking entirely (e.g., Fig. 10); the exception is Dispersed Cuticle #3, which always has at least one modified LCC per stoma (Figs. 11, 12). Second, when a stomatal complex possesses modified LCCs, they may occur along both guard cells (e.g., Fig. 13, P, Lc) or else just one of them (Fig. 13, H). Finally, when a guard cell is flanked by one or more specialized LCCs, they often extend only part of the length of the stoma, rather than the full length (e.g., Fig. 14, arrow). This variation produces stomata that could be classified as anomocytic (Fig. 10, A), hemiparacytic (Fig. 13, H), paracytic (Figs. 9, 11, 13, P), laterocytic (Fig. 13, Lc), weakly cyclocytic (Fig. 13, C), and intermediates. This extreme plasticity in subsidiary cell organization, which is rare in extant flowering plants, produces stomata with a low degree of regularity, analogous to that present in the venation of these and other Zone I leaves.

A survey of extant primitive dicots reveals few groups with stomatal variation approaching that seen in Zone I. Most Magnoliales are paracytic (Baranova, 1972; Bongers, 1973; Koster & Baas,

TABLE 2. Stomatal features of selected Magnoliales.

Family	Winteraceae	Myristicaceae	Magnoliaceae	
Genus	*Drimys* (Old World)	*Knema*	*Manglietia*	*Liriodendron*
Number of contact cells	4–6	4, rarely 5	3–5	4–5
Number of lateral contact cells (LCCs)	2, rarely 3	2	2, very rarely 3	2–3
Stomata with specialized LCCs?	always	always	always	always
Both guard cells of stoma with specialized LCCs?	always	always	always	always
LCCs specialized full length of adjacent guard cell?	always	always	always	always
Number of polar contact cells (PCCs)	2–4	2, rarely 3	1–2	2–3
Stomata with specialized PCCs?	never	never	never	never
PCCs specialized at both poles?	—	—	—	—
Other specialized cells?	sometimes	sometimes	sometimes	sometimes
Position of other specialized cells	lateral	lateral	lateral	lateral
Number of variable features	~3	~3	~3	4
Stomatal types[a]	P, rarely Lc	P, rarely Lc or subdivided P	P, rarely Lc	P and Lc

[a] Key: P = paracytic; Lc = laterocytic.

TABLE 3. Stomatal features of selected Magnoliales.

Family	Canellaceae		Winteraceae	
Genus	*Pleodendron*	*Warburgia*	*Drimys* (New World)	*Takhtajania*
Number of contact cells	4–6	6–9	4–5(–6–7)	4–5
Number of lateral contact cells (LCCs)	2–3(–4)	3–5	2–4	2–3
One or more specialized LCCs in each stoma	always	always	always	sometimes
LCCs specialized for both GCs?	always	always	always	sometimes
LCCs specialized full length GC?	usually, not always	always	often, not always	sometimes (polar contact cell overlaps GC side)
Number of polar contact cells	2–3	3–4	2–3	2
PCCs specialized in each stoma?	rarely	sometimes	never	never
PCCs specialized at both poles?	sometimes	sometimes	—	—
Other specialized cells?	sometimes	always one or more	sometimes	never
Specialization pattern	lateral	lateral, sometimes polar also	lateral	—
Number of variable features	7	6	5	(4–)5
Stomatal types[a]	P, Lc, C	Lc, C	P, Lc	A, P
Remarks			LCCs strongly compressed	4 stomata in photo

[a] Key: P = paracytic; Lc = laterocytic; C = cyclocytic; A = anomocytic.

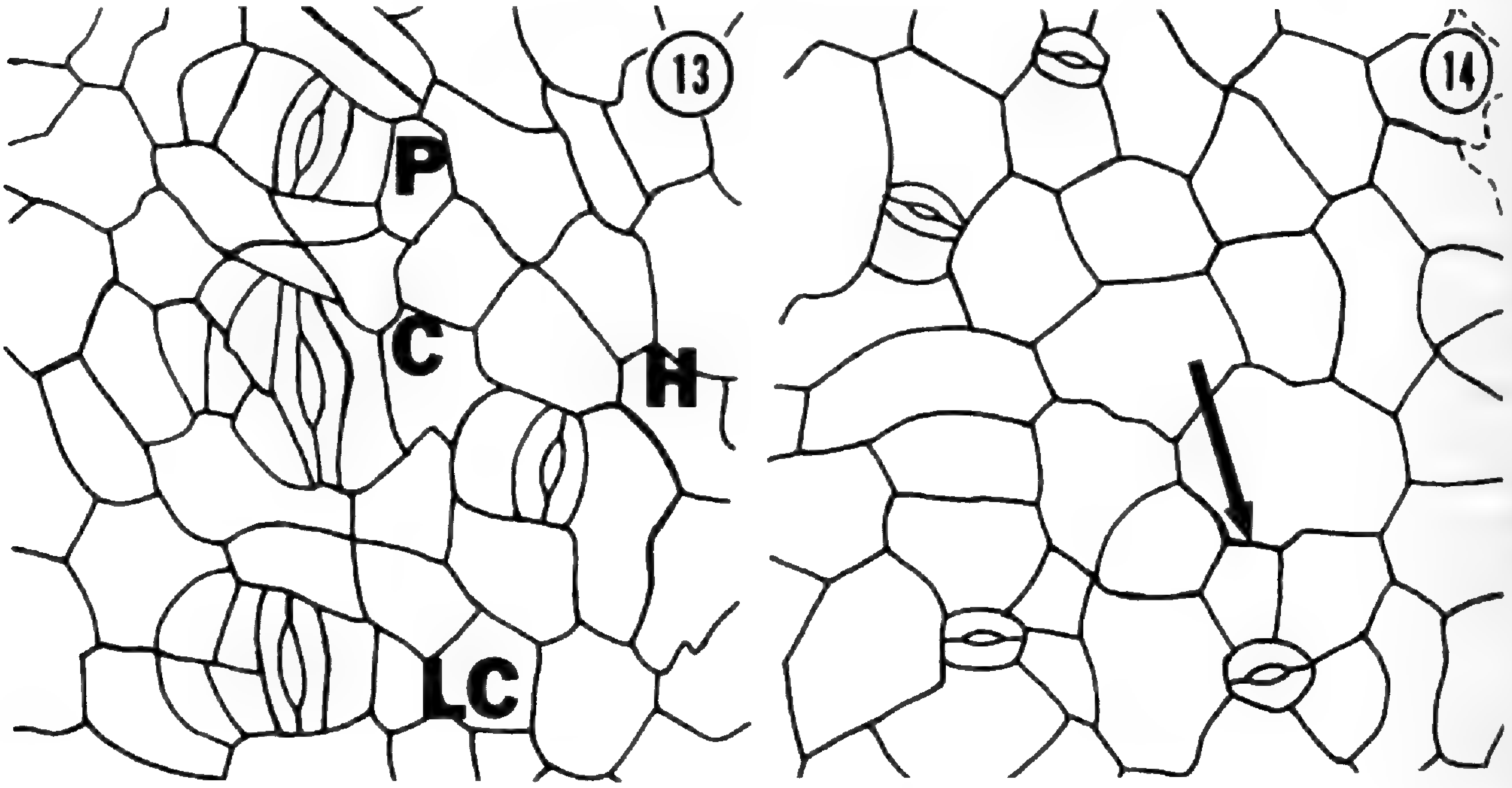
TABLE 4. Stomatal features of selected Laurales and Illiciales.

Family	Amborellaceae	Chloranthaceae		Austrobaileyaceae	Schisandraceae
Genus	*Amborella*	*Chloranthus*	*Sarcandra*	*Austrobaileya*	*Schisandra*
Number of contact cells	4–6	4–5	4–6	4–6	4–6
Number of lateral contact cells (LCCs)	2–3	2–3	2–4	2–4	2–4
Stomata with specialized LCCs?	always	always	always	always	always
Both guard cells of stoma with specialized LCCs?	sometimes	sometimes	always	sometimes	always
LCCs specialized full length of adjacent guard cell?	always for one guard cell, other one variable	sometimes	always	sometimes	sometimes
Number of polar contact cells (PCCs)	2–3	2–3	2–3	2–4	2–4
Stomata with specialized PCCs?	sometimes	occasionally	sometimes	never	never
PCCs specialized at both poles?	sometimes	usually	always	—	—
Other specialized cells?	sometimes	sometimes	sometimes	sometimes	sometimes
Position of other specialized cells	mostly lateral	lateral	mostly lateral	lateral	lateral
Number of variable features	~8	8	5	6	5
Stomatal types[a]	P (common); Lc, H, C, and intermediates (uncommon)	P, Lc (common); H, C, and intermediates between Lc and C (rare)	P, Lc, C	P, Lc (common); H (uncommon)	P, Lc

[a] Key: P = paracytic; Lc = laterocytic; C = cyclocytic; H = hemiparacytic.

1981; Roth, 1981) and those that are not show greater regularity than Zone I forms in the arrangement and specialization of their contact cells (Tables 2, 3). Greater variation is present in some Laurales (including Chloranthaceae) and Illiciales, but few taxa approach the extreme condition found in Zone I. The closest approaches are seen in the vesselless family Amborellaceae (Figs. 15, 16) and at least one species of Chloranthaceae (*Chloranthus serratus*), which are identical to Dispersed Cuticle #3 in almost all of their stomatal features (Table 4). Austrobaileyaceae (Figs. 17, 18) and certain Schisandraceae resemble Zone I forms in most respects, but differ by having uniformly unmodified polar contact cells (Table 4). Finally, the vesselless genus *Sarcandra* (Chloranthaceae) resembles Zone I angiosperms in its number of lateral contact cells and the patterns of specialization in polar and non-contact cells, but differs by having a much more uniform pattern of lateral contact cell modification (Table 4). These similarities suggest that many Laurales and Illiciales are closer to Zone I angiosperms in their level of stomatal advancement than most, if not all, extant Magnoliales.

Only two types of possible hair bases are known from Zone I angiosperms, in contrast to the diverse array found in Tertiary and extant flow-

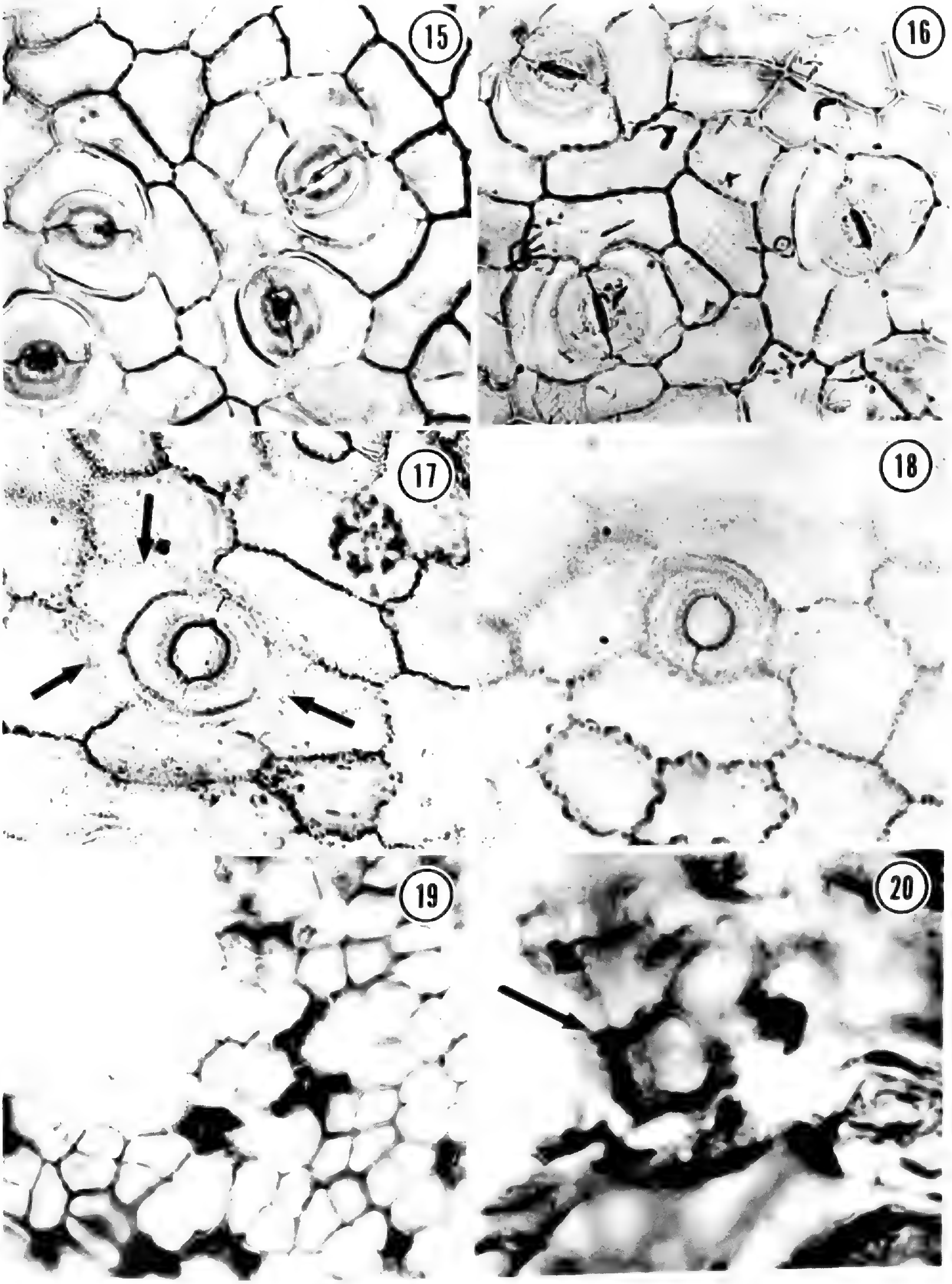


FIGURES 13, 14. Drawings of Zone I angiosperm stomata.—13. *Eucalyptophyllum*, paracytic (P), hemiparacytic (H), laterocytic (Lc), and weakly cyclocytic (C) stomata. UMMP 64892, ×750.—14. Cf. *Ficophyllum*, hemiparacytic and unclassifiable stomata. Note how the lateral contact cells in one stoma are modified for only part of the length of the adjacent guard cell (arrow). UMMP 65107, ×250.

ering plants (cf. Roselt & Schneider, 1969; Dilcher, 1974). Unlike many angiosperm hair bases, which show complex plans of construction, both Zone I types are simple, consisting of a single foot cell (to which the hair was attached) and several unmodified base cells. The first type, found in *Eucalyptophyllum* and DBLT #1, consists of a small, thickened, polygonal foot cell and several base cells that underthrust it (Fig. 19). No attached hairs or distinct abscission scars are known, raising the possibility that the "foot cells" are actually idioblasts, but circular depressions occur on the outer walls of some cells. Similar "foot cells" are found in a variety of extant angiosperm families, including Chloranthaceae, Illiciaceae, and Dilleniaceae (Upchurch, unpubl. data). The second type of hair base, found only in Dispersed Cuticle #3, is similar to the first in its size, shape, and degree of base cell underthrusting. It differs in having a thickened cuticle only on the outer wall of the foot cell and in having a trichome abscission scar, which consists of a pore (Fig. 20). Similar hair bases are found in an Eocene species of Schisandraceae (*Schisandra europaea*, cf. Jähnichen, 1976), but these differ from the Potomac Group type in having a more circular pore and strongly specialized base cells.

Secretory cells are present on the lower epidermis and in the mesophyll of many Zone I leaves and these strongly resemble the oil cells found in extant primitive angiosperms (Table 5). Two major types occur on the lower epidermis. The first, found in *Eucalyptophyllum* and two dispersed cuticle groups (Fig. 21), has a round to somewhat angular outline and a thin, smooth outer cuticle. Similar epidermal oil cells are found today in several groups of Magnoliidae, including Calycanthaceae and Illiciaceae (cf. Jähnichen, 1976; Upchurch, unpubl. data). The second type of secretory cell, found in *Eucalyptophyllum*, DBLT #1, and Dispersed Cuticle #6, and here termed the radiostriate type (Fig. 22), has an angular outline and striations that radiate from its periphery. Similar oil cells are present on the lower epidermis of a few Magnoliales, many Laurales (Fig. 23), both families of Illiciales, and Saururaceae of the Piperales (Bailey & Nast, 1948; Upchurch, unpubl. data). Finally, mesophyll secretory cells are present in cf. *Ficophyllum* and both species of *Celastrophyllum* (Fig. 24). These cells are round, about 10 μm in diameter, and contain dark substances. They resemble the mesophyll oil cells of diverse modern Magnoliidae in their size, shape, and appearance of macerated contents (cf. Jähnichen, 1976; Upchurch, unpubl. data).

Several types of cuticle sculpture are found in Zone I angiosperms. Surface sculpture conforms to three of the four major types listed by Dilcher



FIGURES 15–20. Cuticles of extant and Zone I angiosperms.—15. *Amborella trichopoda,* lower cuticle, stomata showing variation in the pattern of lateral contact cell (LCC) specialization along the length of each guard cell. Gray Herbarium, R. F. Thorne #28348, ×400.—16. *Amborella trichopoda,* lower cuticle, stomata showing variation in the number of guard cells with specialized LCCs. Gray Herbarium, R. F. Thorne #28348, ×400.—17. *Austrobaileya* sp., laterocytic stoma. The subsidiary cells (arrows) typically have thinly cuticized tangential walls. Arnold Arboretum, L. J. Bass #18160, ×400.—18. *Austrobaileya* sp., anomocytic (?) stoma. Arnold Arboretum, L. J. Bass #18160, ×400.—19. *Eucalyptophyllum,* upper cuticle showing probable hair bases. UMMP 64860, ×400.—20. Dispersed Cuticle #3, hair base (arrow). UMMP 65126-56, ×1,000.

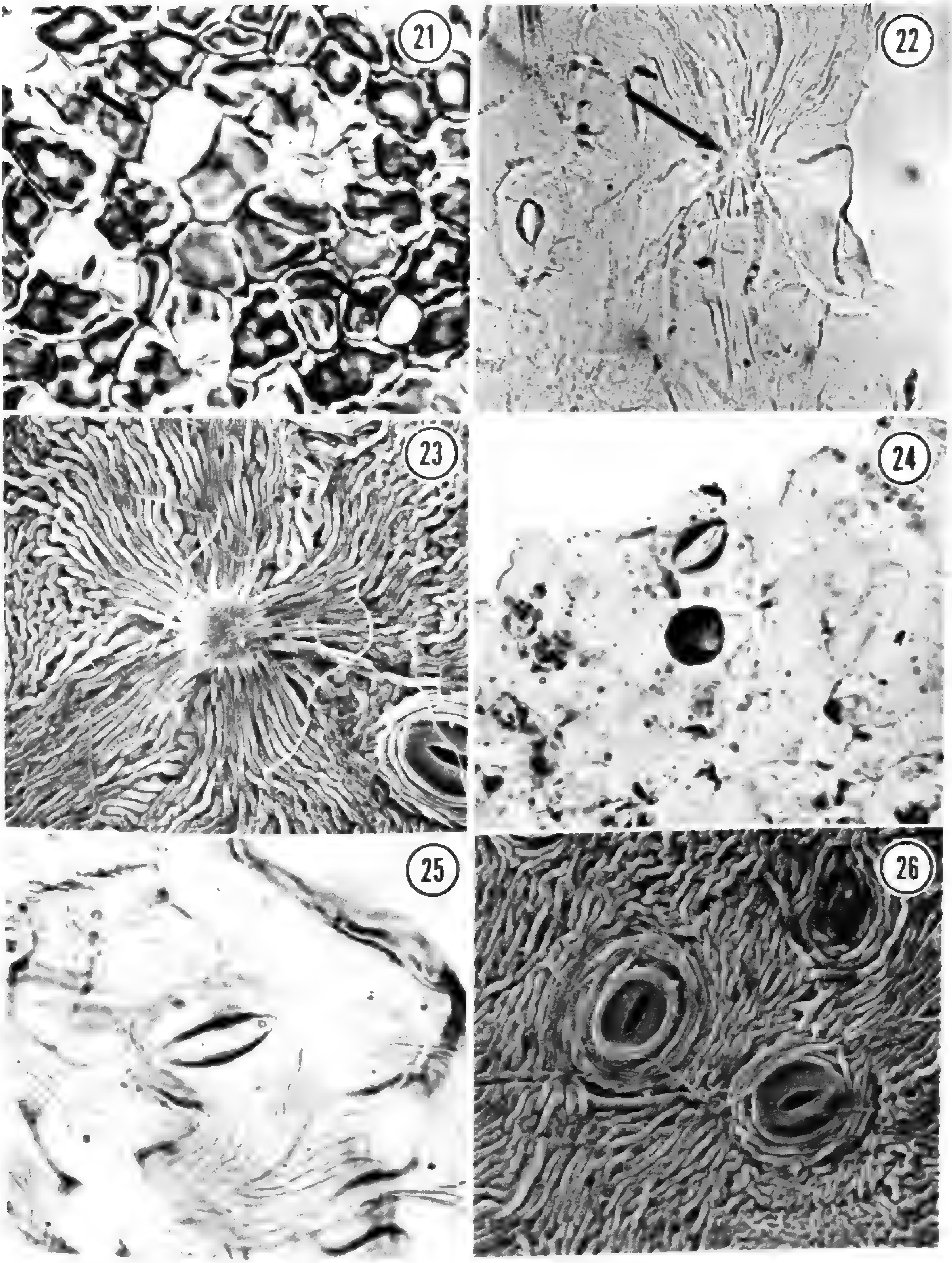
TABLE 5. Secretory cell types of Zone I angiosperms.

Location	Description	Systematic Distribution, Zone I	Systematic Distribution, Modern Flora	
1. Lower epidermis	round-subangular in surface view, outer cuticle smooth	*Eucalyptophyllum* Dispersed Cuticle #5 Dispersed Cuticle #6	Laurales:	Calycanthaceae Chloranthaceae
			Illiciales:	Illiciaceae Schisandraceae
2. Lower epidermis	strongly angular in surface view, outer cuticle with radiating striations	*Eucalyptophyllum* DBLT #1 Dispersed Cuticle #6	Magnoliales:	Annonaceae? Eupomatiaceae
			Laurales:	Austrobaileyaceae Chloranthaceae Gomortegaceae Monimiaceae Trimeniaceae
			Illiciales:	Illiciaceae Schisandraceae
			Piperales:	Saururaceae
3. Mesophyll	spherical, with thin walls and dark contents	*Celastrophyllum* sp. cf. *C. obovatum* cf. *Ficophyllum*	Magnoliales:	all families
			Laurales:	most families
			Illiciales:	both families
			Piperales:	both families
			Aristolochiales:	single family

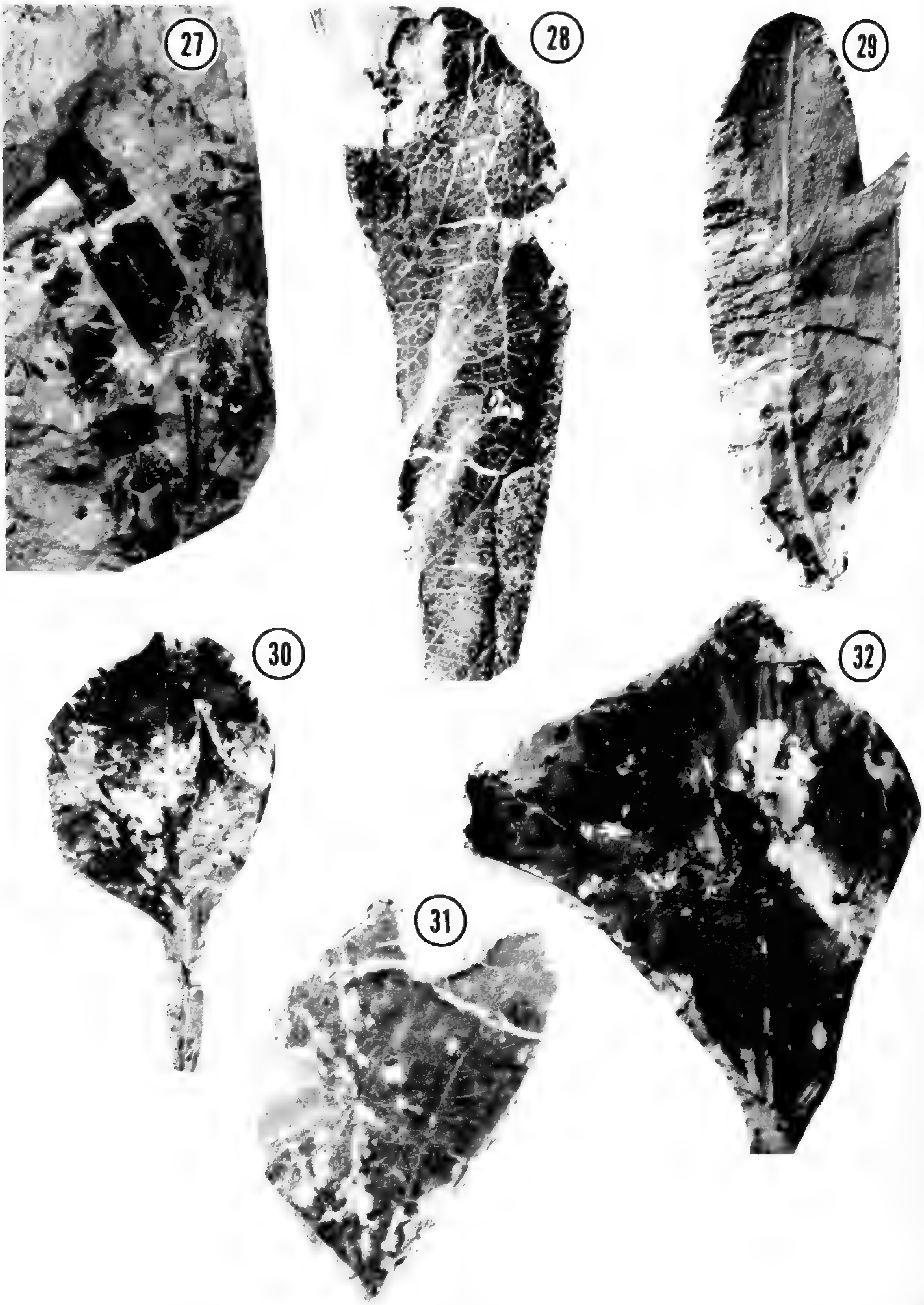
(1974). Psilate (or smooth) sculpture occurs in several different cuticle types. Papillate (or knobbed) sculpture is present in several dispersed cuticle types and commonly the papillae are partially solid, as in Dispersed Cuticle #3 (Fig. 11). Finally, striate (or ridged) sculpture is present in many Zone I groups; this is organized into two distinct patterns. The first, found in both DBLT #1 and Dispersed Cuticle #3, consists of striations which traverse cell boundaries and display two orientations near the stomata: some striations are oriented concentric to the stomatal pore while others either have a random arrangement or radiate from the stomata (Fig. 25). This condition is characteristic of many extant primitive dicot groups, including Illiciales, many Laurales (Fig. 26), and at least some Piperales (Saururaceae, Upchurch, unpubl. data). The second, found only in *Eucalyptophyllum,* consists of two distinct size-classes of striations that display markedly different behavior: the smaller ones traverse cell boundaries and radiate from the stomata, while the larger ones are confined to one cell each and enclose polygonal areas that mimic the shape of the underlying cell (Fig. 7). To date this pattern has not been observed in any extant group of angiosperms, but individual elements occur in scattered families, including Chloranthaceae (Upchurch, unpubl. data).

SUBZONE II-B ANGIOSPERM LEAVES

Subzone II-B angiosperm leaves show a much greater diversity of leaf architectural features than Zone I forms, but still less than in Late Cretaceous and modern flowering plants. Unlike Zone I angiosperms, Subzone II-B leaves include both simple and compound forms and possess several new types of primary venation. *Populophyllum* has actinodromous primary venation, with primaries that all radiate from a single point (Fig. 35). The "platanoids" are palinactinodromous, with primary veins that all diverge from different points (e.g., Fig. 31), and *Menispermites potomacensis* is acrodromous, with lateral primaries that curve towards the apex (Hickey & Doyle, 1977). Secondary venation is also more diverse, with both festooned brochidodromous and several new types present. At least some of the "platanoids" possess simple brochidodromous secondary venation, with secondary veins that form only one order of loops (cf. Hickey & Doyle, 1977; Upchurch, unpubl. data). Some *Sapindopsis* leaflets have eucamptodromous secondary venation, with secondaries that gradually thin towards the apex and do not join with the suprAadjacent secondary veins (Fig. 28), while others possess mixed craspedodromous secondary venation, with a mixture of craspedodromous



FIGURES 21–26. Cuticles of extant and Zone I angiosperms.—21. *Eucalyptophyllum*, epidermal secretory cells (arrows). UMMP 64862, ×400.—22. Dispersed Cuticle #6, radiostriate secretory cell (arrow). UMMP 65123A, ×400.—23. *Austrobaileya* sp., scanning electron micrograph of radiostriate secretory cell. Arnold Arboretum, L. J. Bass #18160, ×400.—24. Cf. *Celastrophyllum obovatum*, mesophyll secretory cell. UMMP 64865, ×600.—25. DBLT #1, anomocytic stoma with concentric and radiating striations. UMMP 64884-G157, ×600.—26. *Austrobaileya* sp., scanning electron micrograph of stomata showing concentric striations. Arnold Arboretum, L. J. Bass #18160, ×400.



FIGURES 27–32. Organically preserved Subzone II-B leaf types.—27. *Sapindopsis variabilis*, pinnatifid leaf. UMMP 65110, ×1.—28. Leaflet of pinnately compound *Sapindopsis* showing eucamptodromous secondary venation. UMMP 65111, ×2.—29. Toothed leaflet of pinnately compound *Sapindopsis* showing mixed craspedodromous secondary venation. UMMP 65112, ×2.—30. Platanoid #3, basal portion of leaf. UMMP 65103, ×1.—31. Platanoid #2. UMMP 65105, ×1.—32. Platanoid #3, apical portion of leaf. UMMP 65104, ×1.

and camptodromous secondary veins (Fig. 29). Finally, there are more tooth types present in Subzone II-B than in Zone I: in addition to convex-convex (A-1) teeth there are concave-convex (C-1) teeth with features of the Rosoid tooth type of Hickey and Wolfe (1975) in some pinnately compound specimens of *Sapindopsis* (Fig. 29) and straight-convex (B-1) teeth in a new serrate leaf from the Red Point locality of Hickey and Doyle (1977).

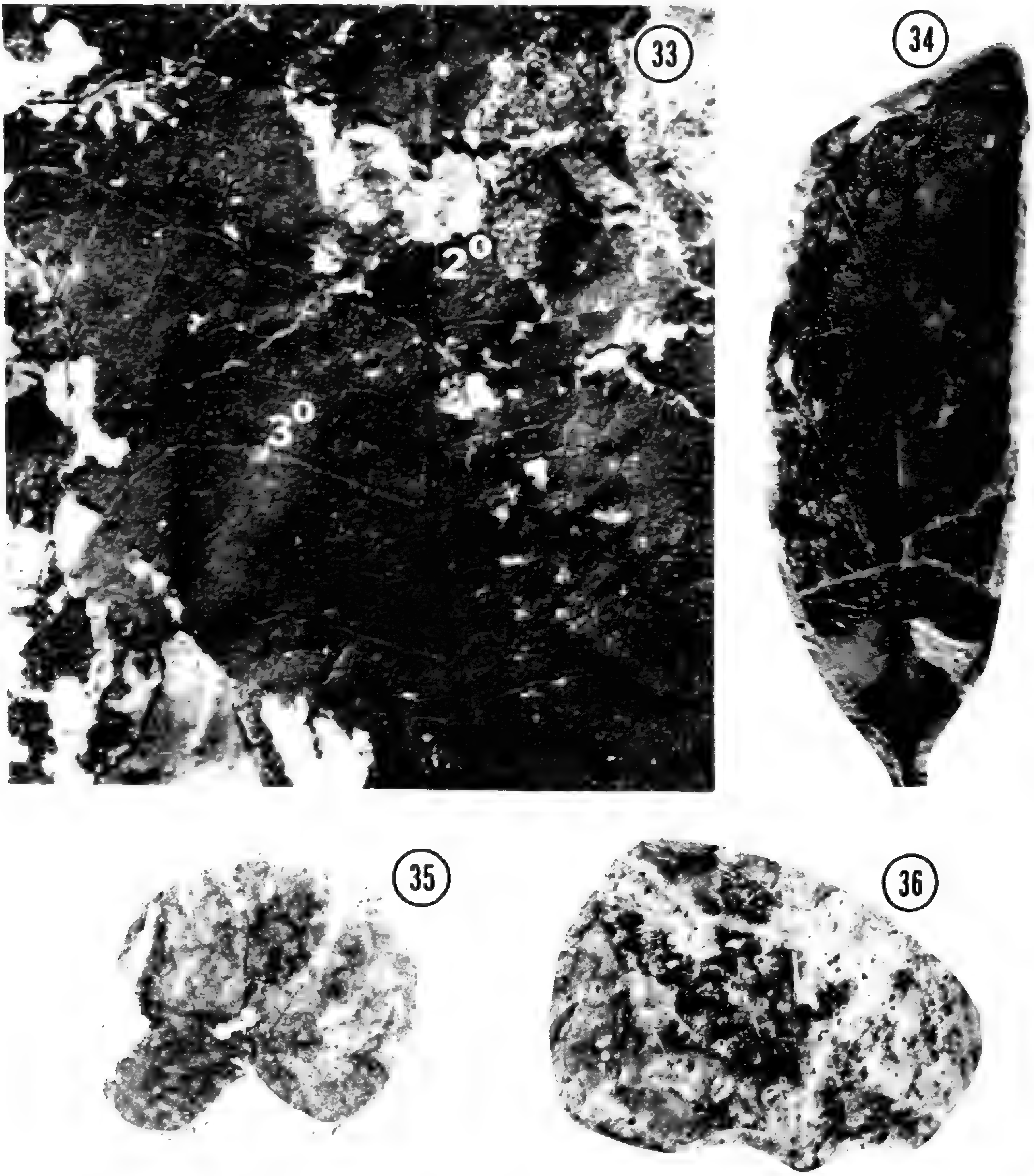
A key difference between Zone I and Subzone II-B dicotyledonous leaves is the strong tendency in the latter for greater vein regularity: generally the veins have a more regular course and the different vein orders are easier to distinguish from one another. While the older "first rank" syndrome is retained in many leaf groups, some, such as many pinnately compound *Sapindopsis,* are "second rank," with secondary veins that are regularly spaced and enclose areas of similar size and shape. Others, such as Platanoid #3, have regularly organized secondary and tertiary venation and hence conform to Hickey's "third rank" syndrome. This greater venational regularity suggests that many Subzone II-B leaves are more advanced than their Zone I counterparts. However, the fact that leaves with "fourth rank" venation, with an organized system of areoles, do not appear until the Late Cretaceous indicates that Subzone II-B angiosperms still do not have the level of advancement of many Late Cretaceous and modern flowering plants (Hickey, 1978).

Cuticular angiosperm leaves are known from four of the major leaf localities of Hickey and Doyle (1977). One, the Bank near Brooke locality in northern Virginia, falls in the lower or middle part of Subzone II-B. The other three, all found in Maryland, are assigned to the upper part of Subzone II-B: (1) West Brothers, near Washington, D.C., (2) Stump Neck, southeast of Washington, D.C. near the Potomac River, and (3) Red Point, at the head of the Chesapeake Bay. Only eight of the over 30 leaf types recognized for this interval are known with cuticle, but these belong to six major leaf groups that represent a large part of the range in morphology present. They are: (1) pinnatifid leaves and similar fragments belonging to *Sapindopsis variabilis* Font. (Fig. 27), (2) pinnately compound leaves and isolated leaflets of the type related to *Sapindopsis* by Hickey and Doyle (1977) (Figs. 28, 29), (3) three types of palinactinodromous, trilobate leaves and similar fragments belonging to the "platanoid" complex (Figs. 30–33), (4) actinodromous cordate leaves belonging to *Populophyllum reniforme* Font. (Fig. 35), (5) a leaf with a lobate base referable to *Menispermites potomacensis* Berry (Fig. 36), and (6) a new species of small, elongate leaf with numerous straight-convex (B-1) serrations (Fig. 34). These forms represent a large part of the range in morphology seen in Subzone II-B leaves, even though they constitute only a small fraction of the species (cf. Hickey & Doyle, 1977).

Subzone II-B angiosperm leaves show greater diversity in their cuticular structure than Zone I forms, particularly in stomatal organization. Three new patterns of variation in subsidiary cell arrangement are present in addition to the older one, but all of the stomatal types in each new pattern occur as variants in the Zone I pattern. New types of secretory structures (and their homologous hair bases) also are found and these show numerous similarities to Zone I types, suggesting their derivation from them. The systematic distribution of new cuticular features shows a strong correspondence with many of the leaf architectural groups recognized by Hickey and Doyle (1977); as a result they are described by group rather than by character.

The fewest new stomatal features are found in *Populophyllum reniforme* Font., a cordate, actinodromous leaf from the Bank near Brooke (Fig. 35). The guard cells differ from those in many Zone I forms by possessing outer stomatal ledges but lacking lamellar thickenings entirely (Figs. 37, 38). In addition, the guard cells often appear to be embedded in the adjacent cells, unlike earlier forms (Fig. 38). But despite these new features *Populophyllum* retains the pattern of contact cell arrangement and specialization found in Zone I, having up to ten variable features in some specimens (Table 6). This pattern most closely resembles that of cf. *Ficophyllum* in its low percentage of paracytic stomata, but differs by its specialized non-contact cells.

More new stomatal features occur in the new serrate leaf from Red Point, which has a characteristically papillate lower epidermis (Figs. 39, 40). The guard cells possess lamellar thickenings identical to those found in Zone I, but lack stomatal ledges entirely (Fig. 40). The number of contact cells is higher than in any Zone I form (Table 6) and the pattern of contact cell specialization is more regular, with each contact cell having a papilla that overarches the adjacent guard cell (Fig. 39). This stomatal pattern has

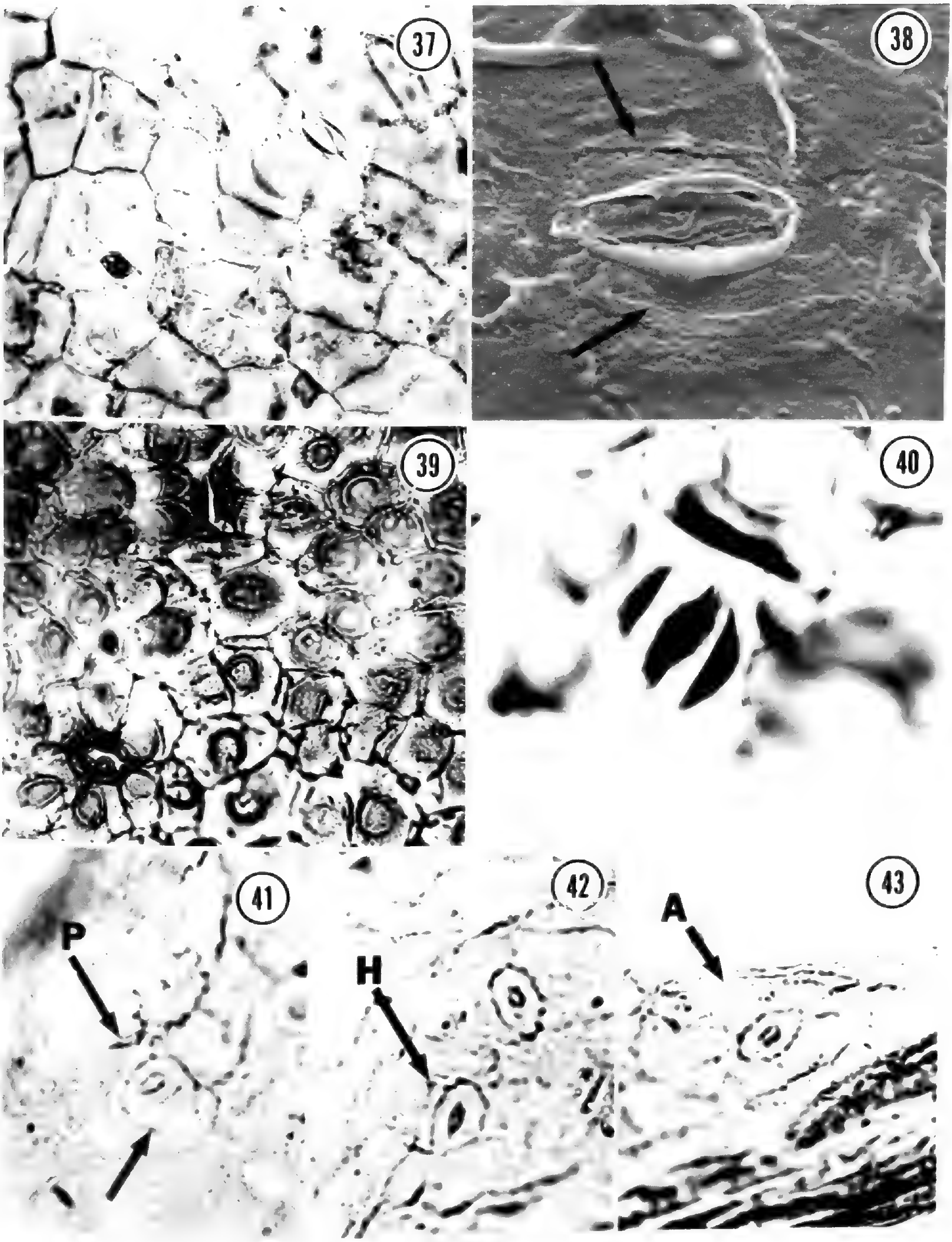


FIGURES 33–36. Organically preserved Subzone II-B leaf types.—33. Platanoid #3, close-up of venation showing tertiary (3°) and higher order venation. UMMP 65104, ×5.—34. New Serrate, Red Point. USNM 222856, ×2.—35. *Populophyllum reniforme.* UMMP 65108, ×1.—36. *Menispermites potomacensis.* UMMP 65102, ×1.

only five variable features, as opposed to seven to ten in Zone I forms (Table 6), and is best classified as weakly cyclocytic.

The second new stomatal pattern occurs in *Menispermites potomacensis* Berry from Stump Neck (Figs. 41–43). The guard cells in this species are smaller than those in all other Potomac Group angiosperms (8–15 μm long), but, as in most other Subzone II-B forms, they lack lamellar thickenings. The contact cells show some variation in arrangement and specialization, but less than that seen in Zone I (Table 6). Specialized LCCs never number more than one per guard cell and always extend the full length of the stoma. PCCs are always unspecialized and number two, while modified non-contact cells are always lateral. This pattern possesses only five variable features and has stomata that conform to three major types: paracytic (Fig. 41, P), hemiparacytic (Fig. 42, H), and anomocytic (Fig. 43, A).

The largest number of new cuticular features is shared by two groups of Subzone II-B leaves



FIGURES 37–43. Cuticles of Subzone II-B angiosperms.—37. *Populophyllum reniforme,* stomata. UMMP 65109, ×250.—38. *Populophyllum reniforme,* scanning electron micrograph of stoma showing outer stomatal ledges and embedded guard cells (arrows). UMMP 65109, ×2,000.—39. New Serrate, Red Point, stomata. Note how the papillae overarch the guard cells. USNM 222856, ×400.—40. New Serrate, Red Point, close-up of stoma showing outer and inner lamellar thickenings. USNM 222856, ×1,000. 41–43. *Menispermites potomacensis.* UMMP 65102.—41. Paracytic stoma, ×600.—42. Hemiparacytic stoma, ×600.—43. Anomocytic stoma, ×600.

that have been related to one another on the basis of leaf architecture: pinnatifid and pinnately compound leaves assigned to *Sapindopsis* (Figs. 27–29) and trilobate, palinactinodromous leaves of the "platanoid" complex (Figs. 30–33). In both groups the guard cells lack lamellar thickenings and tend to be slightly sunken (Fig. 44). The contact cells also show greater regularity in ar-

TABLE 6. Comparison of Zone I and Subzone II-B stomatal patterns.

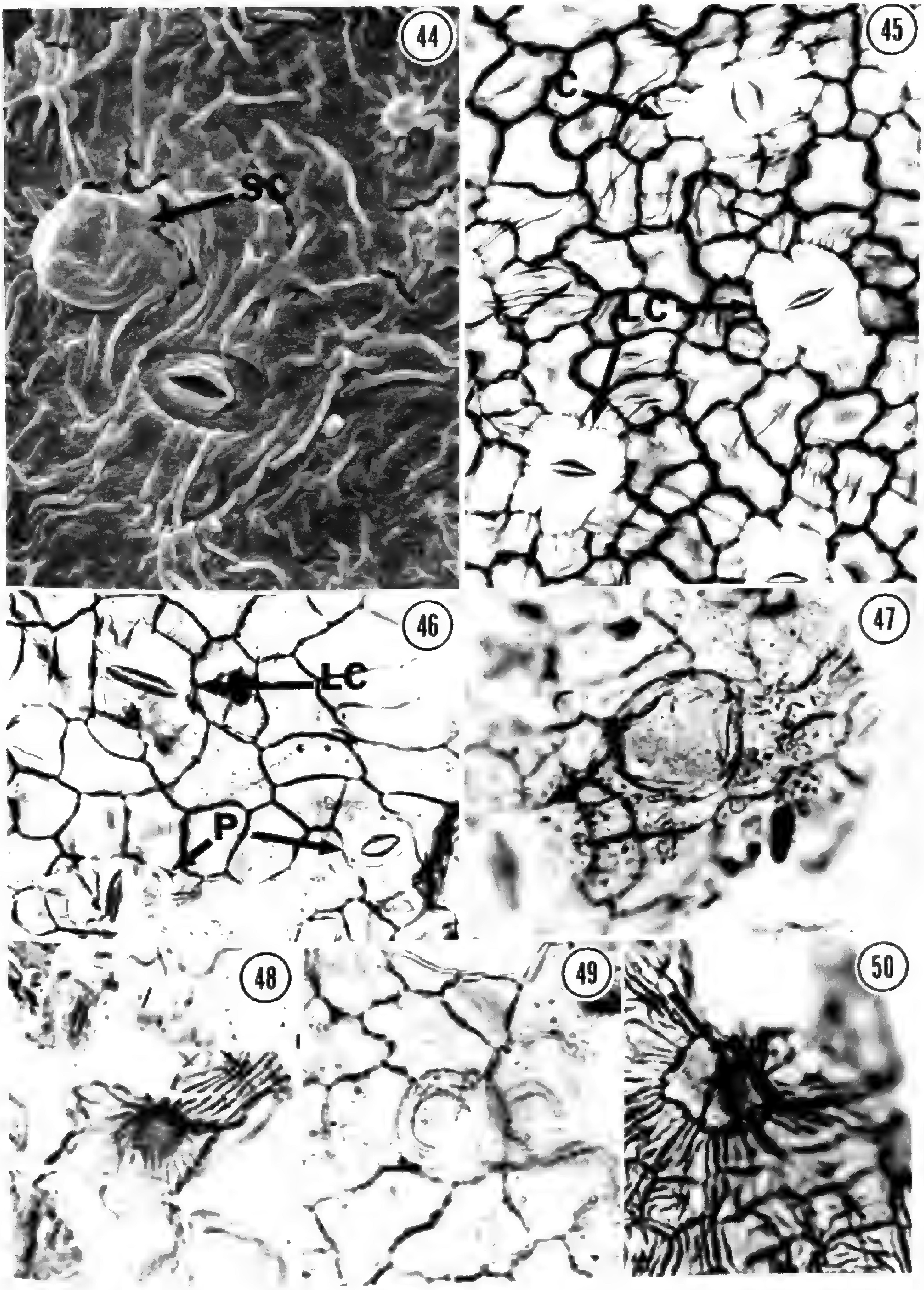
Taxon	Zone I Pattern	*Populophyllum*	New Serrate	*Menispermites*	*Sapindopsis*/ Platanoids
Number of contact cells	4–5(–7)	4–7	6–7	4–5	4–6(–8)
Number of lateral contact cells (LCCs)	2–3, 2–4	2–5	3–5	2–3	2–4(–5)
Specialized LCCs in every stoma?	sometimes/ always	sometimes	always	sometimes	always
LCCs specialized length of stoma?	sometimes	sometimes	always	always	almost always
Number of polar contact cells	2, 2–3	2–3	1–3	2	2–3
PCCs specialized in each stoma?	sometimes	sometimes	always	never	sometimes
PCCs specialized at both poles?	sometimes	sometimes	always	—	sometimes
Other specialized cells?	sometimes/ never	sometimes	sometimes	sometimes	sometimes
Position	variable	variable	variable	lateral	lateral
Number of variable features	7–10	10	5	5	6(–7)
Stomatal types[a]	—	A (common); P, H, and weakly C (rare)	weakly C	P, H, and A	P, Lc, and weakly C

[a] Key: P = paracytic; Lc = laterocytic; C = cyclocytic; H = hemiparacytic; A = anomocytic.

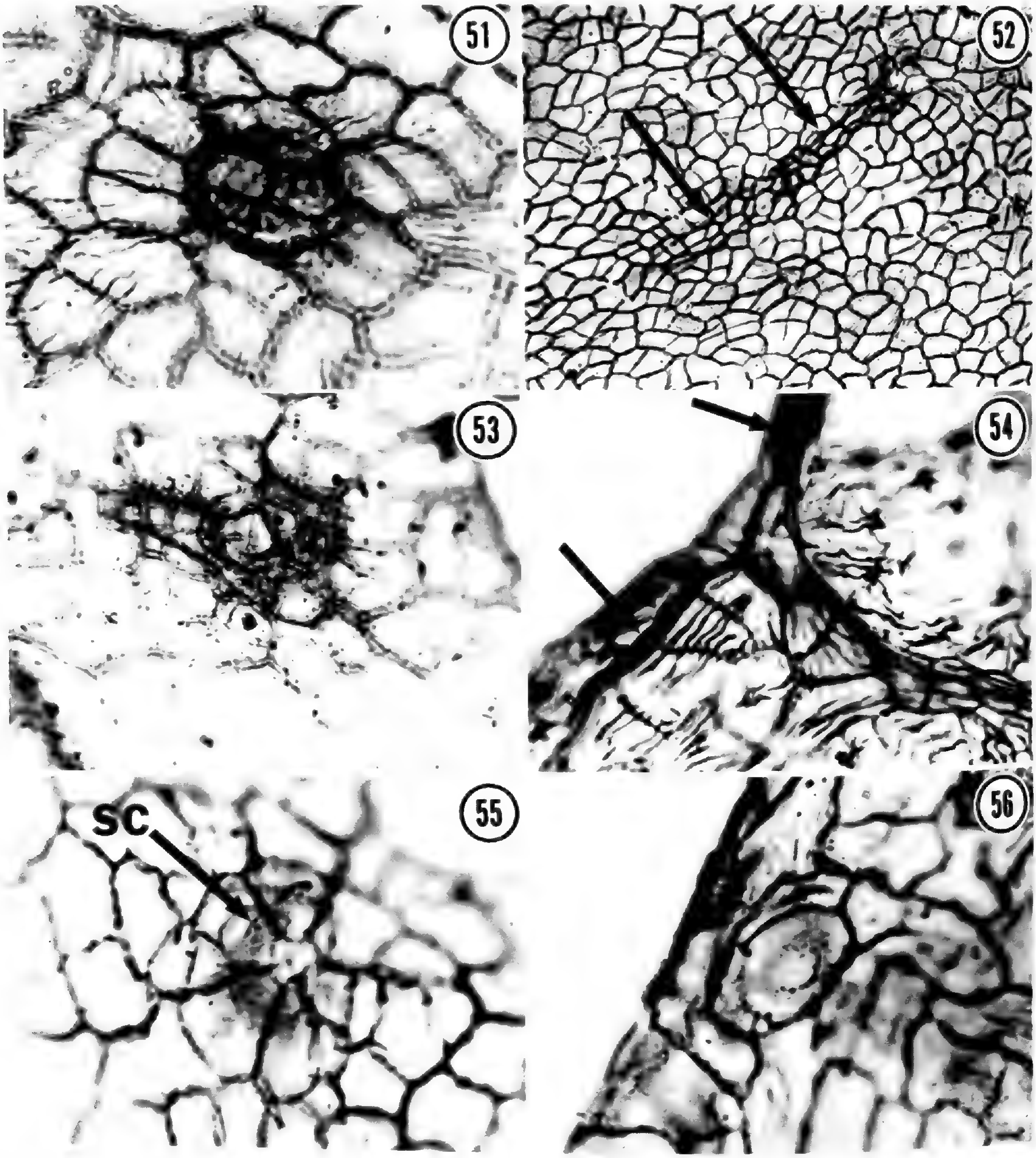
rangement and specialization than in Zone I forms, but less than in *Menispermites* and the new serrate (Table 6). Specialized LCCs occur next to every guard cell on a leaf and they almost always extend the full length of the stoma (Figs. 45, 46). PCCs and other associated cells, in contrast, show the same variation as in Zone I. This pattern has six to seven variable features and produces stomata that conform to three major types: paracytic (Fig. 46, P), laterocytic (Figs. 45, 46, Lc), and weakly cyclocytic (Fig. 45, C).

This same group of leaves also possesses four new patterns of secretory/hair base construction, all of which appear to be homologous. The first (and most variable) is found in both pinnatifid and pinnately compound species of *Sapindopsis* (Table 7). In this pattern there are some secretory cells that strongly resemble their counterparts in Zone I (e.g., Figs. 47, 48), but these intergrade with other types of secretory cells and even rare hair bases on the same leaf. Secretory cells (or SCs) range from level with the epidermis, as in Zone I, to raised, and in the latter case each SC is commonly asymmetrically positioned over the junction of two or more subtending cells (Fig. 50). These subtending cells are unspecialized adjacent to some SCs (Fig. 51) but modified adjacent to others (Fig. 50). SC shape in surface view is often angular or circular, as in Zone I (Figs. 47, 48) but many times it is broadly to narrowly elliptical (Fig. 52) to lobate (Fig. 53) and in some cases one or more heavily cutinized lateral protrusions also are present (Fig. 54). The outer wall of the SC is commonly level with the leaf surface, but sometimes it is strongly protruding (Fig. 55); this latter condition is found only on the lower epidermis. Finally, many secretory cells possess radiating striations and/or a ring of thickened cuticle (e.g., Figs. 51, 56), but this is sometimes missing (e.g., Figs. 47, 55). Hair bases strongly resemble certain types of protruding secretory cells that lack striations, but differ from them in having an apical hair abscission scar (Fig. 49).

The three other plans of secretory cell/hair base construction, found in the "platanoid" complex, represent portions of the spectrum of variation present in *Sapindopsis*. The largest amount of variation is present in Platanoid #1 (Table 7), whose secretory cells differ from those in *Sapindopsis* in only three respects. First, the SCs are always raised, rather than level with the epidermis in some cases (Fig. 57). Second, the SCs are



FIGURES 44–50. *Sapindopsis,* lower cuticle.—44. Scanning electron micrograph showing slightly sunken stoma and round, slightly underthrust secretory cell. UMMP 65113-G72, ×1,000.—45. Stomatal complexes. UMMP 65120, ×500.—46. Stomatal complexes. UMMP 65116, ×500.—47. Epidermal secretory cell of the round, flat Zone I type. UMMP 65117, ×600.—48. Epidermal secretory cell similar to the radiostriate type of Zone I. UMMP 65118, ×600.—49. Hair base which resembles protruding secretory cells. The flat top is interpreted as a hair abscission scar. UMMP 65119, ×600.—50. Radiostriate epidermal secretory cell that is irregularly positioned over two subtending cells. UMMP 65114-G77, ×400.



FIGURES 51–56. Secretory cells, *Sapindopsis.*—51. Round radiostriate secretory cell completely subtended by several cells. UMMP 65121, ×600.—52. Attachment scar of an elongate secretory cell. UMMP 65112, ×400.—53. Irregularly lobate secretory cell subtended by numerous small epidermal cells. UMMP 65115, ×400.—54. Radiostriate secretory cell with heavily cuticized protrusions (arrows). UMMP 65114-G77, ×400.—55. Torn bulbous secretory cell of the type found in some Rosidae. UMMP 65115-G98, ×600.—56. Secretory cell with a diffuse ring of thickened cuticle that defines a possible operculum. UMMP 65117, ×600.

always circular to elliptical, rather than angular in some cases. Finally, the subtending cells are never modified in non-veinal regions (Fig. 58), but often are smaller than the adjacent cells in veinal regions (Fig. 59).

The other two plans of secretory cell/hair base construction represent different subsets of the variation present in Platanoid #1 (Table 7). In Platanoid #2, there are only secretory cells. These are raised above the epidermis and are always symmetrically positioned over the junctions of at least two cells (Figs. 61, 62). Also present in this species are mesophyll secretory cells (Fig. 60). In Platanoid #3, there are only hair bases. These are similar to the hair bases of Platanoid #1, except that the foot cells always are symmetrically positioned over the junctions of two or more cells, and the base of the foot cell often has a ring of thickened cuticle (Figs. 63, 64). In addition, the base cells show a pattern of size

TABLE 7. Secretory cells and homologous epidermal structures of Zone I and Subzone II-B angiosperms.

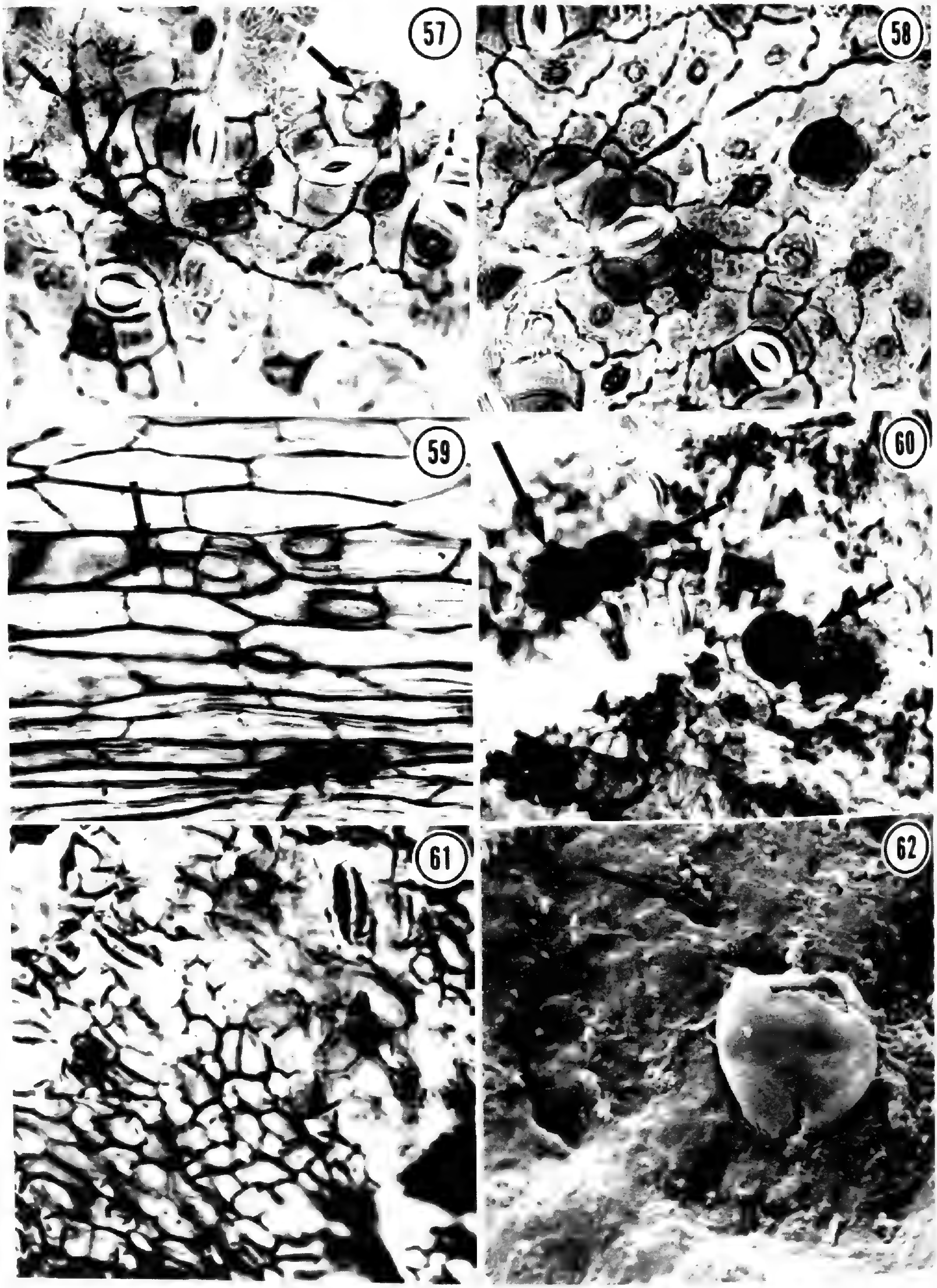
Taxon	Zone I Angiosperms	*Sapindopsis*	Platanoid #1	Platanoid #2	Platanoid #3
Type of epidermal structure	Secretory cells (SCs) only	SCs and rare hair bases	SCs and rare hair bases	SCs only	Hair bases only
Position relative to epidermis	level	level-raised	raised	raised	raised
Specialization of adjacent/underlying cells, veinal regions	—	variable	variable	—	variable
Specialization of adjacent/underlying cells, non-veinal regions	none	variable	none	none	none
Shape of SC or foot cell, surface view	polygonal or rounded	polygonal to circular and elliptical	circular to elliptical	circular	circular
Lateral protrusions from SC or foot cell?	none	sometimes	sometimes	none	none
SC or foot cell shape, outer wall	flat	flat to protruding	protruding	protruding	protruding
Cuticular sculpture	smooth or striate	smooth to striate	smooth to striate	smooth	smooth
Ring of thickened cuticle?	present in one species	sometimes	sometimes	never	sometimes

variation that is identical to that for the cells that subtend the secretory cells in Platanoid #1: they are scarcely modified in non-veinal regions (Fig. 63), but are often smaller than the adjacent cells underneath major veins (Fig. 64). This suite of characters is identical to that found in the hair bases of all extant Platanaceae (Figs. 65, 66).

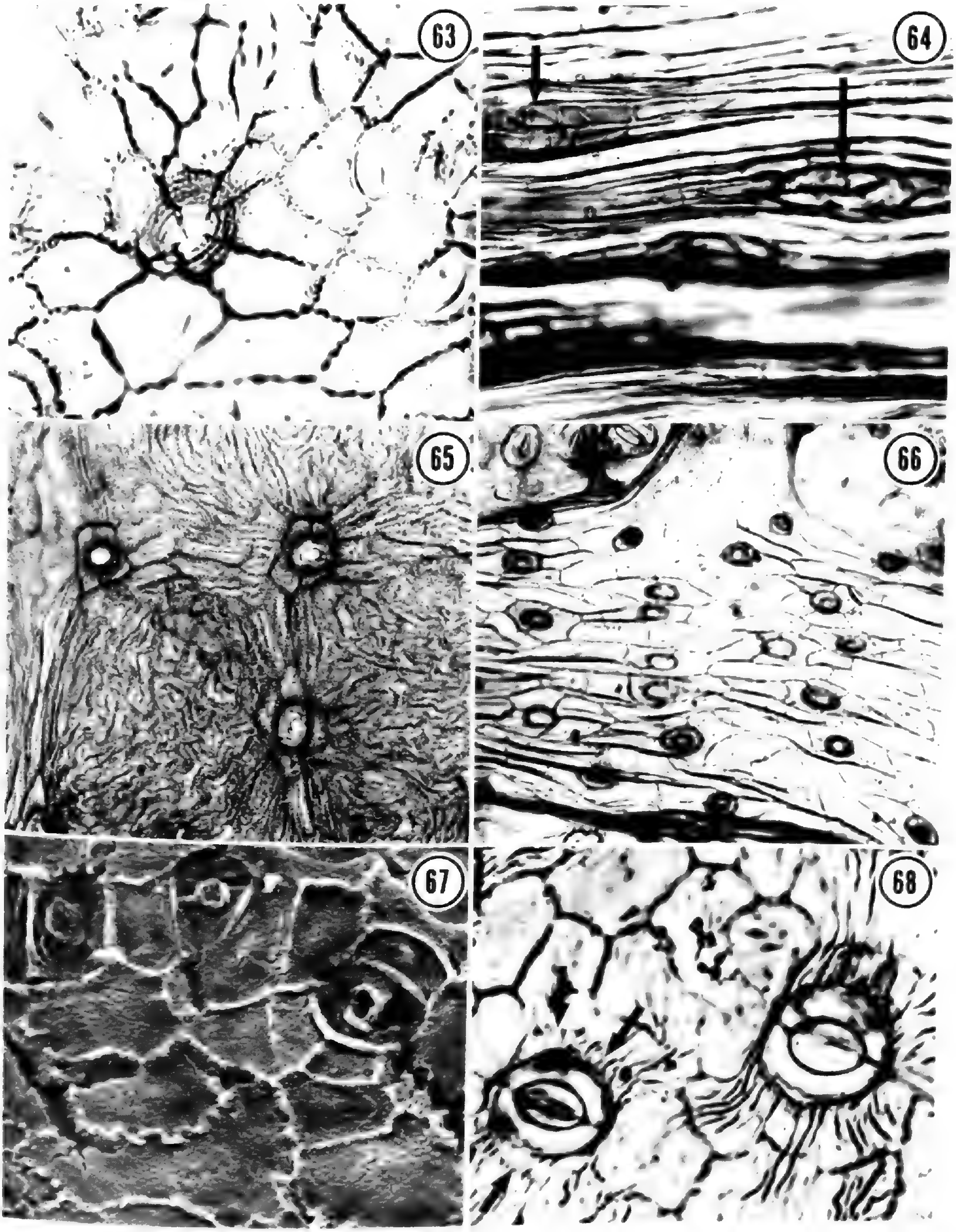
DISCUSSION

The stratigraphic distribution of cuticle types supplements previous evidence from palynology and leaf architecture on the direction and timing of early flowering plant evolution. First, cuticular anatomy strongly supports the concept of a Cretaceous (rather than pre-Cretaceous) angiosperm adaptive radiation. Zone I flowering plants show a limited range of structural diversity compared to later Potomac Group forms, and these in turn are less diverse than Tertiary and modern angiosperms. The guard cells of all Zone I species bear outer stomatal ledges, which are often associated with maceration-resistant lamellae; in contrast, Subzone II-B forms bear either outer stomatal ledges or lamellar thickenings, but never both. The stomata of Zone I angiosperms all conform to a similar pattern of variation in subsidiary cell specialization, which is characterized by a large number of stomatal types. In contrast, the stomata of Subzone II-B angiosperms conform to both the Zone I pattern and three new ones, each of which possesses one or more of the stomatal types found in the earlier leaves. Finally, the epidermal secretory cells of Zone I leaves conform to two basic types, while those of Subzone II-B leaves (along with their homologous hair bases) conform to many different types that fall into four major patterns of organization. This increase in structural diversity through time is similar to that seen for leaf architecture and pollen morphology: Subzone II-B angiosperms are structurally diverse compared to Zone I forms but have features that can be derived from the earlier types.

The similarities seen between Potomac Group angiosperm leaf cuticles and those of modern groups also provide evidence for classical theories of flowering plant evolution, which postulate subclass Magnoliidae (but not necessarily the order Magnoliales!) as the most primitive living group. A survey of many primitive and intermediate level angiosperm families (Tables 2–4, 8) suggests that Zone I forms, when comparable to extant families and orders, most closely re-



Figures 57–62. Platanoids, lower cuticle.—57. Platanoid #1, epidermal secretory cells (arrows) and diverse stomatal types. UMMP 65106, ×400.—58. Platanoid #1, strongly protruding secretory cell and numerous papillate cells. UMMP 65106, ×400.—59. Platanoid #1, secretory cells beneath a primary vein showing irregular placement relative to the subtending cells. Also note the heavily cutinized protrusion on one secretory cell (arrow) and the tendency for the subtending cells to be smaller than the others. UMMP 65106, ×400.—60. Platanoid #2, mesophyll secretory cells. UMMP 64105, ×400.—61. Platanoid #2, laterocytic stoma and numerous attachment spots for epidermal secretory cells (light areas). UMMP 64105, ×600.—62. Platanoid #2, scanning electron micrograph of collapsed secretory cell and the attachment scars for two others (arrows). UMMP 64105. ×4,000.



FIGURES 63–68. Platanoid #3 and extant Platanaceae.—63. Platanoid #3, hair base, non-veinal region, showing symmetrical positioning of the hair over the base cells. Note the flat top of the foot cell and the ring of thickened at its base. UMMP 65103, ×600.—64. Platanoid #3, hair bases beneath a primary vein (arrows). Note the tendency for the base cells to be smaller than the others. UMMP 65104, ×400.—65. *Platanus chiapensis*, upper cuticle, hair bases over small veins. Note the ring of thickened cuticle at the base of each foot cell and the smaller size of the base cells. Michigan, D. E. Breedlove #9796, ×160.—66. *Platanus chiapensis*, hair bases beneath major vein showing the symmetrical positioning of the foot cells over the junctions of two or more base cells. Michigan, D. E. Breedlove #9796, ×160.—67. Platanoid #3, scanning electron micrograph of laterocytic and weakly paracytic stomata. UMMP 65103, ×1,000.—68. *Platanus* sp., laterocytic stomata. Note the thinly cutinized tangential walls of the subsidiary cells (arrows), ×400.

TABLE 8. Stomatal patterns of *Sapindopsis* and selected Rosidae.

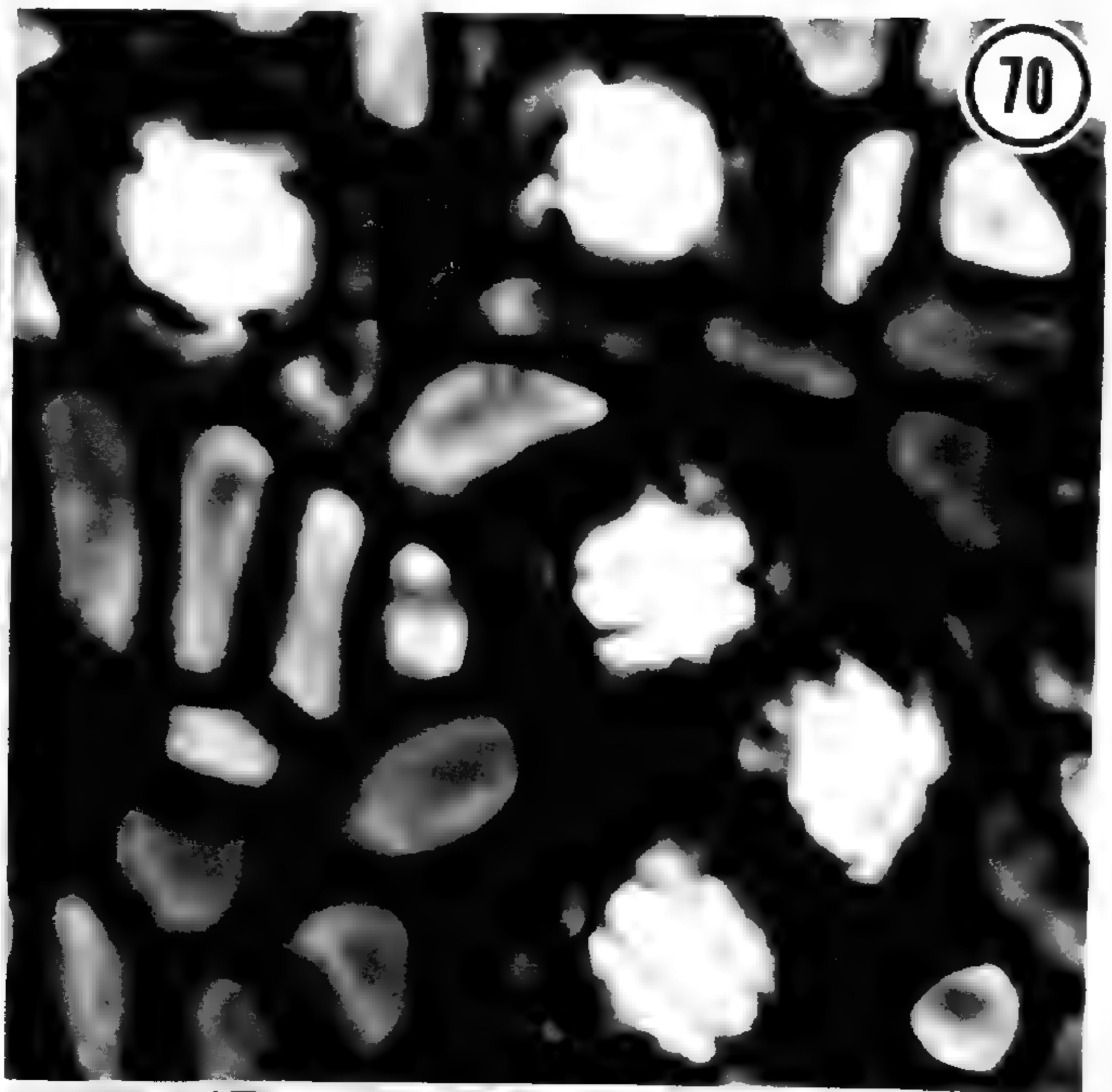
Taxon	*Sapindopsis*	Sapindaceae *Allophylus*	Cunoniaceae *Weinmannia*	Rhamnaceae Extant Members	Rosaceae *Quillaja*
Number of contact cells	4–8	4–6(–7)	4–5	4–6	5–6(–7)
Number of lateral contact cells (LCCs)	2–5	2–4(–5)	2–4	2–3, 2–4	3–5
Specialized LCCs in every stoma?	always	always	always	always	always
Specialized LCCs for each GC?	always	always	always	always	always
LCCs specialized length of stoma?	almost always	almost always	almost always	always	always
Number of polar contact cells	2–3	2–3	2–3	2–3	2–3
PCCs specialized in each stoma?	sometimes	sometimes	sometimes	sometimes	sometimes
PCCs specialized at both poles?	sometimes	sometimes	sometimes	sometimes	never
Other specialized cells?	sometimes	sometimes	sometimes	never	sometimes
Position	lateral	lateral	lateral	—	lateral
Number of variable features	6(–7)	6(–7)	7	5	5
Stomatal types[a]	P, Lc, and weakly C	P, Lc, and weakly C	P, Lc, and weakly C	P, Lc, and weakly C	Lc and transitional to C

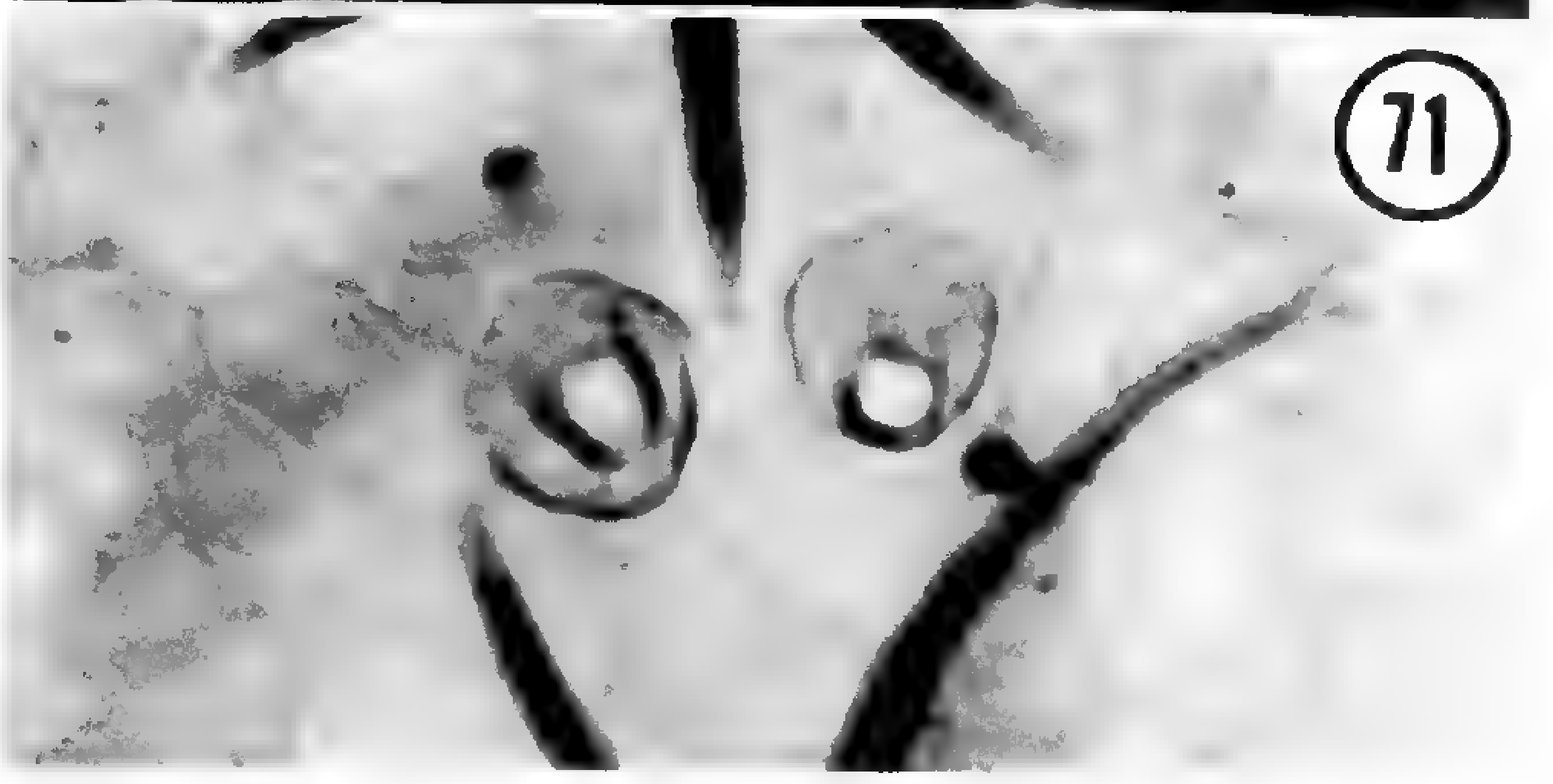
[a] Key: P = paracytic; Lc = laterocytic; C = cyclocytic.

semble Laurales (including Chloranthaceae) and Illiciales, but cannot be assigned to a single family. Two leaf groups and one dispersed cuticle type deserve special mention. The first, Drewrys Bluff Leaf Type #1 (Figs. 1, 4, 25), is similar to Chloranthaceae. The combination of stomata longer than 30 μm, striations that run concentric to the stomatal pore, and radiostriate epidermal secretory cells is found only in some Laurales and Illiciales. The "hair bases" of DBLT #1 today occur in many angiosperm families, but in Magnoliidae have been observed only in Illiciaceae and Chloranthaceae. Finally, the Zone I pattern of variation in subsidiary cell arrangement is known only from Amborellaceae and certain Chloranthaceae, while other Chloranthaceae and Schisandraceae differ in only two to three features (Tables 1, 4). These similarities, along with the Chloranthoid teeth, strongly suggest affinities with the family Chloranthaceae; however, simple craspedodromous secondary venation is absent from the family (Hickey & Wolfe, 1975; Upchurch, unpubl. data). Hence, DBLT #1 may belong to a group that includes the ancestor of modern Chloranthaceae but represents an extinct taxon within the alliance.

The second leaf group, *Eucalyptophyllum oblongifolium* (Figs. 3, 7, 9, 10, 19), most closely resembles Chloranthaceae and Illiciales but has a number of features unknown from either group. This taxon has always been difficult to place systematically because its combination of venational features is unknown in extant angiosperms (Wolfe et al., 1975; Hickey & Doyle, 1977). Cuticular anatomy, however, clearly indicates angiospermous affinities because *Eucalyptophyllum* possesses the same stomatal features, "hair base" type, and epidermal secretory cell types as other Zone I and certain extant flowering plants. In fact, this combination of features today is restricted to Chloranthaceae, and Illiciales differ only in their less variable stomatal complexes. In spite of these similarities, however, the fossil differs from both modern taxa in its elongate sunken stomata, truncate stomatal poles, pattern of striations, and distinctive leaf architecture. Hence, *Eucalyptophyllum* probably represents an extinct group of at least ordinal rank (cf. Hickey & Doyle, 1977) that is related in some way to Chloranthaceae and Illiciales.

The third group, Dispersed Cuticle #3 (Figs. 11, 12, 21), most strongly resembles extant Illici-





FIGURES 69–71. Lower cuticles, extant Rosidae.—69. *Weinmannia crenata* (Cunoniaceae), stomata showing *Sapindopsis* pattern of variation in subsidiary cell arrangement. Michigan, B. A. Krukoff #11053, ×600.—70. *Allophylus apetata* (Sapindaceae), stomata showing *Sapindopsis* pattern of variation in subsidiary cell arrangement. Indiana University Cuticle Slide #308, Yale, Wright #1604, ×600.—71. *Flindersia schottiana* (Rutaceae), abaxial secretory cells. Compare these with the one in Figure 55. National Cleared Leaf Collection #5958, ×600.

ales. The striation pattern around the stomatal complex is typical of that found in Illiciales and Laurales (Fig. 26), whereas the pronounced T-shaped thickenings at the poles are characteristic of Illiciaceae (Bailey & Nast, 1948). The variable pattern of contact cell arrangement and specialization differs from the paracytic condition in Illiciaceae, but it does resemble the pattern found in Schisandraceae in most respects (cf. Tables 1, 4). In addition, the one known hair base is similar to the type found in *Schisandra europaea*, an Eocene member of the order. Despite these similarities, however, the fossil has smaller stomata than modern Illiciales (27 μm long versus 30–70 μm) and appears to lack both the lamellar guard cell thickenings and epidermal oil cells characteristic of the order. Hence, Dispersed Cuticle #3 may be related to Illiciales but represents an extinct taxon within the alliance.

These results indicate the need for caution in interpreting similarities between the pollen of Zone I and modern angiosperms. While monosulcate pollen grains assigned to *Clavatipollenites* cf. *hughesii* as described by Doyle et al. (1975) closely resemble *Ascarina* of the Chloranthaceae (Walker, 1976; Walker & Walker, 1984; Muller, 1981), no angiosperm leaf with preserved cuticle or dispersed cuticle type possesses all of the characters needed to be assigned confidently to extant Chloranthaceae. Since the *Ascarina*-type pollen is inferred to be ancestral to the other pollen types within the family (Walker, 1976), similar pollen could also have been characteristic of the larger Early Cretaceous ancestral complex from which the Chloranthaceae are derived, which may have been much more primitive than the modern family in non-palynological characters.

In contrast to Zone I forms, Subzone II-B angiosperm leaf cuticles are most similar to the subclasses Hamamelididae and Rosidae. The closest resemblances are seen between Platanoid #3 and extant Platanaceae (Hamamelididae). Platanoid #3, like many other Potomac Group platanoids, shares several important venational characters with extant Platanaceae, which include probable palinactinodromous primary venation, closely spaced, percurrent tertiary veins, and orthogonal higher order venation (Figs. 30, 32, 33). Cuticle structure shows an equally strong resemblance. In both groups, contact cell arrangement and specialization conform to the same basic pattern, with the fossil differing in having fewer lateral contact cells that tend to have thicker cuticular flanges along their tangential walls (cf. Figs. 67, 68). Hair base structure is even more similar. In both groups the basal cell of each hair has the shape of a flat-topped cone and is the only cell present in the mature leaf. This cell often possesses a ring of thickened cuticle where it joins the underlying cells, which in veinal areas tend to be smaller than the adjacent cells (Figs. 63–66). These features of both leaf architecture and cuticle structure readily distinguish Platanaceae from other groups and thus strongly suggest a relationship between this family and Platanoid #3. These resemblances, in conjunction with the similarities shown between Platanoid #3 and the other platanoids (cf. above), support the concept that the Potomac Group platanoids represent the Early Cretaceous complex that gave rise to modern Platanaceae (cf. Hickey & Doyle, 1977).

Cuticular anatomy is also consistent with the proposed relationships of *Sapindopsis* and subclass Rosidae (Hickey & Wolfe, 1975; Hickey & Doyle, 1977), but it is not known whether the similarities shared by the two groups are restricted to the subclass. Pinnately compound organization of the *Sapindopsis*-type is almost entirely restricted to Rosidae and inferred derivatives (Hickey & Wolfe, 1975) and admedially oriented tertiary venation of the type present in many *Sapindopsis* leaflets is common within the subclass (Upchurch, unpubl. data). In addition, some West Brothers specimens possess teeth with numerous Rosid features, which include a concave-convex (C-1) shape, symmetrically placed medial vein, and a pair of converging lateral veins, as in the Rosoid tooth type of Hickey and Wolfe (1975) (Fig. 29). The stomatal structure of *Sapindopsis* has many counterparts in extant Rosidae and some of its secretory cells resemble those of a few Rosids. In *Sapindopsis* each guard cell is flanked by at least one specialized lateral contact cell (LCC) and these cells generally extend the full length of the stoma. Polar contact cells (PCC) and other associated cells are variable in their number and patterns of modification. All modified cells are weakly differentiated from the surrounding cells but characteristically have a thinner cuticle, at least adjacent to the guard cells. Many Rosidae have similar stomatal patterns, except that the region of thin cuticle, when present, is almost always restricted to a distinct zone next to the guard cells. Some Cunoniaceae (Fig. 69) and Sapindaceae (Fig. 70) conform to the basic *Sapindopsis* stomatal pattern, while Rhamnaceae and primitive Rosaceae such as *Quillaja* differ only in lacking specialized non-contact cells (Table 8). Other Rosidae with comparable stomatal patterns include Nyssaceae, Alangiaceae, and certain members of Rutaceae, Cornaceae, Celastraceae, and Anacardiaceae (cf. den Hartog & Baas, 1978; Upchurch, unpubl. data). Implications of secretory cell structure are problematic, since no extant angiosperm has been observed with the variable pattern present in *Sapindopsis*; however, the abaxial unicellular, glandular hairs of *Knightia* (Proteaceae), *Platea* (Icacinaceae), and *Flindersia* (Rutaceae, Fig. 71) are similar in shape and position to some protruding *Sapindopsis* secretory cells (cf. Dilcher & Mehrota, 1969; van Staveren & Baas, 1973). Other Rosidae, such as Sapindaceae, Anacardiaceae, and certain Juglandaceae, bear multicellular, generally abaxial glands that are either uniseriate or have a uniseriate stalk, suggesting that they may be derived from the protruding type of secretory structure found in *Sapindopsis*. Additional studies of leaf cuticles from extant angiosperms, along with a detailed phylogenetic analysis of possible *Sapindopsis* relatives from the Late Cretaceous (such as *Anacardites* and "*Rhus*" *powelliana*), are needed to test further the idea of a *Sapindopsis*-Rosidae relationship.

The morphological relationships of Potomac Group cuticle types, in conjunction with their stratigraphic distribution, suggest two previously unsuspected evolutionary trends in the epidermis of early flowering plants. First, stratigraphic and morphologic evidence suggests that the Zone I pattern of secretory cell (SC) construction, with its two distinct types of SCs, gave rise to the highly variable *Sapindopsis* pattern through an increase in developmental plasticity; conversely, the related platanoid patterns appear to be derived through the canalization of one part of this variation (Fig. 72). The epidermal secretory structures of Zone I angiosperms are all unicellular and level with the leaf surface. They conform to two distinct types: one is rounded and has a smooth outer cuticle, while the other is angular and bears radiating striations. The *Sapindopsis* pattern produces variants that are identical to Zone I forms, but these intergrade with

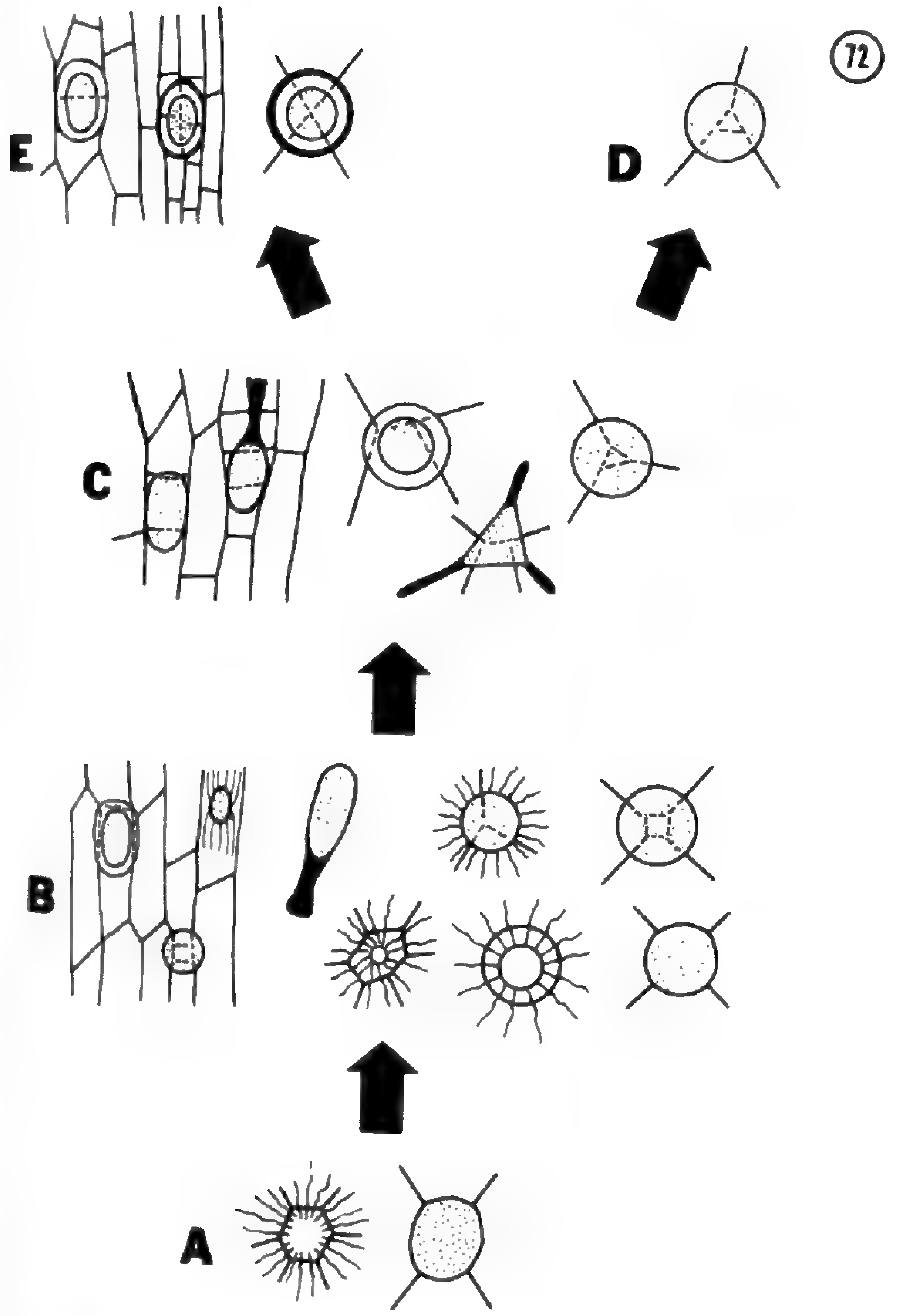


FIGURE 72. Evolution of epidermal secretory cells and homologous hair bases in Potomac Group angiosperm leaves. Legend: A = Zone I secretory cell types. B = *Sapindopsis* pattern of secretory cell and hair base organization. C = Platanoid #1 pattern of secretory cell and hair base organization. D = Platanoid #2 pattern of secretory cell organization. E = Platanoid #3 pattern of hair base organization.

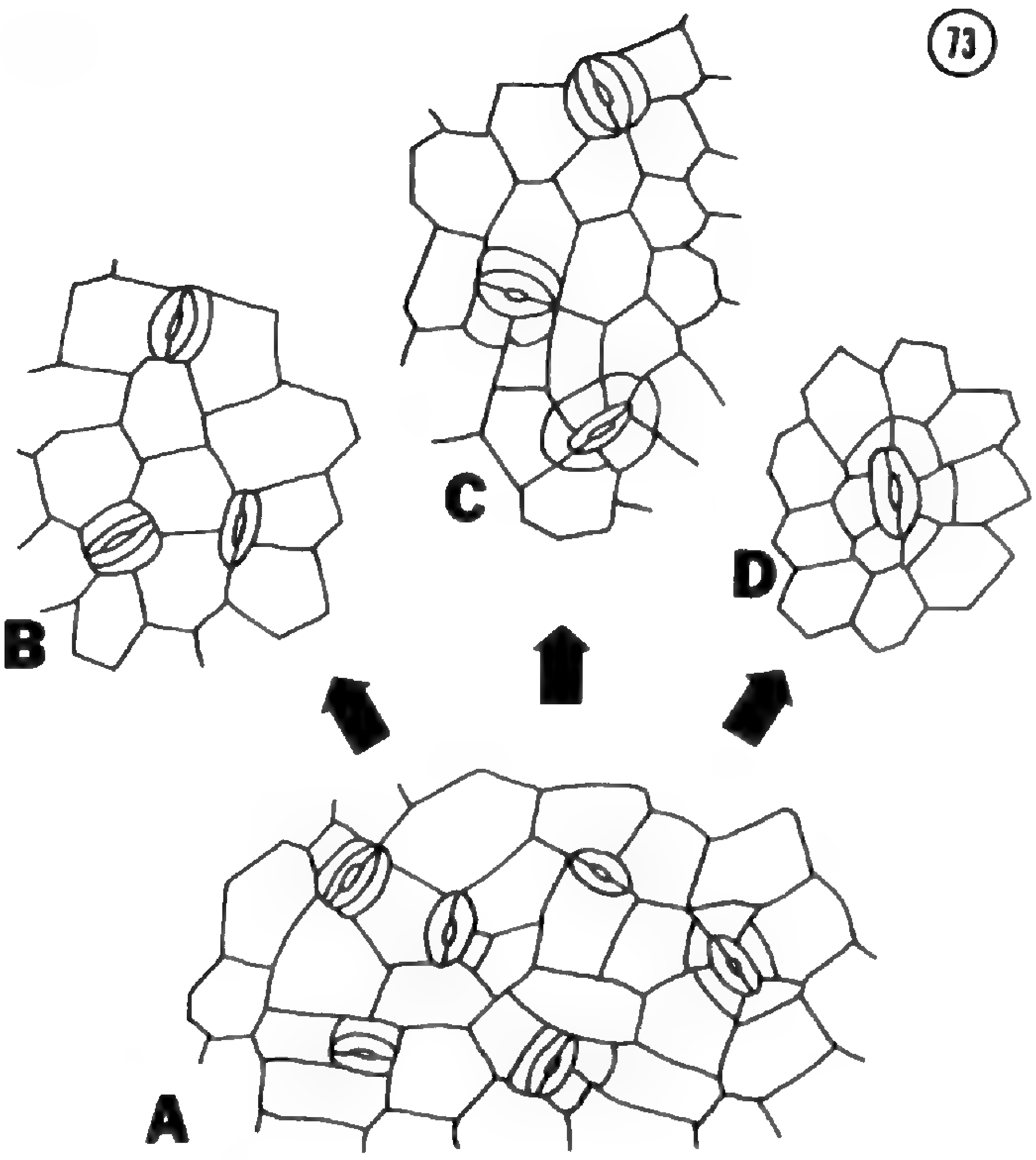


FIGURE 73. Evolution of patterns of variation in subsidiary cell arrangement, Potomac Group angiosperms. Each derived pattern represents one portion of the range of variation present in the ancestral pattern. Legend: A = Zone I pattern. B = *Menispermites potomacensis* pattern. C = *Sapindopsis*/Platanoid pattern. D = New Serrate, Red Point pattern.

each other, divergent types of secretory cells, and the bases of uniseriate hairs. Some secretory structures are level with the epidermis and have flat outer walls, but most rest at least partially on top of other epidermal cells and have protruding outer walls; in addition, they have a variable pattern of positioning relative to the subtending cells. Hair bases resemble this latter type of SC except that each foot cell bears an apical hair abscission scar. The pattern of variation for secretory cells and hair bases in Platanoid #1 is similar to that for *Sapindopsis* except that the Zone I types of secretory cells appear to be absent. The secretory cells of Platanoid #2 and the hair bases of Platanoid #3 are interpreted as independent fixations of different portions of the variation in Platanoid #1 because they resemble different sets of structures found in the latter group. If indeed these proposed homologies among secretory cell and hair base types are correct, then the deciduous hairs of extant Platanaceae are an evolutionary modification of the radiostriate epidermal oil cells present in diverse Magnoliidae. In addition, this proposed series would indicate that the transition between these two structural types was characterized by a stage of extreme developmental plasticity.

The stratigraphic and morphological relationships of the different patterns of variation in stomatal structure also suggest an evolutionary trend towards decreased stomatal variation in early angiosperms, with the later patterns representing independent fixations of a portion of the variation found in Zone I (Fig. 73). The Zone I pattern of variation in subsidiary cell arrangement shows an average of nine out of ten variable features, ranging from seven in cf. *Ficophyllum* to ten in *Eucalyptophyllum*. Stomatal types on a single leaf include paracytic, hemiparacytic, laterocytic, weakly cyclocytic, and (in most groups) anomocytic. Subzone II-B patterns of stomatal variation, in contrast, show an average of only six non-uniform features, with three new, less variable patterns present in addition to the older one. The number of non-uniform features ranges from five in the new serrate from Red Point to

TABLE 9. Stomatal features of Late Cretaceous angiosperms.

Taxon	*Araliephyllum polevoi*	*Debeya tikhonevichii*	*Araliopsis wellingtoniana*	*Dewalquea westerhausiana*	*Dryophyllum cretaceum*
Number of contact cells	4–5(–6)	4–6(–7)	5–7	5–8	5–8
Number of lateral contact cells (LCCs)	2(–3)	2–4	2–4	3–4	3–5
Specialized LCCs in every stoma?	always	always	always	always	always
Specialized LCCs for each GC?	sometimes	always	always	always	always
LCCs specialized full length of stoma?	always	always	mostly	always	always
Number of polar contact cells	2–3(–4)	2–3	2–4	3	2–4
PCCs specialized in each stoma?	never	sometimes	sometimes	sometimes	sometimes
PCCs specialized at both poles?	—	sometimes	sometimes	sometimes	sometimes
Other specialized cells?	sometimes	sometimes	sometimes	sometimes	sometimes
Position	lateral	lateral	variable	variable	variable
Number of variable features	5	6	7	6	7
Stomatal types[a]	P, H	Lc, weakly C	Lc, C	Lc, C	Lc, C

[a] Key: P = paracytic; Lc = laterocytic; C = cyclocytic; H = hemiparacytic.

ten in *Populophyllum*, and the stomatal types present in each new pattern represent a subset of those found in Zone I. Judging from the illustrations of Krassilov (1973), Němejc and Kvaček (1975), and Rüffle and Knappe (1977), Late Cretaceous angiosperms show even less stomatal variation than their Subzone II-B counterparts. The stomata of these angiosperms have an average of 5.5 non-uniform features, ranging from three in *Debeya insignis* to seven in *Araliopsis wellingtoniana* and *Dryophyllum cretaceum* (Tables 9, 10). Usually a leaf possesses no more than

TABLE 10. Stomatal features of Late Cretaceous angiosperms.

Taxon	*Proteophyllum laminarium*	*Grevilleophyllum constans*	*Cocculophyllum extinctum*	*Debeya insignis*
Number of contact cells	4–6	4–6	4–6	5–6
Number of lateral contact cells (LCCs)	2	2	2–4	3–4
Specialized LCCs in every stoma?	always	always	always	always
Specialized LCCs for each GC?	always	always	sometimes	always
LCCs specialized full length of stoma?	always	always	always	always
Number of polar contact cells	2–4	2–4	2–4	2–3
PCCs specialized in each stoma?	sometimes	never	never	always
PCCs specialized at both poles?	never	—	—	always
Other specialized cells?	sometimes	sometimes	sometimes	always
Position	lateral	lateral	lateral	form ring
Number of variable features	6	3	5	3
Stomatal types[a]	P	P	P, Lc	C

[a] Key: P = paracytic; Lc = laterocytic; C = cyclocytic.

two distinct stomatal types, but these belong to the categories found in the Potomac Group. This progressive decrease in stomatal variation, analogous to the contemporaneous trend towards greater vein regularity, suggests that the uniform stomatal patterns characteristic of many extant angiosperms were derived from less uniform patterns through the canalization of the variation in subsidiary cell arrangement. If indeed this trend turns out to be valid for the angiosperms as a whole, then the uniformly paracytic condition of many Magnoliales, considered primitive for the angiosperms by Takhtajan (1969, 1980), Baranova (1972), and Thorne (1976), would be derived. Thus, groups such as Amborellaceae, Austrobaileyaceae, Schisandraceae, and certain Chloranthaceae would be more primitive in their stomatal structure than Magnoliales. In addition, this would suggest that Magnoliales with relatively low stomatal regularity, such as Canellaceae and the New World and Madagascar groups of Winteraceae, are more primitive in stomatal anatomy than uniformly paracytic groups such as Annonaceae and Myristicaceae. Tests of this hypothesis will come from the study of other Early Cretaceous angiosperm leaf floras from low and middle paleolatitudes along with the detailed cladistic analysis of modern and select fossil flowering plants.

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SEED SIZE, DISPERSAL SYNDROMES, AND THE RISE OF THE ANGIOSPERMS: EVIDENCE AND HYPOTHESIS[1]

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The seeds and fruits of angiosperms serve the functions of nurturing, protecting, and dispersing the embryonic plant, and thus form an evolutionarily sensitive portion of the life cycle of the whole organism. Two of these functions also enhance the probability of fossilization of these disseminules. Protection is often achieved through lignification of the fruit or seed wall, predisposing the organ to preservation. Dispersal increases the probability of a propagule arriving at a fossilizing environment. It is, therefore, not surprising that fruits and seeds are a major source of information on the fossil record of the angiosperms, particularly from the Tertiary (Tiffney, 1977a).

This information has generally appeared in descriptive reports of fossil floras and their composition [e.g., the Eocene London Clay Flora (Reid & Chandler, 1933) and the middle Tertiary floras of central Europe (Mai, 1964)]. These floristic studies have formed the basis for synthetic undertakings such as the elucidation of biogeographic patterns (Wood, 1972; Wolfe, 1975; Tiffney, 1980; Mazer & Tiffney, 1982) and the inference of climatic history (Leopold, 1967; Mai, 1970; Friis, 1975; Gregor, 1980a; Collinson et al., 1981). Consideration of evolutionary questions has been largely restricted to the demonstration of species sequences within single genera (e.g., *Stratiotes* L., Chandler, 1923; *Aldrovanda* L., Dorofeev, 1968; *Toddalia* Juss., Gregor, 1979) and families (e.g., Juglandaceae, Manchester & Dilcher, 1981, unpubl. data). However, fruits and seeds additionally offer an excellent starting point for paleobiological inquiry based on modern ecological studies. Of particular note are two considerations: (1) the relation of seed size to the habit and habitat of the parent plant, and (2) dispersal syndromes.

Harper et al. (1970) [after Salisbury (1942)] have demonstrated a strong correlation between seed weight and the stature and successional status of the parent plant. Herbaceous plants, and those of early successional stages, tend to have small propagules, while dominant forest trees and plants of late successional status tend to have large propagules. Some shrubs and "weedy" trees tend to have propagules of intermediate sizes. The mode of dispersal of a living plant may often be inferred from the morphology of the fruit or seed, together with the mode of its presentation to the dispersal agent (Ridley, 1930; van der Pijl, 1969). While fossilization precludes knowledge of the mode of presentation, many of the morphological characters of the fossils permit inference of the mode of dispersal in at least a broad sense. These two features, propagule size and dispersal, have been examined only in modern plants and generally have been treated separately. In the present paper I extend observations on propagule size and dispersal type through the fossil record and propose that these (1) have been related throughout the history of the angiosperms and (2) underwent an intensive period of change in the latest Cretaceous and early Tertiary. My emphasis will be on propagule size; the subject of dispersal syndromes through time warrants a separate study and is not treated in detail here.

METHODS

In the following discussion, I will use the general term "diaspore" to indicate the reproductive unit that is dispersed or sown. Thus, in the case of a capsule, which releases its contents, the term will apply to the morphological seed. In the case of a drupe or berry, the term will encompass fruit tissue. However, in cases in which reference is

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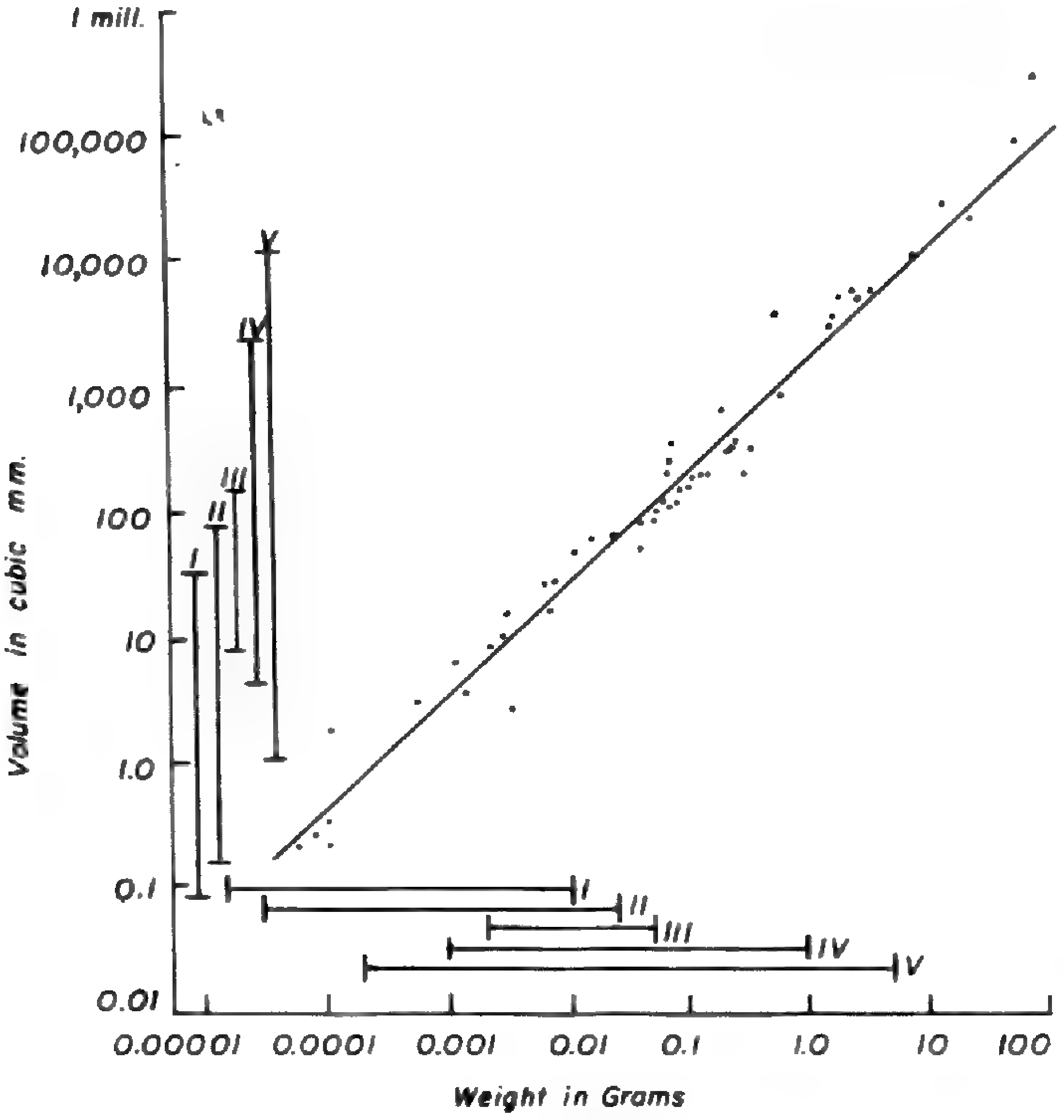

FIGURE 1. Log-log plot of weight versus volume for the propagules of 52 modern angiosperms. The five categories of seed weight (after Harper et al., 1970) on the horizontal axis (weight) are transposed to the vertical axis (volume) by use of the regression line. Categories of plants: I. open habitat; II. woodland margin; III. woodland ground; IV. woodland shrubs; V. woodland trees.

to a specific morphological structure, and particularly when discussing the nutrient reserves of a dispersed seed, I will use the appropriate morphological term.

Salisbury (1942), Harper et al. (1970), and other workers have quantified diaspore size using weight. This approach cannot be applied to a comparative study of fossil seeds because they may be preserved as original organic matter or by replacement with minerals; while lignin has a specific gravity of about 1.2, silicon dioxide has one of 2.65, and pyrite of 5.01. Linear measurements (e.g., length) are also inappropriate because they do not account for variation in three-dimensional shape. I have, therefore, chosen to estimate size from volume. This also permits the calculation of diaspore size from published reports as well as from actual specimens. The use of volume involves two assumptions: (1) that weight and volume are related in fruits and seeds, and (2) that the volumes may be calculated in an accurate and repeatable manner. To test these assumptions, the diaspores of 52 modern species were weighed to the nearest one thousandth of a gram and measured to the nearest tenth of a millimeter. The results are plotted in Figure 1. A regression of weight versus volume yields $r = 0.928$, indicating a significant correlation between the two. This correlation further suggests that the measurement of volume was sufficiently accurate for the purposes of this study.

Diaspore volumes of seven Cretaceous and 20 representative Tertiary and Quaternary floras were then calculated from specimens and the literature (Table 2). In order to obtain accurate identification and measurement of the individual diaspores, only floras with three-dimensional, well-preserved fossils were used. Volumes were obtained only for those fossils that represented diaspores as defined above. Calculations were based on average width, length, and thickness of the specimens as described. In cases where one or more dimensions were not cited, the missing value(s) was estimated from illustrations. In cases of extreme compaction, thickness was assumed to be a value equal to $0.66 \times$ the width. This value was arrived at empirically, and is an outgrowth of the ⅔ power law governing the relation of surface area to volume. The volume of spherical diaspores was estimated at $\frac{4}{3}\pi r^3$. On those occasions where spines or other projections seriously hampered accurate measurement, estimates were made of the volume. The stratigraphic ages of the deposits are those provided by the authors, with modification in light of recent data (Gregor, 1980b) as appropriate. The conversion of stratigraphic age to absolute age is made from van Eysinga (1975) and Gregor (1980b). Assignment of absolute age is necessary to permit calculation of regression values and aids in the relative location of the floras. However, the ages are *approximate* and should be recognized as such. Regression values were calculated using a pre-programmed Texas Instruments TI-55 calculator. Readers are cautioned that the use of numbers with regard to these fossils may convey a false sense of precision. While the numbers used are certainly valid within the relative framework of the present discussion, they often involve subjective judgements and should be regarded as educated approximations, not as absolutes.

DATA

CRETACEOUS FRUITS AND SEEDS

The consideration of Cretaceous fruits and seeds falls into two sections, since floras of three-dimensional fruits and seeds have, to date, only been found in the Late Cretaceous. Before this time, the record of angiosperm reproductive structures involves isolated fossils.

A summary of the better documented fruits and seeds of Early Cretaceous and Cenomanian age (115–95 million years ago, henceforth Ma) is presented in Table 1. The majority of these are preserved as casts or impressions; of the compressions, only a few can be or have been studied in anatomical detail. As a result, many of the earliest reported forms cannot be clearly assigned to the angiosperms and may well be gymnospermous. This has been suggested in the case of *Onoana californica* Chandl. & Axelr. (Chandler & Axelrod, 1961), and by inference *Onoana nicanica* Krass. (Krassilov, 1967), by Wolfe et al. (1975). The same arguments apply to several other Early Cretaceous endocarp-like forms including "*Carpolithus*" (Chandler, 1958), *Nyssidium* Saml. (Samylina, 1961), *Prototrapa* Vas. (Vasil'yev, 1967), *Araliaecarpum* Saml. and *Caricopsis* Saml. (Samylina, 1960) and *Knella* Saml. (Samylina, 1968). Retallack and Dilcher (1981) have similarly viewed many of the above reports as potentially non-angiospermous. These reports will not be considered further.

The remaining reports tabulated in Table 1 fall into two categories. The first includes several structures reported by Fontaine (1889) under the genus "*Carpolithus*" and interpreted by Dilcher (1979) and Retallack and Dilcher (1981) to represent multifollicles. I have not personally examined these specimens and accept the judgement of these authors. The second category includes well-preserved fruits, often containing seeds. These involve clearly angiospermous material such as *Caspiocarpus paniculiger* Vach. & Krass. (Vachrameev & Krassilov, 1979), *Ranunculaecarpus quinquiecarpellatus* Saml. (Samylina, 1960), *Carpites liriophylli* Lesq. (Dilcher et al., 1976) and a host of forms from the Dakota Formation of central North America.

The majority of these Early Cretaceous angiosperm fruits are small, individual carpels ranging from 1 to 15 mm in length and from 0.5 to 8 mm in width, or are capsules of from 10 to 12 mm in diameter. In the five cases where seeds are known from these fruits, the seeds are small, ranging from 0.2 mm^3 (*Caspiocarpus paniculiger*) to approximately 7.5 mm^3 (estimated for the "unpublished five-carpellate fruit" from the Dakota Group; Dilcher, 1979). The one exception to this tendency to small size is *Carpolithus curvatus* Font., which is a carpel about 40 mm long and 15 mm wide. This specimen is not well preserved, and there is no indication as to the size of the included seeds.

The most common fruit morphology is a dehiscent follicle, borne on a central axis, although capsules are also frequently observed. This is in keeping with the classic hypothesis that the conduplicate carpel, and dispersal by morphological seeds, are the primitive conditions in the group (Cronquist, 1968; Takhtajan, 1969). The one potential exception to this pattern is the report of a fleshy fruit from the Cenomanian (98 Ma; Dilcher, 1979). However, the status of this fossil is not clear because Retallack and Dilcher (1981: 49) imply that no fleshy fruits are known from Cenomanian and older sediments. The reported seeds are all apparently thin-walled and without any distinctive features related to dispersal. The capsular-follicular morphology of the fruits and the small, unspecialized, nature of the seeds are characters indicative of a general adaptation to abiotic dispersal mechanisms, a conclusion also reached by Retallack and Dilcher (1981).

Individual fruits are also reported in the Late Cretaceous, often as constituents of compression or impression leaf floras, and several reports exist of isolated occurrences of seeds or seed-like objects (Miner, 1935; Schemel, 1950; Hall, 1963, 1967; Binda, 1968; Colin, 1973; Knobloch, 1981). However, of greater importance to the present work are several fairly diverse (10–50 species) floras of three dimensionally preserved fruits and seeds from fluvial and lacustrine sediments. The most important of these are listed in rows 1–7 of Table 2; several others of lower diversity have not been included but are of a similar nature (Knobloch, 1971, 1977). Although some of these seeds have been assigned to extant families (Caryophyllaceae, Cyperaceae, Menispermaceae, Myricaceae, Theaceae, Urticaceae: Knobloch, 1977; Jung et al., 1978) and orders (Juglandales: Friis, 1984), the majority have been placed in the organ genus *Microcarpolithes* Vangerow erected for seeds or one-seeded fruits of angiospermous affinities. [This genus requires renaming. The type species, *M. hexagonalis* Vangerow (Hall, 1963) has been shown to be an insect coprolite (Knobloch, 1977).]

The average size of the seeds in these floras is approximately 1.7 mm^3 (see Table 2, column $\bar{x}$ and Fig. 2, floras 1–7). This small size does not appear to be a function of mechanical sorting, or of ecological separation, for a variety of reasons. The Santonian-Campanian floras (about 77 Ma) reported by Friis (1984) from Åsen, Sweden, and

TABLE 1. Summary of individually reported fruits and seeds of presumed angiospermous affinities from Early Cretaceous and Cenomanian localities. Judgement of angiospermous affinities in the "comment" column is by the present author unless otherwise noted. "No distinguishing angiospermous features" only implies that the specimen is not *clearly* angiospermous.

Age[a]	Name	Locality	Type	Size	Reference	Comment
Tithonian-Berrasian (134)	"*Tyrmocarpus*"	Tyrma R., Siberia	"capsule-like fruit"	ca. 6 mm diam.	Krassilov (1973) Hughes (1976)	No distinguishing angiospermous features.
Valangian (127)	*Carpolithus*	Vaucluse, France	unclear	22 mm × 12 mm	Chandler (1958)	The original (now lost) was a sandstone cast with no distinctively angiospermous features.
Barremian (117)[b]	*Nyssidium orientale* Sam.	Siberia, U.S.S.R.	unclear—inferred as endocarp	10 mm × 6 mm	Samylina (1961)	No distinguishing angiospermous features. Illustrated specimens show little relation to *Nyssa*. Found in a totally gymnospermous flora.[a]
Barremian (117)[b]	*Nyssidium* Sp.	Siberia, U.S.S.R.	unclear—inferred as endocarp	10 mm × 5 mm	Samylina (1961)	
Barremian (117)[b]	*Onoana californica* Chand. & Axelr.	California, U.S.A.	unclear—inferred as endocarp	20 mm × 15 mm	Chandler and Axelrod (1961)	No distinguishing angiospermous features (Wolfe et al., 1975).[c]
Late Barremian-Early Aptian (112)[d]	*Carpolithus geminatus* Font.	Virginia, U.S.A.	multifollicle	6 mm × 9 mm[e]	Fontaine (1889)	Footnote f.
Late Barremian-Early Aptian (112)[d]	*Carpolithus sessilis* Font.	Virginia, U.S.A.	multifollicle	12 mm × 4 mm	Fontaine (1889)	Footnote f.
Late Barremian-Early Aptian (112)[d]	*Carpolithus virginiensis* Font.	Virginia, U.S.A.	multifollicle	7–10 mm × 4–6.5 mm	Fontaine (1889)	Footnote f.
Aptian (110)	*Onoana nicanica* Krass.	Primorye, U.S.S.R.	unclear—inferred as endocarp	8–10 mm × 5.5–7.5 mm	Krassilov (1967)	No distinguishing angiospermous features (cf. Wolfe et al., 1975). Preservation poor.[c]
Aptian-Albian (107.5)	*Prototrapa douglasi* Vass.	Victoria, Australia	endocarp	1–3 mm × 0.5–1.5 mm	Vasil'yev (1967)	Resemblance to *Trapa* is superficial; angiospermous affinities unclear. Impression.

TABLE 1. (Continued).

Age[a]	Name	Locality	Type	Size	Reference	Comment
Aptian-Albian (107.5)	*Prototrapa praepomelii* Vass.	Victoria, Australia	endocarp	2 mm × 1 mm	Vasil'yev (1967)	Resemblance to *Trapa* is superficial; angiospermous affinities unclear. Impression.
Aptian-Albian (107.5)	*Prototrapa tenuirostrata* Vass.	Victoria, Australia	endocarp	1.2 mm × 0.5 mm	Vasil'yev (1967)	Resemblance to *Trapa* is superficial; angiospermous affinities unclear. Impression.
Albian (105)[b]	*Araliaecarpum kolymensis* Sam.	Siberia, U.S.S.R.	unclear; possibly a winged endocarp?	6 mm × 6 mm	Samylina (1960)	Affinities unclear to present author.
Albian (105)[b]	*Caricopsis compacta* Sam.	Siberia, U.S.S.R.	unclear	3–5 mm × 2 mm	Samylina (1960)	Affinities unclear to present author.
Albian (105)[d]	*Carpolithus conjugatus* Font.	Virginia, U.S.A.	multifollicle	7.5 mm × 3.6 mm[e]	Fontaine (1889)	Footnote f.
Albian (105)[d]	*Carpolithus curvatus* Font.	Virginia, U.S.A.	multifollicle	42 mm × 14.2 mm[e]	Fontaine (1889)	Footnote f.
Albian (105)[d]	*Carpolithus fasiculatus* Font.	Virginia, U.S.A.	multifollicle	15 mm × 8 mm[e]	Fontaine (1889)	Footnote f.
Albian (105)[d]	*Carpolithus ternatus* Font.	Virginia, U.S.A.	multifollicle	8–11 mm × 4–7 mm[e]	Fontaine (1889)	Footnote f.
Albian (105)[g]	*Carpolithus karatscheensis* Vachr.	Kazakhstan, U.S.S.R.	multifollicle	—	Vachrameev (1952)	Original article not seen; data from Retallack and Dilcher (1981).
Albian (105)	*Caspiocarpus paniculiger* Vachr. & Krass.	Kazakhstan, U.S.S.R.	dehiscent follicle	Fruit—1 mm × 0.5 mm Seed—0.8 × 0.5 mm	Vachrameev and Krassilov (1979)	Clear angiospermous affinities.
Albian (105)[b]	*Knella harrisiana* Sam.	Kolyma R., U.S.S.R.	unclear—endocarp?	16 mm × 5 mm	Samylina (1968)	Poor preservation, angiospermous affinities not demonstrated. See also Hughes (1976).[c]

TABLE 1. (Continued).

Age[a]	Name	Locality	Type	Size	Reference	Comment
Albian (105)[b]	*Ranunculaecarpus quinquiecarpellatus* Sam.	Kolyma R., U.S.S.R.	Dehiscent follicle	Fruit—10 mm × 5 mm × 2 mm Seed—1.5 mm × 0.6 mm	Samylina (1960)	Angiospermous affinities fairly certain.
Cenomanian (97.5)	*Carpites liriophylli* Lesq.	Dakota Group, U.S.A.	Dehiscent follicle	Fruit—15–20 mm × 3–4 mm Seed—1.4 mm × 0.6 mm	Dilcher et al. (1976); Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	*Carpites tiliaceus* Lesq.	Dakota Group, U.S.A.	Five-valved capsule	ca. 10 mm diam.[h]	Lesquereux (1892); Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	*Laurus macrocarpa* Lesq.	Dakota Group, U.S.A.	Syncarpous fruit	12 mm × 8.3 mm[h]	Lesquereux (1874); Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	*Platanus primaeva* Lesq.	Dakota Group, U.S.A.	Spherical mass of individual fruits	head ca. 3–4 mm diam.[h]	Lesquereux (1892); Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	"*Salix*"	Dakota Group, U.S.A.	Dehiscent follicle	3.3 mm × 1.5 mm[h]	Lesquereux (1892); Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	un-named	Dakota Group, U.S.A.	Fleshy fruit	5–6 mm diam.[h]	Dilcher (1979)	Dilcher (1979) interprets as angiospermous.

TABLE 1. (Continued).

Age[a]	Name	Locality	Type	Size	Reference	Comment
Cenomanian (97.5)	"unpublished 5-carpellate fruit"[i]	Dakota Group, U.S.A.	Five-valved capsule	Fruit—10 mm diam. Seeds—3.3 mm × 2.5 mm × 1.2 mm[i]	Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	"un-named follicular axis associated with *Magnoliaephyllum*"	Dakota Group, U.S.A.	Dehiscent follicle	Fruit—2.7 mm × 2.0 mm Seed—0.8 mm × 0.5 mm[h]	Dilcher (1979)	Clear angiospermous affinities.
Cenomanian (97.5)	"un-named globose heads"	Dakota Group, U.S.A.	Globose mass of individual fruits	Head ca. 10 mm × 7.5 mm diam.[h]	Dilcher (1979)	Fairly clear angiospermous affinities.
Cenomanian (94)	Platanaceae	Dakota Group, U.S.A.	Spherical mass of individual fruits	Not given	Schwarzwalder and Dilcher (1981)	Infructescences and leaves demonstrably related to Platanaceae.

[a] Absolute ages after van Eysinga (1975).

[b] Age after Hughes (1976).

[c] Retallack and Dilcher (1981) consider the angiospermous affinities of this species to be unproven.

[d] Age after Doyle and Hickey (1976).

[e] Measurements are approximate; made from Fontaine's (1889) illustrations.

[f] The identification of this species as a multifollicle is provided by Retallack and Dilcher (1981), although Fontaine (1889) placed it as a seed of a gymnosperm. I have not viewed this material.

[g] Age after Vachrameev and Krassilov (1979).

[h] Measurements are approximate; made from Dilcher's (1979) illustrations.

[i] This unpublished specimen may be the same as *Carpites tiliaceus* Lesq. (Dilcher, 1979). Since the measurements given for both seed and fruit are made from Dilcher's illustrations, they must be viewed as approximate. The measurements for the seed are taken from the presumed seed-cavity cast.

TABLE 2. Data on individual Late Cretaceous and Tertiary fruit and seed floras. N = total number of seeds measured in flora, $\bar{x}$ = average value, s.d. = standard deviation, CV = covariance.

Stratigraphic Age	Estimated Numeric Age[a]	Locality	Reference	N	$\bar{x}$ (mm^3)	s.d.	Co. var. (s.d./$\bar{x}$)	Largest (mm^3)	Smallest (mm^3)
1. Santonian-Campanian	77	Åsen, Sweden	Friis (1984)	>50	–	–	–	27[b]	0.02[b]
2. Santonian-Campanian	77	Gay Head, Massachusetts, U.S.A.	Tiffney (unpubl. data)	41	5.7	10.5	1.82	55	0.03
3. Santonian-lower Campanian	77	Staré Hamry 1, Czechoslovakia	Knobloch (1977)	19	1.4	0.7	0.5	3	0.41
4. Senonian	75[c]	Aachen, West Germany	Vangerow (1954)	11	0.2	0.17	0.83	0.5	0.03
5. Senonian	75[c]	Petrovice, Czechoslovakia	Knobloch (1964)	11	0.3	0.2	0.625	0.73	0.11
6. Campanian-Early Paleocene	73–63?[d]	Horní, Bečva, Czechoslovakia	Knobloch (1977)	29	1.5	1.4	0.91	6.4	0.15
7. Late Senonian	69	Kössen, Austria	Knobloch (1975)	9	1.3	0.9	0.69	3	0.15
8. Late Senonian	69	Kössen, Austria	Jung et al. (1978)	13	1.5	1.2	0.82	3	0.15
9. Maastrichtian-Middle Paleocene	67–61?[d]	Rusava, Czechoslovakia	Knobloch (1977)	20	1.2	0.8	0.66	3	0.06
10. Late Paleocene	55	Woolwich and Reading Beds, England	Chandler (1961)	18	129	234	1.82	731	1.2
11. Ypresian (Early Eocene)	52	London Clay, England	Reid and Chandler (1933)	202	1,957	5,932	3.03	61,318	0.25
12. Lutetian (Middle Eocene)	45	Geiseltal, East Germany	Mai (1976)	25	308	643	2.1	3,182	2.1
13. Auversian (Late Eocene)	42	Clarno, Oregon, U.S.A.	Scott (1954); Bones (1979)	33	3,729	10,626	2.8	59,150	0.25
14. Middle Oligocene	32	Haselbach, East Germany	Mai and Walther (1978)	79	268	1,220	4.5	9,294	0.07
15. Middle Oligocene	30	Bovey Tracey, England	Chandler (1957)	33	68	225	3.3	1,300	0.35
16. Late Oligocene	25	Tomsk, Siberia U.S.S.R.	Nikitin (1965)	95	19	123	6.4	1,200	0.07
17. Lower to Middle Ottnangian (Lower Miocene)	18.5	Chomutov-Most-Teplice Basin, Czechoslovakia	Bůžek and Holý (1964)	22	19	38.6	2	180	1.27

TABLE 2. (Continued).

Stratigraphic Age	Estimated Numeric Age[a]	Locality	Reference	N	$\bar{x}$ (mm^3)	s.d.	Co. var. (s.d./$\bar{x}$)	Largest (mm^3)	Smallest (mm^3)
18. Lower Miocene	18	Rusinga, Kenya	Chesters (1957)	29	1,319	2,044	1.6	10,935	63
19. Middle Ottnangian (Lower Miocene)	18	Wiesa, East Germany	Mai (1964)	71	1,410	3,263	2.3	15,611	0.25
20. Middle to Upper Ottnangian (Lower Miocene)	18	Hartau, East Germany	Mai (1964)	51	774	2,303	3	11,600	1
21. Upper Ottnangian (Lower Miocene)	17.5	Turów, Poland	Czeczott and Skirgiello (1959, 1961a, 1961b, 1967, 1975, 1980a, 1980b)	47	2,501	4,340	1.7	15,096	2
22. Carpathian (Lower Miocene)	17	Nowy Sącz Basin, Poland	Łancucka-Środoniowa (1979)	79	7	22.8	3.3	179	0.014
23. Badenian (Middle Miocene)	14.5	"Gdów Bay," Poland	Łancucka-Środoniowa (1966)	52	95	366	3.9	2,125	0.04
24. Pliocene	3.5	Kranichfeld, East Germany	Mai (1965)	35	13	63	5	1,215	0.1
25. Pliocene	3.5	Bergheim, West Germany	van der Burgh (1978)	83	100	245.5	2.5	1,400	0.9
26. Plio-Pleistocene	1.8	Rippersroda, East Germany	Mai et al. (1963)	66	68.1	301	4.4	2,125[e]	0.014
27. Holocene	0.035 0.068	New Haven, Connecticut, U.S.A.	Pierce and Tiffney (unpubl. data)	43	1,077	4,116	3.8	25,000[f]	1.1

[a] Numerical ages after van Eysinga (1975), millions of years (Ma).

[b] Estimated from absolute possible smallest and largest sizes of angiosperm fruiting remains presented in Friis (1984). The largest fruiting remain is a seed-bearing fruit (Friis, pers. comm.) and is likely not the unit of dispersal.

[c] Deposit cited as "Senonian;" 75 Ma is taken as the midpoint of the Senonian.

[d] Exact stratigraphic position of deposit not determined; possible range indicated.

[e] This value is for a nut of *Corylus*.

[f] Value for *Juglans cinera*; the next largest value is 8,000 mm^3 for *Carya*.

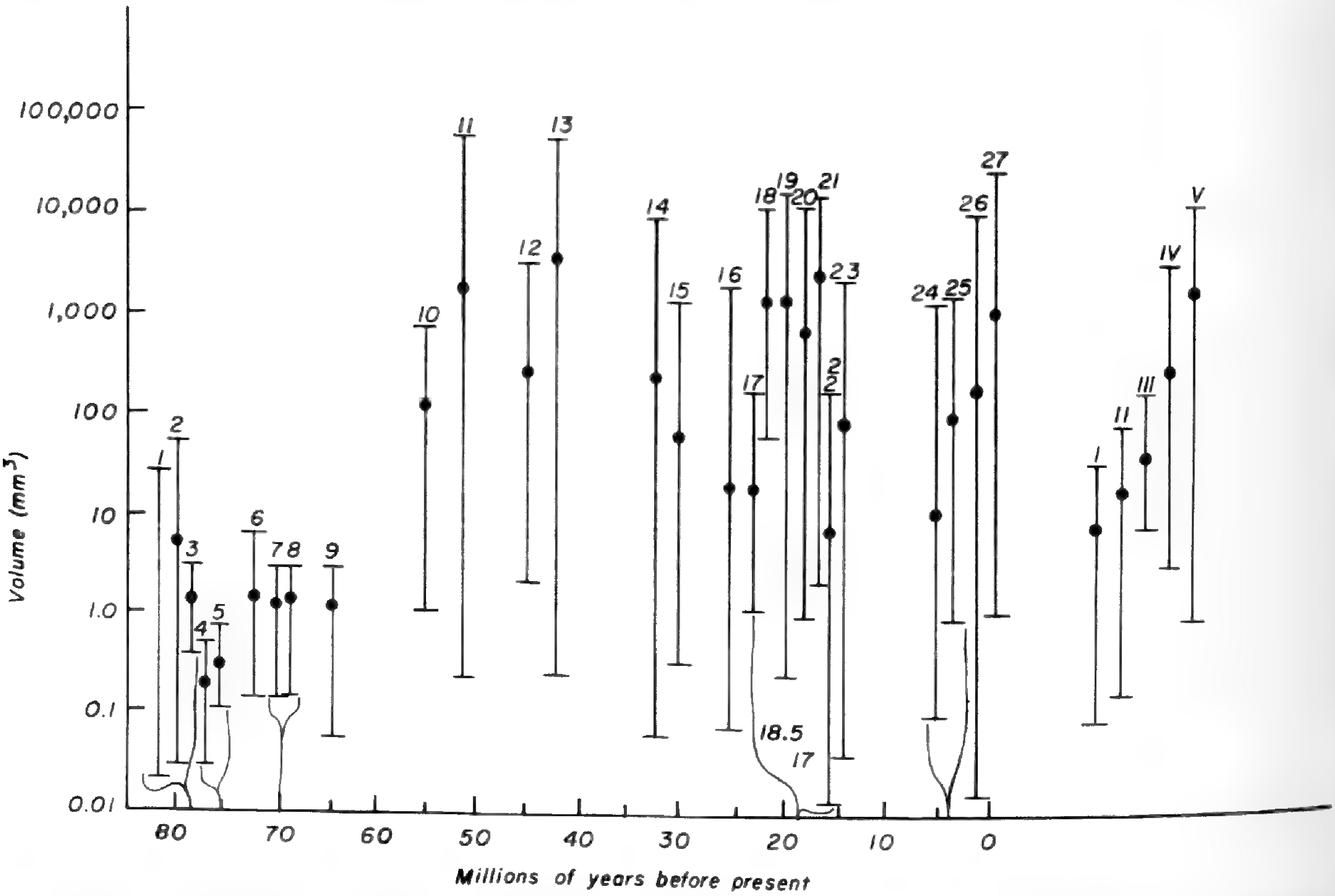

FIGURE 2. Plot of seed volume (vertical axis, logarithmic) versus time (horizontal axis) for 27 Cretaceous and Tertiary fruit and seed floras. The vertical line for each flora indicates the range of diaspore volume; the central dot, the average diaspore volume. The lines I–V at the far right correspond to the volume equivalents of the ecological classes of Harper et al. (1970) as derived in Figure 1. (I. Open habitat; II. woodland margins; III. woodland ground; IV. woodland shrubs; V. woodland trees.) Note that the average volume is not available for flora #1, and that in several cases (floras 1–3, 7, 8, 17–22, 24, 25), more than one flora occurs at a single time.—1. Åsen, Sweden (Friis, 1984).—2. Gay Head, Massachusetts, U.S.A. (Tiffney, unpubl. data).—3. Staré Hamry 1, Czechoslovakia (Knobloch, 1977).—4. Aachen, West Germany (Vangerow, 1954).—5. Petrovice, Czechoslovakia (Knobloch, 1964).—6. Horní Bečva, Czechoslovakia (Knobloch, 1977).—7. Kössen, Austria (Knobloch, 1975).—8. Kössen, Austria (Jung et al., 1978).—9. Rusava, Czechoslovakia (Knobloch, 1977).—10. Woolwich and Reading beds, England (Chandler, 1961).—11. London Clay, England (Reid & Chandler, 1933).—12. Geiseltal, East Germany (Mai, 1976).—13. Clarno, Oregon, U.S.A. (Scott, 1954; Bones, 1979).—14. Haselbach, East Germany (Mai & Walther, 1978).—15. Bovey Tracey, England (Chandler, 1957).—16. Tomsk, Siberia, U.S.S.R. (Nikitin, 1965).—17. Chomutov-Most-Teplice Basin, Czechoslovakia (Bůžek & Holý, 1964).—18. Rusinga, Kenya (Chesters, 1957).—19. Wiesa, East Germany (Mai, 1964).—20. Hartau, East Germany (Mai, 1964).—21. Turów, Poland (Czeczott & Skirgiello, 1959, 1961a, 1961b, 1967, 1975, 1980a, 1980b).—22. Nowy Sącz Basin, Poland (Łancucka-Środoniowa, 1979).—23. "Gdów Bay," Poland (Łancucka-Środoniowa, 1966).—24. Kranichfeld, East Germany (Mai, 1965).—25. Bergheim, West Germany (van der Burgh, 1978).—26. Rippersroda, West Germany (Mai et al., 1963).—27. New Haven, Connecticut, U.S.A. (Pierce & Tiffney, unpubl. data).

by Tiffney (unpubl. data, see Tiffney, 1977b) from Massachusetts, U.S.A., are both in fluvial deposits containing large pieces of wood and, in the case of Tiffney's material, conifer cones (Miller & Robison, 1975). The same situation exists in lagoonal sediments of a similar age from Cliffwood Beach, New Jersey, U.S.A. (Tiffney, unpubl. data). Thus, the size of the angiosperm reproductive remains from these deposits cannot be explained by mechanical sorting.

It is possible that a uniformly small seed size could result from the derivation of the fossils from a single, ecologically-specialized aquatic community, or a combination of aquatic and river-floodplain communities. At the outset, it is noteworthy that in one case (Petrovice, Czechoslovakia, flora #4) Knobloch (1964) described a seed flora of 11 species of *Microcarpolithes* comparable in all respects with other central European Cretaceous fruit and seed floras, but in the same sample as a flora of large leaves including *Araliophyllum* sp. Ett., *Debeya bohemica* Knob., *Pseudoprotophyllum senonense* Knob., *Quercophyllum triangulodentatum* Knob., *Laurophyl-*

lum elegans Holl., *Proteophyllum* sp., *Platanophyllum* sp., *Cinnamomophyllum* sp., and three species of *Dicotylophyllum.* This clearly suggests that at least some of these seeds were borne by woody, nonaquatic vegetation. The question remains, do these floras sample only unstable floodplain forests? The answer lies in an examination of Tertiary and modern deposits, where we have a better idea of the community affinity of the fossils through their taxonomy. The fluvial deposits of the Tertiary (e.g., Bergheim, or those described by Gregor, 1978, 1980b) often include a wide range of fruit and seed sizes that are presumed on taxonomic grounds to be derived from several separate communities, including upland mesic ones. This is further supported by the New Haven, Connecticut flora (#27), which is of Holocene age and includes many upland taxa. Even those Tertiary floras least affected by transport include occasional samples of plants growing in the mesic sites surrounding the water. For example, the Oligocene (30 Ma) lacustrine Bovey Tracey flora of England (Chandler, 1957) includes larger seeds of such trees as *Magnolia* L., *Fagus* L., and *Nyssa* Gronov. ex L. In conclusion, it seems unlikely that these Cretaceous floras are solely records of aquatic or floodplain vegetation.

The morphology of these Late Cretaceous fruits and seeds is somewhat more diverse than that of the Early Cretaceous and Cenomanian remains. Follicles and capsules are still common (Massachusetts and New Jersey deposits), but some evidence is at hand for nuts and drupes (Friis, 1984; Tiffney, unpubl. data). While many of the seeds in these deposits have thin or fragile walls, others have rather thick walls and well-developed surficial sculpture. The dehiscent fruits and thin-walled small seeds suggest the continuing importance of abiotic dispersal mechanisms. However, the presence of drupes and seeds with thick walls is circumstantial evidence for at least the potential for adaptation to animal dispersal, if not for its presence in a limited degree.

Exceptions exist to the general rule of small Cretaceous diaspores. Monteillet and Lappartient (1981) reported a Late Campanian to Maastrichtian (70–66 Ma) flora from Senegal, including seven species of angiosperm fruits with an average volume of 51,950 mm^3. The fossils are poorly preserved, and in the cases of "*Annona*" L., "*Cola*" Schott, and perhaps "*Cordyla*" Lour. and "*Trichilia*" P.Br., I am not convinced that the specimens are of plants. The illustrated specimens of *Borassus* L., *Meliacea* (? new form genus), and perhaps *Nauclea* L. are more convincing. Chesters (1955) has also reported large fruits of Annonaceae, Icacinaceae, and possible other angiosperms from the Maastrichtian (68 Ma) of Nigeria. Although large fruit size is no guarantee of large seed size (*Nauclea* has tiny seeds, Willis, 1973); it appears that larger diaspores were becoming more common in the late Cretaceous.

TERTIARY FRUITS AND SEEDS

Individual large diaspores are known from the Paleocene (Brown, 1962; Koch, 1972a, 1972b), but the only published fruit and seed floras are those of the Woolwich and Reading beds of southern England and possibly Horní Bečva and Rusava, Czechoslovakia. The Rusava flora (Knobloch, 1977) is between latest Cretaceous (67 Ma) and middle Paleocene (60 Ma) in age, while Horní Bečva is inferred from Table 1 of Knobloch (1977) as being between Campanian (73 Ma) and Early Paleocene (63 Ma) in age. Both floras are quite similar to those of Staré Hamry 1 and Petrovice, to which they are geographically close.

By contrast, the flora of the Late Paleocene (55 Ma) Woolwich and Reading beds (Chandler, 1961) includes a diverse array of large and small diaspores with an average volume of 129 mm^3. This sets the pattern for the remaining Tertiary floras, which vary in percentage composition of larger and smaller diaspores, but which always include both. The basic trends can be discerned from columns "$\bar{x}$," "largest diaspore," and "smallest diaspore" in Table 2, and from floras 10–27 of Figure 2. Very large diaspores first appear in numbers in the Early Eocene (52 Ma) London Clay flora and dominate the Middle Eocene (45–42 Ma) Geiseltal and Clarno floras and the mid-Oligocene (32 Ma) Haselbach flora, resulting in high average diaspore sizes for these floras. From the Late Oligocene, there is a general tendency for the average diaspore size of a flora to decrease through Pliocene/Pleistocene time, although this trend is not statistically significant. This decrease in average diaspore size is not due to a decrease in the size of the largest diaspores in each flora (by regression of largest seed size versus age ($P = 0.1$; $r = 0.40$, $N = 18$), but to the occurrence of fewer large diaspores in each flora.

Herbaceous angiosperms began to diversify dramatically in the latest Paleogene and the early Neogene (Tiffney, 1981). Herbs normally have small seeds (Harper et al., 1970), and their increasing importance during this time is reflected in the reduced average diaspore volumes of the floras commencing with the Lagernogo Sad deposit (Tomsk, Siberia; age from Dorofeev, 1963) and carrying through the later Tertiary floras from the Chumotov-Most-Teplice basin (Czechoslovakia), Nowy Sącz basin (Poland), and Kranichfeld (East Germany). While the average diaspore volume (ADV) of these floras is small relative to that of other Tertiary floras, it is markedly larger than the ADV of the Cretaceous floras. The large average volumes for the Miocene Gdów Bay (Poland) and Pliocene Rippersroda (East Germany) floras are due to the presence of a few large diaspores. Deletion of *Corylus* L., *Fagus* L., and *Carya* Nutt. from the former flora brings the average volume down to 9.2 mm³, and deletion of *Trapa* L. and *Corylus* L. from the Rippersroda flora brings the average volume down to 21.5 mm³. The large average volume for the Pliocene Bergheim flora (Mine Fortuna-Garsdorf 1) of West Germany results from the river sands of this deposit having a large allochthonous component derived from upland forest trees (e.g., *Magnolia* L., *Persea* Mill., *Corylus* L., *Castanea* Mill., *Quercus* L., *Halesia* J. Ellis ex L., *Styrax* L.). In spite of these individual differences in ecological and taphonomic setting, it is interesting that each of these floras shows a greater range of diaspore size and a higher average diaspore volume than the Cretaceous floras.

The dispersal mechanisms and syndromes of Tertiary angiosperm fruits and seeds may be inferred from their morphology and from their living relatives. Neither source is totally satisfactory; many morphological features are not preserved, and present dispersal adaptations of a genus or family are no guarantee of past mechanisms. However, both lines of evidence suggest that a wide range of fruits and seeds adapted to animal dispersal were present by the Eocene and Oligocene. This included a variety of sizes from the smaller berries of the Vitaceae to the larger aggregate fruits of the Annonaceae or the drupes of the Mastixiaceae. This diversity of fruit types and sizes offered opportunities to a range of dispersal agents, but particularly to those able to deal with larger disseminules. With the Miocene diversification of herbaceous angiosperms (Retallack, 1981; Tiffney, 1981), an array of small seeds and fruits became available, which was probably important to ground-dwelling rodents and granivorous birds. Thus, the Tertiary appears to be the time in which major dispersal patterns (diaspore morphologies, relations with particular agents) first achieved their modern form and diversified among angiosperms.

SUMMARY

Cretaceous diaspores are generally small. Cretaceous seed floras are marked by a small average diaspore volume (ADV) and a limited range of diaspore volume (RDV). Early Tertiary floras exhibit a major increase in ADV. Succeeding floras show a broad trend of decreasing ADV, but with no decrease in RDV. The change in ADV through the Tertiary is a result of changes in the relative proportions of large and small diaspores in each flora. Small diaspores show no trend in size change through the Cretaceous and Tertiary, and after their appearance in the Tertiary, large diaspores also show no trend in size change. The increase in diaspore size is paralleled by an apparent change from the dominance of abiotic dispersal mechanisms in the Cretaceous to the increasing importance of biotic dispersal agents commencing in the earliest Tertiary.

This pattern of change in size and mode of dispersal cannot be ascribed to taphonomic or ecologic factors because similar depositional environments are sampled in both Cretaceous and Tertiary deposits. Certainly the deposits of Åsen and Massachusetts demonstrate that larger fruits and seeds could have been carried into the deposit and preserved if present. Many of the Tertiary deposits (e.g., Nowy Sącz, Kranichfeld) demonstrate that even deposits dominated by aquatic vegetation may be expected to include some elements of mesic communities.

Climate could have influenced the composition of the vegetation or the presence of dispersal agents. However, Cretaceous climates from the first appearance of the angiosperms through to the latest Cretaceous are generally felt to have been as warm as those of the early Tertiary (Savin, 1977; Barron et al., 1981; Thompson & Barron, 1981), although there is good evidence for a latest Cretaceous–Paleocene cool phase (Hickey, 1981). In addition, the European Pliocene and Quaternary include climates that were cooler than those of any period of angiosperm history, but floras from these epochs have at least a few large diaspores. Perhaps the only unanswerable bias is that all the fruit and seed data are derived from northern hemisphere, primarily European, localities. It is possible that different patterns in the evolution of diaspore size could have taken place in other portions of the world, but this cannot be evaluated from existing paleontological data. However, extant tropical (Levin, 1974) and temperate (Salisbury, 1942; Harper et al., 1970) angiosperm fruits and seeds apparently exhibit the same range of sizes.

The timing of this transition from small to large diaspores, and from the dominance of abiotic dispersal to the increased importance of biotic dispersal, is not clear from present knowledge. Since the mid- to Late Cretaceous and the early to mid-Tertiary of Europe both possessed warm climates, they presumably had a similar potential to host tropical plants. If plants with large diaspores were present in the Cretaceous tropics, they should have been seen in the European Cretaceous, much as they were in the Tertiary. However, a Cretaceous-Tertiary boundary cooling at higher latitudes (Hickey, 1981) could have masked the evolution of angiosperms with large diaspores in the tropics in the latest Cretaceous. These could have then appeared in northerly latitudes with the return of subtropical climates in the early Tertiary.

INTERPRETATIONS

The observed pattern in seed size can be explained most simply as a response to one or both of two ecological factors. The first is the relation between seed size and the habit or ecological site of the parent plant. The second is the importance of dispersal agents, which exert pressure on the morphology and size of fruits and seeds, as evidenced by the existence of distinct "dispersal syndromes" in the angiosperms (van der Pijl, 1969). Each of these factors will be treated in turn.

SEED SIZE AND PARENT PLANT HABIT/HABITAT

Harper et al. (1970) and Silvertown (1981), following on the classic work by Salisbury (1942), have demonstrated a correlation between the habit, habitat, and diaspore weight of individual plants. Short-lived or weedy plants of open or unstable habitats generally have many small diaspores that may be dispersed widely, often by abiotic mechanisms (wind, water). These seeds provide very little nutrient reserve to the germinating seedling, so that seedlings generally survive only in open, sunny habitats. However, the large numbers and wide dispersal of these diaspores increase the likelihood that a few seedlings will germinate in suitable habitats. At the other end of the scale, dominant, long-lived, forest trees of large stature tend to bear fewer, larger diaspores, often involving large seeds. Because of their mass, such diaspores are often dispersed by biotic vectors, although less frequently they may be transported by gravity or water. A large seed provides a massive reserve of nutrients to the young seedling and enables it to become established in the shade of the deep forest. Between the two extremes are groups of plants with intermediate habit, habitat, diaspore, and seed size including (in order of decreasing stature and seed size) woodland shrubs, woodland herbs, and herbs of woodland margins.

It should be noted that this is a general tendency, rather than an invariant rule. Habit and habitat adaptation may interact in a complicated manner and influence seed weight. Several early seral (weedy) trees have seeds as small as those of herbs, but possess a tree habit. However, such species (e.g., *Populus* L., *Betula* L., and *Fraxinus* L. in temperate forests; *Cecropia* Loefl. in the New World tropics) are often fast-growing and short-lived, and tend not to form time-stable, closed communities. Further, other features, including water availability and degree of seasonality, may influence diaspore and seed size (Baker, 1972; Levin & Kerster, 1974), and seed sizes in each ecological class appear to be slightly larger in tropical communities than in temperate ones (Levin, 1974). However, an overview of this variation suggests that the basic pattern of correlation of seed size with the habit and ecology of the parent plant holds as a broad principle in a wide range of environments.

A graphic summary of the average diaspore volume and range of diaspore volume for several modern ecological groups is presented in Figure 2 (cf. Harper et al., 1970). The values for each category were originally calculated by weight (Salisbury, 1942; Levin, 1974), but I have converted this to cubic millimeters by use of the graph presented in Figure 1.

Comparison of the values for the average and range of diaspore volumes (ADV, RDV) for each of these ecological groups with the ADV and RDV for the fossil floras reveals a clear pattern. Cretaceous floras (#1–7) have ADVs equal to or less than that for modern plants of open communities. Further, only in the case of the flora from Massachusetts (#2) does the RDV exceed that seen in modern plants of open habitats. The sedimentary context (Doyle & Hickey, 1976;

Hickey & Doyle, 1977), and the small seeds of the earliest angiosperms, support the contention that they were "weedy" plants of unstable or transient habitats outside of the climax gymnosperm forest (Takhtajan, 1976; Hickey & Doyle, 1977; Doyle, 1978; Niklas et al., 1980; Tiffney, 1981). Note that this statement does not exclude the possibility that the Cretaceous floras included trees, for the ADVs of several Cretaceous floras overlap with the lower end of the range of tree diaspore volumes. However, although trees and shrubs may have been present in these communities, the small sizes of the diaspores involved imply that these were likely early successional plants rather than canopy dominants. An example may be provided by *Platanus* L., which is probably present as early as the Cenomanian (97 Ma) (Dilcher, 1979; Schwarzwalder & Dilcher, 1981). *Platanus* is an early successional tree in modern floras (Braun, 1950) and has been demonstrated to occupy unstable, stream-side habitats in the Eocene (Wing, 1981).

By contrast, the Tertiary floras possess a wide range of diaspore volumes embracing all five ecological categories of diaspore size. This suggests that each flora has the potential to contain plants of any and all habits and habitats. It is not possible to be certain that any one flora was dominated by plants of a particular habit or habitat from diaspore size for three reasons. First, the diaspore sizes for the five modern ecological categories do overlap. Second, taphonomic factors have resulted in the mixing of disseminules from different communities in the fossil record. Third, the average diaspore volume (ADV) for each fossil flora is not a fully trustworthy indicator of the dominant physiognomy of the community; one or two large fruits can drastically affect the ADV of a flora. For example, the elimination of the three largest diaspores (two species of *Carya* and one of *Juglans*) from the New Haven flora (Fig. 2, #27; N = 43 species) drops the ADV from 1,077 mm^3 to 133 mm^3. The degree of influence of large specimens on the ADV may be approximated by the coefficient of variation ($s.d./\bar{x}$, see Table 2). Large values of the coefficient of variation indicate that the mean is not that of a randomly distributed population but is an artifact of a polymodal distribution. The value of this coefficient is high through the Tertiary and shows no significant directional change during this time (commencing with the Woolwich and Reading beds, a regression of the coefficient of variation with time yields $P > 0.20$; $r = -0.27$, N = 18).

In a broad manner, the ADV decreases through the Tertiary, although not in a statistically-significant manner (regression of ADV versus time yields $r = 0.27$, N = 18). The floras (Fig. 2) of the London Clay and Clarno have ADVs very close to that for trees in the modern day. This is not unexpected, as both floras are presumed on taxonomic bases to be related to the modern forests of Indomalaysia (Chandler, 1964). From this high, the ADV falls off through the Tertiary to values close to those for modern plants of open environments (note flora #22, Nowy Sącz, and #24, Kranichfeld). This trend indicates an increasing dominance of smaller-seeded plants and parallels the climatic deterioration and increase in climatic variability that occurred in temperate regions in the later Tertiary (Mai, 1970; Buchardt, 1978). These cooler and more variable temperate climates could be expected to result in the evolution of new, open, unstable communities, populated by plants with a rapid life cycle. This is what is observed in the taxonomic composition of late Tertiary communities, which show a diversification of herbaceous angiosperms (Niklas et al., 1980; Tiffney, 1981). However, it is of great importance to note that while small-seeded forms dominated in the later Tertiary, large-seeded trees remained as part of the flora, although diminished in importance.

In summary, the diaspore size data suggest that Cretaceous angiosperms were small and/or opportunistic plants, and that only in the latest Cretaceous or early Tertiary did the group clearly evolve to include physiognomically-dominant trees of stable, climax forests. This does not exclude angiosperms from forming forests in the Cretaceous, but the diaspore size data suggest that such forests would be restricted to unstable environments, while gymnosperms would be the physiognomic dominants in stable environments. These predictions can be tested in part by examining the sedimentological settings of Cretaceous angiosperm and gymnosperm floras. Angiosperm floras should be more commonly associated with sediments indicative of unstable environments (e.g., river margins), while gymnosperms should be associated with sediments representative of more stable environments (e.g., back swamps or uplands).

The foregoing interpretation rests on at least two assumptions that require consideration. First, does the correlation of diaspore size and habit/habitat witnessed in the modern day hold with respect to Cretaceous angiosperms, for which there are few modern homologues? I cannot answer this question directly, but suggest that Cretaceous angiosperms do indeed follow the same pattern as modern ones since the relation of diaspore size and habit/habitat holds across a wide range of taxonomic groups. Chaloner and Sheerin (1981) have successfully applied this concept to an explanation of early land plant reproductive strategies, in which the evolution of larger plant size is directly correlated with an increase in disseminule size. Also, while the fact that these Carboniferous plants are extinct makes the inference of successional status tenuous, it appears that the dominants of the relatively more stable lowland swamp communities (e.g., medullosans and certain arborescent lycopods) had larger disseminules than plants of less stable habitats (e.g., calamitaleans, cordaitaleans, and conifers). The Mesozoic flora was dominated by the gymnosperms, members of which had a wide range of diaspore sizes. Some (cycads, araucarian conifers) had quite large seeds that appear to have necessitated biotic dispersal (van der Pijl, 1969), while others had small seeds (some seed ferns, cycadeoids, and taxodioid conifers) morphologically adapted to abiotic dispersal. Retallack and Dilcher (1981) suggested that cycadeoids may have been restricted to unstable stream margins in the Cretaceous, while conifers dominated the more stable upland communities. With the advent of large-seeded angiosperms in the latest Cretaceous and Tertiary, gymnosperms declined in importance (Niklas et al., 1980; Tiffney, 1981). It is unclear if this was an unrelated event or a direct result of the expansion of the angiosperms. The latter possibility deserves consideration, because the dominant modern group of gymnosperms in the Northern Hemisphere are the Pinaceae, which have relatively small seeds and are generally restricted to early successional positions or to sites from which angiosperms are excluded by physiological factors. These elements of circumstantial evidence suggest that the correlation of diaspore size and the habit and/or habitat of the parent plant generally holds for land plants and may be assumed to have done so for early angiosperms.

Second, the association between diaspore size and habit/habitat was demonstrated using temperate plants (Salisbury, 1942; Harper et al., 1970). Does it hold with warm-temperate to often tropical taxa, which commonly occur in the Tertiary? Again, the answer is circumstantial but positive. The relationship of seed size to habit/habitat of the parent plant seems to be general among land plants, and anecdotal evidence suggests that it holds in the modern tropics (van der Pijl, 1969; Stebbins, 1971; Opler et al., 1980; Janzen & Martin, 1982). In one case where seeds of plants of the five ecological categories were measured (Levin, 1974), the average seed size in each category was a bit larger (two to five times) than observed in the temperate flora. While interesting, the magnitude of this variation is too small to affect the hypothesis of Cretaceous and Tertiary angiosperm seed size presented here.

SEED SIZE AND MODE OF DISPERSAL

Seed (diaspore) dispersal is an important element in the life cycle of seed plants (cf. Levin & Kerster, 1974). Abiotic dispersal (wind, water) is successfully employed by a wide range of angiosperms, including many trees. However, there is little question that biotic dispersal is of greater importance, if not dominant, among angiosperms in the modern day. Biotic dispersal agents exert a strong selective pressure on angiosperm fruit and seed size and morphology, as evidenced by the evolution of a wide range of adaptations for animal dispersal (cf. Ridley, 1930; van der Pijl, 1969). I am unaware of any estimate of the absolute proportion of the world's angiosperm flora that is animal-dispersed, but in the few reports of individual communities, the proportion of biotically-dispersed species is often high (Jones, 1956; Smythe, 1970; Stiles, 1980; Handel et al., 1981) and reaches 90% in some Central American examples (Frankie et al., 1974; Janzen, 1977). This may be affected by edaphic factors, however, as suggested by Janzen's (1977) observation that a low degree of biotic dispersal occurs in some Indomalaysian forests growing on nutrient-poor soils.

There are five animal groups commonly involved in the dispersal of angiosperm fruits and seeds; ants, fish, reptiles, birds, and mammals (including bats). All have, to greater or lesser degrees, affected the size and shape of angiosperm disseminules. The history and general influence of each group is considered in turn.

Ants. Ant dispersal (myrmecochory) is primarily known among forest floor herbs, particularly in the temperate zone (van der Pijl, 1969; Handel et al., 1981) although it is also reported from other areas (e.g., Berg, 1975). Morphological adaptations to ants usually involve small diaspore size and the presence of an oil body or elaiosome as a food source on the exterior of the diaspore. Although ants are known from the Cretaceous (Burnham, 1978), they would affect only small seeds.

Fish. Fish are generally assumed to have a minor role in the dispersal of angiosperms (Ridley, 1930; van der Pijl, 1969), although a recent study of Amazonian plant communities (Golding, 1980) suggested that fish may disperse diaspores, particularly in time of high water. The degree to which this dispersal syndrome involves adaptations in diaspore morphology and size, and its importance outside the Amazon basin, are not clear. It may not be so much a "coevolved syndrome" as a glorified case of scavenging. Fish have been around since the Paleozoic (Romer, 1966) and may well have served as generalist dispersal agents in swamps and rivers since the Carboniferous.

Reptiles. Reptilian dispersal (saurochory) is a recognized syndrome, often involving brightly colored and odoriferous seeds or fruits borne near the ground and of a wide range of sizes (van der Pijl, 1969). The important modern representatives include turtles and tortoises, which first spread as a group in the Triassic (Romer, 1966), and lizards, particularly iguanas. The latter group appears in the Eocene, although its forerunners may go back to the Upper Jurassic (Romer, 1966). Perhaps the decline of the reptiles at the end of the Cretaceous, just as the angiosperms were undergoing a major expansion, explains the relative lack of dispersal syndromes involving the two groups in the modern day. The possibility must also be entertained that the primary dispersal vectors of the large seeds of the physiognomically-dominant Mesozoic gymnosperms were reptiles, and that the decline of the reptiles may have influenced the demise of some gymnosperm groups in the late Cretaceous (Krassilov, 1978). If so, this would also imply that Late Cretaceous and early Tertiary plant communities were in a state of flux, and open to angiosperm invasion.

Birds. Birds are among the most important of angiosperm dispersal agents, affecting very small to very large diaspores in temperate and tropical communities (Ridley, 1930; van der Pijl, 1969). There are many morphological adaptations of angiosperm disseminules to bird dispersal (ornithochory) because transport may be internal or external. The most common syndrome involves odorless, brightly colored, edible, fleshy fruits with hard, resistant, inner seeds. These are often clearly displayed; and, in dehiscent fruits, the seeds often dangle from the fruit at maturity.

The fossil record of the birds has been reviewed at the family level by Brodkorb (1971), to which I have added data provided by Kurochkin (1976) (Fig. 3). Bird families often contain organisms of diverse dietary habits, but, based on information provided by van Tyne and Berger (1976), individual families can be described as "carnivorous" (no plant material consumed), "omnivorous" (some plant material consumed), or "vegetarian" (dominantly plant material consumed). Figure 3 presents a summary of the diversity of bird families from the Early Cretaceous to the present, broken into these three dietary groups. No fossil families are included; they are few in number, and it would be difficult to ascertain their dietary affinities. The family level is used for ease of tabulation. A generic or specific level summary is beyond the scope of this paper and would not greatly alter the trends seen in Figure 3, although the family level does mask the effect of the late Tertiary diversification of the species-rich, dominantly omnivorous or vegetarian, passerines (Brodkorb, 1971).

Cretaceous families for which diets may be surmised from modern relatives are predominantly carnivorous and marine; one omnivorous family is present (Cracraft, 1973; Brodkorb, 1976). This conclusion is generally supported by the beak morphology of the fossils. The fossil record of the birds diversifies greatly in the Eocene, and the number of modern families continues to increase throughout the Tertiary. The proportion of omnivores remains steady during this time, but the proportion of vegetarian families (which first appear in the Eocene) rises consistently, while that of the carnivorous families falls.

As displayed in Figure 3, the avian fossil record would suggest that birds were not important in angiosperm dispersal until the early Tertiary, whereupon they became increasingly important and continued to mount in significance to the present day. However, the available fossil record of any group may be seen either as a real reflection of evolutionary events, or as too biased to be trusted directly. Cracraft (1973) considered the fossil record to be less important than the information that can be drawn from a comparison of the timing of Cretaceous and Cenozoic continental movements with the modern distri-

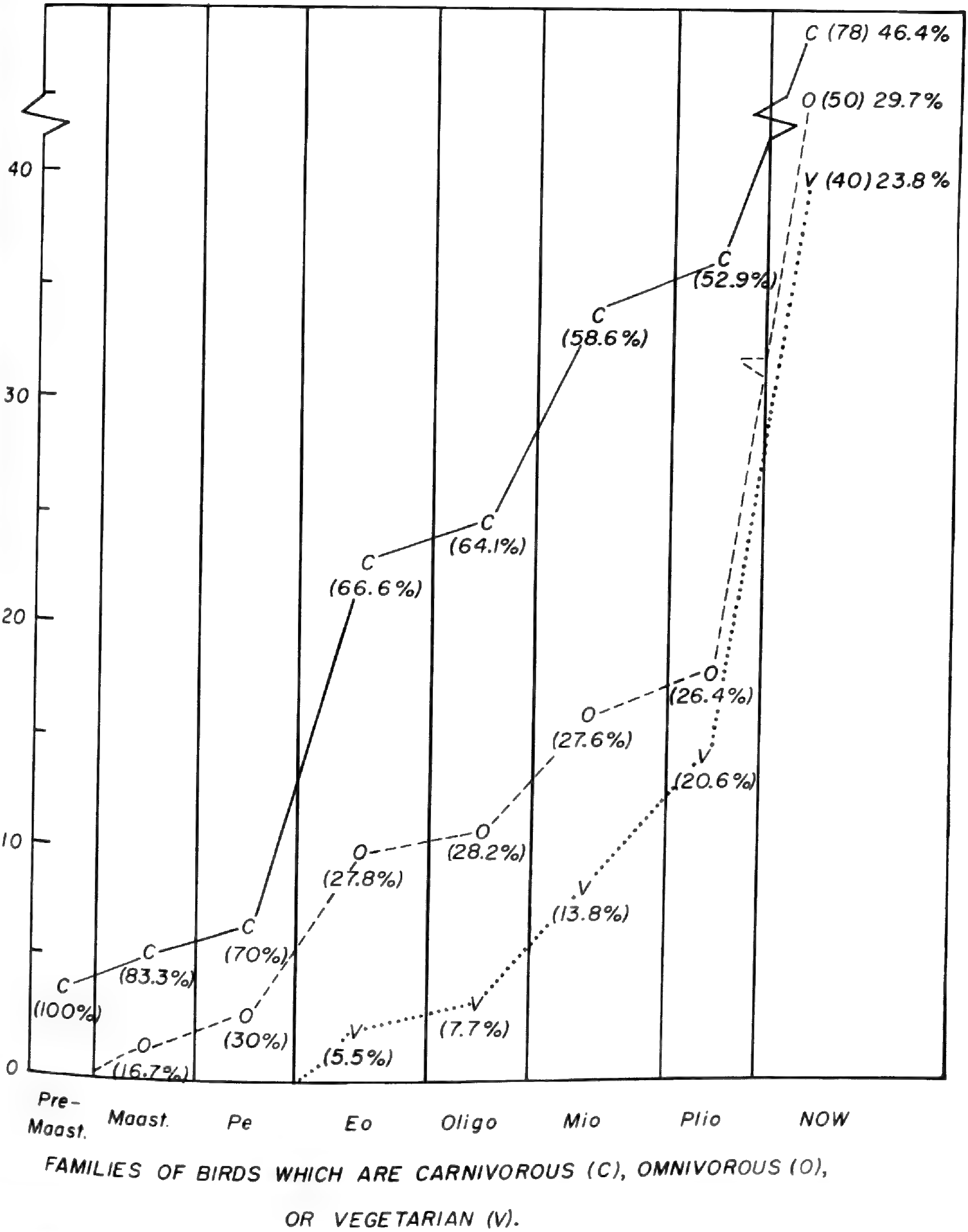

FIGURE 3. Cumulative diversity of modern families of birds through the Cretaceous and Tertiary broken into three dietary groups: carnivorous (c), omnivorous (o), and vegetarian (v). Percentages are of the total number of families in each epoch. Data from Brodkorb (1971, 1976); Kurochkin (1976); van Tyne and Berger (1976). Pre-Maast = pre-Maastrichtian, Maas = Maastrichtian, Pe = Paleocene, Eo = Eocene, Oligo = Oligocene, Mio = Miocene, Plio = Pliocene.

butional patterns of bird families. On this basis, he inferred that the immediate ancestors, if not the actual families, of modern birds were present by the mid- and Late Cretaceous. Brodkorb (1971) also suggested that modern families were present in the mid- and Late Cretaceous. He reasoned that the modern appearance, specialization, and diversity of early Tertiary birds argue for considerable antecedent evolution of the group.

Neither author accepts the fossil record at face value. This logic is reminiscent of the school of paleobotany that sought the origins of the angiosperms in the latest Paleozoic and early Mesozoic on the basis of their "diverse" Cretaceous record (Axelrod, 1960, 1970). Subsequent study of the angiosperms (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Doyle, 1978) has demonstrated that the initial radiation of the angiosperms was confined to the Cretaceous and matches the known fossil record of the group. I choose to accept the fossil record of the birds as indicative of a major radiation in the Tertiary, perhaps with its beginnings in the latest Cretaceous, paralleling that of mammals (Colbert, 1969) and of modern angiosperm families (Niklas et al., 1980; Tiffney, 1981; Muller, 1981). A recent consideration of avian evolution (Cracraft, 1982) does not alter this view, because it emphasizes the aquatic and presumably carnivorous nature of Mesozoic birds as they are presently understood.

Mammals (excluding bats). The dispersal of angiosperm seeds by mammals is probably only a little less important than that by birds (Ridley, 1930; Martin et al., 1951; van der Pijl, 1969; Halls, 1977). Van der Pijl gives the impression that it is of greater importance in the tropics than in the temperate regions. The fruit and seed characters associated with mammal dispersal are quite varied and may involve internal or external transport. Mammals often possess a good sense of smell and thus many mammal-dispersed fruits have a distinctive odor (van der Pijl, 1969). The thickness of the seed wall tends to vary with seed size. Small seeds that would probably be passed through the digestive tract do not require hard coats, whereas large ones with edible contents require protection against direct predation. One important aspect of mammal dispersal is that mammals can move seeds of quite large sizes, often from within the forest canopy (Ridley, 1930; van der Pijl, 1969). Mammal-dispersed fruits of more open habitats are often adapted to external transport (van der Pijl, 1969).

The Tertiary is the "age of mammals," and is the time of radiation of a host of important dispersalist groups (Romer, 1966; Colbert, 1969). Rodents, lagomorphs, primates, artiodactyls, and perissodactyls all commenced radiations in the Eocene. Other, more specialized omnivorous lineages appeared in the mid-Tertiary. While modern terrestrial mammals are almost entirely products of Tertiary radiations, the possibility remains that some Cretaceous lineages of mammals could have been important dispersal agents. Lillegraven (1979) suggested that perhaps mammals and flowering plants were establishing the basic features of their coevolutionary relationship in the Cretaceous. Certainly, several major groups of Cretaceous mammals are presumed to be omnivorous and a few herbivorous (Kron, 1979; Clemens & Kielan-Jaworowska, 1979; Clemens, 1979), although all are generally of small size (Lillegraven, 1979). While I do not doubt that Cretaceous mammals had some interactions with angiosperms, it seems unlikely to me that such interactions were significant and widespread. The known Cretaceous thick-walled seeds are not especially common, and they show no trends in morphology or size to suggest their specialized adaptation to biotic dispersal. Further, if such interactions were established to a significant degree in the Cretaceous, it is surprising that they should not have carried over into the Tertiary and the present. Instead, today the fruits of primitive families or of primitive lineages in families are more commonly abiotically-dispersed, while derived families and lineages are dispersed by organisms of Tertiary origin (Schuster, 1976). Parallel to this pattern is a second one, demonstrated by the Rosaceae, for the geographic co-occurrence of fleshy-fruited angiosperm lineages and "advanced" (products of Tertiary radiations) mammalian lineages (Schuster, 1976). This information, while circumstantial, suggests that mammals became important as dispersal agents only in the Tertiary.

Bats. Bats are important in the dispersal of angiosperm propagules in the warmer regions of the world where fruiting occurs throughout the year. This is borne out by a wide range of anecdotal and scientific observations (Constantine, 1970; Smith, 1976). Bat-dispersed disseminules are normally large, odoriferous, fleshy fruits with a hard stone, or a similar seed with a sarcotesta or aril (van der Pijl, 1957, 1969).

The fossil record of bats (Smith, 1976) is limited and often fragmentary. Bats first appear in the Early Eocene and possess dentition indicative of an insectivorous diet. The first frugivorous bat was thought to be *Archaeopteropus transiens* Meschin. of the Italian Oligocene (Jepsen, 1970), but more recent investigation reveals that the dentition of this specimen is that of an insectivore (Smith, 1976). At present, the earliest record of a frugivore is of a phyllostomatid bat from the late Pleistocene (Smith, 1976).

While some authors feel that bats may have been present in the Late Cretaceous (Jepsen, 1970; Smith, 1976), the absence of pre-Eocene bats, and the rapid diversification of the group in the Eocene and Oligocene, suggests that bats were unimportant, if extant, in pre-Eocene time. Further, the earliest bats were insectivores, and frugivory appears to be a derived condition (Smith, 1976). It is thus likely that the morphological characters of the bat-dispersed fruit evolved as a dispersal syndrome at the earliest in the Eocene.

In summary, pre-Tertiary angiosperm dispersal agents probably included ants, fish, reptiles, and certain groups of archaic mammals. Of these, the last group was probably the most significant, but probably was generalized in its adaptations and of restricted influence on the angiosperms. It appears that the important groups of modern biotic dispersal vectors all underwent their most important period of radiation in the early Tertiary. The sudden appearance of such a wide variety of dispersal agents would be expected to lead to clear changes in seed morphology and size. Such changes are seen in the early Tertiary.

CONCLUSIONS

Two separate features have been explored in an attempt to explain the observed pattern of diaspore size change. The first involves the relationship between seed size and the habit and habitat of the parent plant. This leads to the conclusion that the observed increase in diaspore size is related to the angiosperms becoming physiognomically-dominant plants of stable forest communities. The second approach turns to the evolution of dispersal strategies as inferred from the fossil record of the dispersal agents and from the morphology of the disseminules themselves. This suggests that biotic dispersal vectors influenced angiosperm fruit and seed morphology only in the latest Cretaceous or early Tertiary. Each hypothesis provides an adequate explanation of the observed pattern, although the first does not explain its timing. However, the two are not mutually exclusive and may be synthesized to provide a new perspective on angiosperm evolution. As a preamble to this synthetic interpretation, it is necessary to explore briefly the assumption that canopy dominance generally requires large seeds, which, in turn, normally require biotic dispersal agents.

For an angiosperm to achieve dominance (in a physiognomic, not a numerical, sense) of the community, its seedlings must be able to grow in the shade of the parent (or other) trees, thus insuring the continuity of the population. Any increase in seed size in an abiotically-dispersed plant would provide the seedlings with more nutrients and the capability of growing in a more shaded habitat. Logically, one could envision a slow increase in the seed size and shade tolerance of seedlings in one population, ultimately leading to in situ dominance of the community. However, larger seeds generally have a reduced radius of dispersal, particularly in closed communities or in the absence of means of water transport. Thus, in an abiotically-dispersed plant, increased seed size would result in smaller population sizes and perhaps increased endemism and a higher potential for extinction. All this implies that angiosperms required the presence of biotic dispersal agents in order to attain canopy dominance in a closed community. This conclusion appears correct in light of examples of forest trees that have lost their dispersal agents. *Ginkgo* L. attained a wide distribution in the Mesozoic, and maintained it into the Tertiary (Tralau, 1968), but is now a highly restricted endemic in its natural state. Its fleshy and odoriferous seed seems well-adapted to attracting reptiles, and perhaps these were the vectors by which it spread in the Mesozoic. The loss of these vectors in the early Tertiary would be of little immediate importance, because the genus had a wide distribution in this time of warm climate. However, with the climatic changes of the later Tertiary, its range became severely restricted, and, in the absence of a dispersal vector, it was unable to re-expand its range in periods of favorable climate, thus coming to the brink of extinction in the Holocene. Similar, although less dramatic, examples of the effect of the loss of a dispersal agent on range and population structure have been described by Janzen and Martin (1982) for angiosperms in Central America. These circumstantial examples support the tentative conclusion that attainment of canopy dominance and the maintenance of a stable population structure in closed forests are generally linked to the establishment of biotically-mediated dispersal.

The scenario involving seed size and dispersal in the evolution of the angiosperms is simple. Our understanding of Early Cretaceous land plant communities is limited but conveys the impression that there were few existing seed plants of an early successional nature. The angiosperms first appeared about 120 Ma as an "*r*" strategy (weedy generalist) group with small stature, rapid life cycle, and small, abiotically-dispersed seeds. They spread to occupy a wide variety of early-successional sites (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Doyle, 1978). This diversification was probably paralleled by the appearance of a variety of adaptive vegetative morphologies and may have resulted in the "blocking out" of the general character complexes of several modern suprageneric groups. Evidence from leaf architecture (Doyle & Hickey, 1976; Hickey & Doyle, 1977) indicates that the angiosperms had attained shrub and tree stature by the late Albian or early Cenomanian (about 100 Ma). These plants may have formed extensive angiosperm-dominated communities in consistently unstable environments (e.g., aggradational river bottoms) but probably were displaced by the large-seeded and dominant gymnosperms in more stable habitats. Some angiosperms may have formed an understory of shrubs and small trees in open-canopied gymnosperm forests such as those of the uplands of New Caledonia in the present day (L. J. Hickey, pers. comm.).

Therefore, while Cretaceous angiosperms were probably diverse in certain habitats and perhaps numerically-dominant over the gymnosperms, they did not dominate the world vegetation in the physiognomic sense that they do in the modern day. Rather, they were a more specialized "weedy" group that initially radiated to fill a specific aspect of the community, but that did not continue their radiation at the same rate throughout the Cretaceous. This implies that angiosperm diversity should have risen slowly, rather than dramatically, during the later Cretaceous, which is what is observed (Krassilov, 1977; Niklas et al., 1980; Tiffney, 1981). That the Cretaceous angiosperms included few if any large canopy trees capable of sustaining a closed climax forest is inferred strictly from the paucity of large angiosperm diaspores. While large seeds would have permitted the angiosperms to achieve physiognomic dominance of the community, their size would necessitate association with biotic dispersal agents. Both the record of diaspore size and of animals in the Cretaceous suggest that the appropriate dispersal agents for angiosperms were few, and that the advantages of large seeds were outweighed by the disadvantage of their poor dispersal.

This impasse was broken by the radiation of birds and mammals (including bats) in the early Tertiary or perhaps latest Cretaceous, leading to the swift development of many biotic dispersal syndromes, which in turn influenced the evolution of the angiosperms in the Tertiary.

The total diversity of angiosperms increased dramatically in the early Tertiary (Niklas et al., 1980; Tiffney, 1981). This is to be expected as a result of the development of plant-animal dispersal interactions for three reasons. First, coevolution favored increasing specialization and speciation (cf. Regal, 1977). Second, greater distance of dispersal favored allopatric speciation, an ultimate example of which is the modern eastern North America–eastern Asia pattern of disjunction (Wood, 1972; Wolfe, 1975). Finally, the establishment of dispersal syndromes with animals opened the way for angiosperms to explore all possible habits and habitats within the community. This is partially reflected in the high value of the coefficients of correlation (Table 2) in the Tertiary, indicating the increased polymodality of diaspore size in Tertiary floras. Increased seed size led to an arborescent community with decreased light penetration, diversified biotic competition, and presumably tighter species packing, all features favoring increased diversity. Further, all the changes in the rate of diversification initiated by the interaction of dispersal agents and angiosperms would both accentuate and be accentuated by parallel coevolutionary interactions with insect pollinators (Crepet, 1979, 1984).

The latest Cretaceous and early Tertiary is also remarkable as a time of rapid "modernization" of the world's flora. This involves two aspects; the sudden appearance of large numbers of modern families and genera (Niklas et al., 1980; Muller, 1981; Tiffney, 1981) and their swift spread over the Northern Hemisphere (Wolfe, 1975). Both follow logically from the establishment of dispersal relationships. The rapid appearance of modern taxa results from the increased rate of speciation occasioned by the initiation of the coevolutionary spiral that extends to the present day. The rapid spread of these taxa follows from their association with the effective dispersal agents, although three other factors were of importance. First, the Late Paleocene and the Eocene were periods of warm climate in the northern hemisphere (Buchardt, 1978; Wolfe, 1978). Second, apparently both North Atlantic and North Pacific land bridges were available to terrestrial organisms in the Early Tertiary (Lehmann, 1973; McKenna, 1975; Tiffney, 1980). Finally, and perhaps most importantly, the newly-evolved angiosperm taxa probably included many adaptations to previously unfilled "niches" and were spreading at a time when several gymnosperm groups had recently declined or gone extinct (Krassilov, 1978; Niklas et al., 1980; Tiffney, 1981; Vachrameev, 1982).

The question remains: what initiated the increased level of interaction between plants and dispersal agents in the latest Cretaceous and early Tertiary? Did external factors (e.g., the decline of the reptiles) lead to the evolution of new groups of birds and mammals, which in turn spurred angiosperm evolution? Alternatively, did angiosperms (perhaps responding to the appearance of new groups of insect pollinators, Crepet, 1984) begin to diversify first and thereby stimulate the evolution of potential dispersal agents? I do not believe that the data given here will support interpretations of cause and effect, if indeed, such considerations are not rendered irrelevant by the synergistic nature of coevolutionary relationships. Further, while I have emphasized the historical importance of the development of angiosperm dispersal syndromes in this paper, it is only one of three coevolutionary features that must have had a strong influence on the course of angiosperm evolution. Pollination syndromes have perhaps had an even greater influence in view of the vast array of morphological and ethological permutations involved. Indeed, the interactions of angiosperms with modern pollinators may have been established at a slightly earlier date than the interactions with modern dispersal agents (cf. Crepet, 1984). Additionally, interactions between herbivores and plants have not been explored in the fossil record but must also have been of significance (cf. Niklas, 1978).

Finally, I would like to explore briefly three ancillary points.

First, the evidence presented here suggests that the "Durian Theory" (Corner, 1949, 1964) is untenable. The "Durian Theory" assumes that the primitive angiosperm seed was arillate, of moderate size, probably animal dispersed, and was contained in a dehiscent fruit borne of a large, pachycaulous tree. According to the fossil record of angiosperm seeds, such a combination of characters could have evolved only in the Tertiary, following the establishment of widespread biotic dispersal syndromes. Certainly no evidence is seen of "moderate-sized" angiosperm seeds in the Cretaceous: they are all small. Further, no evidence is seen of widespread animal dispersal in the Cretaceous, or of pachycauly, although the scarcity of Cretaceous angiosperm wood (Wolfe et al., 1975) renders the last a statement based on negative evidence.

Second, the minimum and maximum seed sizes did not appear to have undergone any significant directional change of size during the time period measured. Two regressions were run: (1) the size of the smallest seed of each of the floras examined (Table 2) against time, and (2) the size of the largest seed from each of the Tertiary floras against time. The first regression was not significant ($0.20 > P > 0.10$; $r = 0.29$, $N = 26$); the Rusinga flora was excluded on account of its anomalously large "smallest seed"—probably a function of the collection of the flora from surficial lag deposits. In the second case ($N = 18$, $r = 0.40$), the r value is marginally insignificant ($P = 0.10$), however, this figure may be influenced by the temperate adaptations of the source plants of the later Tertiary. This suggests that the two seed classes have achieved some form of balance between the selective features that affect size. The time stability of small seed size implies that the appearance of larger seeds in the early Tertiary did not alter the selective advantage of small seed size in certain environments. This could be further extended to imply that the basic habitats available to smaller-seeded plants have not greatly altered during the history of the angiosperms, although in some times habitats favoring opportunistic forms are less widespread (early Tertiary) than in others (late Tertiary, Pleistocene). With respect to the larger seeds, it appears that there has been no distinct trend of size increase through the Tertiary. This could imply that there is an optimal upper limit for seed size, one that strikes a balance between available endosperm and efficiency of dispersal, and that was achieved by the early Tertiary. However, this observation may be influenced by climate. The fossils are primarily from Europe and sample a tropical vegetation in the early Tertiary, but an increasingly more temperate one through the later Tertiary. Limited data (Levin, 1974) suggest that modern tropical lowland communities have slightly larger seeds than modern temperate ones. If so, then possibly the size of the largest seeds did increase slightly through the Tertiary.

Finally, both Harper (1961) and Margelef (1968) have suggested that the evolutionary history of a group should tend to parallel its successional history, and that an evolving group should "climb its own seral tree." This is what is seen in the fossil record, with the angiosperms initially appearing as weedy plants and in due time evolving to become dominant members of the climax community. The fossil record suggests that this transition required the appearance of dispersal vectors to permit the dispersal of large seeds of the plants of later seral stages. This implies that the unique characters of the angiosperms (rapidity of life cycle, potential for insect pollination, specialized conducting tissue, etc.) were not sufficient separately or jointly to directly ensure the final dominance of the group. However, the developmental plasticity of the angiosperms did permit them to evolve a diversity of fruit and seed dispersal adaptations in response to the appearance of dispersal agents. This observation raises interesting questions about the structure and function of pre-angiosperm communities. Were dispersal agents involved in previous climax communities? Do climax communities in which dispersal agents are not available have a different, perhaps more open, canopy structure than those in which dispersal agents are present? [For example, could the seeming diversity of lowland Carboniferous coal swamps as contrasted to the upland Carboniferous vegetation be influenced by the availability of mechanisms permitting the dispersal of large seeds in the lowland community (water, fish) and their absence in the upland communities?]

SUMMARY

Analysis of Cretaceous and Tertiary fruit and seed floras from the Northern Hemisphere reveals a change in the average size and range of size of angiosperm diaspores through time. Cretaceous floras are composed almost entirely of small diaspores. Early Tertiary floras are dominated by large diaspores but include many as small as those of the Cretaceous. Later Tertiary floras are primarily composed of smaller diaspores but consistently include a few very large ones. Analyses suggest that the minimum diaspore size for angiosperms has not changed since their appearance in the Cretaceous, and that their maximum size has not increased greatly, if at all, from the time of appearance of large diaspores in the earliest Tertiary to the present. There are two major features that influence diaspore size: (1) the relation between seed size and the ecological characteristics of the parent plant, and (2) dispersal mechanisms. The observed pattern in angiosperm diaspore size through time may be interpreted in light of these two selective forces. Cretaceous angiosperms were primarily small-seeded, abiotically dispersed shrubs or opportunistic trees, perhaps occupying marginal or open habitats in the gymnosperm-dominated vegetation, but probably not forming a closed-canopy climax community. The relative paucity of dispersal agents in the Cretaceous limited the success of large angiosperm diaspores and the closed-canopy forest that they could be expected to give rise to. The latest Cretaceous or early Tertiary radiation of birds, bats, and terrestrial mammals reversed this situation, permitting a biotic interaction favoring large, animal-dispersed propagules. This in turn allowed the establishment of angiosperm seedlings in areas of low light intensity and led to the development of stable, closed-canopy, climax communities, physiognomically- as well as numerically-dominated by angiosperms, and similar in structure for the first time to those of the modern day. This interaction of seed size and dispersal agents may have occurred with, or slightly later than, the establishment of interactions between angiosperms and modern pollinators. Regardless of sequence, the establishment of biological interactions between angiosperms and their pollinators and dispersers was reflected in the rapid appearance of modern families and genera, and of their swift spread around the northern hemisphere, in the latest Cretaceous and early Tertiary.

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NEW PALEOBOTANICAL DATA ON ORIGIN AND EARLY EVOLUTION OF ANGIOSPERMY

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ABSTRACT

The author's contributions to the problem of angiosperm origin since 1975 are summarized. Jurassic *Hirmerella* is assigned to proangiosperms based on its fruit-like diaspores. Achenes with persistent receptacles bearing long trusses of hairs came from the Lower Cretaceous of Lake Baikal province. They resemble cyperaceous achenes but could have arisen from bennettitalean ovulate receptacles by reduction of ovules to one and fusion of interseminal scales. Angiosperm fruits, grass-like leaves, and several kinds of spikes and spiked heads are found in the Lower Cretaceous of Mongolia. A middle Albian fructification from Kazakhstan with bitegmic ovules is related to Ranunculidae. Some minor findings are mentioned in discussion. The "spotted layer" of *Caytonia* is interpreted as inner integument. Mesogenous stomata and incipient vessel members are revealed in bennettites. Possible links of proangiospermous *Caytonia, Dirhopalostachys,* and *Leptostrobus* with angiosperms are indicated.

I have reported on proangiosperms—a rather loose group, comprising *Caytonia, Leptostrobus,* and *Dirhopalostachys* which, together with some other plants, such as bennettites, formally not included in the group, provided a "character pool" for arising angiosperms (Krassilov, 1977a). Since then another proangiosperm plant, supposedly of bennettitalean affinity, was found in Baisa, Lake Baikal province. Early Cretaceous angiosperms and angiosperm-like plants were found in Mongolia. Some Albian angiosperm fructifications from Kazakhstan have been restudied (Vakhrameev & Krassilov, 1979). Some new data on *Hirmerella, Caytonia,* and bennettites are also, I believe, relevant to the problem of angiosperm ancestry. These results and their implications are discussed below.

"OVULIFEROUS SCALES" OF *HIRMERELLA*

This name is applied to ovulate cones of a Jurassic plant that produced pollen grains of *Classopollis* type. *Classopollis* shows some angiosperm-like features (columellate ectexine, striated belt) comparable with equatorial harmomegathus of *Nymphaea.* Ovulate organs of this genus also have angiosperm-like features. *Hirmerella* dispersed rather bulky winged bodies conventionally described as seed scales. However, seeds occurred not on, but within these bodies, which are fruits rather than scales. Harris (1979) found two megaspore membranes within the "scales" and I found two overlapping nucelli in a "scale" from the Lower Jurassic of Poland (courtesy of Dr. Maria Reymanowna, Krakow and Dr. Maya Doludenko, Moscow).

My interpretation is that there were two ovules per fruit, closely packed and filling a locule. In both British and Polish fruits there were cuticles of the locule adnate to integumental cuticles (Fig. 1). If the ovules were merely embedded in the "scales" there would be no internal cuticle lining the locule.

A lot of pollen grains stick to the papillate surface of the "scales," but none have been observed within the nucelli, which had inconspicuous beaks.

Hirmerella radically differs from all known conifers and is perhaps closer to *Ephedra,* which sometimes show two ovules per cupule (Mehra, 1950). Based on its fruit-like diaspores, *Hirmerella* can be included in proangiosperms. It may represent an extinct order of gnetophytes.

BAISIAN ACHENES

One of the most fascinating discoveries was made recently in the Lake Baikal province. Lower Cretaceous paper shales and marls cropping out along the Vitim River near Baisa camp are well known as the richest Mesozoic locality of terrestrial insects and diverse lacustrine fauna. Fossil plants are less abundant and of trivial Early Cretaceous Siberian aspect (ginkgoaleans, czekanowskias, pinaceous conifers). However, a decade ago paleoentomologists from the Paleontological Institute, Moscow, were lucky to find a single angiosperm-like leaf described by Vakh-

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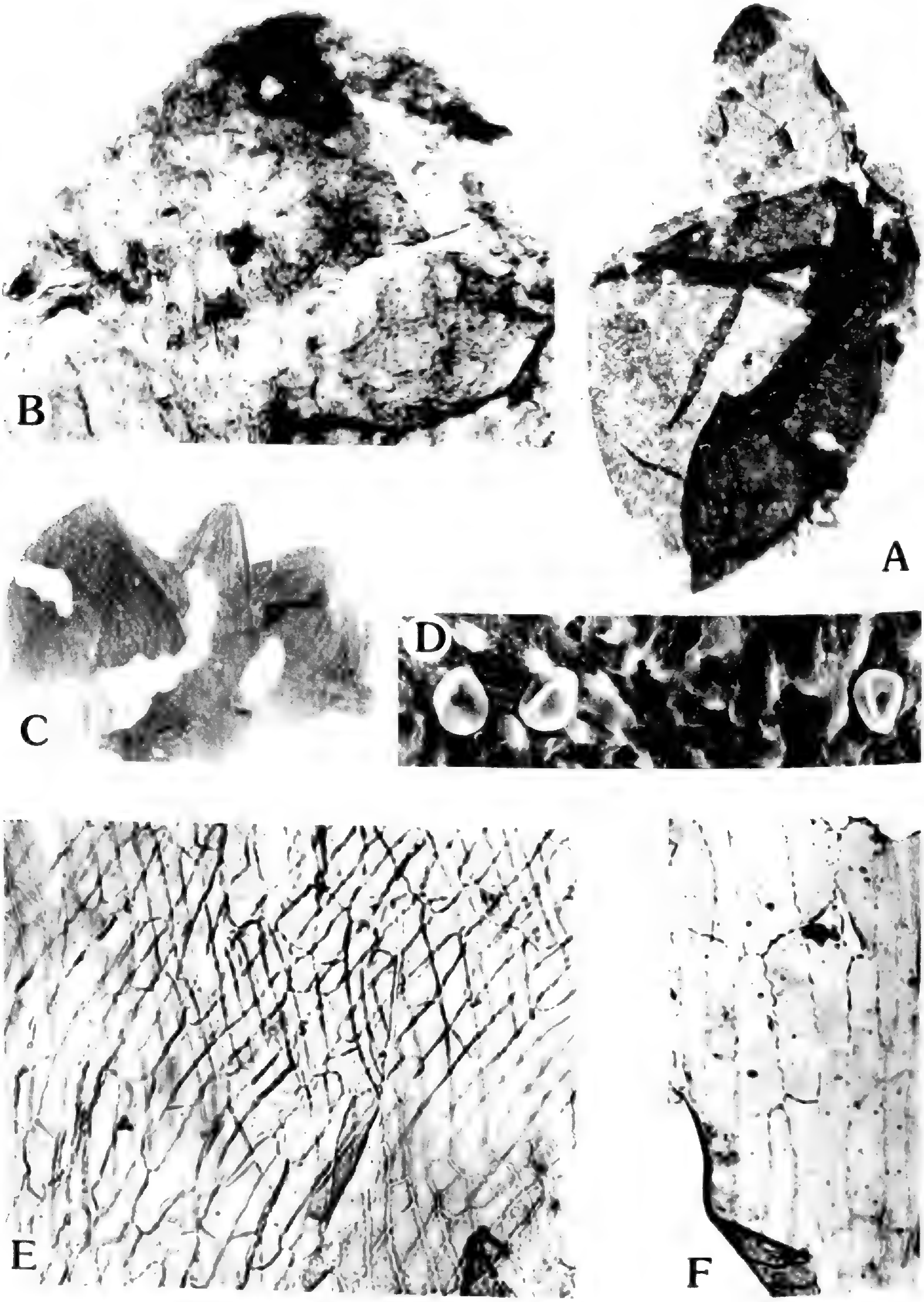

FIGURE 1. *Hirmerella* sp., lower Liassic of Odrovaz (Poland).—A. Two overlapping nucelli from an "ovuliferous scale" shown in C, 15×.—B. Upper portion of a nucellus, 500×.—C. "Ovuliferous scale," 5×.—D. Scanning electron micrograph of pollen grains on the cuticle of a "scale," 500×.—E. Joint cuticles of the locule and integument, 170×.—F. Cuticle of the locule, 170×.

rameev (in Vakhrameev & Kotova, 1977) as *Dicotylophyllum pusillum*.

In 1979, I visited this locality together with Dr. V. V. Zherikhin and other paleoentomologists with hopes of collecting more *Dicotylophyllum*. We failed to find it but instead concentrated on abundant enigmatic hirsute bodies previously brushed aside as insignificant "hairs."

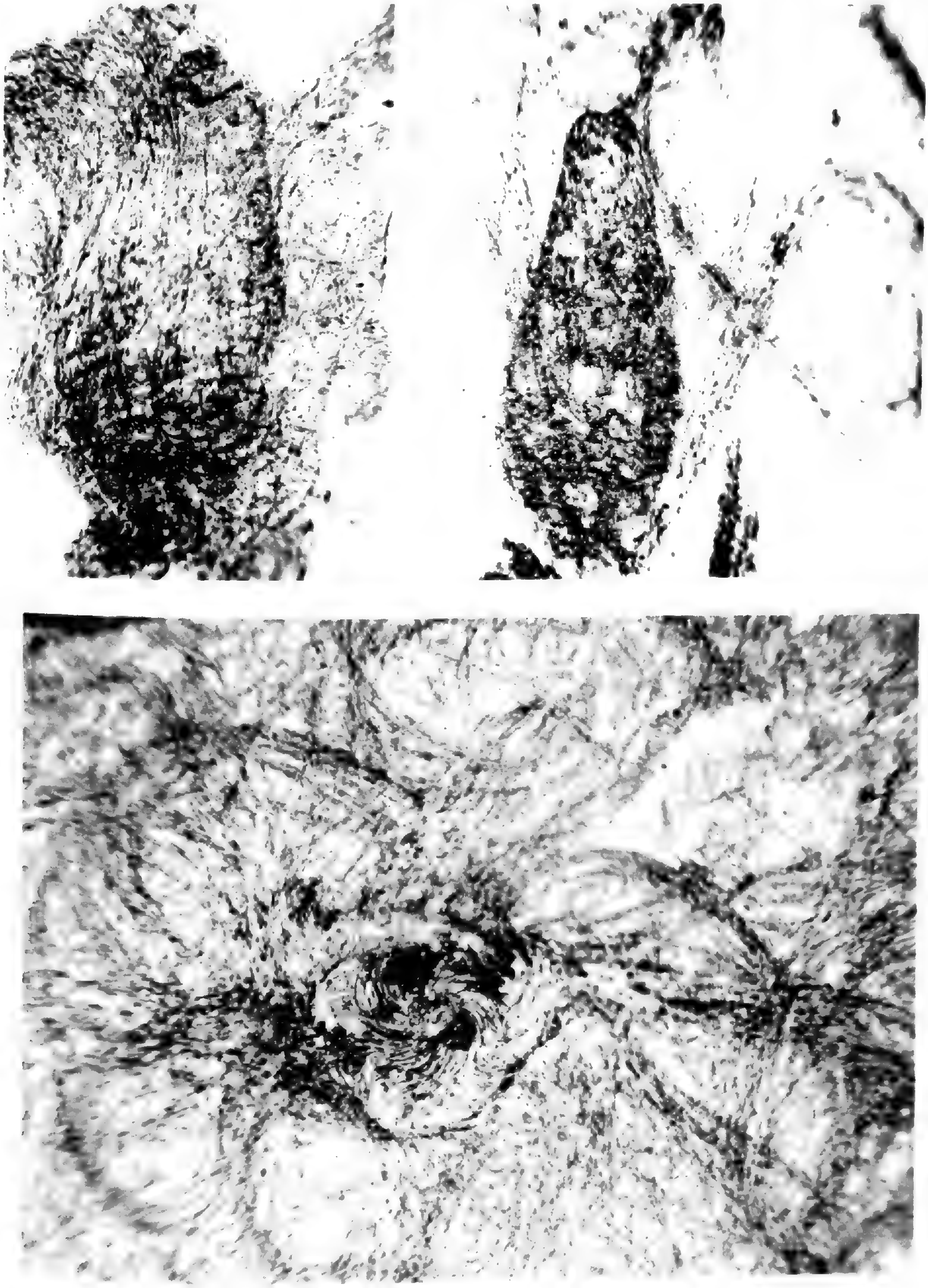

FIGURE 2. Achene-like fossils from the Lower Cretaceous of Baisa, Lake Baikal province. Two achenes showing epidermal cells, "coronas," and long hairs from the receptacles (top), 12×, and a detached receptacle (bottom), 18×.

These bodies were studied with a scanning electron microscope (SEM) and macerated. In effect they were shown to be achene-like diaspores, flask-shaped, with a persistent receptacle bearing long trusses of unicellular hairs (Fig. 2). Detached receptacles also occur abundantly on the bedding planes (Fig. 2). The external coat ("cupule") shows large tubular epidermal cells arranged in longitudinal rows. These are clearly marked on impressions and can be seen under low magnification. The apical portion ("corona") is demarcated by a transverse groove and pitted. The

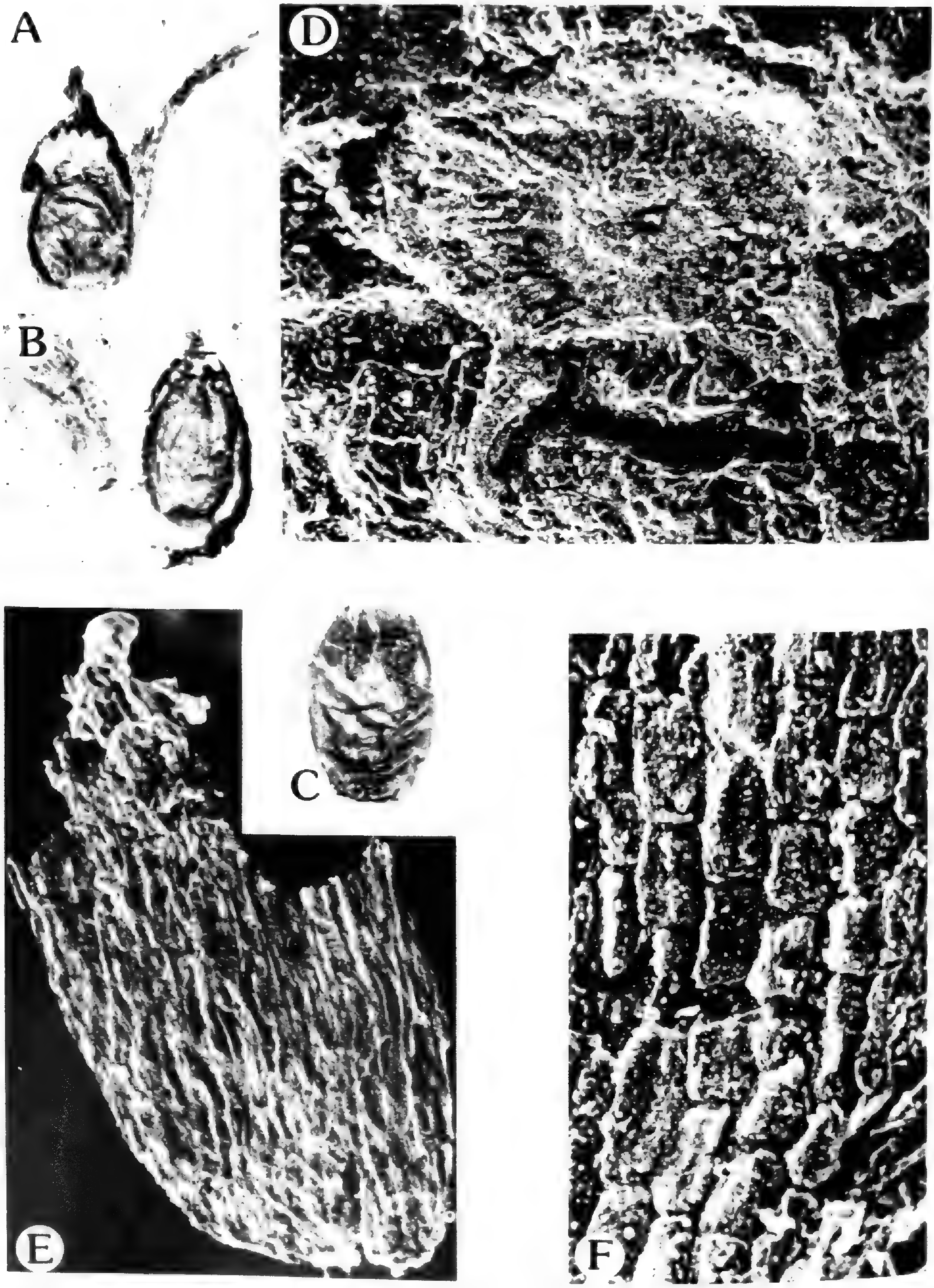

FIGURE 3. Achene-like fossils from the Lower Cretaceous of Baisa, Lake Baikal province.—A, B. Split achenes showing ovules, 12×.—C. Ovule from the achene shown in A, 15×.—D. Scanning electron micrograph of receptacle showing short bracts, 140×.—E. Scanning electron micrograph of nucellus with pollen grains at the top, 60×.—F. Scanning electron micrograph of epidermal cells, 400×.

receptacles show laminar appendages that appear mostly as short rounded lobes. In a favorably preserved specimen there are six small lanceolate bracts at the base (Fig. 3D). Hairs arise in fascicles from these appendages.

A few longitudinally split achenes have an inner cavity with a single ovule almost filling the locule. The ovules are elliptical, with an inconspicuous micropyle.

Externally, the cupules are scarcely cutinized

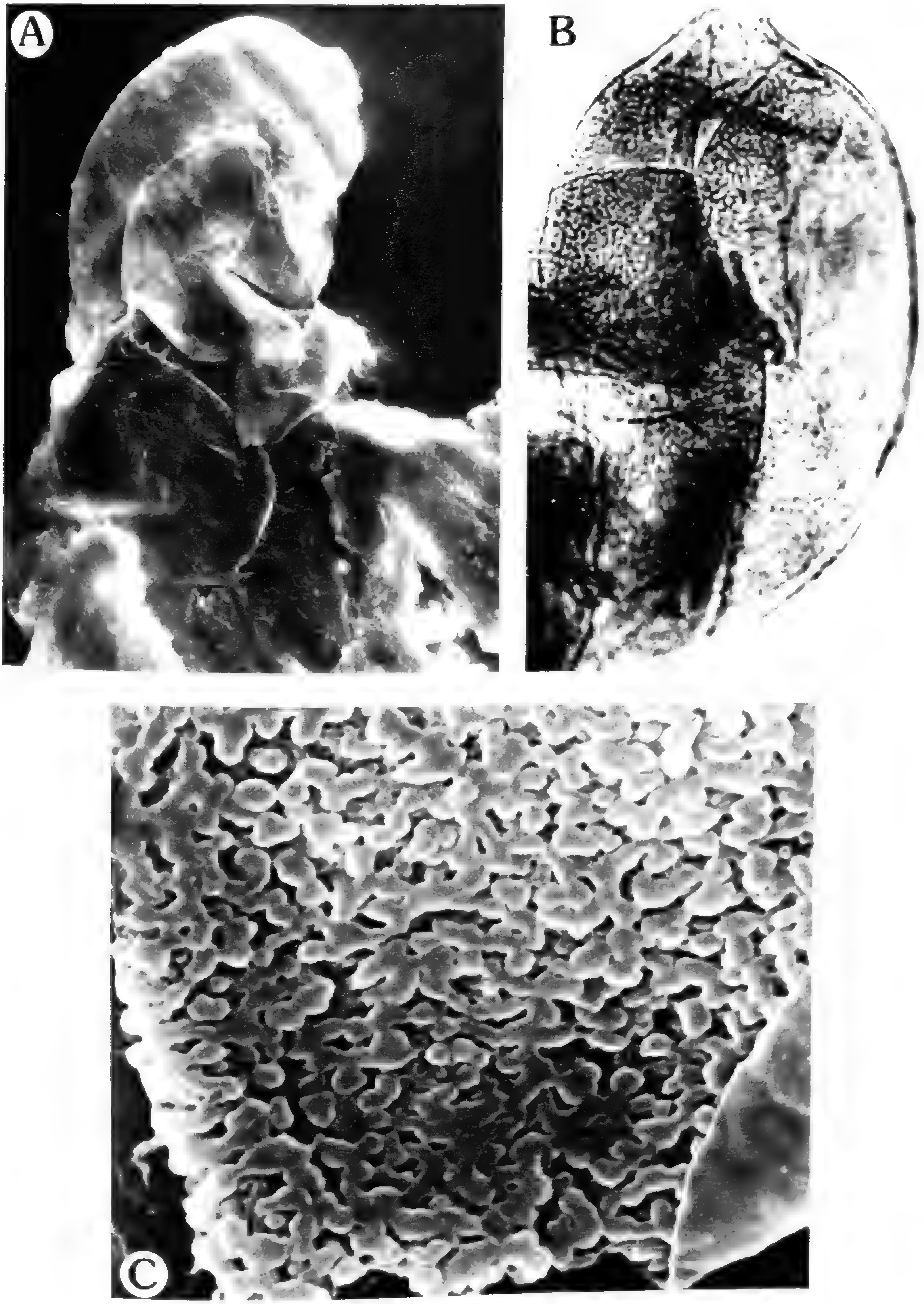

FIGURE 4. Achene-like fossils from the Lower Cretaceous of Baisa, Lake Baikal province.—A. Scanning electron micrograph of pollen grains on the top of a nucellus, same as in Figure 3E, 400×.—B. Top pollen grain showing sulcus, 600×.—C. Scanning electron micrograph showing infratectal clavate-rugulate pattern, 10,000×.

at all; at least I was unable to obtain an outer cuticle. The large-celled epidermis is underlain by a thin fibrous layer and much thicker stone tissue. Fragments of vascular bundles were macerated from the cupule wall. They consist of tracheids with spiral thickenings. The ovules yielded two joint integumental cuticles and a nucellus that is thicker at the base but thin and unfortunately ill-preserved above. However, in one of the nucelli a cluster of pollen grains was observed

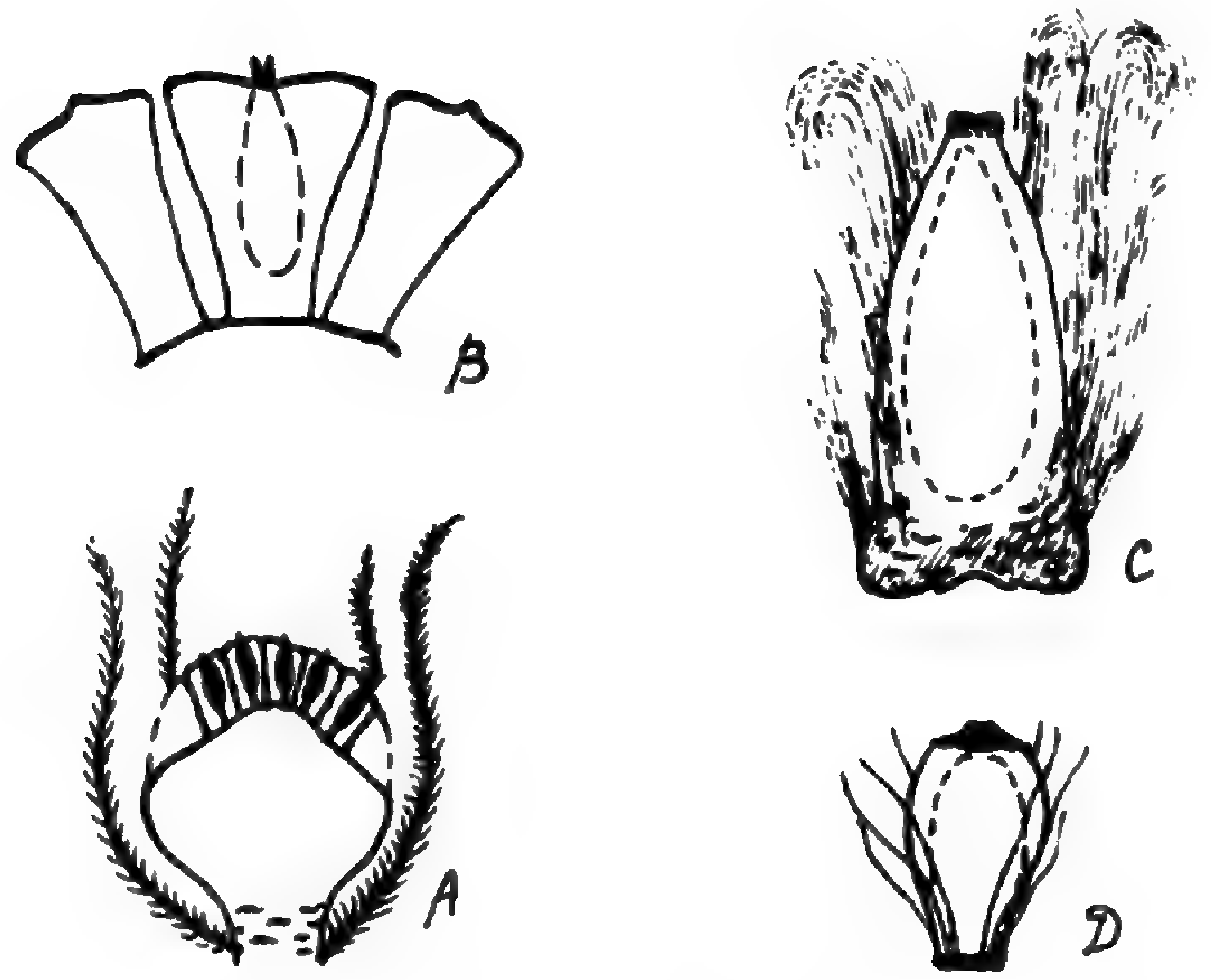

FIGURE 5. Suggested relationships of the Baisian achenes.—A. Bennettitalean flower with hairy bracts, ovules, and interseminal scales.—B. Bennettitalean interseminal scales fused around the ovule as in *Bennetticarpus crossospermum* Harris.—C. Baisian achene.—D. Cyperaceous achene (*Eleocharis* sp.).

at the apex (Fig. 4). They are elliptical, up to 140 μm long, monosulcate, smooth, alveolar, showing clavate-rugulate infratectal structure at places where the tectum is dissolved (by some pollen chamber exudate?).

Superficially, these fossils look much like some cyperaceous achenes, especially those with abundant hypogynous hairs or bristles as in *Eriophorum* or *Carpha* (they might have been mistaken for such if met in geologically younger sediments). In *Eriophorum vaginatum* L., fascicles of bristles on a conical receptacle represent reduced perianth lobes. The shape and dimensions of the Baisian and *Eriophorum* achenes are much alike as well as the large tabular epidermal cells (Fig. 5).

The outer coat of a cyperaceous achene is currently interpreted as either a prophyll-derived membranaceous bladder (utricle) or a cupule formed by hypanthial growth of the receptacle (in Scleriae). Cupules of the Early Cretaceous Baisian achenes might have similar origin. However, on closer inspection they turned out to be neither cyperaceous nor even fully angiospermous because pollen grains occurred on the nucellus.

Among the Mesozoic plants, only bennettites stand for comparison. Their "flowers" have similar receptacles bearing perianth bracts that are often hairy. Reduction was a fashionable evolutionary mode in bennettites (Stidd, 1980). It is conceivable that the bracts were transformed into vestigial outgrowths bearing fascicles of hairs. Similarly, numerous ovules might have been reduced to one while interseminal scales coalesced around it in a kind of a cupule. The clearly demarcated apical portions of the Baisian cupules are analogous to a "corona" of *Williamsonia* formed of the tips of interseminal scales. The nucelli and pollen grains are rather of bennettitalean aspect.

If these considerations were valid, then the Baisian plant could be seen as a development of certain bennettites toward proangiospermy. Whether they progressed further in the direction of monocots, as the similarity to cyperaceous achenes suggests, is an open question. An answer to this problem depends on further paleobotanical discoveries, as well as on new approaches to the cyperacean morphology which, after so many efforts along conventional lines, is still in a mess.

ANGIOSPERMS AND ANGIOSPERM-LIKE FOSSILS FROM THE LOWER CRETACEOUS OF MONGOLIA

Lower Cretaceous lacustrine paper shales are widespread in Central Mongolia, Mongolian Altai, and Gobi. They were extensively studied by the Soviet-Mongolian paleontological expedition. On the evidence of fossil ostracodes, insects, fishes, and recently discovered abundant plant remains, these beds were assigned mostly to the Neocomian-Aptian. Fossil plant assemblages are dominated by conifers (*Brachyphyllum, Araucaria,* pinaceous seeds and seed scales) and ginkgophytes. In the Gurvan-Eren locality (western Mongolia), two species of winged angiosperm fruits were found (Krassilov, 1982). The larger fruit (Fig. 6B) has a spherical endocarp about 6 mm in diameter divided by a thick septa into two locules. The endocarp is embraced by a symmetrical membranaceous wing with reticulate venation and is crowned by a very short style bearing a funnel-shaped stigma. Comparison with superficially similar winged fruits, such as *Eucommia, Pterocaryopsis, Ptelea, Pteleaecarpum, Zygophyllum, Dadonaea, Koelreuteria, Abronia, Dipteronia,* showed that this fossil fruit is hardly assignable to any of the known genera or families. There are, however, some points of resemblance with *Ptelea* and *Eucommia* provided that in the hypothetical ancestral species of the latter both locules were equally developed.

The smaller fruit (Fig. 6A) is elliptical, 2 mm long, having a short stalk and sessile stigma. The

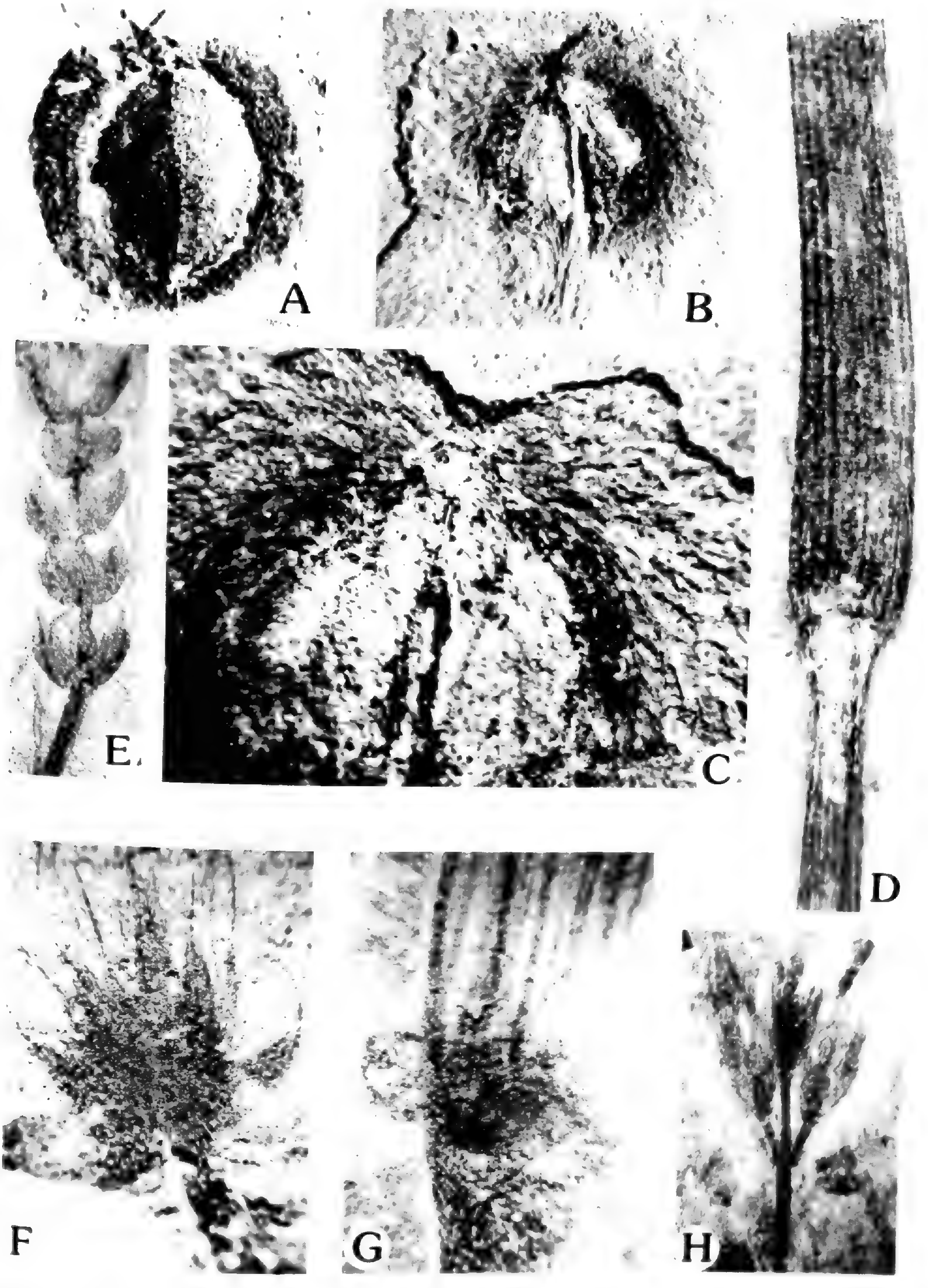

FIGURE 6. Angiosperm fruits and angiosperm-like fossils from the Lower Cretaceous of Mongolia.—A. Biloculate fruit showing a smooth wing, 10×.—B. Larger fruit showing a reticulate wing, 5×.—C. Same as B showing a short style bearing a stigma, 10×.—D. Grass-like leaf showing ligule, 2×.—E. *Potamogeton*-like spike of five whorls of nutlets, 3×.—F. *Sparganium*-like head of awned nutlets, 3×.—G. Grass-like leaf showing auricle (left side of a sheath), 7×.—H. Terminal inflorescence (?) of three spikes showing filamentous bracts, 3×.

wing is narrow, smooth, and encircles the endocarp slightly obliquely to avoid the stalk, as in the winged fruits of Juglandaceae. Evolutionary significance of these findings is at present obscure but they widen the range of pre-Albian fruit diversity.

Another locality, Manlai in eastern Gobi, yielded fragments of articulate stems with sheathing leaves (Fig. 6D). The leaf blade is sessile, flat, having thick parallel veins and longitudinal striation. At the sheath-blade junction there is a conspicuous arched groove, probably representing a ligule. Short reflexed outgrowths are occasionally preserved at the sheath corners. They are comparable to auricules of bambusoid grasses. The general aspect of leaf blade and ligule is rather like in *Ancistrachne* and related southern hemisphere grasses.

There are also several kinds of what appear to be reproductive structures (Fig. 6F–H); (1) a cyme of three stalked spikes or spikelets, terminal on a stem, with three hair-like appendages (inflorescence bracts?) at the base, superficially resembling inflorescences of *Bulbostylis* and some other Cyperaceae; (2) *Potamogeton*-like spike with five whorls of three nutlets each; and (3) *Sparganium*-like fructification consisting of an axis bearing two sessile heads of about ten mucronate nutlets each, the lower one apparently in the axil of a leaf-like bract.

These fossils are approximately contemporaneous with the Baisian achenes. They may indicate initial diversification of marshy herbaceous monocotyledons or plants of the Baisian evolutionary level. Because they are not suitably preserved for detailed study, it is unsafe to draw any definite conclusions.

MIDDLE ALBIAN *CASPIOCARPUS*

Caspiocarpus from the western Kazakhstan is hitherto the most ancient structurally preserved fructification that proves the existence of true angiosperms in the late Early Cretaceous (Vakhrameev & Krassilov, 1979). Its age is determined rather rigorously as middle Albian (Vakhrameev, 1952). The fossil axis bearing two leaves and two paniculate reproductive structures was originally assigned to *Cissites* cf. *parvifolius* (Font.) Bell, the name being applied to the leaves (Vakhrameev, 1952). The details of panicles remained unknown until, in 1977, I was fortunate to obtain a few transfer and cuticular preparations revealing some essential characters. The main axis is flat, grooved, 2 mm wide, branching at an acute angle. Each of the two branches bears a terminal panicle. One of them (the left one in Fig. 7A) is placed 5 mm above the leaf node. The panicles were shown to consist of two larger basal racemes and a number of much shorter crowded racemes above them. The latter are about 4 mm long bearing up to ten (mostly four or five), spirally arranged, overlapping follicles that are better seen in the loose apical portion of the right panicle (Fig. 7C). The follicles are elliptical, to 1 mm long, shortly beaked, attached by a short stalk and mostly opened.

It is seen on the casts and cleared preparations that they opened along the ventral suture and, in the upper quarter, also along the dorsal one (Fig. 8A). Their valves are mostly spreading at about 60° but sometimes they are flattened under pressure. No vestiges of stamens or perianths were found. The rounded pits on the casts of the follicles seen under SEM are hair bases or (less probably) stomata (Fig. 7F).

Several follicles contained intact ovules. In one of them, I found three ovules; two in one half of the follicle, one above the other (Fig. 8B), and a third one (Fig. 8C) juxtaposed to them. The ovules are about 0.8 mm by 0.5 mm, pointed, and broadly truncate at the hilar end. Two integuments are discernable, the inner one wedging out in the upper half (Fig. 8D) or occasionally near the middle of the ovule. The outer integument consists of two layers of tabular cells. Short unicellular hairs are scattered in the upper portion (Fig. 8D). The inner integument shows three layers of narrow spindle-shaped cells in the basal region. Some ovules are divided longitudinally into two halves (Fig. 8C). My suggestion that this feature represented a raphe in the cleared ovules was justly criticized by Retallack and Dilcher (1981), but at present I have no better explanation.

The taxonomic position of *Caspiocarpus* is uncertain. Because the seeds were retained in the dehiscent carpels, one can assume that they were attached by their funicles—a magnolialean feature. However, in the Magnoliaceae the carpels open along the ventral suture (with a single exception of *Kmeria*, see Canright, 1960). The thin-walled, ventrally dehiscent follicles are more characteristic of the Ranunculidae. In *Glaucidium*, an isolated genus related to Ranunculaceae and Berberidaceae, the follicles open at both ventral and dorsal sutures (Tamura, 1963).

The ovules are also of ranunculoid aspect, bi-

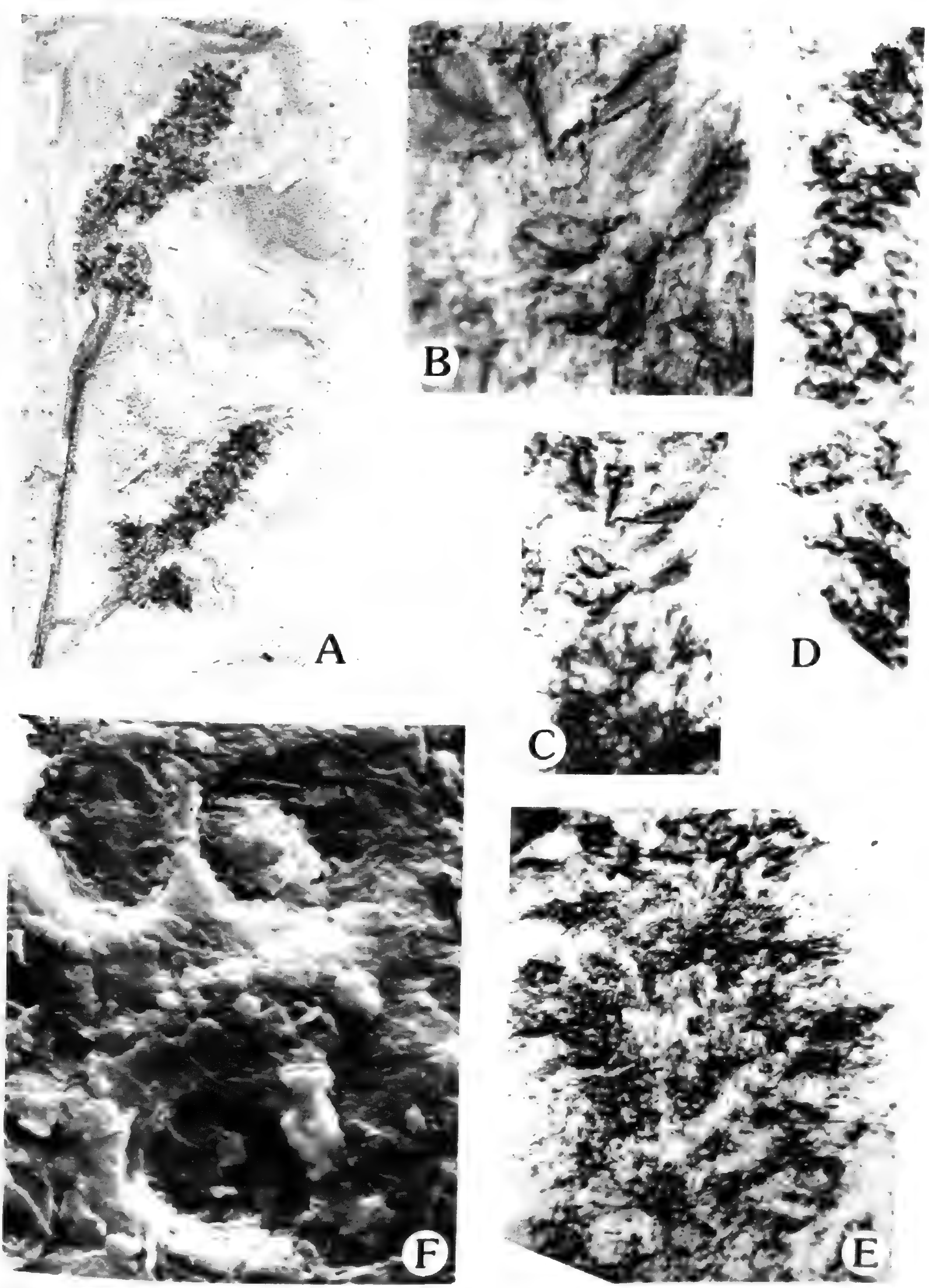

FIGURE 7. *Caspiocarpus* from the middle Albian of Kazakhstan.—A. Shoot bearing two leaves (light impressions inconspicuous on light matrix) and two panicles (1 = a leaf node), 2×.—B, C. Apex of the right panicle showing loosely arranged follicles, 25 and 12×.—D, F. Parts of the right panicle showing short lateral racemes with follicles, 10×.—F. Scanning electron micrograph of pits (hair bases or stomata?) on the follicle, 2,000×.

tegmic, with fairly thin integuments. In most Ranunculaceae the outer integument is typically shorter than the inner one, but the reverse relations occur in Berberidaceae, *Aquilegia, Hydrastis, Paeonia,* and some other genera within Ranunculidae. Extreme reduction of the outer integument is peculiar for *Ranunculus* and especially for *Circaeaster* where it is only two cells

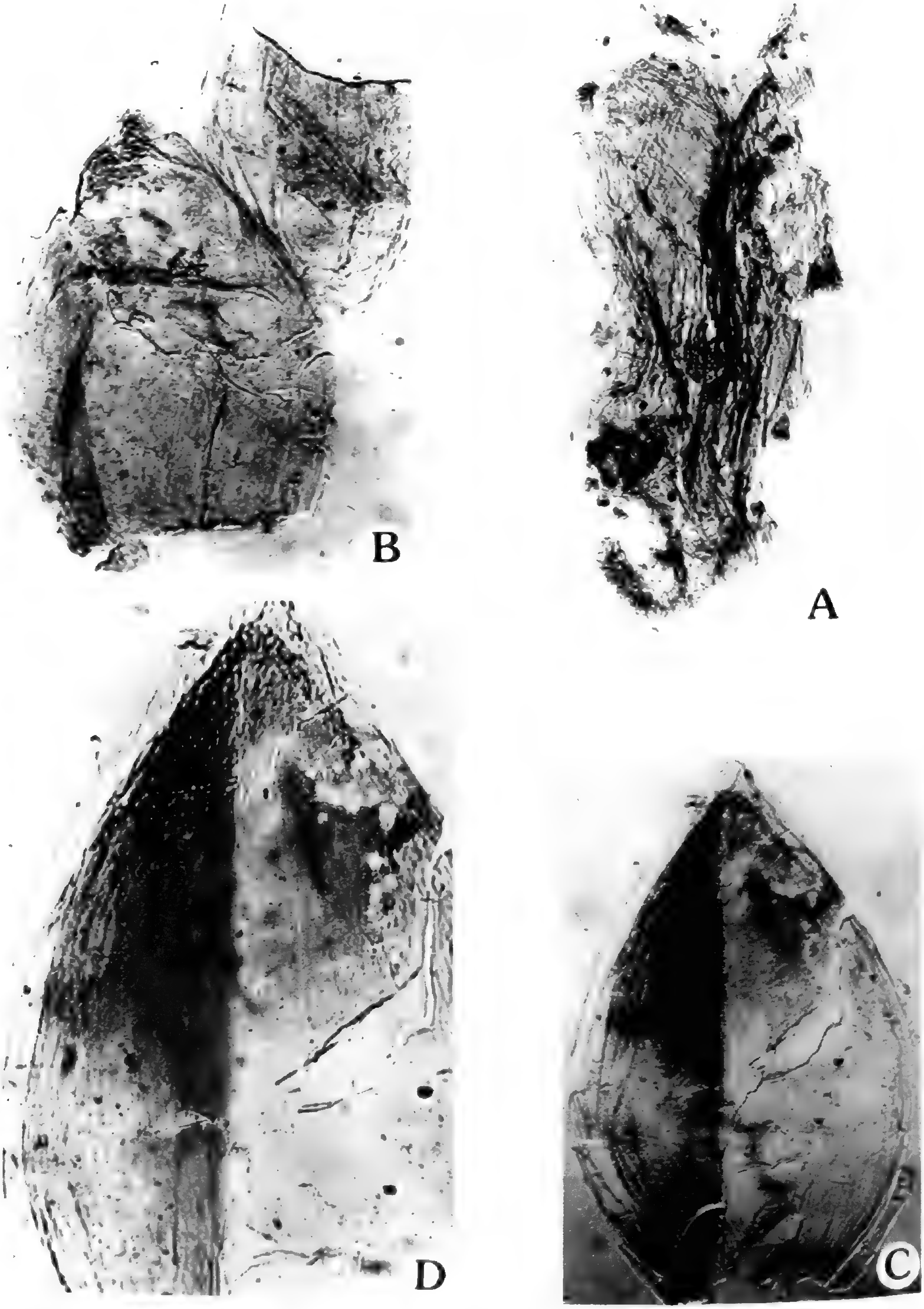

FIGURE 8. *Caspiocarpus* from the middle Albian of Kazakhstan.—A. Small cleared follicle, dorsal view, 150×.—B. Two ovules, 100×.–C. Third ovule from the same follicle, 100×. Portion of the same ovule showing wedging out of the inner integument and one of the integumental hairs, 150×.

thick. Integumentary hairs are characteristic of *Helleborus.* Branching racemose inflorescences are known in *Aconitum* and *Cimicifuga,* but *Thalictrum* has panicles. Leaves of *Cissites* morphotype occur in such extant Ranunculaceae as *Delphinium, Aconitum,* and *Ranunculus.* I believe, therefore, that *Caspiocarpus* was most closely related to Ranunculidae, though possibly not assignable to any existing family.

DISCUSSION

Hickey and Doyle (1977) have stated that "the identification of any Jurassic plants as proangiosperms (as attempted by Krassilov, 1973, 1975) will probably be a difficult task requiring a detailed comparative analysis of all organs as rigorous as that which was required to establish the relationship between cordaites and conifers (Florin, 1971) or the role of Devonian Aneurophytales and Archaeopteridales as progymnosperms." Needless to say, the rigorous analysis of all organs is desirable, but Florin actually drew his conclusions from his studies of the seed scale complexes—which did prove the relationship between cordaites and lebachiacean plants (probably a specialized line of cordaites with reduced leaves), but which left the problem of conifer ancestry unsolved. Evidence that progymnosperms are related to gymnosperms comes mostly from wood anatomy.

Similarly, the proangiosperms, as I understand them, share with true angiosperms a few characters of critical importance, and among them the angiospermy itself. They have a kind of ovary that is supposedly monocarpellate involuted (*Caytonia, Dirhopalostachys*) or bicarpellate with open carpels (*Leptostrobus*). The question is whether any kind of angiospermous ovary could arise from these structures or whether they represented "blind alleys" of angiospermization while the mainstream progenitors are still to be found.

Thomas (1931) has suggested derivation of a ranunculoid follicle from two joined caytonialean cupules fused to the rachis. His ideas were rejected by leading contemporaneous morphologists because in *Caytonia* the ovules are orthotropous and supposedly unitegmic whereas in ranunculoid angiosperms they are mostly bitegmic and anatropous. To overcome the difficulty of a de novo formation of the second integument, Gaussen (1946) has postulated its derivation from the caytonialean cupule while the rachis expanded into a carpel. Stebbins (1974) and Doyle (1978) have supported this suggestion but Retallack and Dilcher (1981) found it intuitively unattractive. In their opinion, the outer integument might have been derived from a glossopteridalean leaf bearing an epiphyllous ovulate structure. But in the case of *Caytonia* there is no need of going to those lengths because its ovules are, in fact, bitegmic.

I suggested (Krassilov, 1970) that the enigmatic "spotted layer" of *Caytonia* (supposedly an aleurone layer) might be a vestigious inner integument. Recently I studied a few *Caytonia* ovules from Yorkshire kindly sent to me by T. M. Harris. I found nothing essentially new except some fine external features of the micropyle (Fig. 9). I also reaffirmed my suspicions about the "spotted layer." The aleurone layer is a layer of endosperm. It is situated inside, not outside the nucellar cuticle. The "spotted layer" of *Caytonia* envelopes the nucellus (Fig. 10). It consists of two layers of cells and it is cutinized. Its small spots and larger patches of dark matter look not like aleurone grains but rather like metamorphosed oil cells and blocks of tannin filling inner integuments of angiosperm seeds. Harris (1964) noticed that the "spotted layer" never extended into the micropyle. Thus, the micropyle was formed by the outer integument only. I discussed the problem of bitegmy elsewhere (Krassilov, 1970). Double integuments can be traced back to early Carboniferous *Eurystoma angulare* (Camp & Hubbard, 1963). In many Paleozoic seeds the inner integument had been lost in fusion with the nucellus (hence, vascularized nucelli), but it was restored in gnetalean plants, some bennettites (*Vardekloeftia,* Harris, 1932), and *Caytonia.* About half of the dicotyledons and three quarters of monocotyledons have bitegmic ovules that are consentaneously recognized as the primitive condition. However, in the families that appeared early in the fossil record, such as Ranunculaceae, Menispermaceae, Piperaceae, Fabaceae, Rosaceae, and Poaceae, there are both uni- and bitegmic ovules. Such flexibility might be due to frequent atavistic mutations. Even vascularized nucelli have been restored in some angiosperm lineages (e.g., Thymeliaceae). Tritegmic forms, as in *Sarcandra,* can also be expected among early angiosperms.

It was shown (Krassilov, 1978) that the "mouth" of *Caytonia* can be shifted from its position at the base of the pedicel. One can imagine that a continuation of this process (due to

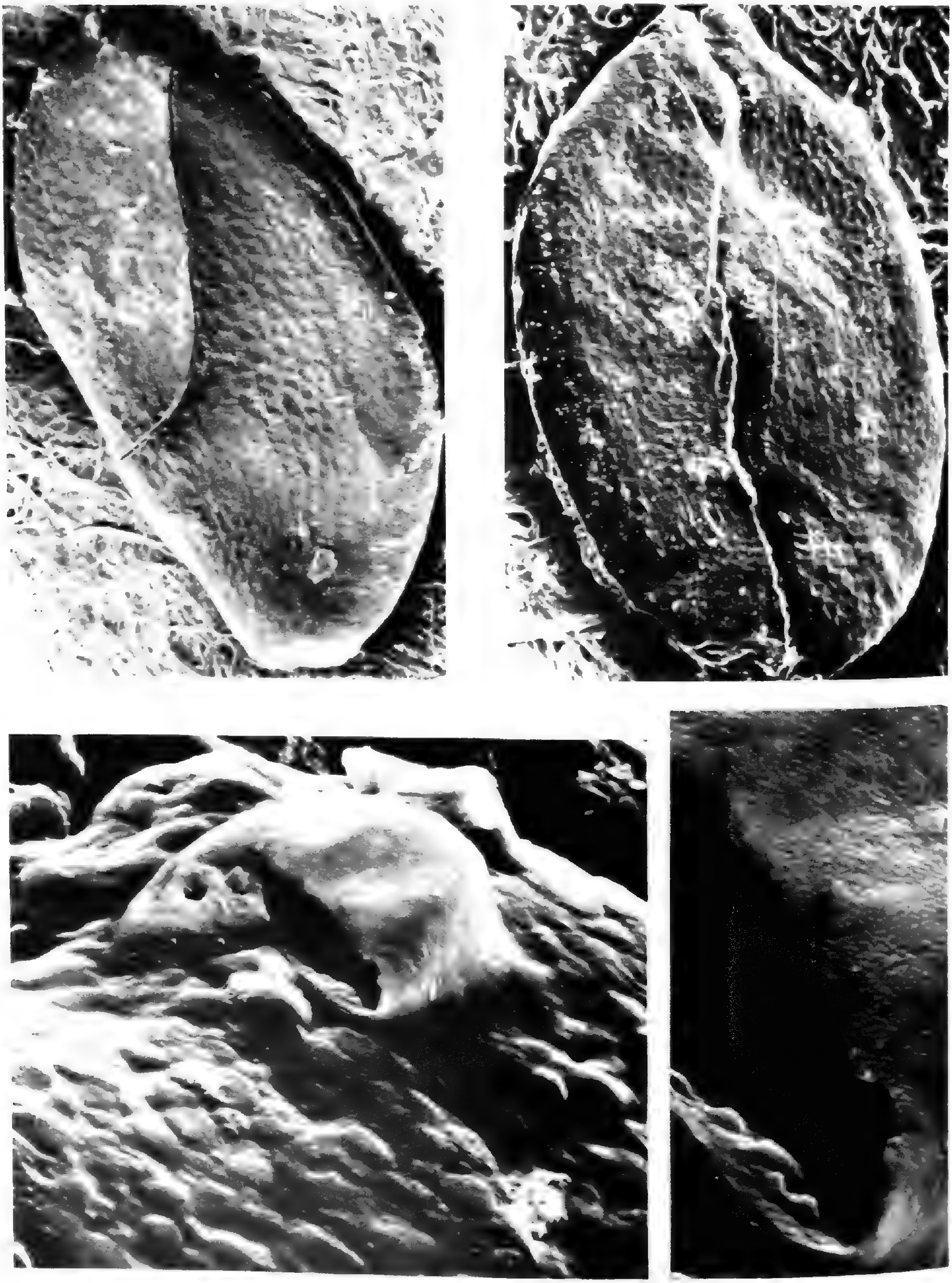

FIGURE 9. *Caytonia sewardii* Thomas from the Jurassic of Yorkshire. Scanning electron micrograph of two ovules, 100×, and scanning electron micrograph of details of the micropyle of the left ovule, 1,200 and 4,000×.

adaptation to some pollination vector?) could bring the "mouth" into apical position, at the same time affecting the position of ovules. The resultant urn-shaped ovary, styleless, with sessile stigma, would not be unlike those of a vesselless angiosperm, *Sarcandra irvingbailleyi* Swamy (Fig. 11). In this species, the ovules are bitegmic (occasionally tritegmic), orthotropous but brought to pseudoanatropous position by the curvature of the carpel (Vijayaraghavan, 1964). Intercarpellary pollen grains, as in *Caytonia* (Krassilov, 1977b) occur as an atavistic or recurrent feature in *Annona, Lilium,* and some other angiosperms (Vasil & Johri, 1964).

FIGURE 10. *Caytonia sewardii* Thomas from the Jurassic of Yorkshire.—A. Nucellus of an ovule shown in Figure 9, right, with the remnants of a "spotted layer," outer integument is removed completely, 70×.—B. "Spotted layer" of another ovule, 150×.—C. Cells of the "spotted layer," 300×.—D. "Spotted layer" wedging out below the micropyle, 150×.

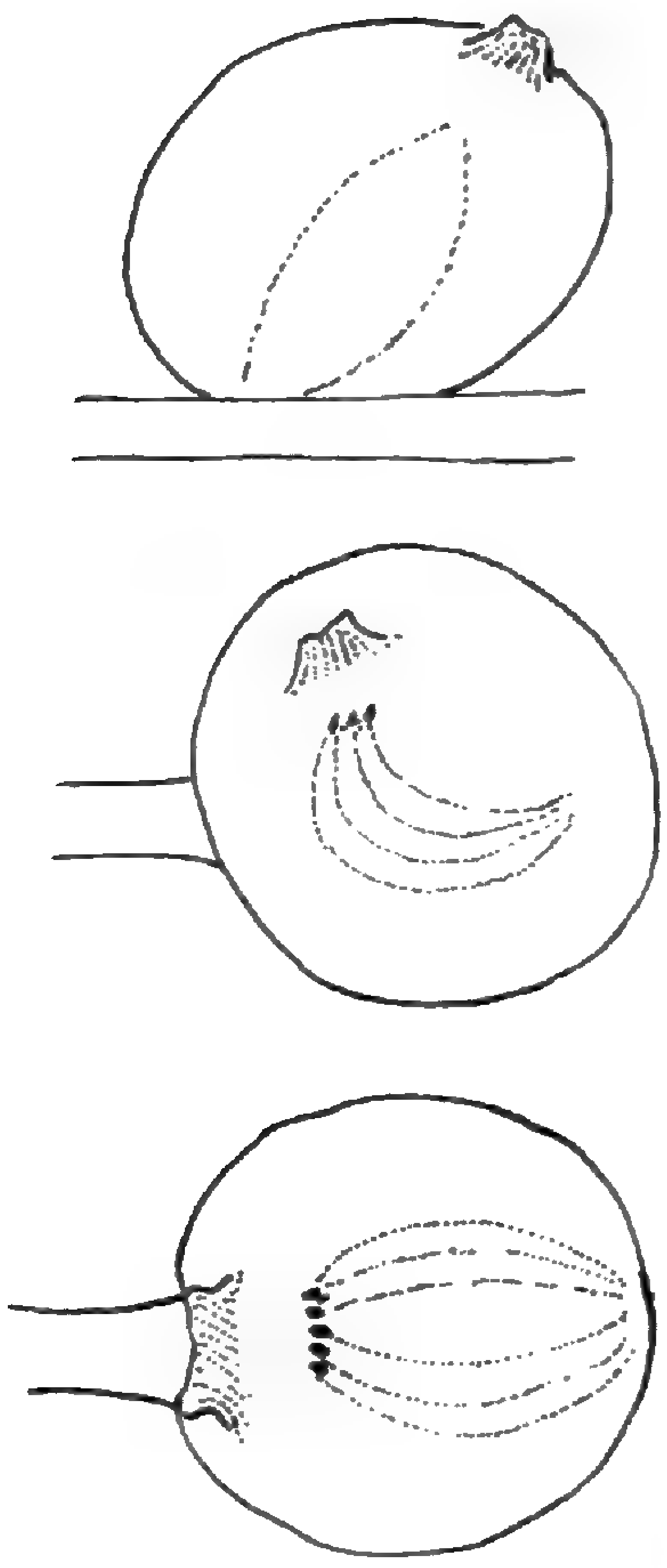

FIGURE 11. Suggested derivation of a *Sarcandra*-like carpel from *Caytonia*-like cupule by the shifting of a mouth.

This simple mode of transforming the caytonialean cupule into a carpel is partially supported by the evidence of the shifted "mouth" in the mid-Jurassic *Caytonia sewardii,* but final proof or repudiation should come from detailed study of the late Jurassic and Cretaceous species.

Dirhopalostachys is a raceme of paired follicle-like one-seeded beaked cupules having a ventral suture (Krassilov, 1975). The pairing of cupules reminds one of the Hamamelidaceae—one of the most ancient angiosperm families. However, the cupules are even more similar to the carpels of *Kingdonia* (Foster, 1961). In this archaic east-Asiatic genus, the gynoecium consists of 5–8 spirally arranged semiclosed carpels that develop into one-seeded fruits with recurved beaks (Fig. 12). Noticeably, the venation in *Kingdonia* is open flabellate in leaves and open pinnate in tepals, resembling *Nilssonia*—supposed foliage leaves of *Dirhopalostachys.* It is conceivable that the apetalous flower of *Kingdonia* arose from androgynous reproductive structure similar to *Irania*—a progymnospermous plant related to *Dirhopalostachys* (Schweitzer, 1977). *Kingdonia* certainly deserves further study. However, many essential features of *Dirhopalostachys* and *Irania,* and first of all the mode of pollination, are still to be learned.

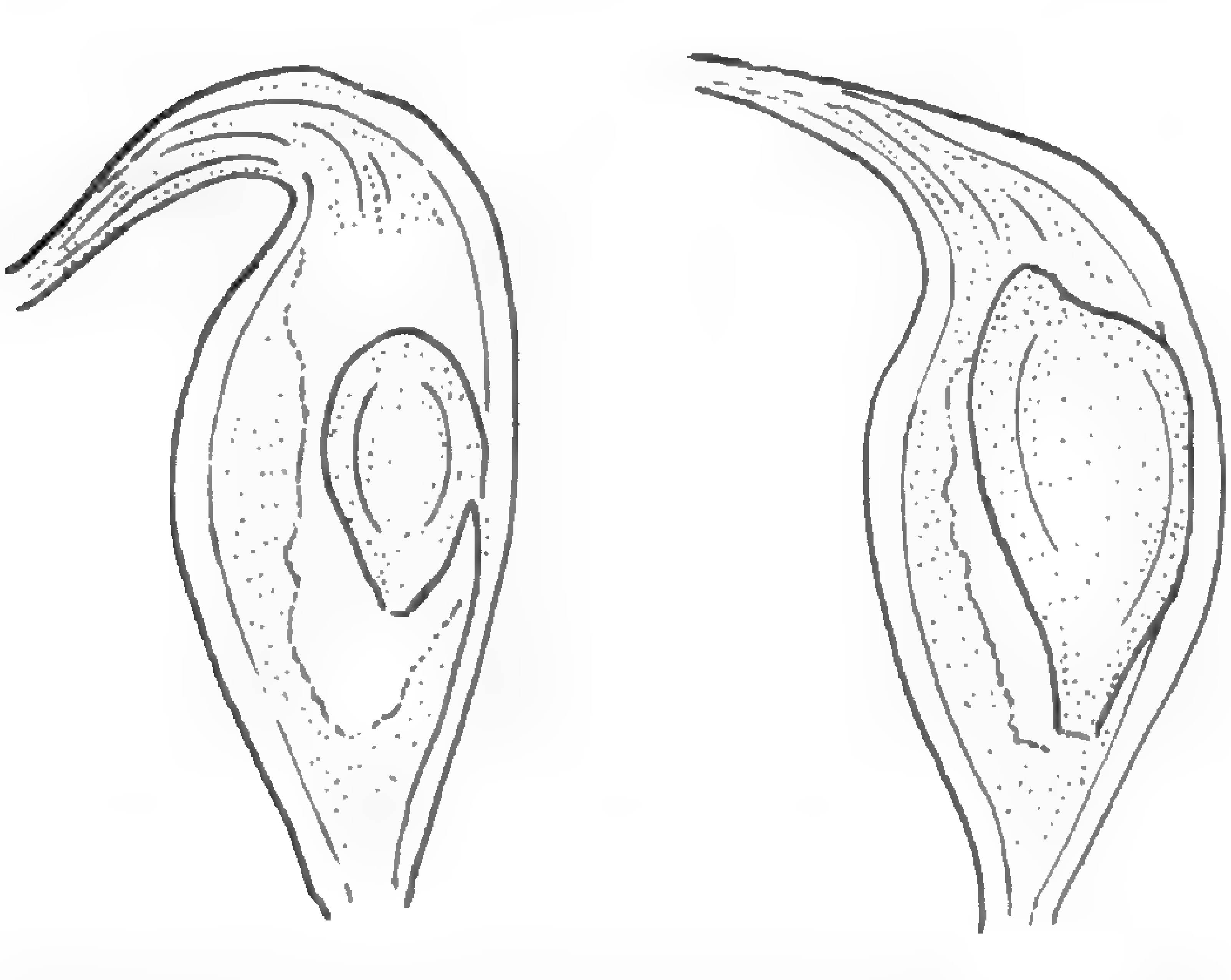

FIGURE 12. Carpels of *Kingdonia,* left (after Foster, 1961) and *Dirhopalostachys* (after Krassilov, 1975).

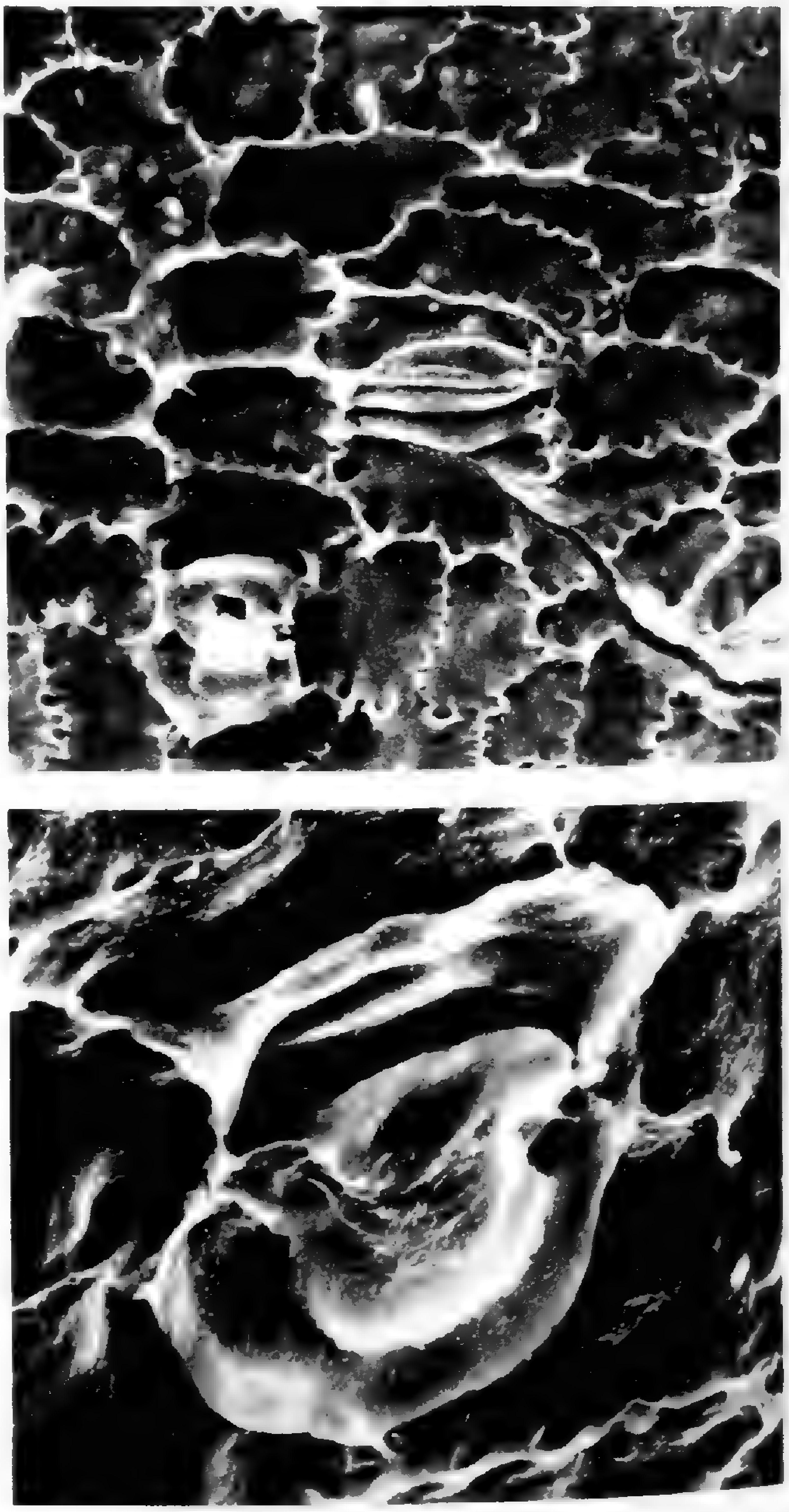

FIGURE 13. Scanning electron micrograph of aborted (top) and normal stomata of a bennettite *Nilssoniopteris amurensis,* 800 and 1,600×.

FIGURE 14. Vessel-like members from the midrib of a *bennettitalean* (*Otozamites*) pinna showing terminal perforations, 300 and 600×.

Paleobotanical discoveries have substantiated almost all theoretically conceivable pathways from open ovulate structure to carpel except conduplication. In the course of my studies of the Late Jurassic *Leptostrobus* (bivalvate capsules with papillate stigmatic fringes), I suggested that the so-called "conduplicate" carpel in Winteraceae is derivable from the leptostrobalean prototype and actually consists of two open carpels fused by their margins (Krassilov, 1970). The conduplicate nature of the winteraceous carpel was questioned by Tucker and Gifford (1964) and recently Leroy (1977) has shown that, at least in some winteraceous genera, the ovary is bicarpellate, with both ventral and dorsal grooves corresponding to the contacts of open carpels as it was, in fact, suggested by me and still earlier, on different grounds, by Long (1966). Vink (1978) noted that in the supposedly unicarpellate ovary of *Drimys*, the dorsal groove is identical to that of the bicarpellate ovaries studied by Leroy. Complete revision of the carpel morphology in Winteraceae, one of the key families of angiosperm phylogeny, is to be expected.

Finally, if the supposed relationships of the Baisian achenes to ovulate structures of bennettites were correct, there should be still another way to angiospermy by fusion of interseminal scales, vaguely preconceived by Fagerlind (1946).

Evolutionary potentials of bennettites look not so gloomy once more. Recently other points of resemblance between them and angiosperms came to light. Florin (1933) suggested that bennettitalean stomata were mesogenous ("syndetocheilic") as in many angiosperms, but his views were disputed because he deduced from mature paracytic apparatuses, which can be ontogenetically mesogenous, perigenous, or mesoperigenous. Recently, I described a few aborted stomata (Fig. 13) that confirm mesogenous development (Krassilov, 1978). In the Mongolian species *Otozamites lacustris* Krassil, it was possible to macerate conducting elements from the midrib of a pinna (Krassilov, 1982). Among the tracheids with scalariform thickenings, there were short vessel-like members showing terminal perforations (Fig. 14).

Thus, bennettites were capable of developing vessels in the primary xylem, reticulate venation (*Dictyozamites*), paracytic stomata, bisexual flowers, and achene-like fruits. It seems unjust to rule them out as possible ancestors of angiosperms. There are also indications that angiosperms first appeared in cycadophyte shrublands dominated by various bennettites and then penetrated coniferous forests (Krassilov, 1973).

CONCLUSION

Not long ago, the origin of angiosperms seemed mysterious because there were no acceptable candidates for ancestors. Now the problem is that there are too many of them.

Traditionalists often pose as defenders of respectable theories (such as monophyletic origin of angiosperms) against irresponsible speculations. Actually, they defend old irresponsible speculations from the new ones. In the case of angiosperm ancestry, however, new speculations even seem somewhat less irresponsible. As more lineages approaching angiospermy emerge from the fossil record, the polyphyletic hypothesis appears more plausible. It is significant also that most proangiosperm records are clustered around the supposed Asiatic center of origin.

Further progress depends on detailed studies of the Late Jurassic and early Cretaceous *Caytonia, Dirhopalostachys,* bennettites, czekanowskialean, and *Classopollis*-producing plants as well as the middle Cretaceous angiosperms.

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MESOSPERM PALYNOLOGIC EVIDENCE AND ANCESTORS OF ANGIOSPERMS

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ABSTRACT

Late Triassic and mid-Cretaceous appear to have been times of evolutionary innovations of seed plant pollen. Between these times dispersed pollen indicates relatively little change, although megafossil studies record the appearance of several new plant groups in the late Jurassic. This incongruity suggests that knowledge of pollination arrangements of Mesozoic seed plants is far from complete; some plants have been described with stigmatic surfaces, and investigation of their morphological intermediate position needs much fuller attention. The search for Mesozoic ancestors of angiosperms is particularly difficult because of the lack of a satisfactory definition of an angiosperm in Cretaceous time. It is suggested that all Mesozoic seed plants should be placed in a Mesosperm Group of fossils and that no living angiosperm taxon should be used for fossil plant remains before the Cenozoic unless at least two separately preserved plant organs in the same beds can be shown to be associated in supporting that taxon. All Mesozoic seed plant taxa should be based solely on evidence from fossils.

In this short paper my object is to attempt to clear some of the obscuring fog around the problem of angiosperm ancestors. Hitherto, on the basis of the current understanding of the terms 'gymnosperm' and 'angiosperm,' I have supported (Hughes, 1976) the view that certain Cretaceous Barremian pollen represented the earliest angiosperms and that any ancestor should properly be sought among gymnosperms in earlier Cretaceous rocks. Progress, however, has been relatively slow because only a small proportion of those interested in the problem work with newly discovered fossil evidence. At the Ninth Botanical Congress (Montreal 1959), the struggle for understanding against obscure diversion (cf. Scott et al., 1960; Hughes, 1961) centered on supposed cryptogenic upland plants; more recently diversions take the form of lightly documented curiosities of comparative morphology of pollen aperture and exine structure (e.g., Klaus, 1979; Cornet, 1980).

In this age of advanced techniques of study of the available abundance of microfossils, a solution to the whole problem actually seems to be attainable by painstaking production of good records of fossils alone. The dangers to such continuous progress by hard work appear to lie in poor communications resulting from ill-defined terms and in the impatience commonly expressed through unnecessary neobotanical association theories. After examining briefly the current progress with fossil gymnosperms, I shall turn to definitions of terms and to those classification procedures that appear to obstruct understanding.

LATE TRIASSIC POLLEN INNOVATIONS

Schulz (1967) described pollen of *Clavatipollenites* type from the late Triassic of Poland. Klaus (1979) amplified the description of the tri-saccate *Dacrycarpites europaeus* Mädler (1964) to include various angiosperm aperture and exine characters that he compared with the pollen of *Schizandra* and other living plants; but these 'prae-angiospermid' characters were observed on 'occasional aberrant' grains. Cornet (1980) referred to a wide range of late Triassic angiospermid apertures but the information is provided only in unillustrated abstract form and is thus difficult to use. If the material referred to by these authors were subjected to rigorous recording with adequate specimen numbers and statistical assistance, it seems likely that some new information would emerge.

In addition, late Triassic is the time of origin of *Classopollis, Eucommiidites,* and *Ovalipollis,* all of undisputed gymnospermid character; Scott (1960) compared *Equisetosporites* with *Ephedra.* In comparison, therefore, with the periods of geologic time just before and just after, these late Triassic floras appeared to have been involved in unusual innovations of pollen characters (Text-fig. 1).

This period of time also produced the megafossil *Sanmiguelia* claimed by Cornet (pers.

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Stratigraphic Scale	'Atlantic-area' Megafloras	Seed Plant Events				
		Pollen	Flower	Fruit	Leaf	Wood
Cenomanian			*F5*			*W2*
Albian	*Potomac 35° Cr N*	*P3*				
Aptian					*L2*	*W1?*
110						
Barremian		*P2*		*Fr1*		
Hauterivian						
Valanginian						
Berriasian	*Wealden 40° Cr N*					
135+						
	Morrison 40° Jr N		*F4*			
Late Jurassic						
Mid Jurassic	*Yorkshire 40° Jr N*		*F3*			
Early Jurassic						
	Scania 40° Jr N					
195+			*F2*			
Rhaetian	*East Greenland 45° Tr N*	*P1*			*L1*	
Norian						
Carnian			*F1*			

TEXT-FIGURE 1. Stratigraphic table of seed plant occurrences and of Atlantic-area floras with approximate paleolatitudes. P1 = Late Triassic pollen innovations; P2 = tectate columellate monocolpate pollen; P3 = tricolpate pollen. F1 = *Sturianthus*; F2 = *Williamsonia*; F3 = *Williamsoniella*; F4 = *Cycadeoidea*; F5 = angiospermid inflorescences. Fr1 = *Onoana*. L1 = *Sanmiguelia*; L2 = Potomac leaves. W1 = *Aptiana* Stopes; W2 = undisputed vessel-bearing wood.

comm.) to be of angiosperm nature. Just such a claim was also made by the original author (Brown, 1956) but had subsequently been doubted because of the state of preservation (Doyle, 1973). The new better preserved material could change opinions.

CRETACEOUS BARREMIAN POLLEN INNOVATIONS

Tectate columellate monosulcate pollen has now been recorded (Hughes et al., 1979) from the British Wealden strata in a succession of many palynologic samples from Berriasian age onwards in which the entry and diversification of such pollen within Barremian time is firmly documented. Unfortunately, there are no useful megafossil plants from the Barremian strata concerned.

Pollen of this type has been recorded by Doyle and Robbins (1977) and others from the Potomac Group of eastern North America where there are well known megafossils redescribed by Hickey and Doyle (1977). The stratigraphic information about these non-marine beds is not complete, but some of the earliest megafossils probably came from approximately Barremian-Aptian boundary times (Potomac—Zone I); there is however an unconformity below and thus no downward succession into earlier beds. Doyle (1982) records a valuable advance in knowledge down-dip, but much more information is still needed.

With the arrival of 'angiospermid pollen' there is a sudden incoming and diversification of large numbers of '*Ephedripites*' pollen. This is also an innovation, but the other palynomorphs in the assemblages are not new and include normal Cretaceous representative species of *Classopollis* (see Alvin, 1982) and *Eucommiidites*.

Although the equivalent beds in West Africa (Doyle et al., 1977) have produced an extended number of types of 'angiospermid' pollen, the stratigraphic succession does not show for certain that the critical palynomorph zones C-V and C-VI are of Barremian rather than of early Aptian age. There are, however, zones C-IV and below, which comprise a downward succession and lack this pollen.

The striking fact about all these Cretaceous successions is that these major Barremian pollen innovations are the first since Rhaetian times. Palynomorphs from many described Hettangian to Hauterivian samples may bear spore innovations such as *Cicatricosisporites* in the late Jurassic and *Aequitriradites* in the early Cretaceous but there are virtually no new or unusual pollen types representing the seed plants.

JURASSIC PLANT MEGAFOSSILS

The relative lack of new variety in seed plant pollen in the Jurassic is contrasted with what is known of the major plant groups themselves. The Bennettitales diversify in the Jurassic into Williamsoniaceae, Wielandiellaceae and, towards the end of the period, Cycadeoidaceae. The Nilssoniales are apparently distinct and diverse throughout; despite attempts using single plant organs as far back as the Permian to identify them with living Cycadales, the situation remains confused and it seems more helpful to confine any discussion of true Cycads to the Cenozoic (cf. Krassilov, 1978: 896). The large group of 'Ginkgophytes,' including *Karkenia* and *Pseudotorellia*, became important in late Jurassic and early Cretaceous time; it is in many ways unfortunate and misleading that the group should even bear the name of the one living species of *Ginkgo*. There is continuous diversification of what are broadly known as Jurassic Coniferales. Entirely new groups such as the Pentoxylales also arose in this time interval.

Despite strong suspicions that some of these plant fossils such as *Caytonia* and *Leptostrobus* (Czekanowskiales) included early kinds of stigmatic surface, there still appears to be no significant appropriate pollen modification. Insect contacts with plant reproductive systems may well have been confined at first to the Coleoptera but in latest Jurassic and early Cretaceous time both the Diptera and the Hymenoptera appear to have evolved far enough to be concerned, but again this is without any apparent response in the pollen morphology before Barremian time.

This striking incongruity of evidence between pollen and megafossils may have some other explanation, but it is probably due to our lack of appreciation of the scope and diversity of the Mesozoic gymnosperms. One of the main causes of this lack is the continued fitting of all fossil plant evidence of this age into a neobotanical hierarchical classification that is inappropriate and irrelevant but is almost always used by custom; the continuation of this procedure perhaps represents the biggest outstanding failure of paleobotany.

Also, as can be seen in Text-figure 1, the main floras, on which most of the interpretations are based, were located in a narrow belt of northern mid-paleolatitudes. Megafossil occurrences in both southern and high northern paleolatitudes are well documented, but the palynologic evidence is more fragmentary as yet.

DEFINITIONS OF MAJOR GROUPS

The term 'angiosperm' is easily and acceptably defined in the world of present-day plants on the basis of a combination of the fossilizable characters of the flower, fruit, pollen, leaf, and wood. However, in mid-Cretaceous time there is normally available, at any one locality, only one plant organ such as pollen or fruit or leaf with its one set of characters. For example, it is by no means certain that the unseen Albian plants providing tectate columellate tricolpate pollen also possessed reticulate-veined laminate leaves; in fact what is known of the order of appearance of organs and characters suggests incongruity of development. Thus it is questionable whether the Barremian tectate monocolpate pollen mentioned above should be included in Angiospermae; but if it is not so included, then no other comparable single organ occurrence can be included either and the question of evolution from ancestors becomes unanswerable. Although an arbitrary decision to include such Barremian pollen in Angiospermae can be made, the case will remain unsatisfactory because the whole of the rest of the Barremian plant concerned could well prove to have gymnospermous characters; no appropriate flower, fruit, leaf, or wood has yet been found at this stratigraphic level.

Correspondingly, the term 'gymnosperm,' in the Mesozoic, is dependent on antithesis and is negative in that it includes any seed plant not shown to be an angiosperm. Further, the term 'flowering plant' must now include Bennettitales and several other pre-Cretaceous gymnospermous fossils and so cannot be used in place of angiosperm.

Thus, if the major terms cannot be defined for Cretaceous time it is meaningless to nominate

MESOZOIC SEED PLANTS

Recommended classification		Terms for Cenozoic use only
MESOSPERM GROUP		Gymnospermae
Brachyphylls		
Cheirolepidiaceae		
Linearphylls		Coniferales
'Ginkgoaceae' (temporary use)		Ginkgoales
Czekanowskiales		
Bennettitales		
Nilsoniales		Cycadales
Caytoniales		
Irania group		
Dirhopalostachys group		
Pentoxylales		
Cretasperm group	For single-organ records	Dicotyledones (Magnoliopsida)
Cretablum group		
Cretapoll group		Monocotyledones (Liliopsida)
Cretaphyll group		Magnoliales
Cretoxyl group		
ANGIOSPERMAE (Only for those pre-Cenozoic records in which two separate organ fossils have been accepted as associated thus confirming the presence of a formally recognized angiosperm taxon.)		

TEXT-FIGURE 2. Scheme of classification of Mesozoic seed plants. List of groups is representative only, but includes some formal groups with latinized name endings. The five Cretaceous single-organ groups are informal. The names in the right-hand column are excluded in this scheme from Mesozoic use.

any Cretaceous, Jurassic, or Triassic fossil as the earliest angiosperm, and such exclusion must apply also to the Barremian pollen.

PROPOSAL FOR MESOZOIC CLASSIFICATION OF SEED PLANTS

The failure of definitions just mentioned can be overcome simply by classifying fossils by those features alone that are observed, omitting all reference to features that are merely supposed. In the present case, there appears to be no dispute that the fossils concerned represent seed plants and that their general sequence age is also known. Hence, it would be logical to attribute all such Mesozoic seed plants to a new 'Mesosperm Group,' which is a name for a group defined to receive all fossil orders or families of Triassic, Jurassic, or Cretaceous age displaying any undisputed seed plant characters; the name 'Mesosperm Group' is neither latinized nor typified so that it remains outside the current neobotanical hierarchy. Thus, the formal name Gymnospermae would not be defined or required in the Mesozoic and would be restricted merely to Recent and Cenozoic plants; any Paleozoic use could be similarly avoided with ease. For the Mesozoic, the use of such subordinate subjective units as Coniferales, Cycadales, Ginkgoales, and Auraucariaceae at the family level could also with advantage be avoided for the same reason. As indicated on Text-figure 2, all currently used fossil seed plant groups would be included in the Mesosperm Group.

ANGIOSPERM TERMINOLOGY TRANSITION FROM MESOZOIC TO CENOZOIC

Even from the late Cretaceous most angiospermous plant evidence is still in the form of individual records of separated flower, fruit, pollen, or leaf; for any records in this state it is appropriate that they should stay in the Mesosperm Group. The criterion, therefore, for change to formal inclusion in Angiospermae could well be the accepted proof of association of two separated organs, e.g., the flowers with Normapolles type pollen referred to by Friis (1981, 1984) and by Skarby (1981). Such a criterion could even provide stimulus to exploration and would greatly enhance the value of fully worked records. Cenozoic angiosperm records would for convenience be free of this restriction.

REFERENCE TO CRETACEOUS ANGIOSPERMID CHARACTERS

From Barremian and Aptian times onwards to the end of the Cretaceous, numerous pollen or leaf or other fossils have already been attributed to extant angiosperm families; although the attributions are harmless expressions of opinion in themselves, the use for the record of a name directly reflecting the indication of affinity is undesirable because it depends, in virtually every case, on the characters of only one organ.

Clearly, such weakly based records should not be accorded the same status as the important cases of accepted confirmation mentioned in the previous section. The undoubted cumulative value of such unconfirmed records can best be expressed by neutral group terms such as 'Cretasperm' and 'Cretaphyll' for communication and listing purposes (see Text-fig. 2); in construction of these words the use of general age and general morphology indications seem unlikely to mislead, but the lack of a latinized ending emphasizes the distinct origin and purpose of such names. The extension of that system of names to include 'Triassopoll' or 'Juraphyll' as required, appears reasonable. Undoubtedly, some authors concerned with 'Cretaphylls' and 'Cretapolls' may consider their single organ evidence to be very strong but the requirement to prove association appears to be an appropriate restraint that will recall for all users the true state of the record.

In this connection, the very well-documented compilation of Muller (1981) appears to present a few cases for exemption from this structure, because he limited his Cretaceous 'acceptances' so severely. Muller (1981: 6) himself drew attention to the problem of lack of information about other organs than pollen, and the logical need for confirmation that remains. It is probably better that work should be stimulated on acceptable confirmation of even these few Cretaceous pollen claims to family or higher group identification, by treating them in the same way as all other single organ records.

ADVANTAGES OF PROPOSED MESOSPERM GROUP SCHEME

1) The scheme outlined above and illustrated in Text-figure 2 involves minimum disturbance to current practice and literature, and calls for additional activity only in classifying Cretaceous 'angiosperms.'

2) The status of records is automatically and much more clearly indicated.

3) Although not directly suggesting a polyphyletic origin for angiospermy, the scheme leaves the matter truly open by removing all trace of classificatory bias towards a monophyletic theory that has no base in geological history nearer to the Cretaceous than 60 million years.

4) The idea, developed for many years in his writings by the late Professor Tom Harris, that paleobotanists are only on the edge of understanding the true biologic range of Mesozoic seed plants, will be strengthened.

CONCLUSIONS

1) Clearly some more-botanically-based colleagues will tend to be dismissive of this scheme, but I ask them to look beyond the apparent iconoclasm. The purpose is to tackle the problem of which the solution has eluded both botanists and geologists for a very long time, by attempting to reorganize the available data, separately from all theory, so that entirely new studies may be encouraged.

2) No solution to the main problem is offered here. Such a solution will appear only gradually when all available evidence has been encompassed. I am personally convinced that there is no abnormal tangible factor involved beyond ordinary paleontological experience.

3) Although perhaps entirely unbiased data handling is unattainable, it appears worthwhile in this way to attempt to free a virtually deadlocked topic.

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FLOWERS FROM THE EOCENE OIL-SHALE OF MESSEL: A PRELIMINARY REPORT

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ABSTRACT

A polycarpous flower perhaps belonging to the Magnoliales, a tiliaceous flower, and a male, branched, sapindalean inflorescence are described from the Middle Eocene oil-shale at Messel near Darmstadt, Germany.

OIL-SHALE OF MESSEL

The oil-shale of Messel, located northeast of Darmstadt (Federal Republic of Germany), occupies an area of about 1 km in diameter and, like a few other small oil-shale deposits in the neighborhood, is surrounded by lower Permian sediments. All are tectonic trenches that originated during sinking of the Rhine valley during the early Tertiary.

The Messel oil-shale originally had a thickness of more than 150 m before it was mined. During mining a large collection of plant and animal fossils were assembled. Among the animal fossils, the vertebrates are of particular significance because they are very well preserved, sometimes showing fine details such as skin, hairs, and feathers (Koenigswald, 1980). The vertebrates are also important for the determination of the age (Lutetian, Middle Eocene; Tobien, 1968), and the occurrence of crocodiles has been taken as indicating a tropical to subtropical climate (Berg, 1966). Like the vertebrates, other fossils such as insects and plant leaves are also well preserved, and there is the potential for reconstructing much of the fauna and flora of the "Messel lake" through further investigations. Because of plans to fill the open cast mine with refuse, the Forschungsinstitut Senckenberg, Frankfurt am Main, and several other institutes have been actively collecting from the locality.

PLANT FOSSILS

Plant fossils, especially leaves, were collected during the mining period. They were first described by Engelhardt (1922) and deposited in the Hessische Landesmuseum Darmstadt and in the Forschungsinstitut Senckenberg, Frankfurt am Main. A more recent revision of the Lauraceae from the locality is published by Sturm (1971). One of the difficulties in preserving the Messel fossils is that the oil-shale splits into small fragments during drying. Recently however, the transfer of animal specimens onto synthetic resins has allowed larger specimens to be salvaged. In the last few years, we have collected a lot of new plant material that consists mainly of leaves; but also fruits as well as five flowers have been collected. Plant remains are not distributed homogeneously in the oil-shale, but there is no area in the mine where a special leaf layer can be found. The leaves occur singly and scattered throughout the sediment and, due to their rarity, we have collected only about 3,000 over the last seven years. During this period several new techniques for their preparation and investigation have been devised (Schaarschmidt, 1982).

The quality of preservation of the leaves is quite variable but can be easily gauged with the use of epi-fluorescence microscopy. Some have well-preserved cuticles but in others the cuticles had been more or less destroyed by decay before fossilization. The water of the Messel lake had little current (Franzen, 1982), and therefore the leaves may have been very slowly deposited. For the same reason flowers are seldom preserved and those present are of fairly large size.

In this paper, I present a preliminary report of the first three flowers, which were found in Messel until 1980. Since this time, the number of collected specimens increased enormously. Particularly, excavations during the summers of 1983 and 1984 brought a lot of small flowers, and by help of fluorescence, it was possible to identify insignificant remains. The more than 1,000 flowers collected so far belong to about 70 genera of several families.

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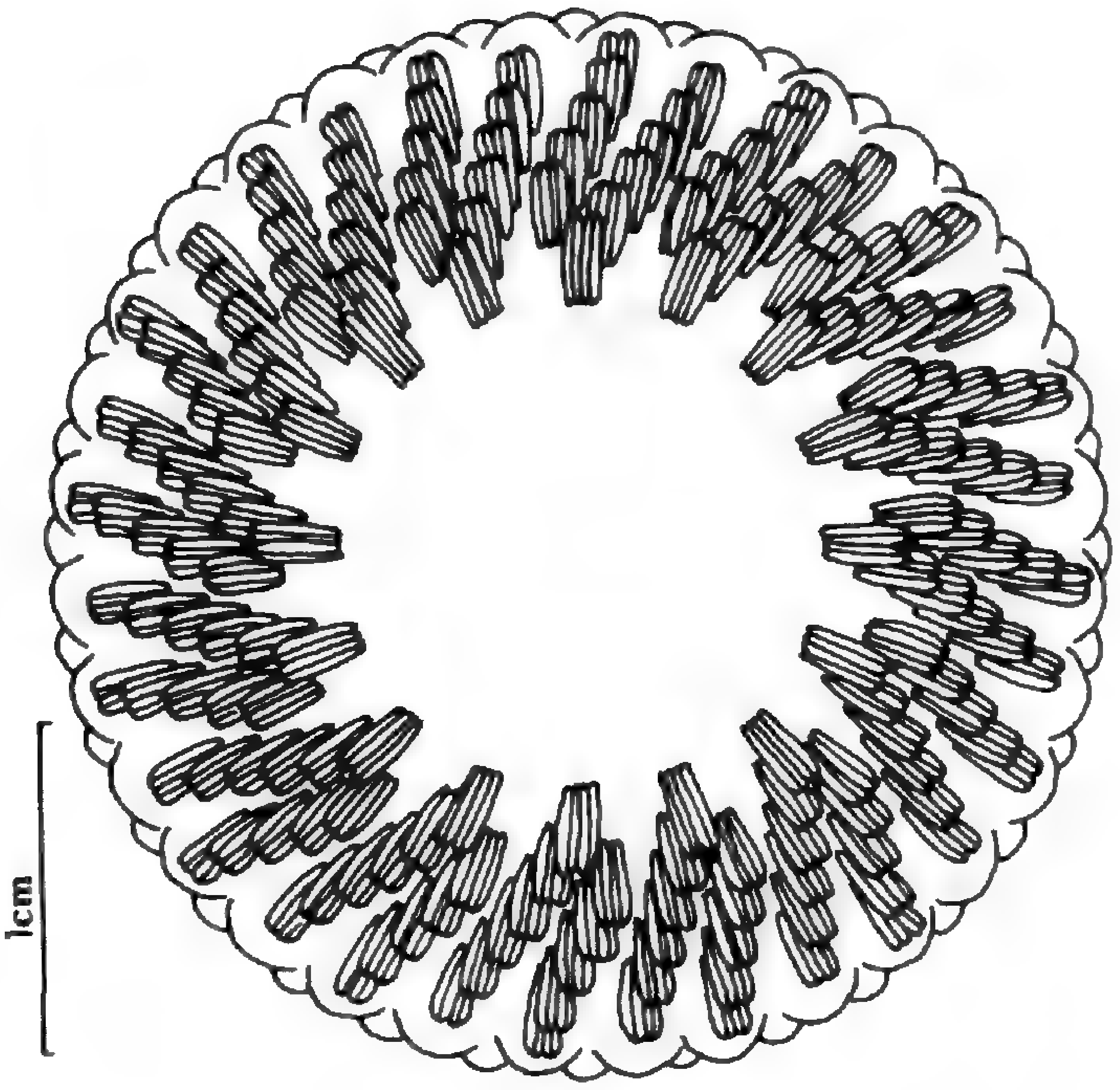


FIGURE 1. Reconstruction of the Magnoliales flower; ×2.

TECHNIQUE

Engelhardt (1922) published only drawings of the leaves, as did Sturm (1971) using an improved drawing technique, because of the difficulties of photographing the black leaves on the black oil-shale. Frequently it is not easy to see the leaf margin or the venation of dry prepared specimens. We have tried several techniques for examining the leaves, and some of these have also been helpful for the study of the flowers (Schaarschmidt, 1982).

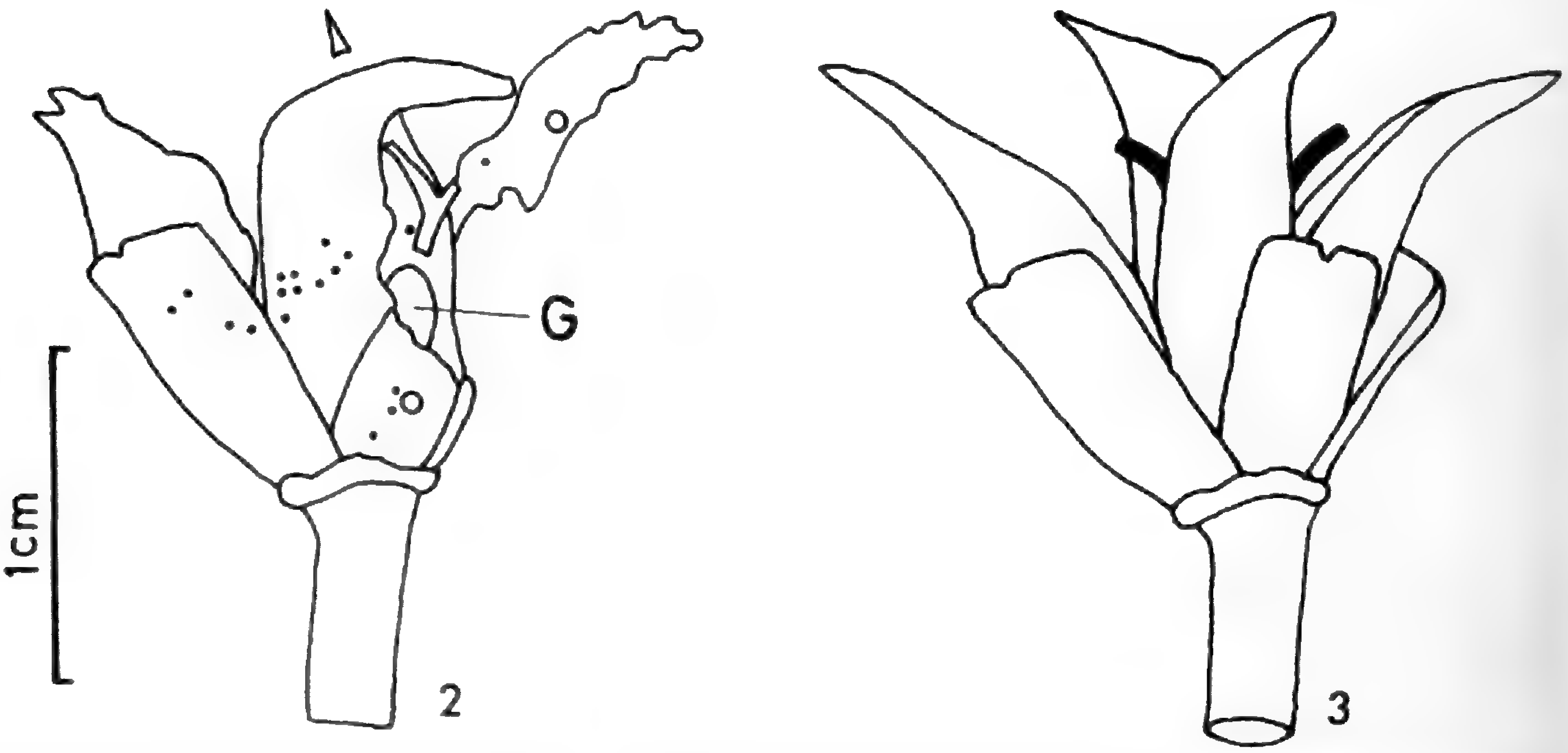
Because the Messel oil-shale breaks during drying, the flowers and other delicate samples are stored in a fluid, either glycerine (disinfected by Thymol) or in liquid Polyethylene-Glycol 200, 400, or 600. Specimens stored in this way are easy to photograph. If necessary, contrast was increased by two polarizing filters, one attached at the lamp, the other below the camera objective (Schaarschmidt, 1973). For one specimen, we obtained clear pictures in infrared light by use of the Wild infrared image intensifier M 520, provided for testing by Ernst Leitz KG, Frankfurt am Main. For fine details, we successfully used the fluorescence technique (Friedrich & Schaarschmidt, 1977, 1979) and were able to observe grains, either isolated or in the anthers, sufficiently well for preliminary determination. Anther wall details could also be seen with this technique.

We have constructed special macrofluorescence equipment for lower power observation (Schaarschmidt & Friedrich, 1981, Schaarschmidt, 1982). At the microscope, we have used the following filters: for excitation, a band pass filter, BP 350–460 and as barrier filter, a long-wave pass filter, LP 515.

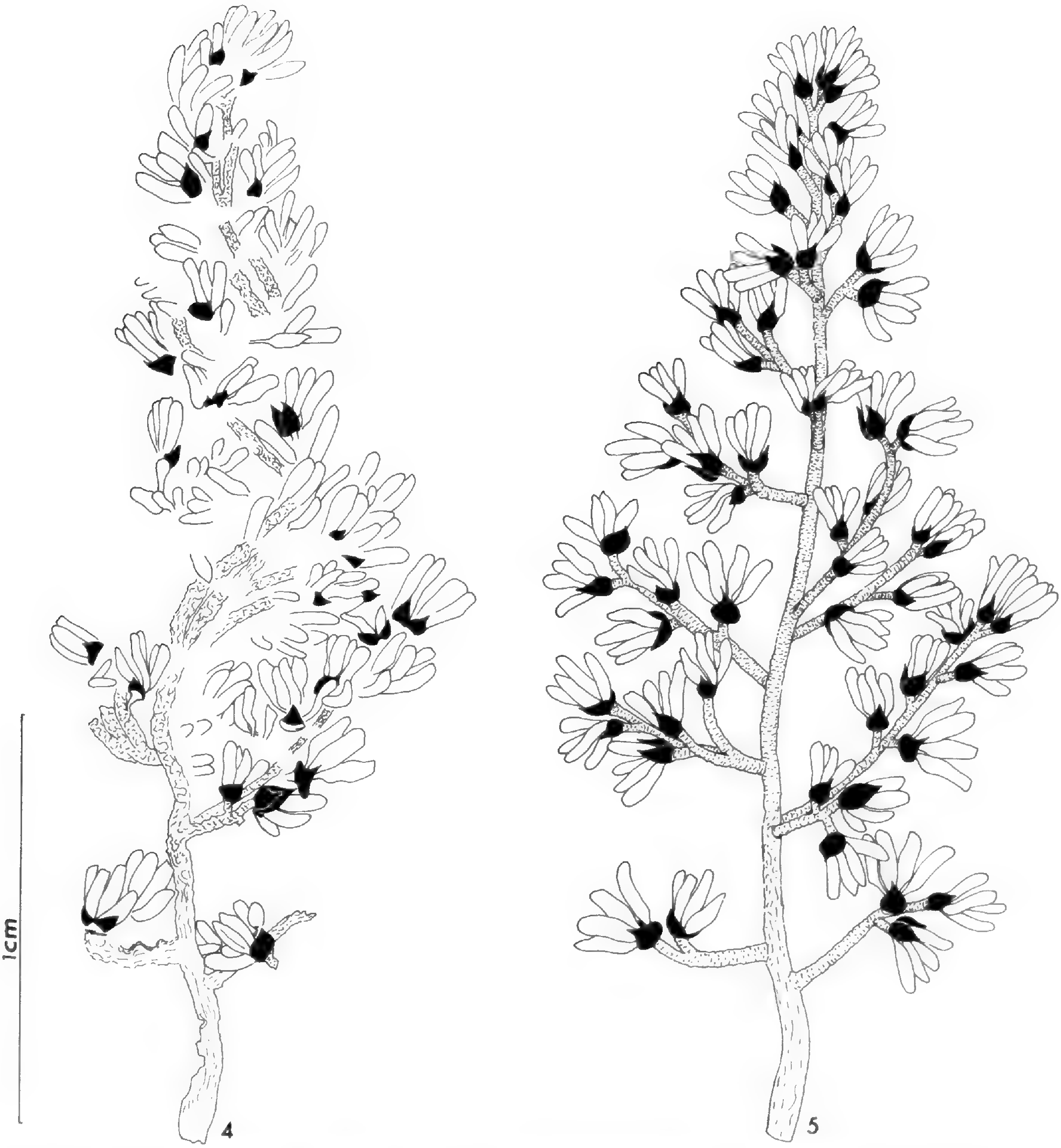
MAGNOLIALES FLOWER

Material. Forschungsinstitut Senckenberg, SM.B. 13476.

Description. The fragment of a disc-like flow-



FIGURES 2, 3. Tiliaceae flower; ×3.—2. Drawing according to the fossil. Three sepals (one complete), 4 petals, ovule (G) and style visible (points = single pollen grains, circles = groups of pollen grains).—3. Reconstruction.

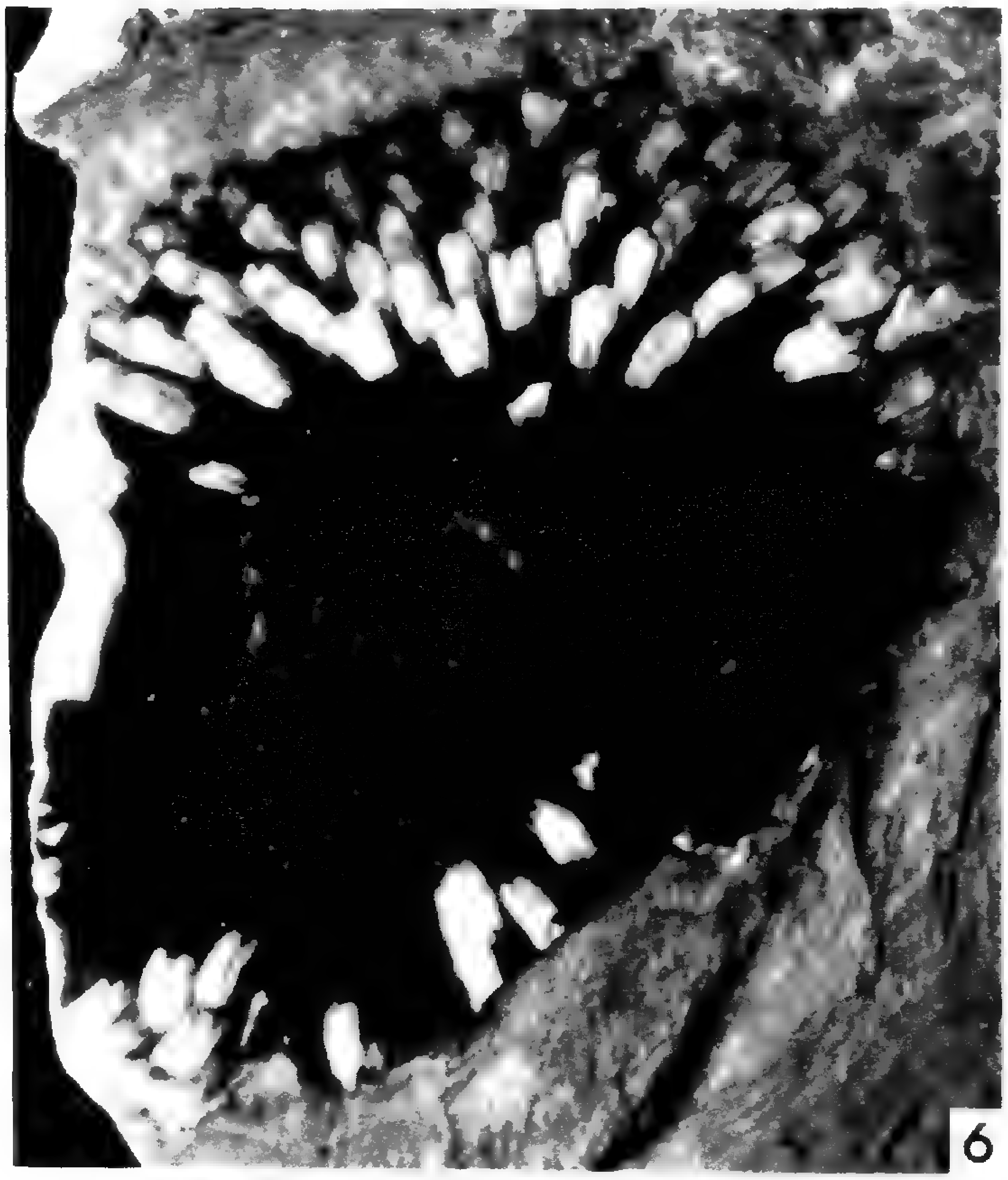


FIGURES 4, 5. Sapindales inflorescence; ×5.—4. Drawing according to the fossil; main axis broken in the middle part and drifted to the right; scales black.—5. Reconstruction.

er has a diameter of 32 mm and shows two groups of helically arranged stamens (Figs. 1, 6). In infrared and fluorescent light, the anthers are clearly seen to consist of four thecae (2–2.5 mm long), which open by a long longitudinal slit (Fig. 7). The filament is attached basally or dorsally. The perianth has an unknown number of rounded parts and is not much longer than the stamens (Fig. 7). It is not possible to decide whether these are sepals or petals. If carpels were present they must have been in the center of the flower, where the fossil is absolutely black. In this area, there seems to be some indistinct objects shaped like *Ranunculus* carpels.

The pollen grains are clearly visible in fluorescent light. Isolated grains are distributed all over the flower, and the pollen sacs are full, suggesting fossilization before anthesis. The prolate tricolporate pollen grains average 22 μm in diameter. The three equatorial colpi have indistinct pores and the exine is fine scabrate (Figs. 8–11).

A reconstruction of the flower is given in Figure 1.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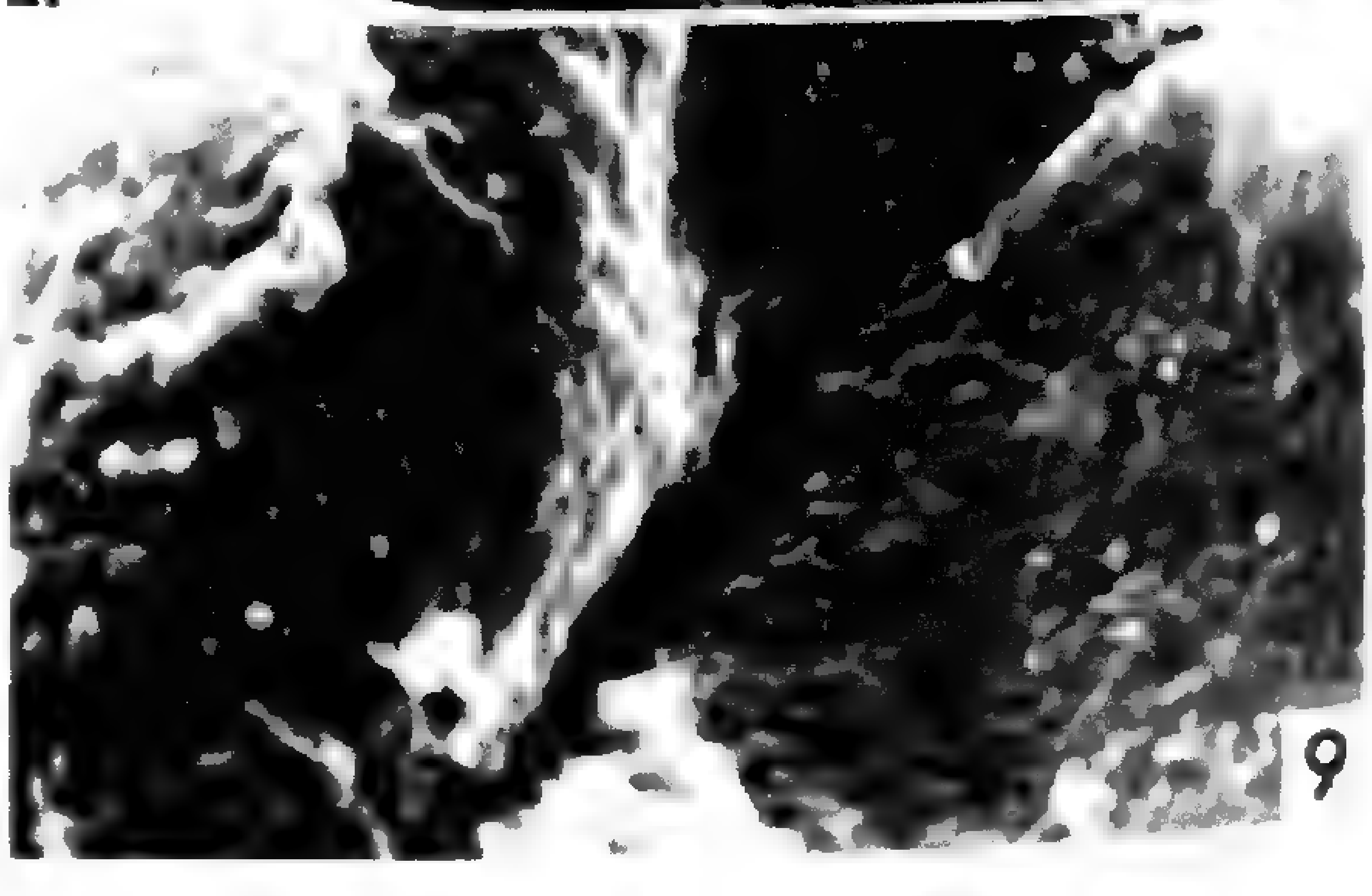
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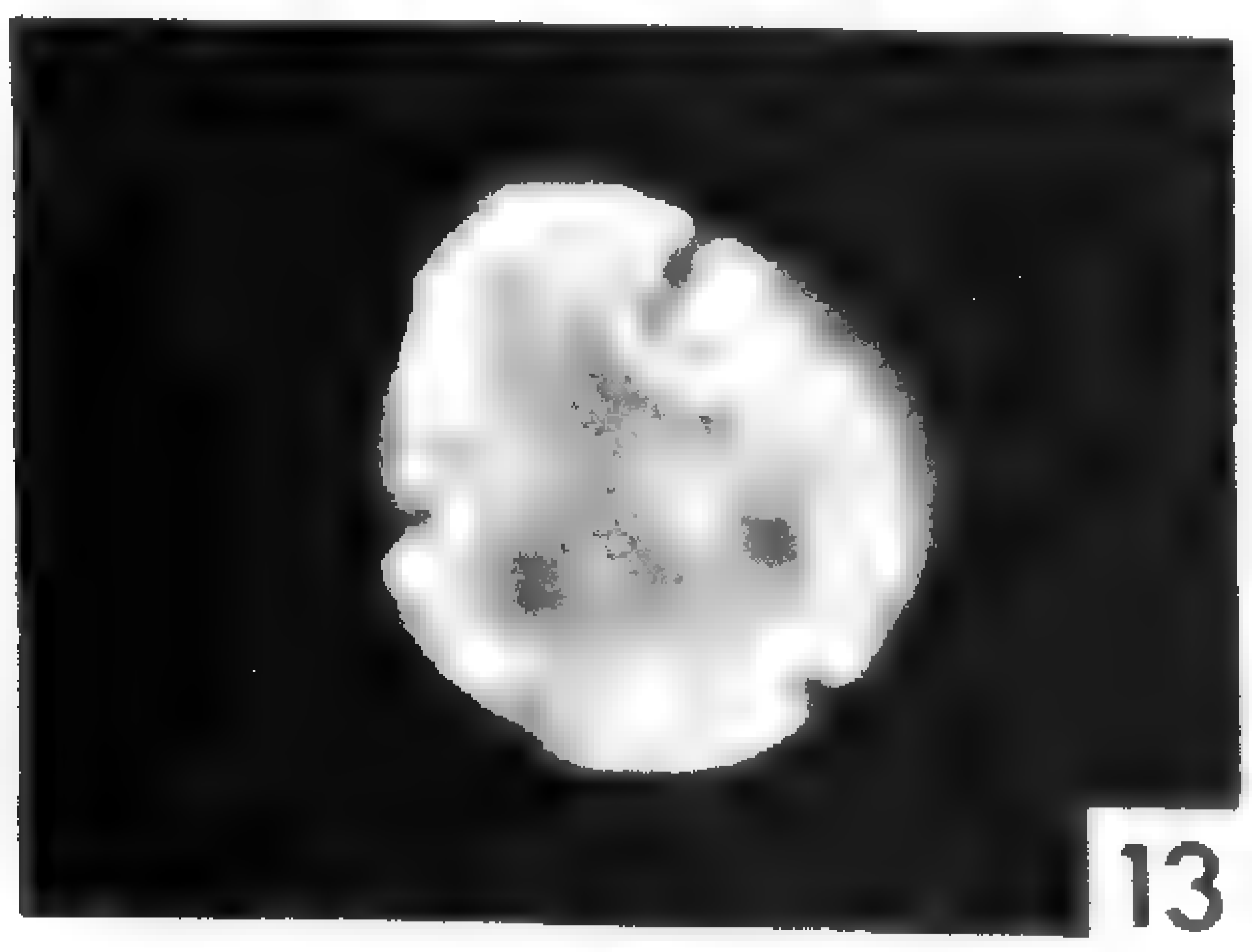
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FIGURES 6–13. 6–11. Magnoliales flower.—6, 7. The specimen in infrared light; 6, ×2.5; 7, ×5.—8. Scanning electron micrograph of the polar view of a pollen grain; ×2,500.—9. Scanning electron micrograph of the structure

Systematic position. This type flower occurs only in the Polycarpicae (Ranales sensu lato), but there seems to be no family that includes all the following features of the specimen: helical arrangement of the stamens, long thecae, a short perianth, and tricolporate pollen grains.

The first two characteristics occur in the Nymphaeaceae, but generally they have longer petals and inaperturate or monosulcate pollen. Tricolpate pollen occurs in *Nelumbo* (Erdtman, 1952: 287). The same arrangement and construction of the stamens also occur in the Magnoliales. In the Magnoliaceae, the pollen grains are monosulcate, but tricolpate pollen does occur in the Illiciaceae and Schisandraceae (Erdtman, 1952: 254–258). Flowers of some Dilleniaceae are also similar; the Dilleniaceae produce tricolpate pollen grains (Erdtman, 1952: 148) and in the Paeoniaceae tricolporate pollen is found. Despite these similarities, without knowledge of the gynoecium it is not possible to assign the flower to an extant family. However, at least, in so far we know it, it may be a flower of one family of the Magnoliales.

TILIACEOUS FLOWER

Material. Landessammlungen für Naturkunde, Karlsruhe, 1 flower.

Description. Flower with a pedicel 15 mm long, four pointed and recurved petals. Three petals are obvious and the tip of a fourth petal can be seen at the upper margin of the flower (Figs. 2, 3, 12). The petals may have been thin, because they are folded. In front of the left and middle petals are remains of two sepals. They are strap-shaped. Ovary and style are preserved but still covered by parts of the flower. No stamens are visible.

Pollen grains are scattered on the surface of the calyx. These pollen grains are all of one morphological type (Fig. 13). The grains are triporeovate and of the tilioid type. Because of their uniformity and because of the absence of other different pollen grains, I believe that they were produced by this flower, which would also indicate bisexuality. The pollen grains are 36–42 μm (average 39.5 μm diameter) and rounded to triangular in outline in polar view. The tilioid pores are located at the straight flank (i.e., planaperturate).

Systematic position. The systematic position is clearly identified by the pollen as tilioid type pollen, which occur only in the Tiliaceae (Mai, 1961: 56), although not in all genera of the family. On the other hand, most of the flowers in this family are pentamerous, but a few subfamilies such as the Tetralicoideae and the Tilioideae pro parte (e.g., *Sparmannia*) are tetramerous (Burret, 1926).

Mai (1961) described a flower of the Tiliaceae: *Burretia instructa* Mai (Brownlowioideae) from the Miocene of Central Germany, but this is quite different from the Messel fossil. It is pentamerous, unisexual, and has a fused calyx. The Messel flower is tetramerous, bisexual, and has free sepals, and may belong to a genus of the Tilioideae with tetramerous flowers but not to *Sparmannia,* which does not have tilioid pollen grains. Also, the *Tilia* flowers described by Hall and Swain (1971) have no similarity to the Messel flower.

Tilioid pollen is abundant in the Tertiary. At Messel, *Intratriporopollenites pseudinstructus* Mai (1961, text-fig. 3), occurs in the dispersed palynoflora and is similar to the pollen grains found in the flower.

SAPINDALES INFLORESCENCE

Material. Forschungsinstitut Senckenberg, SM.B. 13477.

Description. The specimen is a catkin 28 mm long consisting only of stamens. In the lower part it is branched several times. The middle part is broken, slightly distorted, and displaced to the right, perhaps by a weak current during deposition (Figs. 4, 5, 14).

The stamens are arranged in groups, which may be simple flowers (Fig. 15). Unfortunately, it is impossible to count the exact number of the stamens but the number appears to be between three and six. Each flower has one or two pointed scales about 1 mm long at the base. The scales are not conspicuous and both can be seen only in laterally compressed flowers.

The anthers are 2.5 mm long, with a short filament. They open by longitudinal slits. In fluorescent light the epidermis of the anthers is vis-

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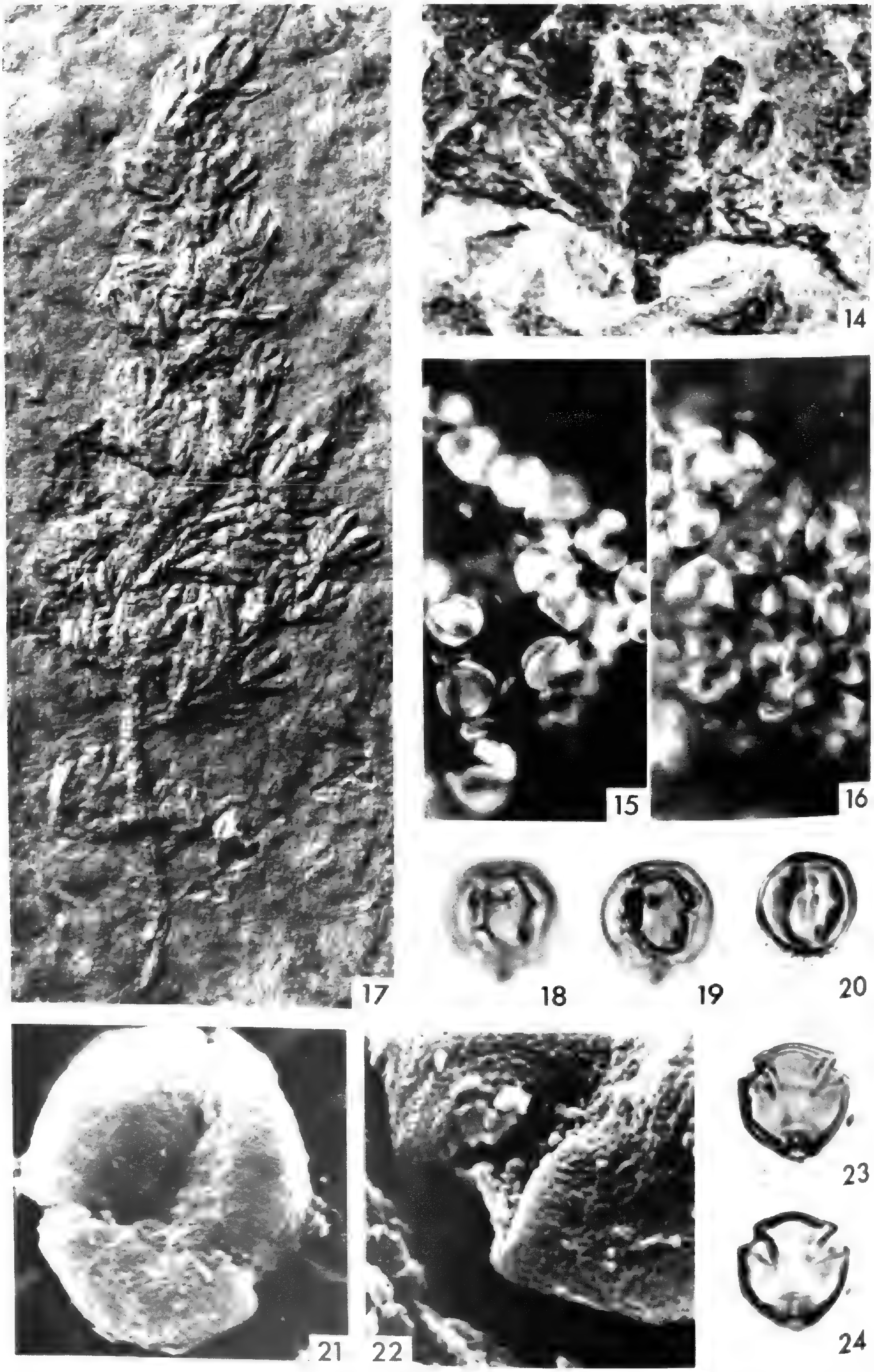
of the colpus and the exine; ×5,000.—10, 11. Polar and lateral views of the pollen grains in transmitted light; ×1,000. 12, 13. Tiliaceae flower.—12. The whole specimen; ×3.—13. Polar view of a pollen grain, epi-fluorescence; ×500.



FIGURES 14–24. Sapindales inflorescence.—14. Cluster of flowers, the scale of one flower visible; ×20.—15, 16. Pollen grains in stamens, epi-fluorescence; ×500.—17. The specimen in flat light; ×5.—18–20, 23, 24. Pollen

ible and consists of longitudinal cells. The epidermis of the scales has polygonal cells.

The pollen grains are fairly small, 18 μm in diameter, circular in equatorial and polar views, and distinctly tricolporate (Figs. 15–24).

Systematic position. Because of the very simple construction, it is not easy to find the right position of the inflorescence. There are two orders of angiosperms that come into question. Both have bisexual flowers but with the tendency to unisexuality and wind pollination.

In one order, Hamamelidales, the single flower of the Messel inflorescence resembles most the Cercidiphyllaceae, which also has flowers with two scales at the base. But in contrast to our specimen, the inflorescences of the Cercidiphyllaceae are close clusters, they have more stamens per "flower" (8–11), and their pollen grains are only tricolpate (Erdtman, 1952: 106–107). The other families of Hamamelidales, Platanaceae, and Hamamelidaceae, are still more different, as well, in their flowers and pollen grains, especially in the construction of the inflorescences, which are normally clusters or globose heads. Only a few genera of Hamamelidaceae have spikes, but none have branched catkins. The related Eucommiaceae also have simple perianthless male flowers. The pollen grains are 3-colporoidate (Erdtman, 1952: 164), but the flowers are also in clusters. It seems that the Messel inflorescence does not belong to the Hamamelidales or any related family.

The second order with a tendency towards unisexuality are the Sapindales. Most families have panicle-like inflorescences, occasionally with unisexual flowers that lack a perianth. It seems that the most similar inflorescences occur in the following families. Several genera of Sapindaceae have paniculate inflorescences. The male flowers of *Dodonaea,* for instance, contain about seven stamens, petals are absent but the four small, conspicuous sepals don't correspond with our flowers. More similar are the male catkin of *Pistacia* (Anacardiaceae). The five stamens are of similar shape and size, and at the base of the single flowers a scale-like bract is visible. However, the flowers of *Pistacia* have a reduced 5-lobed calyx. It may be that the flowers of the Messel inflorescence also had a calyx before fossilization. On the other hand, the relationship to *Pistacia* is not probable, because in this genus the catkins are not branched and the pollen grains are different: they normally have more than three "not sharply delimited" apertures (Erdtman, 1952: 48).

There are still more families in the Sapindales in which unisexual panicles occur—sometimes the flowers without petals—for instance: Staphyleaceae, Sabiaceae, Burseraceae, Simaroubaceae, and Meliaceae. But we have not yet found a living genus that includes all attributes of the Messel inflorescence. Therefore, we classify it as a Sapindales inflorescence.

CONCLUSIONS

There is, with a few exceptions, a long gap between the excellent published record of fossil flowers by Conwentz (1886) from the Eocene Baltic amber and the modern systematic investigation of early Tertiary flowers, especially from the Middle Eocene Clairborne formation by Crepet, Dilcher, and others. It is rapidly becoming clear that fossil flowers are available for investigation and yield important information for our understanding of angiosperm evolution. It seems that, by the early Tertiary, anemophilous flowers were already highly developed, and at nearly the same level of their living relations (Crepet, 1979)—e.g., Juglandaceae (Crepet et al. 1975), Fagaceae (Crepet & Daghlian, 1980), and Ulmaceae (Zavada & Crepet, 1981). Against that, the entomophilous flowers have still been more primitive. Therefore, it is generally not as easy as in the anemophilous flowers to compare them with living plants. Most of the fossil entomophilous flowers are radially symmetrical; bilateral symmetry is still at the beginning. It is also significant that the fossil record of early angiosperms shows both catkins and oligomerous radial flowers. Polycarpous flowers are found rarely as fossils generally. For instance, Seward and Conway (1935: 22. pl. 4. fig. 20) and Bock (1962, text-figs. 498, 499) published seed axes called *Magnoliaestrobus* from Cretaceous of Greenland and Oligocene of Hungaria; Dilcher (1979: 315. figs. 40, 50, 51) and Dilcher and Crane (1984)

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grains in lateral and polar view in transmitted light; ×1,000.—21. Scanning electron micrograph of the polar view of a pollen grain; ×2,500.—22. Scanning electron micrograph of the structure of the colpus and the exine; ×5,000.

have described an archaic elongated axis with a high number of carpels from the middle Cretaceous. Now in Messel the male part of a flower of this important plant group is first found, which was interpreted as the most primitive angiosperm group by many botanists in the past.

Although in the Messel oil-shale flowers are very rare, we hope to contribute more results to this important field of angiosperm paleobotany in the future, because the plant remains of Messel are well preserved and allow several fine-detailed investigations.

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ADVANCED (CONSTANT) INSECT POLLINATION MECHANISMS: PATTERN OF EVOLUTION AND IMPLICATIONS VIS-À-VIS ANGIOSPERM DIVERSITY[1]

WILLIAM L. CREPET[2]

ABSTRACT

The functional/phylogenetic relationship between the angiosperm flower and insects, combined with the correlation between insect pollination and many of the most diverse angiosperm families, suggest that insect pollination has had an important role in angiosperm success. Various advantages of insect pollination at the species level, especially those associated with bee and lepidopteran pollinators, are consistent with these correlations—furthermore, modern angiosperm diversity may be more directly related to insect pollination by the speciation-promoting characteristics of constant pollinators. Until the present time, paleontological data have mitigated against this possibility by illustrating that both advanced insect pollinators and their co-adapted angiosperm flowers evolved too late to have been of major significance in angiosperm radiation. Recent analyses of paleobotanical and biogeographical data together with paleobotanical data indicate that hymenopteran and lepidopteran pollinators, and angiosperm taxa having flowers adapted to them, existed at a time of major angiosperm radiation. Although angiosperm success cannot be confidently related to one feature, the importance of insect pollination in the diversification of the group can no longer be minimized in the context of the fossil record. Angiosperms are distinguished among the tracheophyta by their overwhelming diversity [250/300 families of vascular plants are angiosperms; 240,000/300,000 species of flowering plants are angiosperms (Burger, 1981)]. The angiosperms are also dominant in sheer numbers of individuals and are of extraordinary economic importance. Furthermore, angiosperms demonstrate stunning variation in vegetative and reproductive morphology, anatomy, and habit.

Attempts to explain angiosperm diversity might be directed logically at explaining the potential benefits of unique, basic angiosperm features (i.e., synapomorphic features at the level "Angiospermae"). These are dominated by characters related to floral morphology and function including the hermaphroditic condition, enclosed ovules, monosulcate granular-walled pollen, double fertilization, and insect pollination. Angiosperm flowers are related to insect pollination by functional morphology and phylogeny and they are probably the products of co-evolution with insects (e.g., Grant, 1950; Crepet, 1979; Stebbins, 1981). There are numerous examples of radiations in angiosperm taxa associated with adaptations for various animal pollinators (e.g., the Polemoniaceae, Grant & Grant, 1965), especially faithful pollinators, and particularly the Apoidea (bees). The Apoidea may be temporally (polytropic—a tendency to pollinate one species at a time) or more or less absolutely (oligotropic-monotropic) faithful, and flowers may be adapted to bee (and other) pollinators in a variety of ways (Heinrich, 1979, 1981; Macior, 1974). Correlations between various diverse angiosperm taxa and animal pollinators, particularly constant pollinators, suggest that there may be a fundamental relationship between animal pollination and diversity (Grant, 1949; Grant & Grant, 1965; Baker & Hurd, 1968; Crepet, 1979). Certain aspects of insect pollination may include characteristics that provide competitive advantages to insect-pollinated taxa as well as those more immediately related to speciation (and the production of diversity).

At the species level, these include:

a. Reliable directional pollination with its energetic advantages (Pohl, 1937; Cruden, 1977).
b. The production of outcrossed offspring in a population of relatively widely dispersed individuals (Burger, 1981).

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c. Successful pollination under environmental conditions inappropriate for wind pollination.

Potential advantages at the level "Angiospermae" (i.e., those related directly to diversity) include:

a. The filling of "empty" niches as a result of "b" and "c" above.
b. The deflection of faithful pollinators from their host plant through stochastic change in key floral features (altered developmental patterns) could provide the means for restricting gene flow from parental populations to isolated (peripheral or sympatric) demes (see the scenarios outlined in Fig. 1A and B based on Grant, 1949; Gottlieb, 1982; Tiffney, 1984).

The combination of these features of angiosperm reproductive biology represents a mechanism for increasing the frequency of the formation of small, genetically isolated populations in which evolution can proceed rapidly (due to founder effect/drift, the potentially rapid fixation of mutations, etc.), thus maximizing the probability of speciation and conforming with the punctuated equilibria model of Eldredge and Gould (1972) and Gould and Eldredge (1977). The net result: augmented speciation in angiosperms consistent with their present diversity (Fig. 1).

Many features of the angiosperms can be reasonably regarded as having contributed to their present diversity. For example, Mulcahy has considered the advantages conferred by a reproductive system that allows for gametophytic as well as sporophytic competition (1979) and Tiffney (1984) pointed out the speciation-promoting quality of having animal dispersed seeds (see also the discussion below and Crepet, 1982). Burger (1981) and Stebbins (1981) have independently summarized and evaluated the various features of angiosperms likely to have been important in their present success. Stebbins pointed out the need to consider the fossil record in assessing the impact of insect pollination on present angiosperm diversity. He noted that the types of pollinators most likely to be directly involved in the establishment of diversity (i.e., constant pollinators) evolved too late to have participated in major angiosperm radiation and considered insect pollination to have been supplemental, and not essential. Stebbins (1981) considers attributes he views as following from the reduction of the female gametophyte as having been of major significance in angiosperm success. These include the closed carpel, double fertilization, and the stylar canal. Few would debate the potential advantages of these features (the ultimate role of the carpel, for example, in fruit dispersal), but Stebbins's implicit separation of these characters from co-evolution with insect pollinators is open to question.

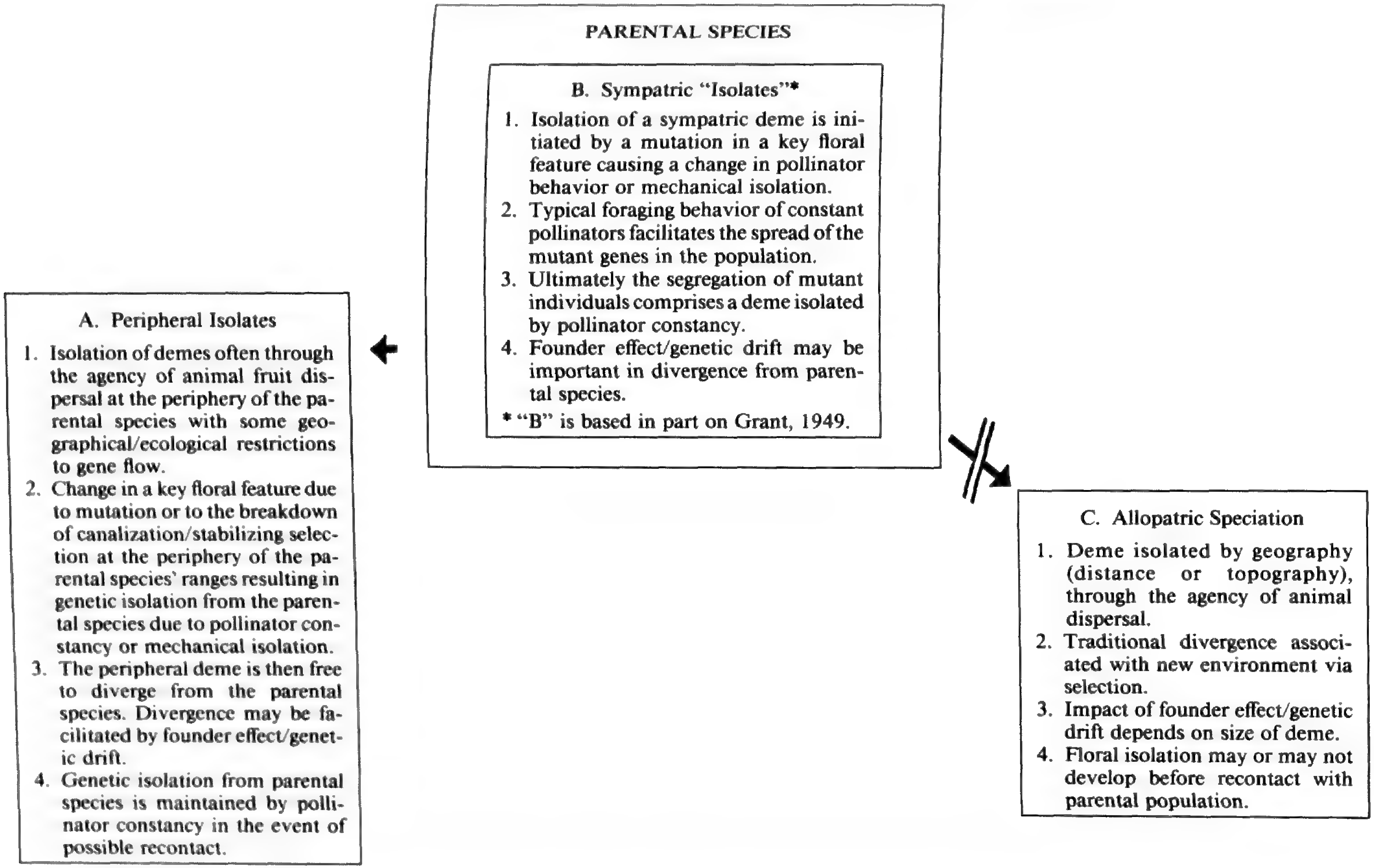
More recent paleontological and neontological information suggests an alternative interpretation of the timing of the evolution of constant pollinators and of the radiation of the angiosperms. It is my intention to offer a preliminary account of the diversification of advanced adaptations to insect pollination likely to have involved constant pollinators and of the possible implications with regard to angiosperm history. The bases for my argument include:

1. The growing fossil record of flowers, inflorescences, and fruits.
2. Bee biogeography and its evolutionary significance, as recently discussed by Michener (1979).
3. Recent data on patterns of diversification in the angiosperms (e.g., Niklas et al., 1980; Muller, 1981; Tiffney, 1981).
4. Improved understanding of the taxonomic value of pollen and leaves combined with growing information on the occurrences and states of different organs representing the same taxa from the same localities or times.

PALEOBOTANICAL EVIDENCE ON THE STATUS OF ADVANCED POLLINATION

Angiosperms with floral morphology indicative of pollination by advanced constant animal pollinators are conspicuous by the Middle Eocene. Appreciation of the past diversity of these taxa has increased recently because of the growing fossil record of flowers and fruits combined with a better understanding of the taxonomic significance of fossil leaves and pollen.

Flower and inflorescence fossils have been important in assessing the status of families with advanced pollination mechanisms at various times in the past. They provide the details of floral morphology that can be used, with proper cautions, to infer pollination mechanisms. Floral data have also been important in confirming the



PARENTAL SPECIES

B. Sympatric "Isolates"*

1. Isolation of a sympatric deme is initiated by a mutation in a key floral feature causing a change in pollinator behavior or mechanical isolation.
2. Typical foraging behavior of constant pollinators facilitates the spread of the mutant genes in the population.
3. Ultimately the segregation of mutant individuals comprises a deme isolated by pollinator constancy.
4. Founder effect/genetic drift may be important in divergence from parental species.

* "B" is based in part on Grant, 1949.

A. Peripheral Isolates

1. Isolation of demes often through the agency of animal fruit dispersal at the periphery of the parental species with some geographical/ecological restrictions to gene flow.
2. Change in a key floral feature due to mutation or to the breakdown of canalization/stabilizing selection at the periphery of the parental species' ranges resulting in genetic isolation from the parental species due to pollinator constancy or mechanical isolation.
3. The peripheral deme is then free to diverge from the parental species. Divergence may be facilitated by founder effect/genetic drift.
4. Genetic isolation from parental species is maintained by pollinator constancy in the event of possible recontact.

C. Allopatric Speciation

1. Deme isolated by geography (distance or topography), through the agency of animal dispersal.
2. Traditional divergence associated with new environment via selection.
3. Impact of founder effect/genetic drift depends on size of deme.
4. Floral isolation may or may not develop before recontact with parental population.

FIGURE 1. Several possible scenarios for the isolation of small populations due to the combination of faithful pollinators, stochastic floral change, and animal seed dispersal.

existence of taxa or of floral character complexes at times when most modern paleobotanists would be reluctant to risk inferring their presence on the basis of other organ evidence alone (e.g., Paleocene Gentianaceae, Crepet & Daghlian, 1981a). Floral data have, in addition, added to the significance of the dispersed palynological record by allowing an assessment of the accuracy with which particular palynomorphs reflect particular suites of associated floral characters and by increasing the taxonomic significance of associated palynomorphs that have been enigmatic when dispersed.

Increasing numbers of in-depth studies of the pollen of extant taxa in conjunction with the increased number of characters used to classify pollen based on scanning electron and transmission electron microscopy have been important in making fossil pollen a valuable diagnostic feature. Fossil leaf studies have also been important in improving our understanding of angiosperm history. Careful studies of leaves have shown that they too may be good taxonomic characters if fine venation patterns and/or cuticular details are determined and analyzed in the context of variation in similar features in extant related taxa (Hickey, 1973; Dilcher, 1974).

A significant problem in interpreting the fossil record of angiosperms has been attempting to deduce the character state of one particular organ from another more commonly preserved organ, in this case, floral structure from pollen, fruit, or leaf evidence. While one character state can never be predicted from another with absolute certainty, neontological data and increasing knowledge of the various organs of particular taxa from specific geological horizons suggest that in recognizably modern families there is a high degree of correlation among the states of the various organs of a taxon [e.g., the Ulmaceae where Eocene celtidoid flowers and pollen both seem reflective of an insect-pollinated ancestry for the now wind-pollinated taxon (Zavada & Crepet, 1981); the Araceae (Crepet, 1978; Dilcher & Daghlian, 1977); the Juglandaceae (Crepet et al., 1975; Manchester, 1981); the Fagaceae (Crepet & Daghlian, 1980; Jones, 1979), etc.].

In certain cases, correlation might be expected. There is a strong functional relationship, for example, between floral and pollen structure that probably extends even to incompatibility mechanisms and pollen ultrastructure (Zavada, unpubl. data). Both flowers and pollen must be adapted to the physical and behavioral characteristics of biotic pollinators or to various physical agencies that might effect pollination. The correlation between fruits and flowers in the past is more complex. Evidence presented by Tiffney (1984) and considered later in this article suggests the possibility that faithful pollinators temporally preceded animal fruit dispersal.

Fruit structure, then, might "lag" evolutionarily behind floral features. Thus, fruit structure of a modern family represented in the fossil record might be too conservative an indicator of the floral condition at a given point in the past. On this basis, it seems unlikely that a modern taxon recognized from a particular geologic horizon on the basis of fruit evidence would have floral features significantly different from what might be expected based on the modern characters circumscribing the taxon.

It is perhaps more difficult to imagine the reasons for correlation between leaf and floral structure other than that both are complex organs and might be united to some extent by character correlations associated with cladogenesis. Yet, growing fossil evidence suggests correlation between leaf and floral structure in the history of extant families.

As more attention is being devoted to all the organs representing a particular taxon from a particular horizon, the possibility that taxa representing unique mosaics of modern characters existed in the past may be evaluated. Such combinations, if sufficiently different, might be misleading in the context of the evolution of pollination mechanisms, but only a few such instances have been adequately demonstrated (Crane, 1982) and in no case has floral morphology, and therefore pollination mechanism, been found to vary significantly from what might have been expected from other organ evidence.

Thus, when the affinities and characters of a particular sufficiently complex organ taxon have been demonstrated *adequately*, it is fairly safe to assume that basic floral morphology and likely pollination mechanism were at a similar evolutionary state. In the present paper, reports of organ taxa other than flowers and inflorescences are occasionally used to infer the presence of the pollination mechanism that is today associated with that taxon. In almost all instances, however, the existence of pollination mechanisms implied in this manner are backed up by contemporaneous floral evidence.

The paleobotanical data. Methods. Two major sources of data other than discrete reports and work in progress were used in assessing the record of angiosperms with advanced pollination syndromes (Muller, 1981; Reid & Chandler, 1933). These were selected because of the proven taxonomic value of pollen and fruits, their likely correlation with floral structure, and because the quality of the identifications is high in each case. Data were selected from individual reports according to the significance of the taxa involved and only if the reports involved clear demonstration of affinities on solid morphological-anatomical grounds. More data on the occurrences of advanced families will doubtlessly come to light in the future and some of the taxa reported in Muller (1981) and Reid and Chandler (1933), even as modified by Chandler (1961), may not stand up to further investigations, but the data presented are a reasonable state of the art representation of the occurrences of various floral characters at various times in the past.

Data. Table 1 is a summary of all data on the occurrences of families with pollination syndromes typical of the Apoidea and Lepidoptera and even some birds/bats. Families with appropriate syndromes are listed chronologically (however, see footnote a, Table 1) and families may be listed more than once to include as many reliable reports as possible based on as many different types of fossil evidence as possible. The table includes the ages, order, family, type of fossil evidence, characters related to the advanced syndrome and type of syndrome, and pollinators usually associated with the family.

Before summarizing the pattern of evolution of various pollination syndromes, I would like to discuss the appearances of several individual taxa: the Fabales, Asteridae, Zingiberales, and Euphorbiaceae. In these instances, evidence for the appearances of certain character complexes is extremely good and the order and timing of the appearances of the features represented by these taxa serves to corroborate the general impression of the evolution of advanced pollination syndromes gained from Table 1.

Fabales-Mimosaceae. Mimosoids have brush-type blossoms and are pollinated by a variety of faithful pollinators including bees, lepidoptera, and bats. Brush-type blossoms are common in Middle Eocene Claiborne deposits (Fig. 2) and inflorescences similar to modern racemose mimosoid inflorescences are known from the Middle Eocene and younger deposits of the southeastern United States (Crepet & Dilcher, 1977; Daghlian et al., 1980). Spicate inflorescences are 6 cm in length with sessile, alternate, perfect flowers (Fig. 3). Floral envelopes consist of a lobed calyx and a corolla with four ovate lobes (Crepet & Dilcher, 1977). There are eight exserted stamens with bilocular, versatile, longitudinally dehiscent anthers (Crepet & Dilcher, 1977). The gynoecium consists of a single carpel with an elongate, pubescent style (Fig. 4). Pollen is borne in tetrads and is tricolporate (Fig. 5).

These inflorescences are very similar to those of modern mimosoids, but subtle palynological differences suggest that they represent an extinct genus. Floral structure and palynological configuration (i.e., why invest units of pollen grains rather than single grains in unfaithful pollinators), suggest that the Eocene mimosoids were also pollinated by faithful pollinators, implying a prior history of co-evolution. Recent discoveries of Paleocene mimosoids support this possibility (Table 1).

Fabales-Caesalpiniaceae. While Paleocene inflorescences are the first reliable reports of the Mimosaceae, the Caesalpiniaceae have been reported as early as the Maestrichtian on the basis of highly distinctive *Sindora* pollen (Table 1). The presence of the Caesalpiniaceae and of myrtaceous pollen (Table 1) in the Maestrichtian also suggests that the brush-type blossom, or one that closely approximates it, originated rather early.

Fabales-Papilionaceae. Studies of paleocene flowers now in progress reveal that the typical highly derived zygomorphic papilionaceous flower already existed at that time. Details will be presented in a subsequent publication (Crepet, unpubl. data).

Asteridae. A recently discovered flower from the Lower Eocene of the Gulf Coastal Plain has several important implications with regard to the tempo of evolution of bee pollination. Flowers are distinctive in having an open, funnelform, sympetalous, seven-parted corolla (Fig. 6) and unusual pollen (Fig. 7). Pollen preserved within compressed anthers is 22 μm in diameter, intectate, triaperturate, and has prominent gemmae (Figs. 7, 8). Pollen is well known as the dispersed Upper Cretaceous-Eocene palynomorph, *Pistillipollenites macgregorii.* Pollen is most common in the Paleocene-Lower Eocene.

The combination of floral and palynological features is suggestive of affinities with the modern Gentianaceae although the taxon is clearly extinct. Floral structure is typical of bee pollination (e.g., Faegri & van der Pijl, 1971) in the angiosperms in general and in the Gentianaceae

TABLE 1. Summary of evidence related to the geological occurrences of angiosperms associated with advanced pollinators.

	Subclass	Order	Family	Evidence	Geography
Upper Eocene					
	Asteridae[a]	Gentianales	1. Apocynaceae	1. *Rauwolfia*-type pollen	1. a) Cameroon b) Venezuela[b]
		Rubiales	2. Rubiaceae	2. *Gardenia*-type pollen	2. Germany
	Rosidae	Fabales	3. Mimosaceae	3. *Acacia*-type pollen	3. Cameroon
			4. Mimosaceae	4. *Adenanthus*-type pollen	4. Cameroon
			5. Mimosaceae	5. *Calpocalyx ngnouniensis*-type pollen	5. Cameroon
			6. Mimosaceae	6. *Parkia*-type pollen	6. Cameroon
		Myrtales	7. Combretaceae	7. *Terminalia*-type pollen	7. Cameroon
			8. Lythraceae	8. *Crenea*-type pollen	8. Northern South America
		Rosales	9. Escalloniaceae	9. *Quintinia*-type pollen	9. New Zealand
		Santalales	10. Loranthaceae	10. *Amylotheca*-type pollen	10. New Zealand
Middle Eocene					
	Asteridae	Dipsacales	11. Caprifoliaceae	11. *Viburnum*-type pollen	11. France
		Scrophulariales	12. Bignoniaceae	12. *Dolichandrone*-type pollen	12. Southeastern United States
		Solanales	13. Convolvulaceae	13. *Merremia macrocalyx*-type pollen	13. a) Brazil b) Nigeria
	Rosidae	Euphorbiales	14. Euphorbiaceae	14. a) *Paleowetherellia* fruit b) Hippomanean flowers	14. a) Egypt b) Tennessee
		Fabales	15. Caesalpiniaceae	15. *Brachystegia*-type pollen	15. Nigeria
			16. Mimosaceae	16. *Eomimosoidea plumosa* floral, pollen	16. Texas
			17. Mimosaceae	17. *Pentaclethra macrophylla*-type pollen	17. Cameroon
		Myrtales	18. Myrtaceae	18. *Eugenia*-type pollen	18. Tennessee
		Polygalales	19. Malpighiaceae	19. *Brachypteris*-type pollen	19. Brazil
		Sapindales	20. Sapindaceae	20. *Diplopeltis huegelii*-type pollen	20. Central America
	Zingiberidae	Zingiberales	21. Heliconiaceae	21. a) Heliconiaceous flowers b) Heliconiaceous leaves	21. a) Tennessee b) Deccan Intertrappean
			22. Musaceae	22. Musaceous fruits	22. Deccan Intertrappean
			23. Zingiberaceae	23. Zingiberaceous fruits	23. Central Europe

TABLE 1. (Continued).

	Subclass	Order	Family	Evidence	Geography
Lower Eocene					
	Asteridae	Gentianales	24. Apocynaceae	24. *Ochrosella ovalis* fruit	24. London Clay
			25. Apocynaceae	25. *Ochrosoidea sheppeyensis* fruit	25. London Clay
			26. Gentianaceae	26. *Pistillipollenites* pollen, floral	26. Northeastern Texas
		Lamiales	27. Boraginaceae	27. *Ehretia ehretioides* fruit	27. London Clay
		Solanales	28. Convolvulaceae	28. *Merremia tridentata* pollen	28. Cameroon
			29. Solanaceae	29. *Cantisolanum daturoides* fruit	29. London Clay
	Rosidae	Euphorbiales	30. Euphorbiaceae	30. *Euphorbiospermum ambiguum* seed	30. London Clay
			31. Euphorbiaceae	31. *Euphorbiotheca minor* fruit	31. London Clay
		Fabales	32. Caesalpiniaceae	32. *Caesalpinia*-type pollen	32. Assam
			33. Mimosaceae	33. *Mimosites browniana* bowerbank, fruit	33. London Clay
		Myrtales	34. Lythraceae	34. *Minsterocarpum alatum* fruit	34. London Clay
				35. *Pachyspermum quinquelocularis* fruit	35. London Clay
			36. Myrtaceae	36. *Palaeorhodomyrtus subangulata* bowerbank, fruit	36. London Clay
			37. Onagraceae	37. *Palaeeucharidium cellulare* fruit	37. London Clay
		Santalales	38. Loranthaceae	38. *Arceuthobium*-type pollen	38. North-central Europe
			39. Loranthaceae	39. *Loranthus elegans*-type pollen	39. Germany
	Zingiberidae	Zingiberales	40. Cannaceae	40. Cannaceous leaves	40. Texas
			41. Zingiberaceae	41. Zingiberaceous leaves	41. Texas
Paleocene					
	Asteridae	Gentianales	42. Apocynaceae	42. *Alyxia*-type pollen	42. Northwest Borneo
			43. Gentianaceae	43. Gentianaceous pollen and associated floral type	43. Mississippi Embayment
	Rosidae	Euphorbiales	44. Euphorbiaceae	44. Inflorescences of the tribe Hippomane	44. Mississippi Embayment

TABLE 1. (Continued).

	Subclass	Order	Family	Evidence	Geography
		Fabales	45. Caesalpiniaceae	45. *Crudia*-type pollen	45. Nigeria
			46. Caesalpiniaceae	46. *Maniltoa grandiflora*-type pollen	46. Texas
			47. Mimosaceae	47. Flowers and inflorescences	47. Mississippi Embayment
			48. Papilionaceae	48. Flowers	48. Mississippi Embayment
		Myrtales	49. Myrtaceae	49. *Leptospermum* and *Metrosederos*-type pollen	49. a) New Zealand b) Ninetyeast Ridge
			50. Myrtaceae	50. *Syncolpites lisamae* pollen	50. Australia
		Polygalales	51. Polygalaceae	51. *Monnina*-type pollen	51. Chile
		Proteales	52. Proteaceae	52. *Adenanthus*-type pollen	52. Australia
			53. Proteaceae	53. *Banksia*-type pollen	53. Australia
			54. Proteaceae	54. *Beauprea*-type pollen	54. South Australia
			55. Proteaceae	55. *Symphyonema*-type pollen	55. Queensland
			56. Proteaceae	56. *Xylomelon*-type pollen	56. Australia
Cretaceous					
Stage					
Maestrichtian	Asteridae	Gentianales	57. Gentianaceae	57. Pollen associated with flowers	57. Northeastern Texas
Coniacian	Rosidae	Euphorbiales	58. Euphorbiaceae	58. *Paraphyllanthoxylon* wood	58. a) Arizona b) South Africa
Maestrichtian		Fabales	59. Caesalpiniaceae	59. *Sindora*-type pollen	59. Siberia
Santonian		Myrtales	60. Myrtaceae	60. *Syncolporites lisamae* pollen	60. Gabon
Maestrichtian			61. Onagraceae	61. *Epilobium*-type pollen	61. a) California b) Brazil
Maestrichtian		Proteales	62. Proteaceae	62. *Helicia*-type pollen	62. California
Maestrichtian			63. Proteaceae	63. *Guevina*-type pollen	63. Northern South America/Central Africa
Upper Senonian			64. Proteaceae	64. *Guevina*-type pollen	64. New Zealand
Lower Senonian		Sapindales	65. Sapindaceae	65. *Cupanopsis*-type pollen	65. a) Gabon b) India
Maestrichtian	Zingiberidae	Zingiberales	66. Zingiberaceae	66. *Zingiberopsis* leaves	66. Wyoming, Colorado

TABLE 1. (Continued).

	Floral Structural Features Related to Advanced Pollination Syndrome	Typical Pollination Syndrome	Literature Cited
Upper Eocene			
	1. Funnel or salverform, sympetalous corolla	1. Melittophily, Psycophily	1. a) Salard-Cheboldaeff (1978) b) Muller (unpubl. data)
	2. Funnelform, sympetalous corolla	2. Melittophyly, Psycophily, Ornithophily	2. Krutzsch (1970)
	3. Brush-type flowers, often with tubular corolla	3. Chiropterophily, Melittophily, Ornithophily, Psycophily	3. Salard-Cheboldaeff (1978)
	4. As above[c]	4. As above	4. Salard-Cheboldaeff (1978)
	5. As above	5. As above	5. Salard-Cheboldaeff (1978)
	6. As above	6. As above	6. Salard-Cheboldaeff (1979)
	7. Trumpet-type flowers formed by prolonged hypanthium	7. Psycophily	7. Salard-Cheboldaeff (1978)
	8. Tubular flowers by an extended hypanthium, some brush-types	8. Chiropterophily, Melittophily, Ornithophily, Psycophily	8. Germeraad et al. (1968)
	9. Flowers pendent, with a prolonged hypanthium	9. Myophily, Ornithophily, Phalaenophily	9. Mildenhall (1980)
	10. Tubular and brush-type flowers	10. Melittophily, Ornithophily	10. Mildenhall (1980)
Middle Eocene			
	11. Sympetalous corolla, tubular, often bilabiate	11. Hymenoptera (wasp), Myophily, Ornithophily, Phalaenophily	11. Gruas-Cavagnetto (1978)
	12. Strongly irregular, sympetalous corolla, trumpet-type, often bilabiate	12. Chiropterophily, Ornithophily	12. Frederiksen (1973, 1977)
	13. Funnelform, sympetalous corolla	13. Myophily, Melittophily	13. a) Pares Regali et al. (1974a, 1974b) b) Legoux (1978)
	14. Tepals connate toward base	14. Hymenoptera (wasp), Myophily, Ornithophily	14. a) Chandler (1954) b) Manchester and Dilcher (1979), Crepet and Daghlian (1981b)
	15. Flag-type flowers, strongly irregular, not papilionaceous	15. Chiropterophily, Melittophily	15. Legoux (1978)
	16. As above	16. Chiropterophily, Melittophily, Ornithophily, Psycophily	16. a) Crepet and Dilcher (1977) b) Daghlian et al. (1980)
	17. As above	17. As above	17. Salard-Cheboldaeff (1978, 1979)
	18. Predominantly brush-type flowers	18. Chiropterophily, Ornithophily, Melittophily	18. Elsik and Dilcher (1974)

TABLE 1. (Continued).

	Floral Structural Features Related to Advanced Pollination Syndrome	Typical Pollination Syndrome	Literature Cited
	19. Irregular, tending to zygomorphy	19. Melittophily	19. Pares Regali et al. (1974a, 1974b)
	20. Irregular, some flag-types	20. Melittophily	20. Kemp (1976)
	21. Strongly irregular, tubular corolla	21. Lepidoptera, Melittophily, Myophily	21. a) Crepet and Daghlian (unpubl. data) b) Trivedi and Verma (1971)
	22. Irregular, strongly nectariferous, briefly tubular	22. Chiropterophily, Ornithophily	22. Jain (1963)
	23. Zygomorphic, flag-type, tubular corolla	23. Melittophily, Ornithophily, Psycophily	23. Koch and Friedrich (1971)
Lower Eocene			
	24. As above	24. As above	24. Reid and Chandler (1933)
	25. As above	25. As above	25. Reid and Chandler (1933)
	26. Slender sympetalous corolla, bell- or trumpet-shaped	26. Melittophily, Psycophily	26. Crepet and Daghlian (1981a)
	27. Corolla generally salverform, sometimes tubular or funnelform	27. Melittophily	27. Chandler (1961)
	28. As above	28. As above	28. Salard-Cheboldaeff (1975)
	29. Various funnelform, tubular, trumpet-like flowers	29. Melittophily, Myophily, Phalaenophily, Chiropterophily	29. Reid and Chandler (1933)
	30. As above	30. As above	30. Reid and Chandler (1933)
	31. As above	31. As above	31. Reid and Chandler (1933)
	32. As above	32. As above	32. Baksi (1972, 1973, 1974), Sah (1974)
	33. As above	33. As above	33. Reid and Chandler (1933)
	34. As above	34. As above	34. Reid and Chandler (1933)
	35. As above	36. As above	35. Reid and Chandler (1933)
	36. As above	37. Melittophily, Myophily, Ornithophily, Phalaenophily	36. Reid and Chandler (1933)
	37. Funnelform to tubular flowers		37. Reid and Chandler (1933)
	38. As above	38. As above	38. Krutzsch (1970)
	39. As above	39. As above	39. Krutzsch (1970)
	40. Erect, tubular, highly irregular symmetry	40. Melittophily, Ornithophily, Psychophily	40. Daghlian (unpubl. data), Ball (1930), Berry (1916), Daghlian (1981)
	41. As above	41. As above	41. Daghlian (unpubl. data)
Paleocene			
	42. As above	42. As above	42. Muller (1968)
	43. As above	43. As above	43. Elsik (1968)

TABLE 1. (Continued).

	Floral Structural Features Related to Advanced Pollination Syndrome	Typical Pollination Syndrome	Literature Cited
	44. As above	44. As above	44. Crepet (unpubl. data)
	45. As above	45. As above	45. Adegoke et al. (1978)
	46. As above	46. As above	46. Elsik (1968)
	47. As above	47. As above	47. Crepet (unpubl. data)
	48. Papilionaceous zygomorphic flowers	48. Melittophily	48. Crepet (unpubl. data)
	49. As above	49. As above	49. a) Mildenhall (1980) b) Harris (1974)
	50. As above	50. As above	50. Harris (1965a), Martin (1978)
	52. Flag-type, strongly irregular symmetry	51. Melittophily	51. Doubinger and Chotin (1975)
	52. Brush-type flowers	52. Ornithophily (some mice and small marsupials)	52. Harris (1965a), Martin (1978), Stover and Partridge (1973)
	53. As above	53. As above	53. Martin (1978)
	54. As above	54. As above	54. Harris (1965a)
	55. As above	55. As above	55. Harris (1965b)
	56. As above	56. As above	56. Stover and Partridge (1973)
Cretaceous			
Stage			
Maestrichtian	57. As above	57. As above	57. Crepet and Daghlian (1981a)
Coniacian	58. As above	58. As above	58. a) Bailey (1924), Webster (1967) b) Madel (1962)
Maestrichtian	59. As above	59. As above	59. Van Campo (1963), Krutzsch (1969)
Santonian	60. As above	60. As above	60. Boltenhagen (1976a, 1976b)
Maestrichtian	61. As above	61. As above	61. a) Chmura (1973) b) Pares Regali et al. (1974a, 1974b)
Maestrichtian	62. As above	62. As above	62. Chmura (1973), Germeraad et al. (1968), Couper (1960)
Maestrichtian	63. As above	63. As above	63. Chmura (1973), Germeraad et al. (1968), Couper (1960)
Upper Senonian	64. As above	64. As above	64. Chmura (1973), Germeraad et al. (1968), Couper (1960)
Lower Senonian	65. As above	65. As above	65. a) Belsky et al. (1965), Boltenhagen 1976b) b) Vinkatachala and Sharma (1974)
Maestrichtian	66. As above	66. As above	66. Hickey and Peterson (1978)

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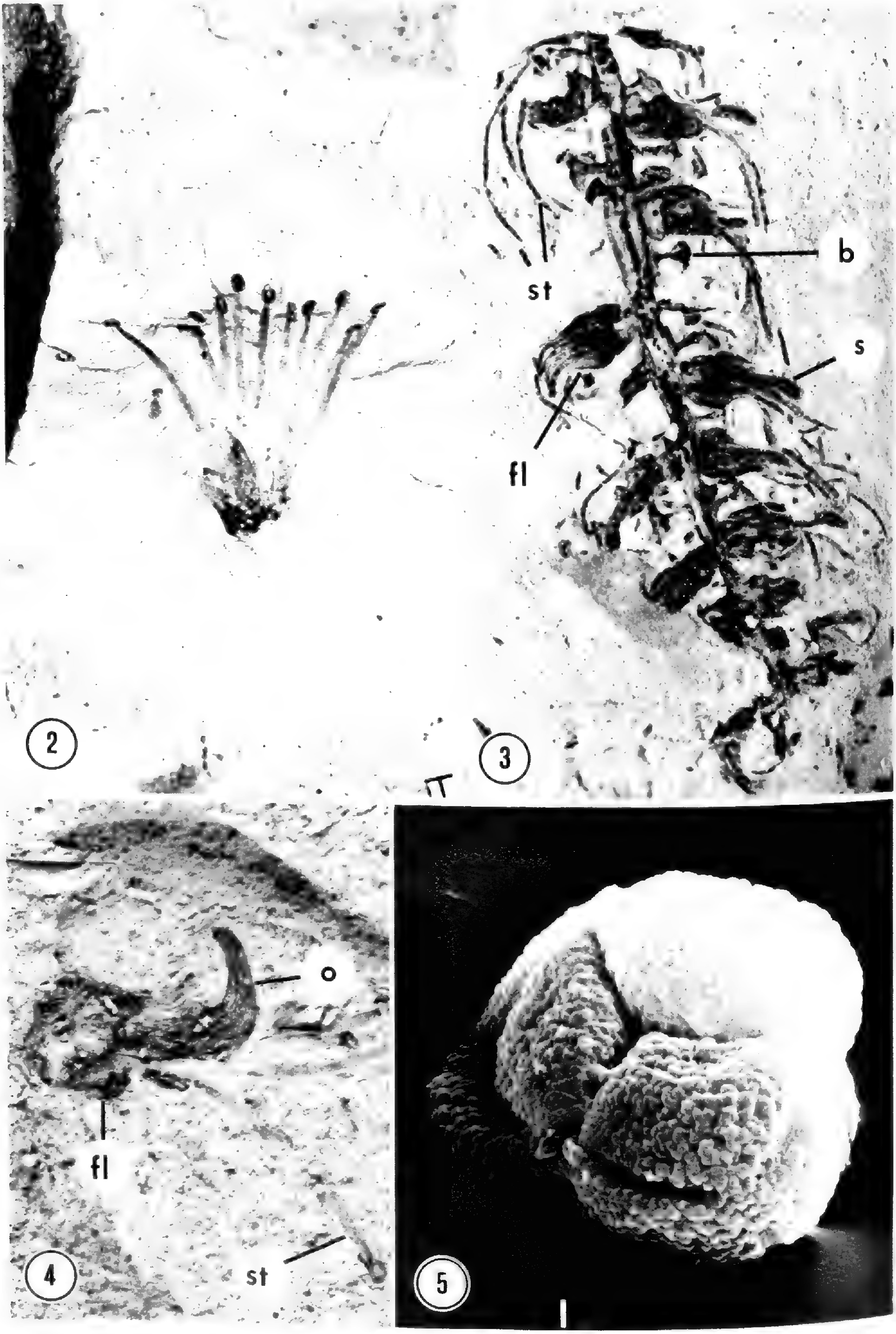
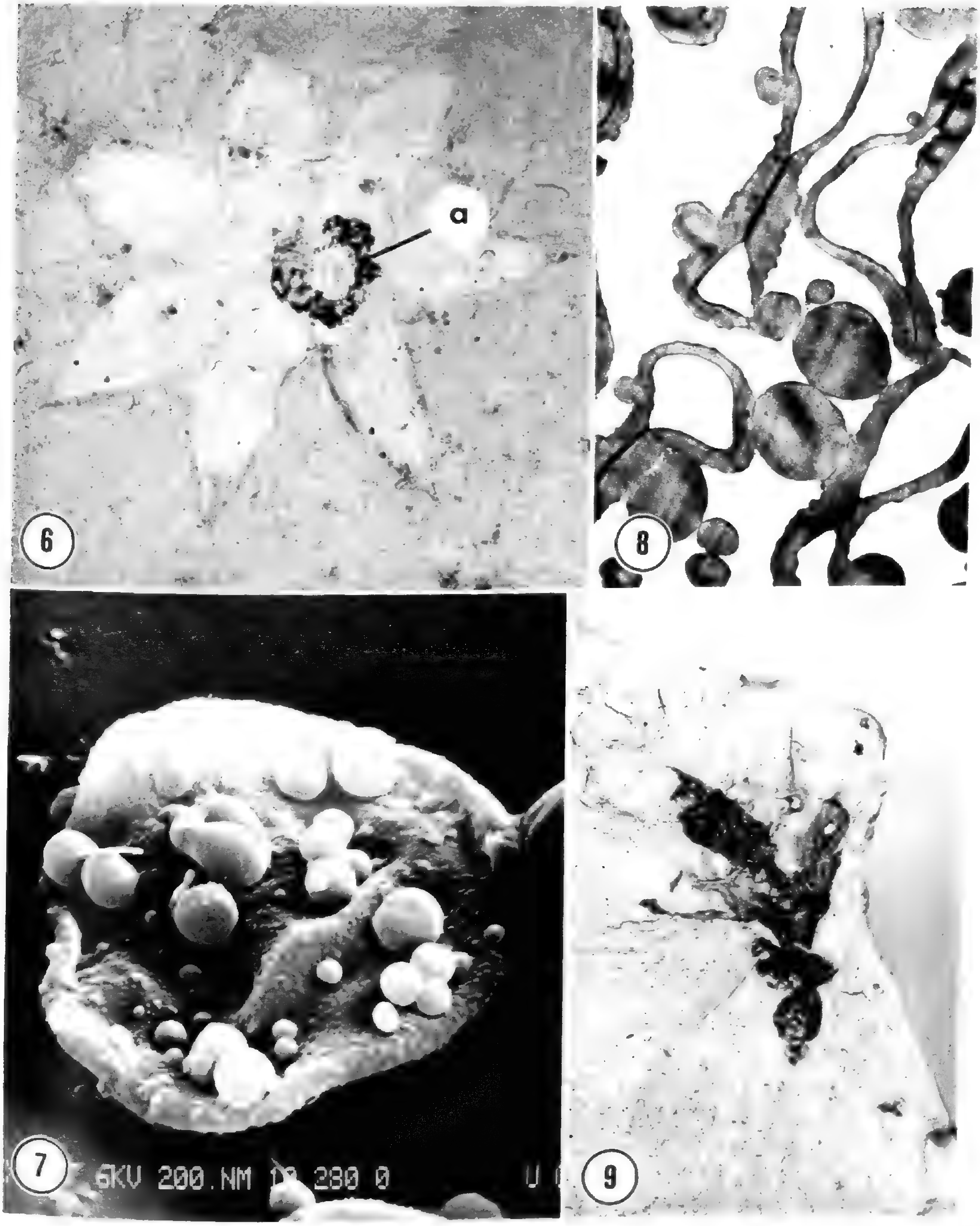
[a] Subclasses are arranged alphabetically within each geologic time unit; their position within that unit is not indicative of their order of appearance.



FIGURES 2–5. 2. Brush blossom. ×2.5. UCPC (University of Connecticut Paleobotanical Collection) B553. 3–5. *Eomimosoïdea plumosa.*—3. Inflorescence, note the floral envelopes (fl), style and stigma (s), stamens (st), and subtending bracts (b). ×5. UCPC H45.—4. Floret with an expanding ovary (o). Note the floral envelope (fl), the stamens (st), and that the carpel is hairy. ×7. UCPC W29.–5. Scanning electron micrograph of a tetrad of tricolporate pollen grains. ×2,500.



FIGURES 6–9. 6. Flower with seven-parted sympetalous corolla. Note the compressed ring of anthers (a). ×3.2. UCPC Ma322.—7. Scanning electron micrograph of pollen (when dispersed *Pistillipollenites macgregorii*) isolated from the flower illustrated in Figure 6. Note the gemmate processes. ×3,180.—8. Transmission electron micrograph of pollen illustrated in Figure 7 illustrating the intectate wall structure, gemmate processes, and residual columellae under certain of the gemmae. ×5,800.—9. Flower with a narrow floral tube. ×3. IUPC (Indiana University Paleobotanical Collection) P2226.

specifically where lepidopteran pollination is also common (Weaver, 1972).

Pollen is particularly important because its unique nature makes its occurrence a reliable indication that the same taxon and thus, floral structure, is involved whenever it occurs. *Pistillipollenites macgregorii* is known to extend into the Maestrichtian, suggesting that a pollination syndrome associated with bee pollination and, therefore, bees existed at that time. Surprisingly advanced Maestrichtian floral morphology may be an indication that bee pollination existed previous to that time. Pollen morphology provides additional corroboration for this assumption. Pollen with ornamentation similar to that of *P. macgregorii* is found in four extant taxa (Nowicke & Skvarla, 1974; Nilsson, 1970; Poole, 1981). In two of these families (Gentianaceae, Euphorbiaceae), variation in pollen is sufficiently well known that the sequence of evolution leading to gemmate pollen can be reconstructed (e.g., Nilsson, 1970). In each case gemmate, intectate pollen results from a breakdown of the muri of reticulate pollen accompanied by the elaboration of the tectum in localized areas. The progession suggests that gemmate pollen is a derived type and likely to be the end product of an evolutionary lineage; possibly one that originated previous to the Maestrichtian.

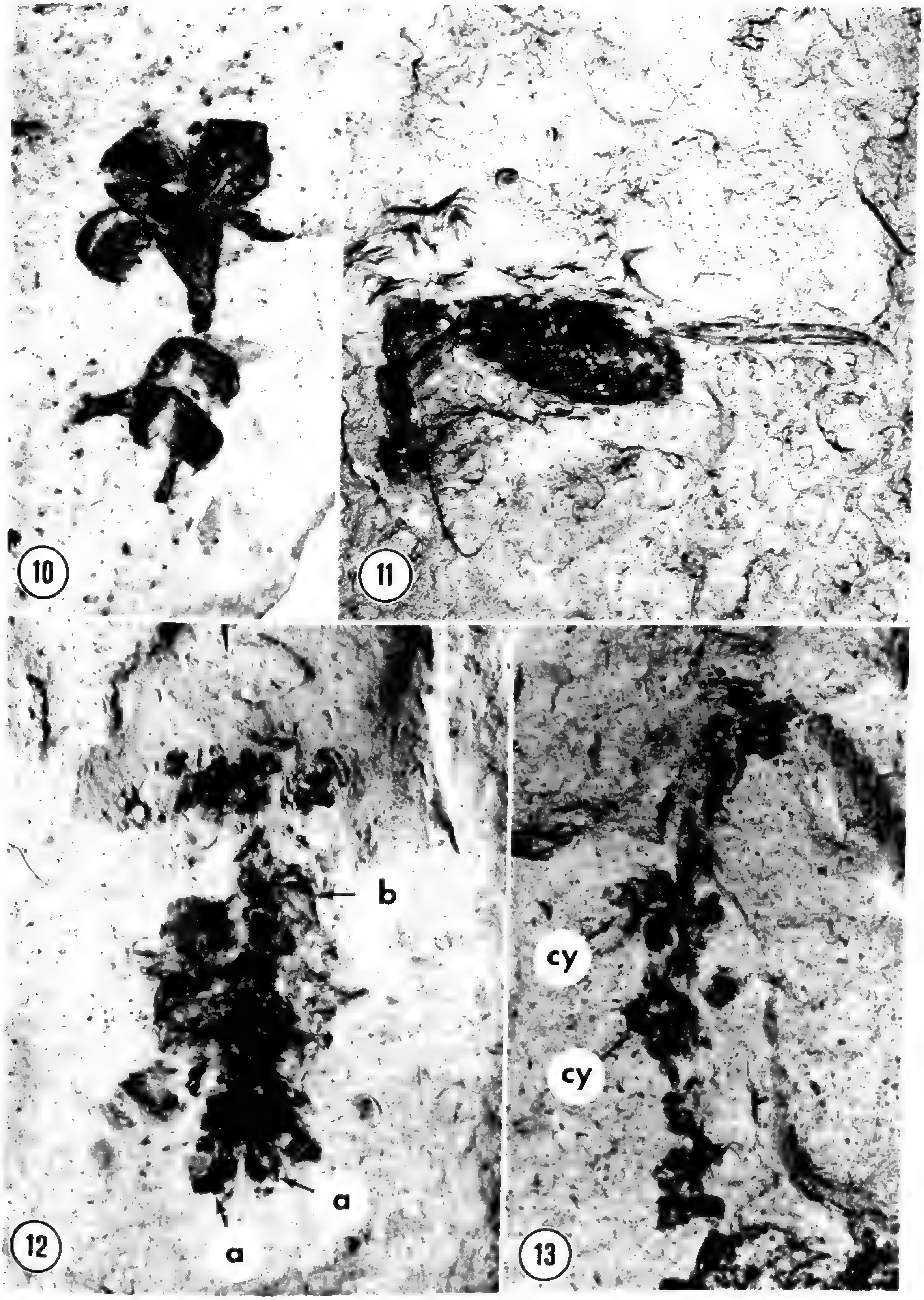
Sympetalous, funnelform-salverform flowers of as yet unknown affinities that have floral tubes narrow enough to suggest lepidopteran pollination (Figs. 9, 10) exist in Middle Eocene sediments of both the Green River Formation and the Claiborne Formation. In these cases the flowers also appear to be radially symmetrical, suggesting probable butterfly, as opposed to moth, pollination.

Zingiberidae. The taxa composing the Zingiberidae are remarkable for their often radical zygomorphy and their adaptations to a variety of advanced pollinators, including bees. Despite the derived nature of the flowers of this taxon, the Zingiberidae seem to be remarkably advanced by the Eocene. Fruits provide some of the most compelling data on the status of the group at this time. The Musaceae have been reported from the Eocene Deccan Intertrappean Series (Jain, 1963) and fruits of the Zingiberaceae have been reported from Eocene through Miocene sediments (Koch & Friedrich, 1971). Due to the highly adapted nature of zingiberidean flowers it has been suggested that floral structure in Paleogene taxa might have been different from floral structure in modern species (Daghlian, 1981). In view of the modern nature of the Paleogene fruits and the close relationship between fruit and flower structure, it seems more likely that they had flowers similar to those of modern taxa. This possibility is supported by a recently discovered zingiberidean flower (Fig. 11), from the Claiborne Formation (Middle Eocene). Although still in preliminary stages of investigation, this flower seems to be closest to the modern Heliconiaceae.

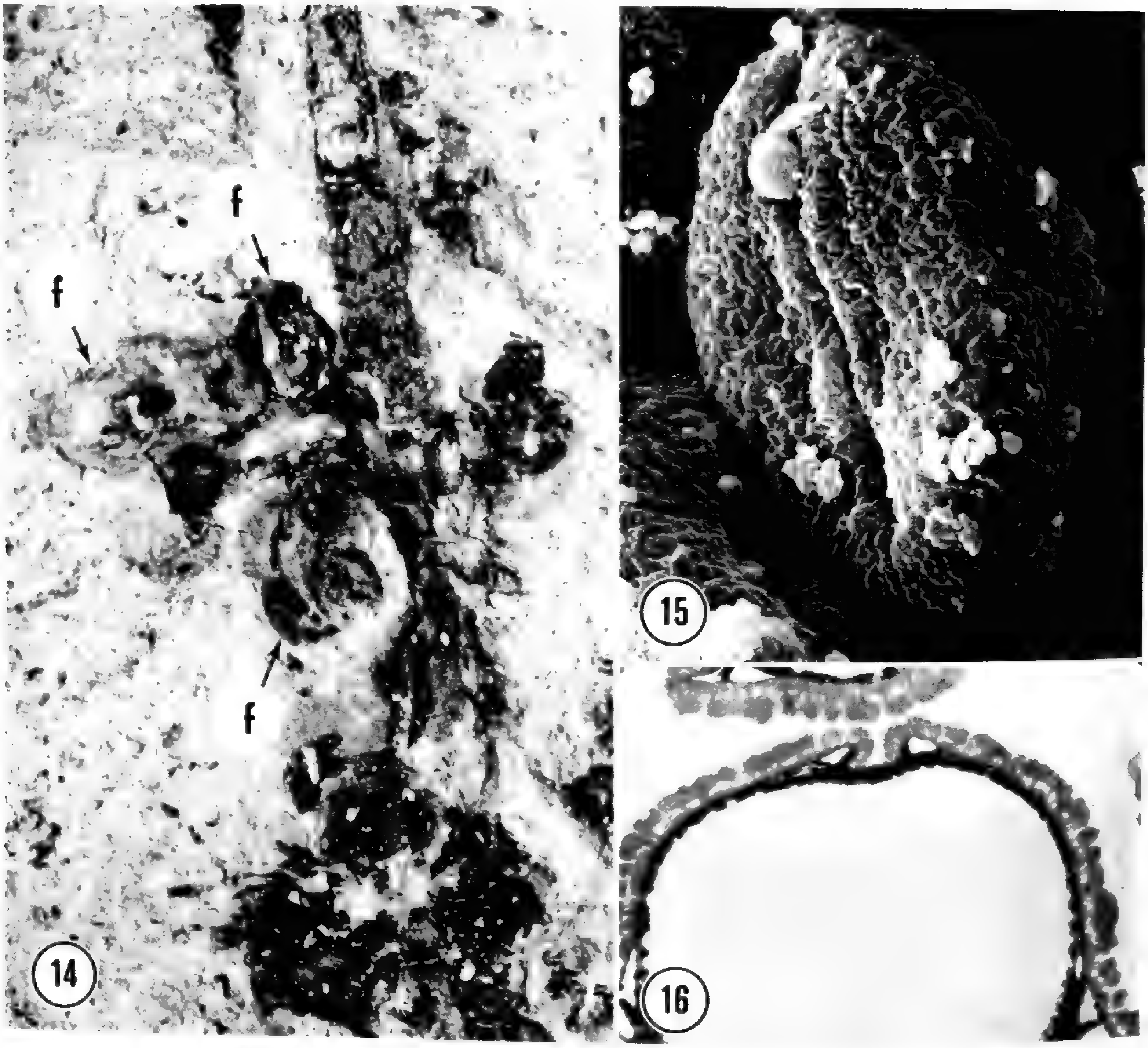
One of the most exciting recent developments relating to monocot history has been the discovery of zingiberalean leaves of Maestrichtian age. These are well documented and suggest the presence of highly advanced pollination syndromes during the Maestrichtian (Hickey & Peterson, 1978).

Euphorbiaceae. The Euphorbiaceae are one of the largest families of flowering plants and one in which diversity has been associated with adaptation to a wide range of insect pollinators (Stebbins, 1981). The state of the Euphorbiaceae by the Middle Eocene is a good indication of the rapidity of radiation of pollination mechanisms associated with insect pollination. The number of discrete fossil euphorbiaceans is small, but their nature makes it possible to infer something of the history of the family. Fruit and flower fossils of Middle Eocene age reveal that one of the most advanced tribes of the Euphorbiaceae, the Hippomane, was diverse and essentially modern by the Middle Eocene. Fruits reported by Manchester and Dilcher (1979) suggest that taxa similar to the hippomanean genera *Hippomane* and *Hura* were extant at that time. Inflorescences provide corroboration that this extremely derived tribe was modern by the Middle Eocene (Crepet & Daghlian, 1981b). Inflorescences were preserved at two ontogenetic stages: before the cymules expanded while the florets were still partially enclosed by a subtending bract (Fig. 12) and at maturity (Fig. 13). Inflorescences are sometimes branched spikes of cymules. Each cymule is composed of at least three staminate florets with at least three anthers each and is subtended by an ovate, cupped bract (Figs. 12, 14). Pollen is tricolporate and prolate with lalongate pores (Fig. 15). Exine is tectate columellate and perforate (Fig. 16). Ornamentation is interesting because the convoluted reticulum has striate muri. Inflorescence, cymule, and pollen morphology are similar to those of the genera *Gymnanthes* and *Senefeldera* in the Hippomane (Crepet & Daghlian, 1981b). The appearance of such modern taxa by the Eocene suggests an earlier origin for the family. This is supported by reliable reports of Cretaceous woods similar to those of certain modern genera (Webster, 1967) and by recently discovered Paleocene hippomanean inflorescences (Crepet, unpubl. data).

What is known of the history of the Euphorbiaceae gives the general impression (consistent with other paleobotanical data) that there was



FIGURES 10–13. 10. Another type of flower with a narrow corolla tube. ×3. UCPC G399.—11. Flower of the Zingiberidae. ×2.3. UCPC 520.—12. Part of an immature inflorescence of *Hippomaneoidea*. Note the cup-shaped bract (b) and the anthers (a) protruding from another bract. ×7.75. UCPC W14.—13. A mature inflorescence of *Hippomaneoidea* showing the expanded cymules (cy). ×4.3. UCPC W55.



FIGURES 14–16. *Hippomaneoidea.*—14. Higher magnification view of UCPC W55 showing two expanded cymules—one compressed laterally and one compressed in face view. Note that the laterally compressed cymule is composed of at least three florets (f) of 3–4 anthers each. ×16.—15. Scanning electron micrograph of pollen isolated from UCPC W55. ×2,500.—16. Transmission electron micrograph of pollen isolated from UCPC W55 illustrating the tectate-columellate wall structure. ×4,800.

relatively early (Upper Cretaceous—early Paleogene) radiation associated with insect pollinators.

SUMMARY OF PALEOBOTANICAL EVIDENCE

Evidence based on carefully investigated organ taxa including flowers and inflorescences suggests that families with pollination syndromes reflective of pollination by Apoidea and Lepidoptera existed by the Middle Eocene. Such advancement indicates an earlier radiation of pollination mechanisms involving faithful pollinators. The earlier Paleogene and Upper Cretaceous records are consistent with this possibility (Table 1) and the nature of pollination syndromes associated with families that occur during the Maestrichtian suggests that co-evolutionary relationships between angiosperms and faithful pollinators began at an earlier time. It is risky to suggest that the appearance of an advanced taxon at a given time implies a lengthy previous history. The projection of speciation models into geologic time by Eldredge and Gould (punctuated equilibria, 1972) and their consistency with angiosperm reproductive biology and the angiosperm fossil record (Crepet, 1982) introduces the possibility that the appearances of relatively modern syndromes at particular times are the culminations of events initiated just prior to their appearances in the fossil record. Nevertheless, the complexity of plant-pollinator interactions and the involvement of co-evolution in their origin do suggest that advanced pollinators, at least at higher taxonomic levels, e.g., superfamily Apoidea, may even have existed earlier than the uppermost Cretaceous, even if their evolution proceeded as in the punctuated equilibria model.

EVOLUTIONARY HISTORY OF FAITHFUL POLLINATORS

The two most important groups of pollinators in terms of promotion of speciation are the Apoidea, and to a slightly lesser degree, Lepidoptera. The discussion of advanced pollinators is consequently directed primarily toward these two groups. Coleoptera and Diptera are certainly important pollinators but do not have the ethologies associated with heightened promotion of speciation events. Both orders were well developed during the entire Mesozoic, especially the Coleoptera, and perhaps both were important in the establishment of basic angiosperm floral features. They undoubtedly contributed to Early Cretaceous radiation and spread of the angiosperms. Birds and bats are also important pollinators; however, they are not numerically as significant as insects, and birds tend to be promiscuous pollinators (Stiles, 1981), while fidelity in bats is poorly understood (Koopman, 1981). However the history of bats and birds suggests that neither were important pollinators until late Paleogene times (see review by Tiffney, 1984).

APOIDEA

It is interesting to examine data on the pattern of evolution of the Apoidea and to contrast these with the inferences obtained from the fossil record of plants. Although the most obvious place to begin is the fossil record of bees, that record is limited and most insights into the pattern of their radiation have been gained from a careful consideration of biogeography in light of their neontological features, including behavior, level of sociality, nesting habits, etc. (Michener, 1979).

The earliest record of fossil bees is either Eocene or Oligocene depending on the interpretation of the age of the Baltic amber. A diversity of fossil bees from various localities occurs at the same time including derived and ancestral tribes and subfamilies (by the Oligocene the Halictinae, Andreninae, Ctenoplectrinae, Melittinae, Anthidiini, Megachilini, Xylocoopini, Anthophorini, Meliponinae, Bombini, and Apini are known) (Michener, 1979). The presence of two of the four tribes of the Apidae by the Oligocene, including one of the two most highly derived tribes of extant bees (the Apini and Meliponini) is an indication that bee origin may have occurred considerably earlier than the Oligocene. Certainly, the known fossils do not help to unravel the pattern of evolution in bees. The strongest evidence related to the antiquity of the Apoidea comes from the interpretation of their disjunct distributions.

Michener (1979) noted that the distributions of most present day bees are probably the result of slow spreading over continents and presently moderate barriers, since most bees are not good dispersers. Most bees do not fly during bad weather, so they are not likely to be dispersed by storm winds and most bees have a tendency to return to their nesting sites. Dispersal is even more restricted in highly social bees due to their mode of colony establishment. Thus, there are certain groups of bees whose disjunct distributions are best explained by continental movements or by dispersal across oceans at a time when they were relatively narrow.

The Colletidae. The Colletidae are a family of short-tongued solitary bees and are considered the most primitive family of extant bees on neontological grounds (important primitive features include bifid glossae similar to those of the sphecid wasps and methods of carrying pollen, i.e., in the crop in two subfamilies (Hylaeinae and Euryglossinae) rather than on body hairs or more specialized structures (scopae; Michener, 1979; Thorp, 1979)). One tribe in particular has a distribution most easily accounted for by continental movements—the Paracolletini. These are presently restricted to temperate parts of three southern continents (Australia, Africa, and South America). Michener (1979) suggested that this disjunction may extend to the Upper Cretaceous when oceanic gaps were narrower. The colletids are an unusual family of bees inasmuch as in Australia, where they are most diverse, they are strongly associated with pollinating one particular family of angiosperms—the Myrtaceae. The presence of myrtaceous pollen in the Santonian (Table 1) supports Michener's suggestion.

The Fideliidae. The most primitive family of long-tongued bees, the Fideliidae, are closely related to the Megacheilidae (they are apparently sister groups, Michener, 1974). They are ground-nesters and particularly poor candidates for dispersal for that reason (i.e., flotation is out as a means of dispersal). Two species live in arid western South Africa and one is native to arid central Chile. Michener (1979) pointed out that the last direct migration route was closed in the lower Upper Cretaceous and that it would have been inaccessible to these bees anyway, because it was through the tropics. He concluded that the family had a distribution during the Upper Cretaceous and dispersed across oceans that were narrower than at present.

The Meliponini. One of the most important indicators of apoidean antiquity is the present distribution of the Meliponini. They are particularly important due to their phylogenetic status, their degree of eusociality, and their inability to disperse. The best biogeographical evidence involves the subgenera of the genus *Trigona* (Michener, 1979). The Meliponini are as highly social as the Apini, and, together with the Apini, represent the most derived bees. The discovery of a genus as modern as *Trigona* in the Upper Eocene-Oligocene Baltic amber suggests an earlier origin for the family. In fact, the distribution of the modern subgenera of *Trigona* is explicable only by a mid-Upper Cretaceous origin of the *subgenera.* Before considering the details of their distribution, it is instructive to examine the features that make the Meliponini particularly bad dispersers. As highly eusocial bees, they are dispersed by swarms and not individuals. Swarms are so highly organized that Michener (1979) considered it impossible for them to cross sizable bodies of water. Even the pattern of swarming mitigates against dispersal. Individuals from a parent colony go back and forth to provision the new nest before the queen migrates. The apparent isolation of species and subspecies in Brazil by rivers (Michener, 1979), and the absence of meliponines from the Antilles, even though these islands are relatively close to major continental populations, represent good evidence for their lack of dispersability.

Despite these difficulties, the genus *Trigona* is worldwide in its distribution with similarities at the subgeneric level between South American taxa and those of all other southern continents except Antarctica. There are three disjunctions in poorly dispersing subgenera as follows:

Plebeia: found in American tropics, Australia, and New Guinea.
Tetragona: American tropics, the oriental region, and Australia.
Hypotrigona-Trigonisca: American tropics, Africa, and the oriental region.

In view of their inability to traverse even rather insignificant bodies of water, Michener (1979) proposed that the principal subgenera of *Trigona* originated in the Middle or Upper Cretaceous when Africa and South America were joined or not yet widely separated at tropical latitudes.

LEPIDOPTERA

The fossil record of the Lepidoptera is better than that of the Apoidea, but it is still far from complete. Nonetheless, certain important aspects of the history of the Lepidoptera are evident from the fossil record.

The first reliable report of the Lepidoptera is based on several moths preserved whole in 100–130 Ma amber. These are related to the extant Micropterigidae (Lepidoptera, Zeugloptera; Whalley, 1977). Even though these fossils are the first evidence of the Lepidoptera, they are well defined micropterigids and are similar to the modern genus *Sabatinca.* Whalley (1977) proposed an origin for the Lepidoptera in the Jurassic based on the specialized nature of these fossils. Micropterigids are considered to be ancestral based on neontological features (Common, 1975) and are interesting because they have well-developed mandibles and no proboscis. Thus, it appears that the earliest lepidopterans were pollen feeders, if not predacious, and not nectar feeders.

There are several other reports of Cretaceous Lepidoptera in amber. One is of the head of a ditrysian larva from 73 Ma, another is of micropterigid scales from 100 Ma (Mackay, 1977; Kühne et al., 1973). In general, reports of Cretaceous Lepidoptera are rare, but what information is available provides an idea of their time of origin and degree of diversification (Monotrysia and Ditrysia are differentiated by the Upper Cretaceous).

A variety of fossil lepidopterans are known from the Paleogene, including one monotrysian moth, 41 ditrysian moths, and 27 butterflies (Durden & Rose, 1978). Perhaps the most interesting of these are three papilionid butterflies known from the Middle Eocene Green River Shale.

A variety of lepidopterous taxa are known from the later Tertiary and most are similar to their modern counterparts (Common, 1975). Common (1975), in his review of the fossil record of the Lepidoptera, concluded that the haustellate Lepidoptera were well established in the Cretaceous and that it is likely that the simple proboscis had evolved by the time angiosperms appeared. He further assumed that the radiation of ditrysian forms paralleled that of the angiosperms. These seem to be reasonable assumptions based on the fossil record. Lepidoptera occur relatively early and ditrysian forms (i.e., usually with a proboscis) occur at least by 73 Ma. Further, a variety of Lepidoptera are present in the Paleogene, including the highly specialized Papilionidae. It seems more than likely that advanced lepidopteran pollinators were available during the Upper Cretaceous.

Patterns of Angiosperm Diversification

The tempo of angiosperm diversification is an essential datum in assessing the possibility of a relationship between advanced faithful pollinators and angiosperm diversity. Until recently (Niklas et al., 1980; Muller, 1981; Tiffney, 1981), there has been no really rigorous attempt to chart the course of angiosperm diversification. The notions that angiosperms arose *de novo* as modern taxa and almost instantaneously became dominant have been debunked by Doyle and Hickey (1976), but the angiosperms have been considered generally to be dominant worldwide by the lower Upper Cretaceous (e.g., Raven & Axelrod, 1974). Recent analyses of angiosperm diversity through time have presented a different picture.

Niklas et al. (1980) have analyzed angiosperm diversification based on reports of various fossil organs in the literature as part of their general survey of patterns of diversification in vascular plants. The results suggest that angiosperm diversity increased slowly and steadily during much of the Cretaceous with angiosperms becoming locally dominant during the Upper Cretaceous and achieving world dominance by the uppermost Cretaceous or Early Tertiary (Niklas et al., 1980). They provide a well thought out discussion defending their use of fossil species as the basis for their diversity curves, and in context (Niklas et al., 1980), species are clearly the fossil taxon of choice. One of the justifications for using fossil species involves inherently greater subjectivity in the designation of higher taxonomic levels. This may be true for higher taxonomic levels that are extinct and it is certainly true in extant taxa, but with fossil angiosperms there are reasons why higher taxonomic levels, particularly the family, may be superior indices of actual diversity. First and perhaps most important, families can be identified with great confidence in the fossil record. This provides an element of reliability and eliminates inevitable distorting redundancy associated with the use of form taxa. Second, the biological validity of angiosperm families can be assessed on the basis of neontological data, since these families exist in the present as well as in the past. Third, using appearances of families as indices of diversity minimizes aberrations that might be associated with having relatively few megafossil localities at certain times. Finally, dominant angiosperm diversity is the result, not only of having certain extremely large families and genera, but predominantly, of having a great number of families. In fact, the average number of species/family in the angiosperms is comparable with the species/family ratio in gymnosperms (Stebbins, 1981). Thus, rate of appearances of families is a reasonable index of angiosperm diversification. Naturally, it is a compromise inasmuch as some diversity is masked, especially diversity preceding the origination of modern families.

Muller recently provided an account of the diversification pattern of angiosperm families based on his analysis of the palynological literature (1981). Muller's analysis is attractive because criteria for accepting or rejecting data on the occurrences of particular families are clearly discussed and because pollen has proven taxonomic value. Muller's analysis (1981) parallels that of Niklas et al. (1980) in illustrating a steady rise in total angiosperm diversity during most of the Cretaceous, but reveals a slightly earlier (Campanian) and more dramatic peak in diversification that reaches a maximum during the Maestrichtian and extends into the Paleogene. Interestingly, diversification patterns for orders and superorders, which would presumably include most angiosperms left out in a consideration of only modern families, are very similar to the pattern of diversification based on families alone (Muller, 1981).

Both analyses of angiosperm diversity are valuable attempts to clarify a pattern that has been predominantly subjectively interpreted. Both have their strengths and weaknesses, but in each instance the major dramatic radiation of angiosperms is revealed at a date later than has commonly been supposed.

Summary of Data

1. Families having flowers adapted for pollination by Apoidea and Lepidoptera probably existed during the uppermost Cretaceous. The taxa

present at that time indicate a probability of earlier co-evolution of angiosperms with apoidean and lepidopteran pollinators.

2. Rigorous analysis of the biogeography of bees suggests that at least three families of the Apoidea were present by the uppermost Cretaceous; the Colletidae, Fideliidae, and Apidae. The Apidae were so well developed by that time that it is likely that three subgenera of the genus *Trigona* already existed.

3. The fossil record of the Lepidoptera indicates an origin for the order previous to 100 Ma with both monotrysian and ditrysian forms present by the Upper Cretaceous.

4. Angiosperm diversity increased steadily during the lower and part of the upper Cretaceous. They may have commenced a major diversification as early as the Campanian, but were certainly experiencing a major radiation by the Cretaceous-Tertiary boundary that continued into the Tertiary.

CONCLUSIONS

It is not reasonable at the present time to attempt to attribute angiosperm success to any single characteristic. In fact, many of the features of angiosperms that have been discussed by Stebbins (1981), Burger (1981), and Mulcahy (1979) have undoubted significance in angiosperm supremacy. Nonetheless, data on the progression of evolution of insect pollination mechanisms in angiosperms suggest that the inception of advanced insect pollination syndromes was either coincident with, or just prior to, a major radiation of flowering plants. Advanced insect pollination can no longer be excluded on the basis of paleontological evidence from having participated in a major radiation of angiosperms. On the contrary, paleontological data are consistent with neontological evidence in suggesting an important role for advanced insect pollinators in establishing contemporary angiosperm diversity.

There were undoubtedly several milestones in the evolution of angiosperm pollination mechanisms during the Cretaceous and Paleogene other than the appearance of advanced faithful pollinators, and these also must have affected angiosperm diversity. What can be inferred from the fossil record at the present time suggests the following sequence of events in the evolution of angiosperm pollination mechanisms:

1. The origin of insect pollination. Angiosperm origin involved co-evolution with insect pollinators (dipteran or coleopteran) that resulted in the ancestral angiosperm flower. The first angiosperms had features conducive to successful radiation, including a truncated life cycle, enclosed ovules, insect pollination, and gametophytic competition (Stebbins, 1981; Doyle & Hickey, 1976; Burger, 1981). Evidence for the early predominance of coleopteran/dipteran pollination in angiosperms is provided by the fossil record, which illustrates the existence of all major magnoliidan pollen types during the Aptian/Albian (Zavada, unpubl. data).

2. During the mid-Cretaceous, wind pollination evolved in angiosperms possibly as a result of the combination of seasonally dry tropical-subtropical environments and competition for insect pollinators (Whitehead, 1969; Crepet, 1981). These taxa were pre-adapted to invade subsequent appropriate habitats, including those created by climatic decay.

3. The appearance of advanced faithful insect pollinators in the Upper Cretaceous/Paleogene.

4. The origin of bat and bird pollinators. These pollen vectors probably became significant no earlier than the mid-Paleogene (e.g., Stiles, 1981; Koopman, 1981; Tiffney, 1984) and, while certainly contributing to angiosperm diversity by increasing the adaptive space associated with animal pollination, they are not as significant numerically as insect pollinators.

5. Finally, the ultimate refinements of the specific plant-pollinator interaction (e.g., the Orchidaceae) and of the non-specific plant pollinator interaction (e.g., the Compositae; Proctor, 1978). These alternative developments must have occurred late in the Tertiary, but there is little germane fossil evidence at this time.

Regal (1977) has pointed out the possibility that synergism between insect pollinators and animal seed dispersal vectors may have been important in the major radiation of angiosperms (although his timing was way off due to his apparent unfamiliarity with such things as the nature of pollinating vs. non-pollinating Hymenoptera, etc.). A modification of this proposal, i.e., that *faithful* insect pollination and animal seed dispersal vectors were of utmost importance in maximizing angiosperm diversification during the uppermost Cretaceous-Lower Tertiary, remains a viable and even exciting possibility (consider the present chapter in conjunction with that of Tiffney, 1984). Animal dispersal maximizes the probability that, given a heterogeneous terrestrial biospace, a small population will be isolated in a new environment (Tiffney, 1984; see discussion also by Vrba, 1980, fig. 1C). Constant pollinators, stochastic floral change, and animal seed dispersal vectors may interact in a variety of ways to further promote speciation (Fig. 1A–C). Because these elements of angiosperm reproductive biology are conducive to the stochastic isolation of small populations and because of the apparent importance of stasis in angiosperm history (Crepet, unpubl. data), I consider the punctuated equilibrium model of evolution to have merit with regard to the angiosperms. Differences in the timing of events; i.e., the coincidence of the appearance of advanced insect pollination mechanisms with the onset of the major angiosperm radiation during the Campanian according to Muller (1981), versus a slightly later date for maximal angiosperm diversification as reported by Niklas et al. (1980) and Tiffney (1981), are probably not significant given the constraints imposed by the degree of resolution presently available from the fossil record. What is important is the understanding that presently available fossil data do show an uppermost Cretaceous-Early Tertiary and not an earlier peak in angiosperm diversification rate.

It now appears that the inception of advanced pollination mechanisms preceded widespread animal seed dispersal (Tiffney, 1984). If future investigations bear out this possibility, it will suggest advanced insect pollination alone might have been responsible for the onset of a major angiosperm radiation while synergism with animal seed dispersal vectors became an important factor at a slightly later time.

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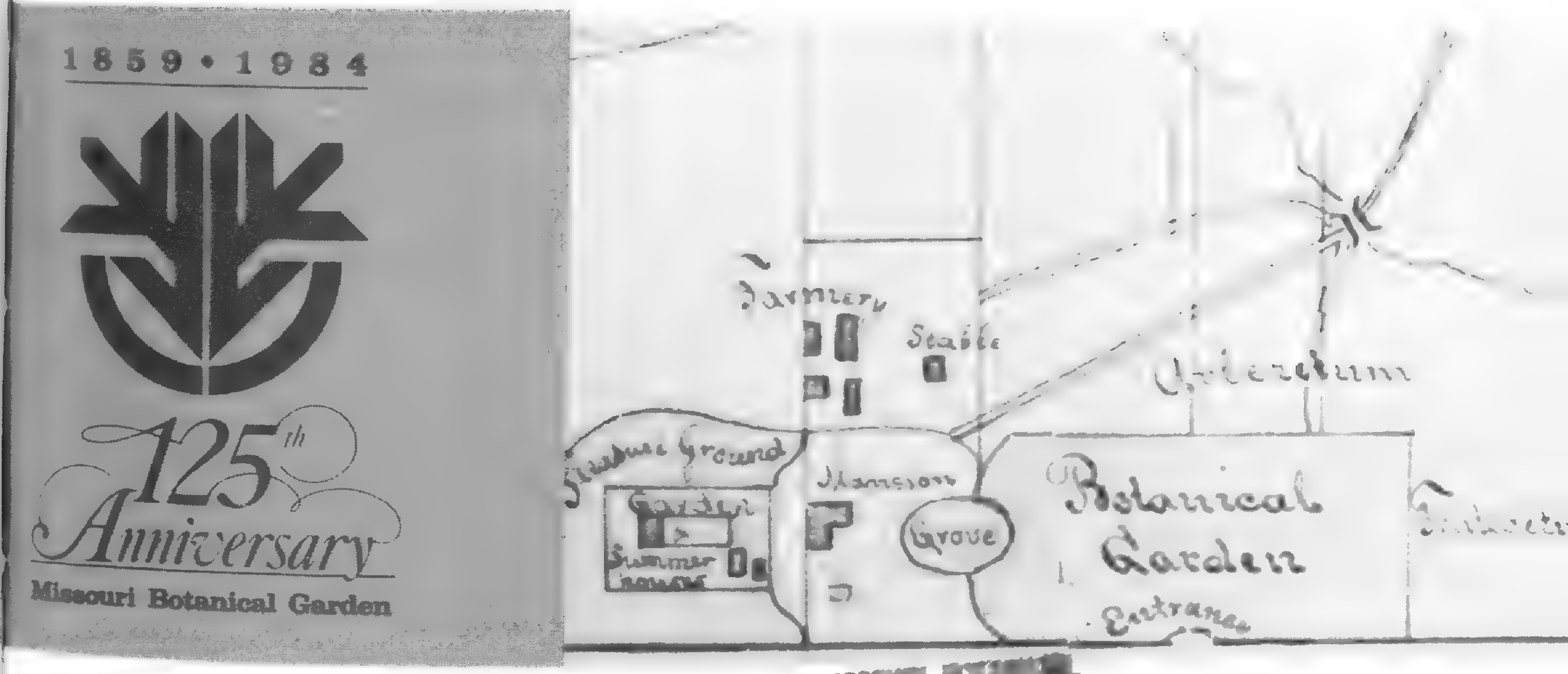

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THE ORDER MYRTALES: A SYMPOSIUM

Peter H. Raven[1]

This symposium was held at the XIII International Botanical Congress, Sydney, Australia, 21–28 August 1981. Much development of the material was carried out subsequent to the Congress, and some of the papers published here have been added to round out the picture of the overall group.

By concensus of the participants in the symposium, Myrtales are a clearly defined group including the following families and subfamilies:

Onagraceae
Trapaceae
Lythraceae subfam. Lythroideae
    subfam. Sonneratioideae
    subfam. Duabangoideae
    subfam. Punicoideae
Oliniaceae
Combretaceae subfam. Combretoideae
    subfam. Strephonematoideae
Alzateaceae
Rhynchocalycaceae
Penaeaceae
Crypteroniaceae
Melastomataceae
Memecylaceae
Psiloxylaceae
Heteropyxidaceae
Myrtaceae

Concerning differences in the delimitation of these groups, the following points are pertinent. Memecylaceae are regarded as a subfamily of Melastomataceae by R. F. Thorne, and *Pternandra* is apparently intermediate between these two groups. Psiloxylaceae and Heteropyxidaceae, each with a single genus, are considered subfamilies of Myrtaceae by Thorne. They clearly are most closely related to that family, constituting with it a distinctive early offshoot within the order. *Strephonema* might be segregated as a distinct family on the basis of several features, but clearly is more closely related to the other genera of Combretaceae than to any other group. Further evaluation of the relationships of *Axinandra, Crypteronia,* and *Dactylocladus,* and of their placement together in the family Crypteroniaceae, is likewise desirable.

Despite the many distinctive features that distinguish it from Myrtales and link it with Euphorbiaceae, Cronquist includes Thymelaeaceae in Myrtales; his point of view is apparently unique among students of the order and participants in this symposium. Contemporary systematists who have considered the order Myrtales, Thymelaeaceae, and Euphorbiaceae from many points of view apparently agree unanimously, with the exception of Cronquist, in grouping the last two families and not linking them with Myrtales.

With the single exception just reviewed, no participant in the symposium argued for the inclusion of any family in the order Myrtales other than those listed above, and none have suggested that any of these families ought to be excluded

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[1] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.

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from the order. In fact, there is no convincing case even for a relatively close relationship between the order Myrtales, as here defined, and any other family of plants. Consequently, Myrtales may be regarded as a highly distinctive group, one of the most clearly delimited of all orders of angiosperms.

The organization and coordination of this symposium were assisted by a grant from the U.S. National Science Foundation.

THE ORDER MYRTALES: CIRCUMSCRIPTION, VARIATION, AND RELATIONSHIPS[1]

ROLF DAHLGREN[2] AND ROBERT F. THORNE[3]

ABSTRACT

The Myrtales are one of the least controversial orders as regards circumscription and characterization. The core families are Onagraceae, Trapaceae, Lythraceae, Oliniaceae, Combretaceae, Alzateaceae, Rhynchocalycaceae, Penaeaceae, Crypteroniaceae, Melastomataceae, Memecylaceae, Psiloxylaceae, Heteropyxidaceae, and Myrtaceae. Psiloxylaceae-Heteropyxidaceae-Myrtaceae and Onagraceae form two somewhat peripheral groups within the order. Alzateaceae and Rhynchocalycaceae are newly recognized at the familial level. Punicaceae and Sonneratiaceae are included in Lythraceae. Crypteroniaceae and Memecylaceae could be included in Melastomataceae and Psiloxylaceae and Heteropyxidaceae in Myrtaceae. Lecythidaceae, Haloragaceae, Rhizophoraceae, and Thymelaeaceae are excluded from Myrtales. Arguments pro and con for this are given. The distribution of a number of attributes in the aforementioned families are discussed, and some distributions are illustrated diagrammatically. These attributes involve wood anatomy, foliar sclereids, phyllotaxy, stipular structures, merous conditions of perianth, inferior versus superior ovary placement, floral tube, pleiomery and developmental succession of stamens, anther connectives, pollen pseudocolpi, embryology, seed coat structure, chromosome numbers, chemistry, etc. Other families that have been associated with Myrtales are also considered. The Myrtales show affinities to Rosales, and fewer ones to Gentianales, Cornales, and possibly Theales.

CIRCUMSCRIPTION OF MYRTALES IN SOME CURRENT SYSTEMS OF CLASSIFICATION

The historical background of the order Myrtales will not be outlined here. We shall restrict ourselves to the circumscription of the order in the following classifications: Emberger (1960), Melchior (1964), Soó (1967), Hutchinson (1926, 1959, 1973), Thorne (1968, 1976, 1981), Cronquist (1968, 1981), Takhtajan (1969, 1980), Stebbins (1974), Dahlgren (1975a, 1980a), and Briggs and Johnson (1979).

Emberger (1960) included in this order: Lythraceae, Crypteroniaceae, Heteropyxidaceae, Sonneratiaceae, Punicaceae, Rhizophoraceae, Lecythidaceae, Combretaceae, Myrtaceae, Melastomataceae, Onagraceae, Trapaceae ("Hydrocaryaceae"), Haloragaceae ("Halorrhagidaceae"), and Gunneraceae, and, as annex families, added Hippuridaceae, Callitrichaceae, and Dialypetalanthaceae. Penaeaceae and Oliniaceae were placed in the adjacent order Thymelaeales, which also included Thymelaeaceae, Geissolomataceae, and Elaeagnaceae.

This wide circumscription may be taken as a relevant starting point in this presentation, as here we have the essential scope of the order in a very wide sense. The general tendency has been to include Penaeaceae and Oliniaceae in Myrtales and to exclude Hippuridaceae and Gunneraceae (in as much as these are segregated from Haloragaceae), and also to exclude Lecythidaceae, Rhizophoraceae, and Haloragaceae sensu stricto. Dialypetalanthaceae have sometimes been very loosely attached to the order. Trapaceae are usually included in Myrtales and Heteropyxidaceae have usually been included in Myrtaceae, whereas, Psiloxylaceae are a recent addition to the Myrtaceae. Other later systems usually do not deviate greatly from this pattern.

In Melchior's (1964) edition of Engler's "Syllabus der Pflanzenfamilien," the following families are included in the order: Lythraceae, Trapaceae, Crypteroniaceae, Myrtaceae (incl.

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[1] The present summary presentation of Myrtales would not have been made without the encouragement from Dr. Peter H. Raven and all the contacts communicated by him. Numerous specialists in different fields for taxa within and without Myrtales have generously contributed information. Their contributions are acknowledged in the above text with the discrete remark, "personal communication." In particular, we wish to acknowledge ample first hand information from P. Baas, B. Briggs, S. A. Graham, A. Graham, L. Johnson, P. Raven, H. Tobe, C. A. Stace, and G. J. C. M. van Vliet. P. Raven, L. A. S. Johnson, B. Briggs, and R. Schmid have kindly read our manuscript and suggested many useful improvements and new data.

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Heteropyxidaceae), Dialypetalanthaceae, Sonneratiaceae, Punicaceae, Lecythidaceae, Melastomataceae, Rhizophoraceae, Combretaceae, Onagraceae, Oliniaceae, Haloragaceae (incl. Gunneraceae), and Theligonaceae, and in separate suborders Hippuridaceae and Cynomoriaceae. Inclusion of the last-mentioned familiy has gained no support. Penaeaceae, as in Emberger's (1960) classification, were placed in Thymelaeales, as were also Geissolomataceae, Dichapetalaceae, and Elaeagnaceae.

Soó (1967, 1975) subdivided his order Myrtales into three suborders: Myrtineae, with Combretaceae, Melastomataceae, Myrtaceae, Oliniaceae, Punicaceae, Sonneratiaceae, Lecythidaceae, and Rhizophoraceae; Lythrineae, with Lythraceae, Onagraceae, and Trapaceae; and Haloragineae, with Haloragaceae, Gunneraceae, and Hippuridaceae. Crypteroniaceae were omitted, and Penaeaceae were included in Thymelaeales.

Hutchinson (1926) in the first edition of his "Families of Flowering Plants" placed the families Lythraceae, Crypteroniaceae, Sonneratiaceae, Punicaceae, Oliniaceae, Onagraceae, Haloragaceae (including *Gunnera* and *Hippuris*), and Callitrichaceae in a separate order Lythrales; and Myrtaceae, Lecythidaceae, Melastomataceae, Combretaceae, and Rhizophoraceae in another order, Myrtales. These orders were at least partly distinguished by being chiefly herbaceous or chiefly woody, respectively, although this distinction had to involve many exceptions.

In the second edition of the same work (Hutchinson, 1959), with the same basic principle of division, the chiefly herbaceous Lythrales were restricted to Lythraceae, Onagraceae, Trapaceae, Haloragaceae, and Callitrichaceae; whereas the chiefly woody Myrtales included Myrtaceae, Lecythidaceae, Rhizophoraceae, Sonneratiaceae, Punicaceae, Combretaceae, and Melastomataceae. Crypteroniaceae and Oliniaceae in that edition were placed in Cunoniales and Penaeaceae in Thymelaeales. It is obvious that Hutchinson's strict adherence to the division of herbaceous versus woody plants has resulted in a less natural classification.

In the third edition of the same work, Hutchinson (1973) presented a new classification, in which an extended woody order Myrtales included Myrtaceae, Barringtoniaceae, Anisophylleaceae, Sonneratiaceae, Lythraceae, Rhizophoraceae, Lecythidaceae, Combretaceae, Punicaceae, Napoleonaceae, and Melastomataceae. Crypteroniaceae and Oliniaceae were retained in Cunoniales and Penaeaceae in Thymelaeales. The herbaceous order Onagrales was there restricted to Onagraceae, Trapaceae, Haloragaceae (incl. *Hippuris* and *Gunnera*), and Callitrichaceae; whereas Dialypetalanthaceae were placed beside Rubiaceae in Rubiales, a very reasonable position in the light of some of its attributes.

Thorne (1968, 1976, 1981) by preference has wider ordinal and familial concepts. He restricts the superorder Myrtiflorae to the Myrtales, in which he now treats Lythraceae (incl. Punicoideae and Sonneratioideae), Penaeaceae, Oliniaceae, Trapaceae, Crypteroniaceae, Melastomataceae (incl. Memecyloideae), Combretaceae (incl. Strephonematoideae), Myrtaceae (incl. Psiloxyloideae), and Onagraceae. In the 1976 version of his classification he had included Thymelaeaceae in Myrtales, but in the latest treatment (Thorne, 1981) has returned Thymelaeaceae to Euphorbiales where he earlier (1968) had placed them. These families comprise what we shall treat as the 'core group' of families in Myrtales. Thorne has placed Rhizophoraceae and Haloragaceae in separate suborders of Cornales, and, in all versions of his classification has treated Lecythidaceae in Theales as the separate suborder Lecythidineae. He has included *Dialypetalanthus* among taxa incertae sedis, however, he now regards this genus as closely related to, or perhaps better included in, Rubiaceae of Gentianales.

Cronquist (1968) in his Myrtales included Sonneratiaceae, Lythraceae, Penaeaceae, Crypteroniaceae, Thymelaeaceae, Trapaceae, Dialypetalanthaceae, Myrtaceae (incl. *Heteropyxis*), Punicaceae, Onagraceae, Oliniaceae, Melastomataceae, and Combretaceae, giving the order approximately the same circumscription as that accepted by Thorne in 1976. Cronquist placed Lecythidaceae in the separate order Lecythidales, and Haloragaceae, Hippuridaceae, Gunneraceae, and Theligonaceae in an order named Haloragales. Further, Rhizophoraceae, as in Thorne's classification, were placed in Cornales, though Cronquist (1981) now prefers to treat Rhizophoraceae in their own order, Rhizophorales.

In his classification of 1981, Cronquist placed Dialypetalanthaceae in his Rosales, Theligonaceae in Rubiales, and Hippuridaceae in Callitrichales, leaving Haloragaceae and Gunneraceae in the order Haloragales.

Takhtajan (1959, 1966, 1969) included in the Myrtales Lythraceae, Sonneratiaceae, Punicaceae, Rhizophoraceae, Anisophylleaceae, Combretaceae, Lecythidaceae (sensu lato), Myrtaceae, Melastomataceae, Oliniaceae, Penaeaceae, Onagraceae, and Trapaceae. He placed Crypteroniaceae in Saxifragales near Brunelliaceae (cf. Cronquist, 1981). Takhtajan's Hippuridales (= Haloragales) included Haloragaceae, Gunneraceae, and Hippuridaceae and were placed next to Myrtales. Thymelaeales, with only Thymelaeaceae, were placed in sequence with Euphorbiales and were not considered by Takhtajan as related to Myrtales.

In a revised version of his angiosperm classification, Takhtajan (1980) widened the circumscription for his order Myrtales, which was divided into four suborders: Myrtineae, with the families of his order Myrtales from 1969 plus Crypteroniaceae; Halorigineae, with Haloragaceae (excl. *Gunnera* and *Hippuris*); Rhizophorineae, with Rhizophoraceae (incl. Anisophylleaceae, Legnotidaceae, and Polygonanthaceae); and Lecythidineae, with Lecythidaceae (incl. Asteranthaceae, Barringtoniaceae, Foetidiaceae, and Napoleonaceae). This new classification approaches closely that of Dahlgren (1980a); wherein, however, the Lecythidaceae are placed in Theales and the ordinal circumscription is slightly different.

Stebbins (1974) basically followed Cronquist (1968), but did include Rhizophoraceae in Myrtales. Like Cronquist, he treated Lecythidaceae in an order of their own.

Dahlgren, in his classification of 1975a, gave Myrtales the following circumscription: Lythraceae (incl. Sonneratiaceae), Punicaceae, Rhizophoraceae (incl. Anisophylleaceae), Crypteroniaceae, Combretaceae, Oliniaceae, Melastomataceae, Penaeaceae, Myrtaceae (incl. *Heteropyxis*), and Onagraceae, and in this order also included Dialypetalanthaceae, but remarked that the position of that family was uncertain. Trapaceae were excluded from the order as a consequence of the lack of endosperm formation and other details [but were reinstated in Myrtales in his later system (Dahlgren, 1980a; Dahlgren et al., 1981)]. Haloragaceae (excl. *Hippuris* and *Gunnera*) were treated in a separate order next to Myrtales, and Lecythidaceae with their segregates were placed in Theales. As in Takhtajan's classification, Thymelaeaceae were placed in Thymelaeales adjacent to Euphorbiales.

In the revised classification of 1980a, Dahlgren included in Myrtales the families Myrtaceae, Psiloxylaceae, Oliniaceae, Melastomataceae, Penaeaceae, Crypteroniaceae, Lythraceae, Sonneratiaceae, Punicaceae, Combretaceae, Onagraceae, and Trapaceae. Haloragaceae and Rhizophoraceae were placed in separate orders next to Myrtales in the Myrtiflorae; whereas, Anisophylleaceae and Dialypetalanthaceae with some reservations were considered to be possibly cornalean.

Briggs and Johnson (1979) suggested a new classification of the former myrtalean families, distributing them in two orders, Myrtales sensu stricto and Lythrales, although these have widely different circumscriptions than have the corresponding orders in Hutchinson's system of 1959. Myrtales sensu stricto of Briggs and Johnson included Myrtaceae, Psiloxylaceae, Melastomataceae, Oliniaceae, and Penaeaceae; whereas, their Lythrales included Lythraceae, Sonneratiaceae, Punicaceae, Trapaceae, Combretaceae, Onagraceae, and Crypteroniaceae. [They have since (this symposium) dropped this division of the myrtalean families into two orders.] Haloragaceae, according to them, are possibly related to Myrtales and Lythrales, and Rhizophoraceae are suspected to be heterogeneous with possibly a thealean affinity. Thymelaeales, in accordance with various previous authors, are believed to be allied to Euphorbiales and Malvales. Lecythidaceae are also excluded, and Dialypetalanthaceae are regarded as gentianalean or rubialean (these orders are united in some systems). This classification will be discussed further in this paper.

Here, the order will be circumscribed largely as by Dahlgren (1980a), and by Thorne (1981), although the familial rank will be treated somewhat differently. One of us (Dahlgren) prefers smaller, homogenous families and recognizes as many as 14 families [Onagraceae, Trapaceae, Lythraceae (incl. Punicaceae and Sonneratiaceae), Oliniaceae, Combretaceae, Alzateaceae, Penaeaceae, Rhynchocalycaceae, Crypteroniaceae, Memecylaceae, Melastomataceae, Psiloxylaceae, Heteropyxidaceae, and Myrtaceae]. For convenience this treatment will be used throughout this survey. Thorne, on the other hand, includes Heteropyxidaceae and Psiloxylaceae in Myrtaceae and Memecylaceae in Melastomataceae. In all other respects, we are in agreement.

DEFINITION OF THE ORDER

Members are woody or herbaceous, terrestrial or rarely aquatic, ranging from huge trees to small annual herbs. The tap root is usually well developed.

Vascular strands are bicollateral in all the families and (as far as known) in nearly all species. Nodes are largely unilacunar (but trilacunar in Alzateaceae). Vessel elements have simple perforation plates (or very rarely scalariform perforation plates) and vestured pits (van Vliet, 1978). (Internal phloem and vestured pitting in this order are extremely important and define the order along with other distinctive features.) Wood rays vary between uni- and pluriseriate (even within most families), are mostly to 3 cells wide, and heterocellular to homocellular; ray cells often have gummy deposits; some of the axial parenchyma in scattered families generally consisting of vertical crystalliferous strands (Cronquist, 1981). Phloem of young twigs is often tangentially stratified into hard and soft layers. Sieve-tube plastids accumulate starch but never protein.

Leaves are typically opposite but quite often alternate, rarely verticillate, simple, either petiolate or sessile, rarely (in Onagraceae; Cronquist, 1981) lyrate-pinnatifid. The leaf margin is generally entire, but several genera of the Onagraceae and certain Lythraceae are provided with teeth ("Fuchsioid teeth") similar to those in Rosaceae, and *Trapa* has unique teeth having a double apex (Hickey, 1981, unpubl. data). Primary venation is pinnate, secondary venation most often brochidodromous, and tertiary venation obliquely and irregularly percurrent (Hickey & Wolfe, 1975). Stipules are present in nearly all families as rudimentary, either lateral or axillary, structures, the latter frequently dissected into several to numerous, small, finger-like projections (rarely long hairs). Ridges or wings of stems often end at the nodes in acute or acuminate tips, which should not be confused with stipules.

Branched sclereid idioblasts (foliar sclereids) are common in several families and tracheoids with spiral or annular wall thickenings are sometimes present. Schizolysigenous secretory cavities are present in the Psiloxylaceae and Myrtaceae. Hairs are sparse or lacking in some groups (e.g., Penaeaceae); when present, they are often unbranched, but especially in Melastomataceae are multicellular and complex, and in Combretaceae often form peltate or scale-like structures. Short, marginal hairs are present on the leaves in certain Onagraceae and Lythraceae. Stomata are anomocytic in most families but often anisocytic or polocytic in at least Onagraceae and Melastomataceae. Paracytic, procytic, and diacytic types also occur.

Inflorescences are variable but fundamentally derivable from an anthotelic primary condition (see Briggs & Johnson, 1979). Suppression or amplification explain diverse inflorescences. Derived are, for example, the racemes (often associated with zygomorphic flowers).

Flowers are usually bisexual, generally adapted to insect or bird pollination, actinomorphic or weakly (to rarely strongly) zygomorphic, mostly 4- or 5-merous although sometimes 3-, 6-, or pleiomerous, perigynous to epigynous or sometimes semi-epigynous, without, or more often with, short to long hypanthium (an expanded, cup-shaped floral tube or receptacle) (Bunniger, 1972; Bunniger & Weberling, 1968), bearing mostly on its rim calyx-lobes, petals, and stamens, some of which may be reduced or absent (filaments are often more or less free from the hypanthium in Lythraceae and some Combretaceae, however). Calyx lobes are green or colored, sometimes conspicuously carnose, rarely shed as a cap at anthesis. Petals are usually present, then mutually free, unguiculate to basally cuneate, mostly red, violet, white, or yellow. Petals, when 5, are mostly with convolute aestivation, but when 4, with decussate aestivation.

The androecium is haplo- or diplostemonous (sometimes superficially obdiplostemonous), or secondarily polyandrous with centripetal or, more rarely, centrifugal developmental sequence, in the latter case often in a few clusters developed from the same number of primordia, associated with trunk-bundles. Reduction in stamen number within isomerous whorls is rare. Stamens have narrow to relatively broad, terete or flat filaments and basifixed or dorsifixed anthers, in some families with a conspicuously enlarged, compact and capitate (Penaeaceae) to variably elongated connective, without or with appendages (many Melastomataceae). Anther dehiscence is mostly by longitudinal slits or, in certain Myrtaceae and most Melastomataceae, by apical pores. The tapetum is glandular and generally binucleate.

Pollen grains are mostly free (tetrads are present in genera of Onagraceae, however), basically 3-colporate, but rarely colpate or porate. In several families they are provided with conspicuous pseudocolpi alternating with the true apertures; more rarely, viz. in some genera of Lythraceae, with twice as many pseudocolpi as true apertures. Viscin threads arise from the pollen grains in nearly all Onagraceae (exception: *Circaea alpina* L.); this family also is more variable in aperture condition than the other families. Pollen grains are usually 2-celled when dispersed (cf. Tobe & Raven, 1984c).

An annular disc structure is often present around the style or ovary, inside the stamens (or hypanthium).

The pistil is syncarpous, consisting of two or more (frequently four or five) carpels and provided with one, two, or more locules, rarely with incomplete septa. The style (almost lacking in *Psiloxylon*) varies from apically branched (branches isomerous with carpels) to simple, with lobate to simple stigma, or with stigmatic areas rarely commissural and separate (as in some Penaeaceae; see below this family). The stigma is usually of the "dry" type (Heslop-Harrison & Shivanna, 1977), but at least in Melastomataceae and Onagraceae often of the "wet" type (Raven, pers. comm.). Placentation is mostly central and axile, or more rarely free-central (as in a few Lythraceae) or basal (as in most Penaeaceae) in the bi- to multilocular ovaries; parietal (as in a few Myrtaceae), or apical (as in all Combretaceae) in the unilocular ovaries.

Ovules are solitary to numerous per carpel, anatropous or rarely hemianatropous or campylotropous, crassinucellate, and generally bitegmic (unitegmic in some Myrtaceae). A primary parietal cell is cut off from the archesporial cell in all families studied (although this has not been verified satisfactorily for Myrtaceae). Embryo sac formation is mostly according to the *Polygonum* type, except in Penaeaceae (with the tetrasporic, 16-nucleate *Penaea* type), Onagraceae (with the monosporic, 4-nucleate *Oenothera* type), and Alzateaceae (with a bisporic, *Allium* type embryo sac; Tobe & Raven, 1984a). Endosperm formation is nuclear (but there is rapid endosperm nucleus degeneration in Trapaceae). The embryology of Myrtales has been reviewed by Tobe and Raven (1983a).

Fruits are most varied: capsules, berries, nuts, or samaras developed from superior or inferior ovaries.

The seed coat varies among the families of the order and tends either to have a fibrous exotegmen (i.e., outer layer of the inner integument) often combined with a sclerotic mesotesta (middle layer of the outer integument) or to lack a fibrous tegmen, then generally having a sclerotic mesotesta. Ripe seeds are generally without any or with a very thin layer of endosperm, this being used up during seed development. The embryo is variously differentiated, straight or more rarely curved or twisted, with anisocotyly in Trapaceae. The embryo stores fatty oils and aleuron in most families but does store starch in Trapaceae, and in some Myrtaceae and Melastomataceae.

Galli- and ellagitannins are normally present; flavonols (including methylated flavonols) are common, but flavones are rare or lacking. Proanthocyanins are present in some families. Triterpenes are common and triterpene saponins are present in at least some families. Various alkaloids are sporadically formed but are diverse and without great taxonomic significance. Cyanogenic compounds likewise are sporadically present in the order. Aluminum accumulation is conspicuous in at least three related families, and silica grains occur in certain Myrtaceae. Clustered or solitary crystals of calcium oxalate are commonly deposited in cells of the parenchymatous tissue; raphides are present in Onagraceae and rarely in Lythraceae. Iridoids, polyacetylenes, sesquiterpene lactones, glucosinolates, and benzylisoquinoline alkaloids are absent. Essential oils are present in secretory cavities in Myrtaceae.

Chromosome numbers tend to be multiples of 11 or especially 12 ($X = 12$ is considered a likely primary basic number by Raven, 1975), but show a considerable range of variation particularly in Onagraceae, Lythraceae, and Melastomataceae.

This description is valid for the Myrtales if restricted to the "core families": Onagraceae, Trapaceae, Lythraceae, Oliniaceae, Combretaceae, Alzateaceae, Penaeaceae, Rhynchocalycaceae, Crypteroniaceae, Memecylaceae, Melastomataceae, Psiloxylaceae, Heteropyxidaceae, and Myrtaceae. With this circumscription the Myrtales seem to be homogeneous, natural, and easily definable. If the order were expanded, as recommended by some taxonomists, to include Thymelaeaceae, Lecythidaceae, Haloragaceae, or Rhizophoraceae, it would require considerable modification in each case. These families, considered by some as serious candidates for inclusion in Myrtales, will be discussed in more detail near the end of this paper.

A Note on the Circumscription of the Families of Myrtales

For the purpose of the following account on distribution of character states, the following notes may be adequate.

The Onagraceae present no problems and are circumscribed and subdivided as by Raven (1979), comprising 17 genera of ca. 675 species distributed among seven tribes.

Trapaceae consist of the genus *Trapa* only.

The family Lythraceae is more widely circumscribed here than in most contemporary literature. It includes Punicaceae, with the genus *Puni-*

ca (Levin, 1980, treats one of the species in the segregate genus *Socotria*), and Sonneratiaceae, with the probably rather distantly related genera *Sonneratia* and *Duabanga*.

The Combretaceae here include Strephonemataceae (Venkateswarlu & Prakasa Rao, 1971), which consist of the single genus *Strephonema*. With the inclusion of the genus *Strephonema*, the Combretaceae (syn. Terminaliaceae) are circumscribed as in current works. The mangrove genera *Lumnitzera* and *Laguncularia* have probably adapted to their mangrove life by convergence.

Oliniaceae consist of the genus *Olinia* only.

Alzatea and *Rhynchocalyx*, which were treated in Crypteroniaceae by van Beusekom-Osinga and van Beusekom (1975), have here been excluded from this family and proved to be so distinct that they are each given family rank (Graham, 1984; Johnson & Briggs, 1984).

Penaeaceae (Dahlgren 1967a, 1967b, 1967c, 1968, 1971) consist of seven genera, *Endonema, Glischrocolla, Saltera, Sonderothamnus, Brachysiphon, Stylapterus,* and *Penaea*.

Crypteroniaceae, after the exclusion of *Alzatea* and *Rhynchocalyx*, consist only of *Crypteronia, Axinandra,* and *Dactylocladus*.

Memecyclaceae with some hesitation are here considered as distinct from Melastomataceae (by Dahlgren). It consists of six to eight genera, *Mouriri, Lijndenia, Memecylon, Votomita, Spathandra,* and *Warneckea*. *Pternandra* is also included, whereas the position of *Astronia* is doubtful.

Remaining are Psiloxylaceae (*Psiloxylon*), Heteropyxidaceae (*Heteropyxis*; Stern & Brizicky, 1958), and Myrtaceae, which are undoubtedly derivatives from the same ancestral stock. (Thorne considers *Heteropyxis* and *Psiloxylon* to represent subfamilies of Myrtaceae.)

DISTRIBUTION OF CERTAIN ATTRIBUTES IN THE FAMILIES OF MYRTALES AND SOME OTHER FAMILIES

The attributes discussed below and outlined as to their distribution in the myrtalean families and some allied families were selected on the basis of the following criteria:

(1) they are either characteristic of the order or part of the order and frequently mentioned as "key" attributes;

(2) most are reasonably well documented, although a few are not; and

(3) they do not exhibit complicated patterns in the order.

Some of the attributes are often neglected to a great extent but deserve inclusion with the others. The selection is somewhat limited and cannot claim to include all the most essential items, but is thought to be representative in some degree, and to give an indication of:

(1) distinctness of the order;

(2) relationship among families of the order; and

(3) degree of consistency of the attributes within families.

WOOD ANATOMY

As the wood anatomy is treated elsewhere in this symposium, by van Vliet and Baas, only a few remarks will be given here.

The core families of Myrtales are all characterized by the combination of bicollateral bundles (intraxylary phloem) (Fig. 1A) and vestured pits (Metcalfe & Chalk, 1950; van Vliet, 1978), a combination which is otherwise very rare in angiosperms and restricted to Thymelaeaceae (excl. Gonystyloideae), certain Euphorbiaceae, a few families of Gentianales, part of Vochysiaceae, and the genus *Centopodium* (= *Emex* pro parte) of Polygonaceae (van Vliet & Baas, 1984). Thymelaeaceae and Loganiaceae, which appear to some as closely allied to Myrtales, will be discussed later. For different reasons each family is considered by us as not directly related to Myrtales.

From a purely wood-anatomical point of view it is obvious (van Vliet & Baas, 1984; Baas & Zweypfenning, 1979) that *Punica* as well as *Rhynchocalyx* (treated here as Rhynchocalycaceae) could well be included in Lythraceae, whereas *Sonneratia* and *Duabanga*, usually treated as the Sonneratiaceae, in different (and not always the same) wood-anatomical respects deviate somewhat more from Lythraceae. Thus the homogeneity of the former Sonneratiaceae must be reconsidered; *Sonneratia* and *Duabanga* diverge also in other respects (see p. 663). On the collected evidence they are both included in Lythraceae.

Further, Crypteroniaceae and Memecylaceae largely differ from Melastomataceae in having distinctly bordered pits and in lacking fiber dimorphism, and Memecylaceae also for the most part have solitary vessels and included phloem, which is not the case in Melastomataceae. This is taken to support treating Crypteroniaceae, Melastomataceae, and Memecylaceae as distinct families.

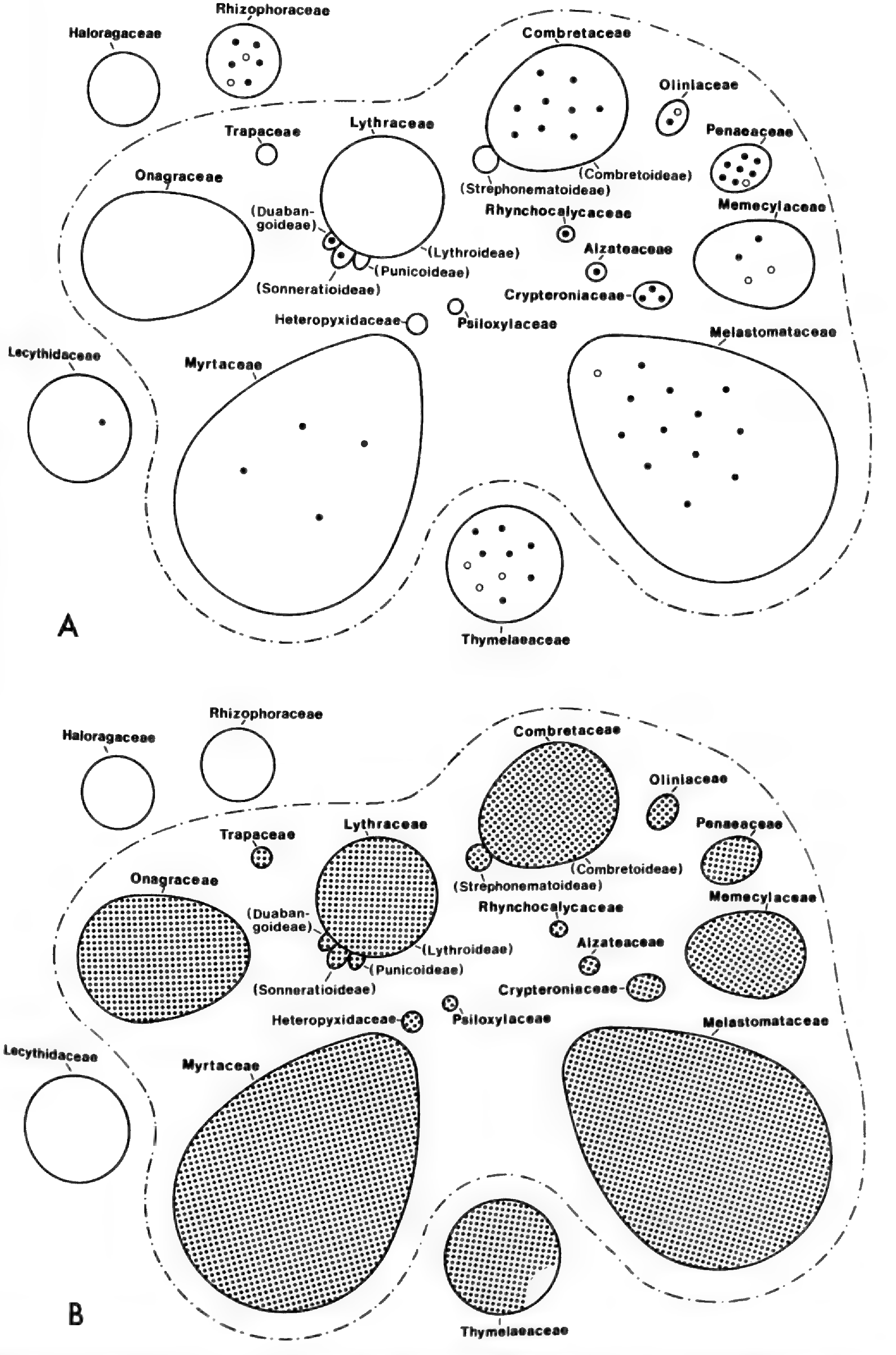


FIGURE 1. Distribution, in the myrtalean and some other families, of:—A. bicollateral vascular strands (dotting).—B. diffuse (●) and terminal (○) sclereids, according to Rao & Das (1979).

Strephonema differs from other Combretaceae in certain wood-anatomical respects, and *Psiloxylon* similarly differs from the Myrtaceae, supporting the treatment of these genera, which for other reasons have been claimed to form separate units, as separate families or, at least, as subfamilies.

Alzatea also appears to be out of place in Lythraceae as well as in Crypteroniaceae, and it now appears it should be placed in a separate family (cf. Graham, 1984). This treatment is supported by various wood-anatomical details.

These indications, all based largely on the data of van Vliet and Baas (1984), are important in the general considerations of rank, circumscription, and interrelationships.

Some trends of evolution in wood anatomy are of significance in the order. An example is the reduction of pit borders and the limitation of pits to the radial walls in the fibers, i.e., the evolution from fiber-tracheids to libriform fibers. This has occurred in Lythraceae (incl. *Punica, Duabanga,* and *Sonneratia*), and in Onagraceae (there are also other similarities between the Lythraceae and Onagraceae), Oliniaceae, Melastomataceae, and Combretaceae, and in many Myrtaceae. In this respect these groups are thus specialized.

On the whole, the differences between the Lythraceae (sensu stricto) and Onagraceae in wood anatomy appear to be conspicuously few. There also seems to be great concordance in wood anatomy between Strephonematoideae and most Myrtaceae. Some of these similarities, as pointed out by van Vliet and Baas (1984), are, most likely, due to retention of primitive features and thus do not form a sound basis for phylogenetic conclusions, but others are similarities of specialization and therefore can be phylogenetically important, although convergent evolution in some of these features has surely occurred.

SCLEREID IDIOBLASTS OR FOLIAR SCLEREIDS

Rao and Das (1979) have surveyed the occurrence of foliar sclereids in angiosperms. Leaf sclereids (Fig. 1B) are common in the Myrtales, and are reported in Lythraceae (rare), Sonneratiaceae, Oliniaceae, Alzateaceae, Penaeaceae, Crypteroniaceae, Memecylaceae, Melastomataceae, and Myrtaceae (rare). In some Lythraceae and in *Rhynchocalyx* (Rhynchocalycaceae) they are unbranched and restricted to the leaf petioles; whereas, in *Alzatea* (Alzateaceae) they are branched and present in the blades, this being possibly of some significance in the consideration of the distinctness of *Alzatea* in relation to Lythraceae. The presence of leaf sclereids in *Sonneratia* and *Duabanga* may also be noted in this context. In Penaeaceae, leaf sclereids are present in all the genera and have been described by Rao (1965) as well as by Dahlgren (1971).

Leaf sclereids are abundant and their shapes useful in the classification of species in Memecylaceae (Foster, 1946, 1947; Rao & Jacques-Félix, 1978; Bremer, 1979; Rao et al., 1980). Morley (1953) noted that the presence of terminal sclereids seems to be typical of this family, whereas their absence seems typical of Melastomataceae. Non-terminal sclereids do occur, however, in various Melastomataceae, e.g., *Plethiandra* (Rao & Bhattacharya, 1977).

In Crypteroniaceae, unbranched sclereids occur in leaf petioles in *Crypteronia* and *Dactylocladus,* but not in *Axinandra* (van Vliet & Baas, 1975). According to Keating (1982), Onagraceae lack foliar sclereids; their absence in the aquatic Trapaceae is expected. Within Myrtaceae, foliar sclereids are known to occur at least in *Angophora, Eucalyptus,* and *Syzygium* (Rao & Das, 1979).

Sclereids have not been recorded in Haloragaceae but are known to occur in several genera of Rhizophoraceae and Thymelaeaceae. Sclereids also occur in various taxa of Theales, perhaps not in the Lecythidaceae, but in Bonnetiaceae, for example, and in several genera of Theaceae sensu stricto. Furthermore, in Primulaceae, foliar sclereids are common, e.g., in *Dionysia* (Bokhari & Wendelbo, 1976, where sclereids are classified).

The presence of sclereids and their variation must not be overemphasized as a taxonomic criterion. Considered at large (Rao & Das, 1979), they give a very scattered picture in the angiosperm system. However, in isolated famlies they may be conspicuously plentiful or may be absent, and in such cases they may be of phylogenetic interest.

SIEVE-ELEMENT PLASTIDS

As is shown by Behnke (1984), all Myrtales yet studied have sieve-tube plastids with starch grains (S-type plastids) but without protein crystalloids (P-type plastids). The fact that the Rhizophoraceae have protein crystalloids, which are numerous, rectangular or variously 4(or 5)-angled, and of variable sizes (type PVc, sensu Behnke, 1981) may be taken as an indication that this family is not myrtalean. However, in dicotyledons a number of isolated families unexpectedly have P-type plastids of various shapes (Rhabdodendraceae, Cyrillaceae, Erythroxylaceae, Oxalidaceae, Connaraceae, Gunneraceae, Vitaceae, Buxaceae), a feature which may not, alone, be sufficient evidence for excluding them from orders with S-type plastids. Of the enumerated families, Erythroxylaceae are the family with the protein bodies most similar to those in Rhizophoraceae and Cyrillaceae, which should be considered in evaluating their phylogenetic relationships.

The fact that Myrtaceae, but not other Myrtales studied, contain crystalline protein in their sieve elements may indicate that they are somewhat isolated in the order.

PHYLLOTAXY

The most common condition in Myrtales is that the leaves are opposite. However, verticillate leaves occur in some genera, and the leaves are quite often disjunct-opposite or "scattered" ("alternate"), as in Psiloxylaceae, Heteropyxidaceae, many Myrtaceae, many Onagraceae (in the tribes Onagreae and Epilobieae), many Combretaceae (e.g., *Terminalia* and *Buchenavia*), and some Lythraceae. Whether in any of these families the leaves have truly spiral (disperse) phyllotaxy is not clear (see Johnson & Briggs, 1984).

To our knowledge all or nearly all taxa of Trapaceae, Oliniaceae, Alzateaceae, Penaeaceae, Rhynchocalycaceae, Crypteroniaceae, Memecylaceae, and Melastomataceae (exceptions, e.g., *Catantherea* and *Medinilla alternifolia* Blume) have truly opposite or verticillate leaves, although they can be disjunct-opposite in fast-growing young shoots. The leaf rosettes of Trapaceae consist of decussate leaf pairs.

Thymelaeaceae, often placed in Myrtales, have disperse or opposite leaves. Among other families sometimes associated with Myrtales, Rhizophoraceae generally, but not consistently, have opposite leaves; Haloragaceae sensu stricto have three genera with exclusively disperse, three with either disperse or opposite, one (*Haloragodendron*) with only opposite, and one (*Myriophyllum*) with chiefly verticillate leaves (Orchard, 1975). Dialypetalanthaceae have opposite, decussate leaves. Finally, Lecythidaceae consistently have disperse leaves. Elaeagnaceae have prevailingly disperse, but sometimes opposite, leaves.

STIPULAR STRUCTURES

(by F. Weberling, Ulm)

In contradiction of the classical opinion, nearly all families belonging to the Myrtales are characterized by the occurrence of stipules (Weberling, 1955, 1956, 1958, 1960, 1963, 1966, 1968). They seem to be lacking usually in the Melastomataceae, and generally so in Memecylaceae, where they occur, however, in at least some taxa of *Mouriri* (Fig. 14B).

In most cases the stipules are diminutive ("rudimentary") and subulate (Fig. 2C), reaching only rarely a length of several millimeters. In most families of the Myrtales stipules represent a rather constant vegetative characteristic, as in Lythraceae (incl. Punicaceae and Sonneratiaceae), Trapaceae, Myrtaceae, Psiloxylaceae, Oliniaceae, Penaeaceae, and Crypteroniaceae (and also in the possibly allied families Rhizophoraceae and Haloragaceae), whereas in the other families they are present in some genera only. In Onagraceae, stipules are characteristic of five relatively primitive tribes, Jussiaeeae (*Ludwigia*), Hauyeae (*Hauya*), Fuchsieae (*Fuchsia*), Lopezieae (*Lopezia*), and Circaeeae (*Circaea*), but are absent in two advanced ones, viz., Epilobieae and Onagreae. In Combretaceae rudimentary stipules could be found only in species of *Terminalia* and in *Buchenavia capitata* Eichl.; perhaps they are present in *Bucida buceras* L. and *Anogeissus leiocarpa* Guill. & Perr. as well.

The ontogeny of the stipules in Myrtales displays usual features in their development. They appear at a very early stage of the leaf development, forming lateral excrescences from the leaf-base (Fig. 2A, D, F). Their further growth shows a more or less pronounced prolepsis. Sometimes they grow so rapidly that they temporarily have nearly the length of the entire leaf (Fig. 2B) or they may even exceed the leaf in length (Fig. 2D). They also attain their final proportions a long time before the leaf-blade does. Thus stipules which are more or less flattened are able to serve as bud-scales, whereas stipules which function as glands contribute to bud-protection by covering the buds with their mucous secretions.

Outside Myrtales as circumscribed here, stipules are present in Haloragaceae. In the pinnate leaves of *Myriophyllum*, more or less complete stipules at the very base of the leaf can be ob-

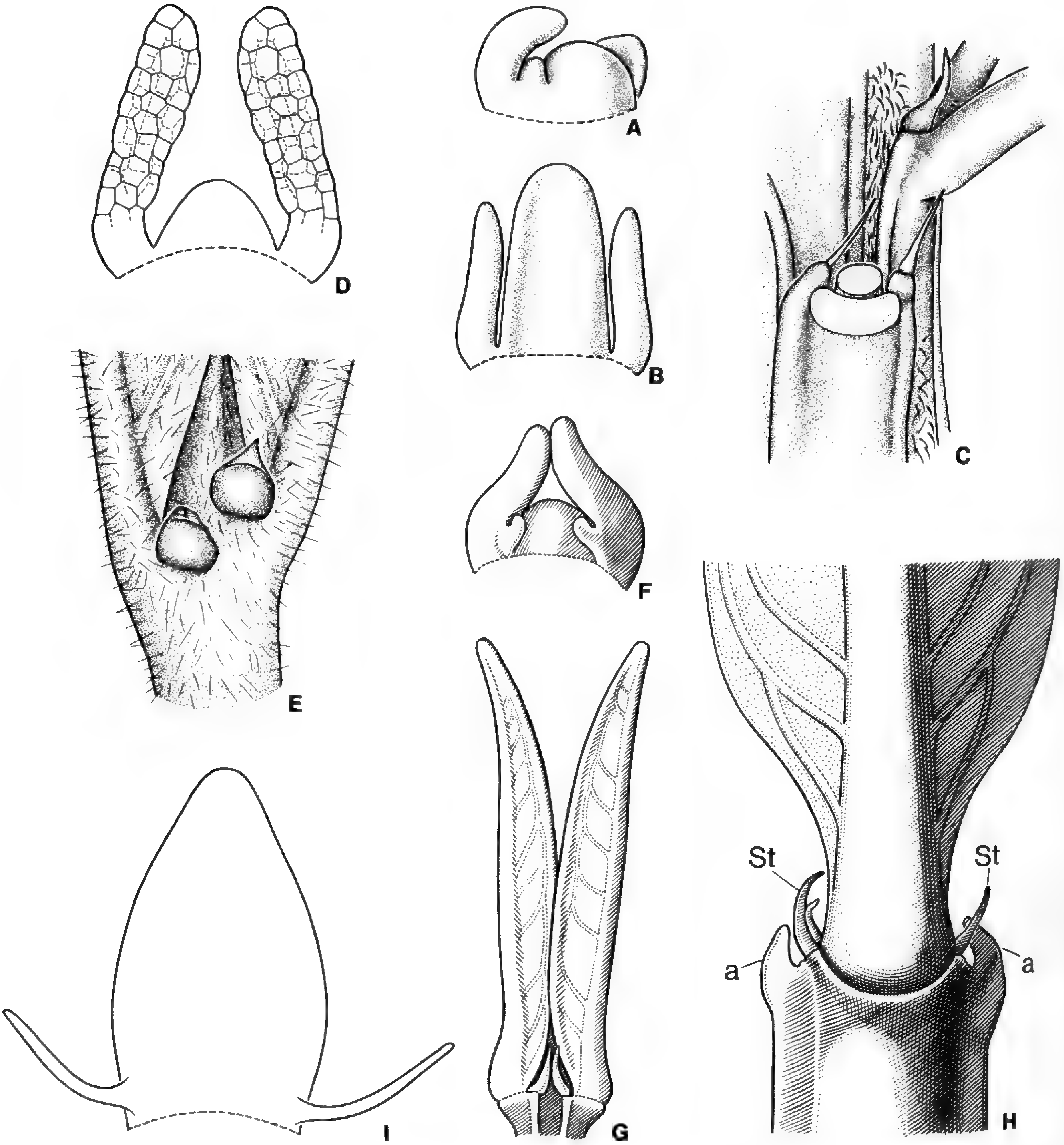


FIGURE 2. Stipules in the Myrtales. A–C. *Lopezia racemosa* Cav. (Onagraceae).—A. growing point with two leaf primordia, the larger one with primordia of stipules.—B. leaf primordium with stipules.—C. part of a stem bearing two leaf bases with stipules on the upper ends of ridges formed by the margins of decurrent leaves.—D. *Circaea lutetiana* L. (Onagraceae): leaf primordium with far developed stipules.—E. *Ludwigia* cf. *uruguayensis* (Camb.) Hara (Onagraceae): part of a stem with lower part of foliage leaves and stipules. F–I. *Punica granatum* L. (Punicaceae).—F–G. stages of leaf development.—H. base of young foliage leaf with decurrent wings ending in auricles (a) and rudimentary stipules (st)—I. cataphyll and stipules.

served. Above their insertion the formation of further leaflets still continues in a basipetal direction (Fig. 3G, H).

Commonly stipules are situated one on either side of the leaf axil. In this position they can be observed in *Lopezia* (Fig. 2C), *Ludwigia* (Fig. 2E), or in *Crypteronia* (Fig. 3C). In many taxa of Myrtales (e.g., many Myrtaceae and *Psiloxylon*), however, they form two or more minute, subulate, or club-shaped processes shifted somewhat deeper into the leaf axil on either side of the leaf-base (Figs. 2H, 3A) or two groups of minute processes forming a transverse row across the base of the petiole (Fig. 3F). The latter type has been reported for most genera of Lythraceae by Koehne (1884, 1893, 1903), though within

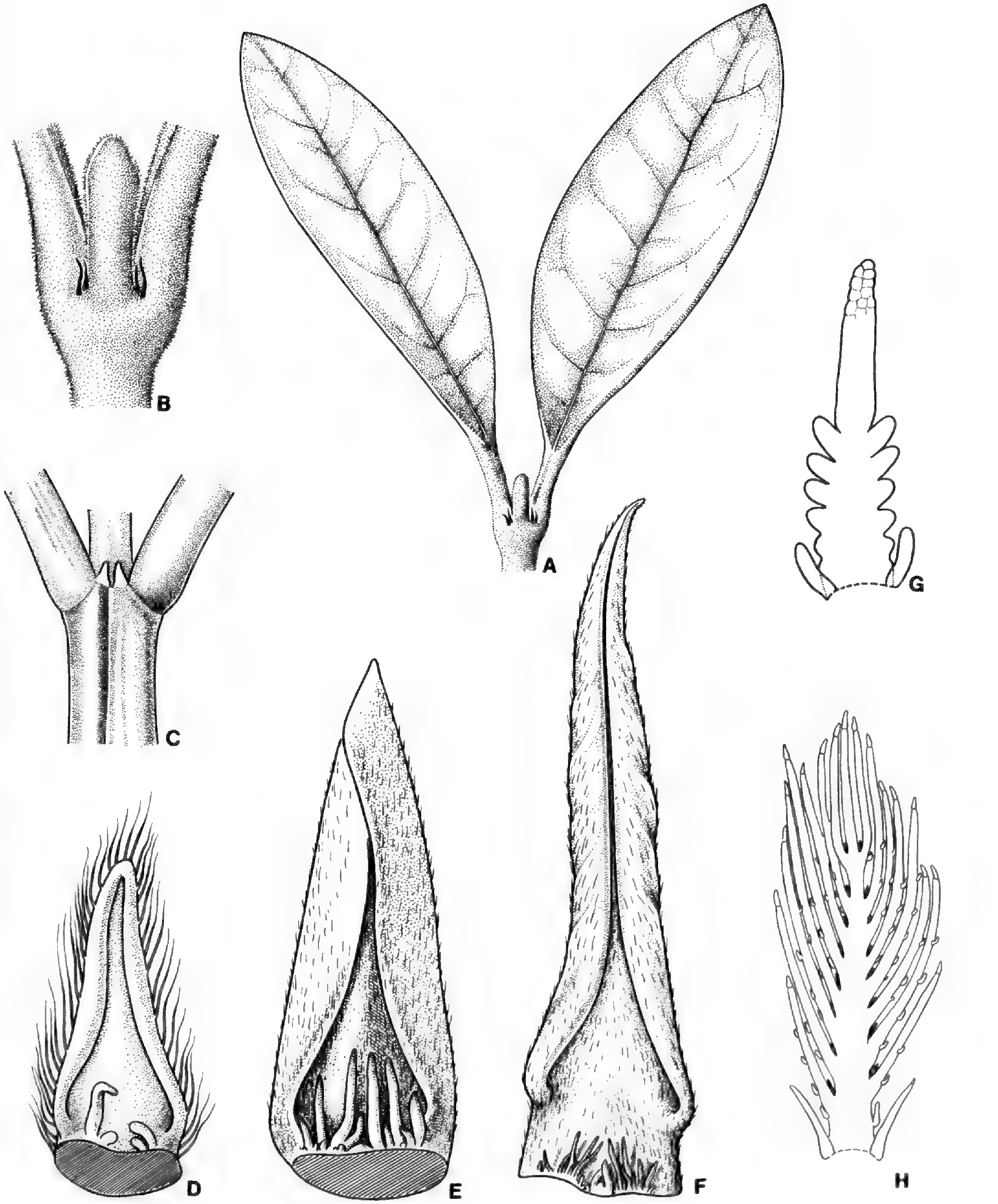


FIGURE 3. Stipules in myrtalean and some other families. A–B. *Feijoa sellowiana* Berg. (Myrtaceae).—A. opposite leaves with rudimentary stipules.—B. leaf bases in detail.—C. *Crypteronia leptostachys* Endl. (Crypteroniaceae); bases of oposite leaves with stipules.—D–F. *Terminalia catappa* L. (Combretaceae); different stages of leaf development (in D, 1.5 mm, in E, 3.5 mm, and in F, 10 mm long).—G–H. *Myriophyllum pinnatum* Britton (Haloragaceae); stages of leaf development, H representing a nearly fully developed leaf.

this family there are also taxa where leaves bear stipules in 'normal' position (e.g., *Lagerstroemia* and *Lawsonia*). Intrapetiolar rows of stipular processes also occur in Trapaceae, Penaeaceae, many Myrtaceae, and some Combretaceae (and also in Lecythidaceae). Continuous morphological lines of intermediary forms (two- or three-lobed stipules a.o.) between stipules in 'normal' number and position, and intrapetiolar rows of stipular processes indicate that the two groups of processes composing an intrapetiolar row are equivalents of two stipules. The same becomes evident from the study of their ontogeny (Fig. 3D–F). The dissection of the stipules may be a symptom of reduction. The displacement of stipular processes into the leaf axil probably is a result of an increased growth of the lower surface of the leaf-base.

In some Myrtales (*Punica granatum* L., Fig. 2F–H, *Lafoënsia microphylla* Pohl, *Lagerstroemia indica* L., *Penaea mucronata* L.) and the lecythidaceous *Napoleona talbotii* E. G. Baker, the stems are winged, apparently by the leaf-bases being decurrent (Fig. 2F, G). These wings are prolonged at their upper ends into auricles situated on either side of the leaf-insertion, like stipules, whereas the true stipules are subulate processes located somewhat deeper in the leaf axil (Fig. 2H).

In Rhizophoraceae, the Rhizophoroideae are characterized by large triangular to lanceolate interpetiolar stipules, whereas the genera of Anisophylleoideae differ by the alternate position of the leaves and the stipules being represented by a variable number of minute processes placed in the leaf axil.

Habitually, in the myrtalean families, stipules are present in connection with all leaves except the cotyledons. But in *Angophora* and *Eucalyptus*, genera in which the foliage leaves of all or most species are destitute of stipules, Carr and Carr (1966) found that the cotyledons of many species have rudimentary stipules. Johnson and Briggs (1984) report on stipules at the cotyledonary stage also in *Arillastrum*. The stipules can be two- or three-lobed or may be represented by several glandular processes situated on or near the margins of the leaf-base. The same is true for some other genera of Myrtaceae (*Leptospermum*, *Callistemon*, *Melaleuca*, etc.). Appendages which might be interpreted as rudimentary stipules have also been observed on the cotyledons in some species of *Ludwigia* (Dekker, pers. comm.). They are, however, missing on the cotyledons of other Onagraceae investigated, even those species in which the leaves are usually provided with stipules (Weberling, unpubl. data). Glandular minute stipules have been detected in the cotyledons of several Lythraceae, e.g., species of *Cuphea* and *Lythrum* (Weberling, unpubl. data).

In many Myrtales stipules also occur at the bases of the cataphylls (Fig. 2I) and at the bases of bracts. This fact indicates that cataphylls and bracts are of laminar origin (also confirmed by their venation).

OTHER LEAF CHARACTERISTICS

The leaves in Myrtales are normally simple and entire and have basically brochidodromous to eucamptodromous venation (Hickey, 1981; Hickey & Wolfe, 1975). In certain lines of evolution, i.e., most Melastomataceae and many Myrtaceae, there are several main secondary veins, which branch out from the base of the blade, with tertiary veins being transverse. The difference between the two families Memecylaceae and Melastomataceae is significant (but not altogether sharp), both types being probably secondary to a typical brochidodromous type. Further trends of venation patterns are demonstrated by Hickey (1981).

As regards marginal teeth, these occur in certain Onagraceae, viz., in the tribes Epilobieae and Onagreae, and also, although less conspicuously so, in some Lythraceae (Hickey, 1981), being in these families conspicuously similar, and of a "Rosoid" basic type with a broad, crater-like apical hollow: the "Fuchsioid" subtype. Another similarity (Hickey, 1981) is the presence on the leaf margins in taxa of the two families of short marginal hairs. Independent origin of both of these structures, the former of which is quite particular, seems to be unlikely, and thus we agree with Hickey that most likely they represent original attributes in the order.

In the Trapaceae (*Trapa*) the teeth have a "unique double apex" (Hickey, 1981), which is quite different from that in the families mentioned. Teeth also occur rarely in the genus *Sonerila*, Melastomataceae (e.g., in *Sonerila tenuifolia* Blume), where they may vary considerably in length (Carlo Hansen, pers. comm.). These teeth do not seem to be of the same kind as in Onagraceae or Lythraceae; their filiform apex may represent a trichome.

The phylogenetic significance of leaf-tooth types is discussed by Hickey and Wolfe (1975), who state that they often show great homogeneity in families, orders, and larger groups and that conclusions can be drawn from their distribution. The Rosoid teeth in some Myrtales, if they are a residual attribute, indicate a possible connection with the Rosales and other orders possessing such teeth, such as Rhamnales, Rutales, Sapindales, Cunoniales, Vitales, and Cornales.

The leaf teeth in Lecythidaceae are of the "Theoid" kind (Hickey & Wolfe, 1975) and so

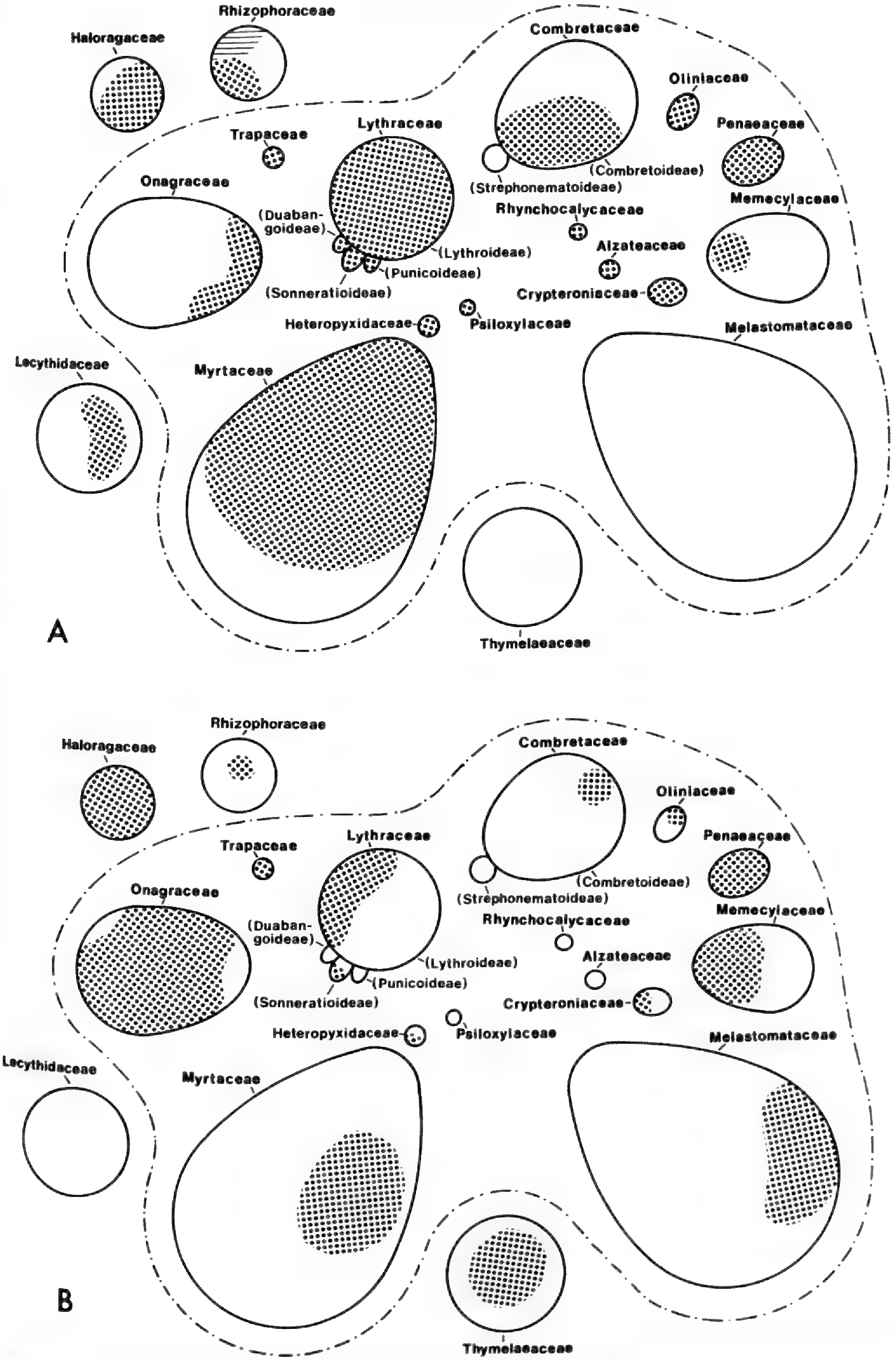


FIGURE 4. Distribution, in the myrtalean and some other families, of:—A. stipules, minute (dotting) or fairly large (hatching).—B. tetramery of perianth (dotting).

TABLE 1. Merous conditions in sepal and petal whorls in Myrtales and possibly related families.

	2-mery	3-mery	4-mery	5-mery	>5-mery
Onagraceae	(+)	(+)	+	(+)	(+)
Trapaceae	–	–	+	–	–
Lythraceae	–	–	+	(+)	+
Oliniaceae	–	–	(+)	+	–
Combretaceae	–	–	+	+	(+)
Alzateaceae	–	–	–	+	–
Penaeaceae	–	–	+	–	–
Rhynchocalycaceae	–	–	–	–	+
Crypteroniaceae	–	–	+	+	–
Memecylaceae	–	–	+	+	–
Melastomataceae	–	(+)	(+)	+	(+)
Psiloxylaceae	–	–	–	+	(+)
Heteropyxidaceae	–	–	–	+	–
Myrtaceae	–	–	(+)	+	(+)
Thymelaeaceae	–	–	+	+	(+)
Haloragaceae	(+)	(+)	+	–	–
Rhizophoraceae	–	(+)	+	+	(+)
Lecythidaceae	–	–	(+)	+	(+)
Elaeagnaceae	–	–	+	–	–

probably do not show connection with those in any myrtalean group.

MEROUS CONDITIONS OF PERIANTH

The merous conditions in sepal and petal whorls are shown in Table 1 and in Figure 4B.

The general trend in angiosperms is usually considered to be that an indefinite number of spirally set tepals, stamens, and carpels form the most primitive state; whereas 3-mery (as in Annonaceae, Aristolochiaceae, etc.) and 5-mery (numerous groups) evolve as secondary states, 4-mery mostly being considered as secondary to 5-mery. However, in the Myrtales 4- and 5-mery are both very common.

Merous conditions in perianth and androecium of the Myrtales have been discussed by Eyde (1977) in connection with the genus *Ludwigia*. This genus, unlike the other, almost consistently 4-merous Onagraceae, has a 5- or 6-merous perianth in a number of species. Eyde stated (1977: 653) that the "higher number of floral parts can occur in association with certain advanced features. For instance, in sect. *Oocarpon*, with 5-merous flowers, and in sect. *Oligospermum*, where 5-mery is the rule and 6-mery occasional, the higher numbers are linked with 1-seriate ovules and a specialized endocarp." Because *Ludwigia* represents a phyletic line separated early from the rest of Onagraceae, 5-mery or more may not be derived in the Onagraceae, although the prevalence of 4-mery in this family suggests that its immediate ancestors might have had 4-merous flowers.

Lythraceae are more or less evenly divided between genera with 4-merous and 6-merous flowers with respect to sepal, petal, and stamen number. However, the locule number is most often 2–4, which suggests that 4-mery is primitive in the family (provided ancestral Myrtales had isomerous floral whorls). Additionally, zygomorphic genera are 6-merous, a further evidence that 6-mery is derived. Not all specialized genera, however, are 6-merous. The aquatic and marsh annuals, *Ammannia* and *Didiplis*, are 4-merous. Pentamerous flowers are common only in *Decodon*. There is variation in merous conditions among populations within species in some genera, but the 4-merous or 6-merous state is clearly dominant in most instances (A. Graham & S. Graham, pers. comm.).

The merous conditions in myrtalean and some other families, somewhat generalized, are shown in Table 1. The commonest conditions are 4-mery and 5-mery. The great frequency of the former state is noteworthy since in most other dicotyledonous orders 5-mery is much more frequent. However, merous conditions are variable in Myrtales, and it is even rather typical in the larger (and some of the small) families that merous conditions vary from (2–)3 to 6 or more. An outgroup comparison combined with an appreciation of the merous conditions in the order indicates that 5-mery is likely to be ancestral, although 4-mery has arisen very early and probably, subsequently become dominant in several evolutionary lines.

Among families often associated with Myrtales, 4-mery is common in Thymelaeaceae and Rhizophoraceae, dominant in Haloragaceae and Elaeagnaceae, and the only condition in Dialypetalanthaceae; whereas, in Lecythidaceae it is rare. Tetramery in floral parts has often been a consideration in regarding most of these families as related to the Myrtales or members of the order in spite of the fact that it is probably not the ancestral state here.

INFERIOR, SEMI-INFERIOR, OR SUPERIOR OVARY

In the Myrtales the floral tube is either adnate to all or part of the ovary walls (epigynous and hemi-epigynous states respectively) or surrounds the ovary either tightly or loosely (perigynous states). The distribution of these states is shown in Table 2 and Figure 5A.

Because hypogyny and perigyny are considered to precede hemi-epigyny and epigyny and because several families are heterogeneous in this respect, it is obvious that adnation between floral tube and ovary has occurred in several evolutionary lines.

The floral tube (or hypanthium) is quite varied in length and may be short or long, and loose or tight around the ovary. Where it can be called a hypanthium, it bears on its edge sepals, petals, and frequently also one or two whorls of stamens or numerous stamens, although stamens can also be borne on the inner side of the hypanthium, or near its base.

In perigynous flowers of most Lythraceae, all the filaments are nearly or wholly free from the hypanthium. This condition may be considered either as an original state or as a separate, derived condition in relation to that where the filaments are inserted on the hypanthium edge. Exceptions are found in *Lawsonia,* where the stamens are inserted on the inner side of the hypanthium, and in *Sonneratia, Duabanga,* and some species of *Cuphea,* where they are inserted on or near its rim. The first two genera, often referred to Sonneratiaceae, thus deviate from most other Lythraceae in having the stamens inserted on the rim of the hypanthium. Also *Rhynchocalyx* (Rhynchocalycaceae), which is sometimes referred to Lythraceae, has the stamens inserted on the rim of the hypanthium.

In epigynous flowers of Myrtales a hypanthium continuing beyond the ovary is sometimes missing, as in *Ludwigia* (Onagraceae).

Within Myrtales the perigynous flower, found in most Lythraceae, and in all Penaeaceae, Rhynchocalycaceae, Alzateaceae, Psiloxylaceae, Heteropyxidaceae, Trapaceae, and in a great part of Melastomataceae but in very few Myrtaceae, is undoubtedly the ancestral condition. In Melastomataceae, there is a range of variation from perigyny to epigyny, and in Combretaceae the flowers are hemi-epigynous (*Strephonema*) or epigynous, and the immediate ancestors of each family must have had perigynous to hemi-epigynous flowers. Memecylaceae, Oliniaceae, Onagraceae, and most Myrtaceae have epigynous flowers. In each of them the epigynous condition apparently evolved early, but the ancestors of each family presumably had perigynous flowers, because other families to which they are closely related have representatives with perigynous flowers. Lythraceae, in which perigynous flowers are combined in various members with a number of other probable ancestral states, therefore take a central position in the order.

TABLE 2. Gynous conditions in Myrtales and possibly related families.

	Hypo/ perigyny	Hemi-epigyny	Epigyny
Onagraceae	–	–	+
Trapaceae	+	(+)	–
Lythraceae	+	(+)	(+)
Oliniaceae	–	–	+
Combretaceae	–	–	+
Alzateaceae	+	–	–
Penaeaceae	+	–	–
Rhynchocalycaceae	+	–	–
Crypteroniaceae	(+)	+	–
Memecylaceae	–	–	+
Melastomataceae	+	+	+
Psiloxylaceae	+	–	–
Heteropyxidaceae	+	–	–
Myrtaceae	(+)	+	+
Thymelaeaceae	+	–	–
Haloragaceae	–	–	+
Rhizophoraceae	(+)	(+)	+
Lecythidaceae	–	–	+
Elaeagnaceae	+	–	–

Among the families often associated with Myrtales, Elaeagnaceae and Thymelaeaceae have perigynous flowers. Rhizophoraceae exhibit a range of variation from perigynous to epigynous flowers, while Dialypetalanthaceae, Haloragaceae, and Lecythidaceae have epigynous flowers.

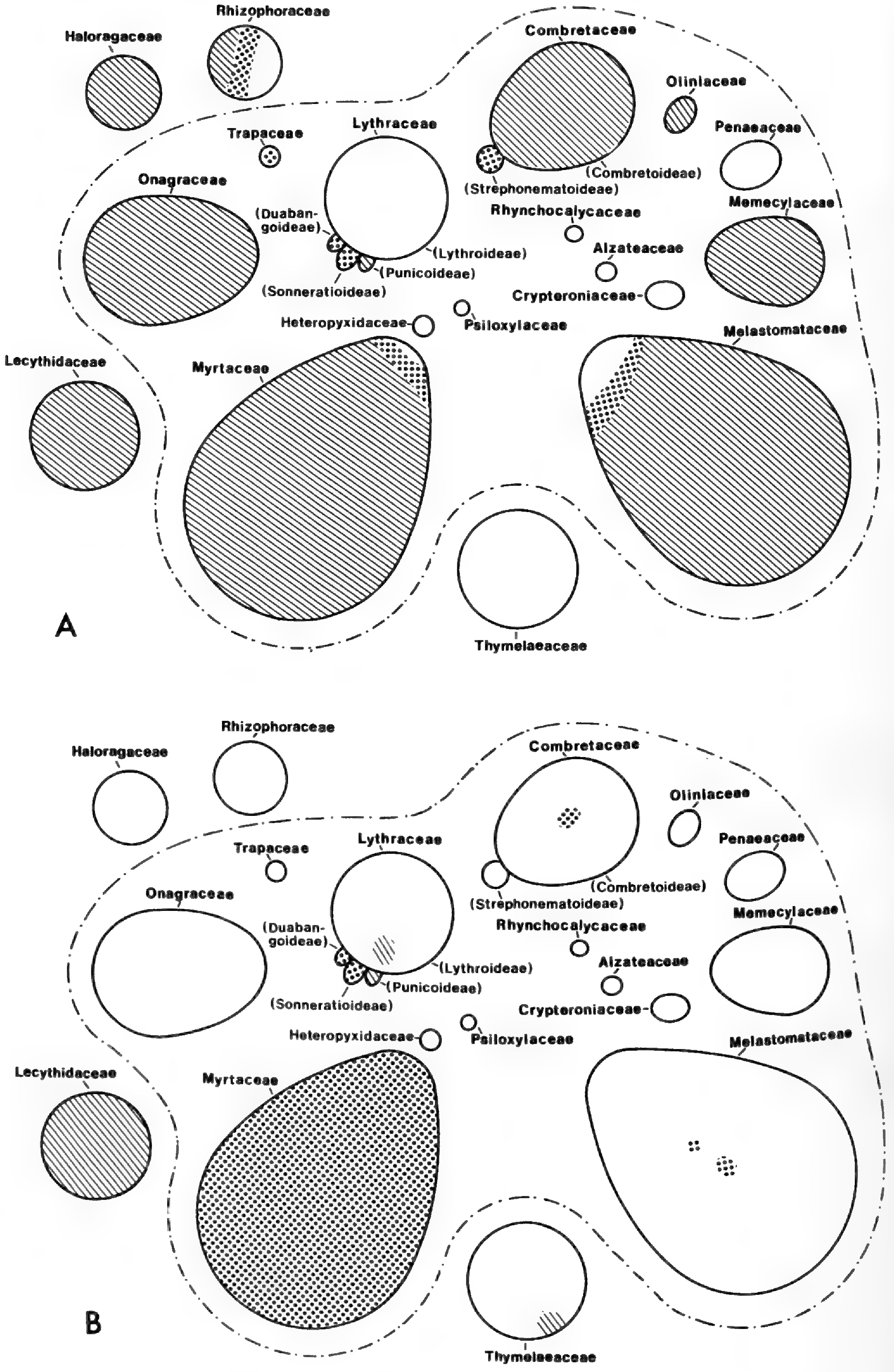
ONTOGENY OF FLORAL PARTS IN SOME MYRTALES

In a study of the ontogeny of the flower in representatives of Lythraceae (incl. *Punica*), Onagraceae, and Myrtaceae, Mayr (1969) found the following features:

The histogenesis of the organs of the flower shows different participation of cell layers, the relative number of cells in the basal level of the primordia being the critical factor.

In Myrtaceae the sepals and petals are more or less simultaneous in ontogeny but in Lythraceae (also in *Punica*) and Onagraceae the petals develop considerably later than the sepals.

The "epicalyx" found in many Lythraceae (see


Rhizophoraceae
Haloragaceae
Combretaceae
Oliniaceae
Trapaceae
Lythraceae
Penaeaceae
(Combretoideae)
(Strephonematoideae)
Onagraceae
Rhynchocalycaceae
Memecylaceae
(Duabangoideae)
(Lythroideae)
Alzateaceae
(Punicoideae)
(Sonneratioideae)
Crypteroniaceae
Heteropyxidaceae
Psiloxylaceae
Melastomataceae
Lecythidaceae
Myrtaceae
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Thymelaeaceae
Rhizophoraceae
Haloragaceae
Combretaceae
Oliniaceae
Trapaceae
Lythraceae
Penaeaceae
Onagraceae
(Combretoideae)
(Strephonematoideae)
Rhynchocalycaceae
Memecylaceae
(Duabangoideae)
(Lythroideae)
Alzateaceae
(Punicoideae)
(Sonneratioideae)
Crypteroniaceae
Heteropyxidaceae
Psiloxylaceae
Melastomataceae
Lecythidaceae
Myrtaceae
B
Thymelaeaceae

Fig. 8G) is interpreted as processes from the congenitally fused sepals (comparable to commissural stigmas). The position of Coridaceae, which is similar in this respect, is discussed on p. 686.

In androecia with numerous, bundled stamens, the organogeny of the stamens within the bundles is centripetal in Myrtaceae but centrifugal in *Lagerstroemia* and *Punica* of the Lythraceae.

The androecium of all taxa with two whorls of stamens is actually diplostemonous. Where it appears obdiplostemonous (as in Onagraceae), this condition depends on primary differences in size and secondary displacement in the course of growth.

Some Onagraceae have commissural stigmas (which is also the case in *Penaea* and *Stylapterus* of the Penaeaceae; see under this family below, and Dahlgren, 1967a, 1968).

Mayr (1969) concluded that, among the families investigated, Myrtaceae stand apart from the other three in several important details.

MERY AND DEVELOPMENTAL SUCCESSION IN ANDROECIA

In the Myrtales, diplostemony is no doubt basic.

Haplostemony occurs in Trapaceae, Oliniaceae, Alzateaceae, Penaeaceae, and Rhynchocalycaceae, and in disparate genera of Lythraceae and Melastomataceae, a few genera of Combretaceae and Onagraceae, two genera (*Crypteronia* and *Dactylocladus*) of three in Crypteroniaceae, and (as a case of reduction in a polystemonous whorl) in at least *Myrrhinium* of Myrtaceae. In Combretaceae, the flowers in *Meiostemon* and *Thiloa* as well as in one species of *Terminalia* are regularly haplostemonous, one species of *Thiloa* having staminodia representing the second whorl; in *Conocarpus* the androecium is sometimes reduced from ten stamens to varying numbers down to five by abortion (Stace, pers. comm.). In Onagraceae, *Circaea, Lopezia,* some species of *Clarkia* and *Ludwigia,* and one species of *Camissonia* have haplostemonous flowers (Eyde, 1977), all these cases being no doubt secondary in relation to diplostemony. In Melastomataceae, haplostemonous androecia are in the minority but are scattered in a number of genera.

It is also fairly obvious that in Lythraceae there have been both reduction and multiplication of stamen number from a diplostemonous condition. Reduction has occurred either as loss of episepalous stamens (*Orias, Lawsonia, Capuronia*), or episepalous stamens (*Tetrataxis, Diplusodon, Galpinia, Pleurophora*). Multiplication has occurred by increase in the epipetalous whorl (*Ginoria, Lagerstroemia*) or increase in the episepalous stamens (*Diplusodon*). Although the evolutionary relationships among the genera are not clear, it does appear that the loss or gain of staminal whorls has occurred independently more than once in Lythraceae and both loss and gain can occur within a single genus. An interesting staminal feature in Lythraceae is that stamens are often of two distinct lengths, with the episepalous ones always longest. (All this according to A. Graham & S. Graham, pers. comm.)

The occurrence of numerous stamens in certain Myrtales, as in other orders, such as Malvales, Theales, Caryophyllales (Chenopodiales), and Loasales, is no doubt a derived condition that has evolved from a diplo- or haplostemonous state (Leins, 1964), providing greater pollen production, especially in large flowers. This does not mean that the original ancestors of the angiosperms could not have had an indefinite number of stamens, which most likely were spirally arranged.

Much emphasis has been laid on the developmental sequence (initials or anthesis, according to authors) of stamens in polyandrous taxa, i.e., whether the groups of stamens develop centrifugally or centripetally. Leins (1964) distinguished three groups for their subdivision, but there must be many more than three evolutionary lines for polymerous androecia. Cronquist (1968) and Takhtajan (1969) have laid much stress on whether orders have centripetal or centrifugal androecial development, and Merxmüller and Leins (1971) have further elucidated the occurrence and taxonomic significance of these types. Multistaminal androecia have surely evolved secondarily in independent lines, examples being the Capparales (Capparaceae), Car-

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FIGURE 5. Distribution, in the myrtalean and some other families, of:—A. perigynous (blank), hemi-epigynous (dotting), and epigynous (hatching) flowers.—B. multistaminate androecia with centrifugal (hatching) and centripetal (dotting) developmental succession.

yophyllales (Aizoaceae, Cactaceae), Loasales (Loasaceae), Theales (several families), Thymelaeales (Thymelaeaceae: *Gonystylus*), Malvales (several families, e.g., Tiliaceae, Sterculiaceae, Malvaceae), Violales (independently from the preceding?: various Flacourtiaceae, Begoniaceae, etc.), perhaps also (?) Rosales (Chrysobalanaceae: *Couepia*), and Myrtales. In Rosales, the stamens are generally arranged in several whorls which tend to have stamens in a multiple number of that in the perianth whorls, and Chrysobalanaceae may not belong here. Also in palms, the stamens, no doubt, have increased secondarily in number, with different developmental sequences as a result (Uhl & Moore, 1980). A similar condition occurs in Velloziaceae; and in Alismataceae a secondarily multistaminal condition develops from initials superposed on the primary fewer ones, resulting in numerous whorls of stamens (Sattler & Singh, 1978, and other papers).

It seems that what is taxonomically important is not the developmental direction in itself but rather along which evolutionary lines these androecia evolved, i.e., whether the multistaminal condition in various Myrtales has evolved along the same lines or not. Within Myrtales there are families with multistaminal as well as diplo- and haplostemonous androecia, e.g., Lythraceae, Myrtaceae, Melastomataceae, and Combretaceae. There seems thus to be a general tendency, within the order, for reduction as well as multiplication of stamens.

There is some regularity in the distribution of these secondarily multistaminal androecia and their initiation. Those of Myrtales are generally known to be centripetal, but Mayr (1969, see above) observed that *Punica* and *Lagerstroemia* (Lythraceae) have centrifugal development, as in most Lecythidaceae and various other Theales (see Fig. 5B).

Within Melastomataceae, the genus *Astrocalyx* may have up to ca. 65 stamens per flower, and in *Plethiandra* the stamens may be 20–30 in number. The developmental sequence of the stamens in these genera has apparently not been studied.

Diplostemony seems to be basic in Myrtales and wide-spread in the order, occurring in several of the larger families: Lythraceae, Combretaceae, Melastomataceae, and Onagraceae.

POLLEN FEATURES, PARTICULARLY OCCURRENCE OF PSEUDOCOLPI

Pollen morphology of Myrtales and possible allied groups is described separately in this symposium by Patel et al. (1984); hence we restrict ourselves to some general comments. The pollen grains in the core families of this order seem to be basically 3-colporate, although two to more than five apertures have been reported. Further the pollen grains are basically tectate and frequently characterized by pseudocolpi (intercolpate furrows or "rugae," sensu Erdtman, 1952). The pseudocolpi are not actual apertures but conspicuously colpus-like thin parts of the exine. In their early ontogeny they differ from true apertures by *not* being subtended by a thick layer of intine (Thanikaimoni, pers. comm.). Pollen tetrads occur in some groups, especially in Onagraceae, where another peculiarity, the occurrence of viscin threads, is a characteristic feature.

Pseudocolpi (Fig. 6) are recorded in the families Lythraceae, Oliniaceae, Combretaceae, Penaeaceae, Rhynchocalycaceae, Crypteroniaceae, Memecylaceae, and Melastomataceae (incl. Memecyloideae) but are absent (or very indistinct) in many Lythraceae (see below, incl. the Punicoideae, Sonneratioideae, and Duabangoideae), Trapaceae, Alzateaceae, Psiloxylaceae, Heteropyxidaceae, Myrtaceae, and Onagraceae. More or less distinct intercolpate depressions in the pollen grains connect the distinctly heterocolpate pollen grains with other types and make the feature somewhat vaguely defined. However, presence of pseudocolpi is so significant in Myrtales, and so rare outside the order, that we attach great phylogenetic significance to its distribution. The significance of pseudocolpi in the Crypteroniaceae (as circumscribed by van Beusekom-Osinga & van Beusekom, 1975), i.e., in the genera *Crypteronia, Dactylocladus, Axinandra, Alzatea,* and *Rhynchocalyx,* was elucidated, for example by Muller (1975). He found *Alzatea* to differ from the others in lacking pseudocolpi, thus contributing toward recognition of the heterogeneity of the family in that circumscription.

The relatively homogeneous family Lythraceae, however, shows great variation in the occurrence of pseudocolpi (see also Patel et al., 1984). Thus according to Erdtman (1952), Campos (1964), and S. Graham (pers. comm.), Lythraceae generally possess 3-colporate pollen grains (in *Lafoënsia* oracolpoidate, Campos, 1964). Nine genera have pseudocolpi, according to S. Graham (pers. comm.). In *Lythrum,* at least there are three pseudocolpi alternating with the three apertures, but in *Ammannia, Crenea, Ginoria,* and *Nesaea* there are six pseudocolpi, two pseudocolpi being present between two successive apertures. Fifteen other genera (according to

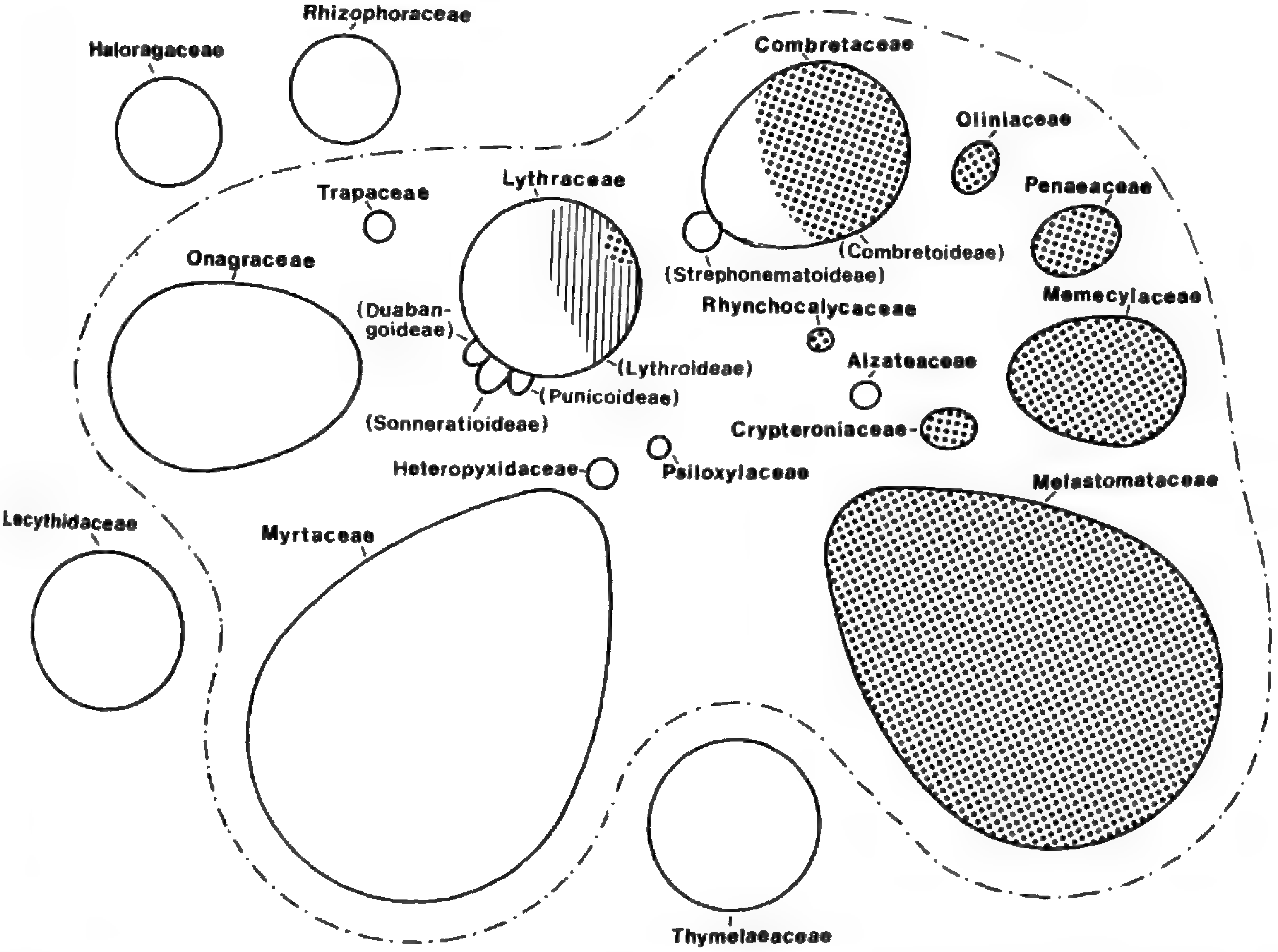


FIGURE 6. Distribution, in the myrtalean and some other families, of pollen grains without (blank) pseudocolpi, with pseudocolpi isomerous with apertures (dotting) and with pseudocolpi double the number of apertures (hatching).

S. Graham, pers. comm.), such as *Adenaria, Cuphea, Diplusodon, Galpinia, Lafoënsia, Lagerstroemia, Pemphis, Pelurophora, Physocalymma,* and *Woodfordia,* lack pseudocolpi. *Rotala* (Campos, 1964) may have incipient (or rudimentary!) pseudocolpi: "*R. ramosior* marquerait le passage entre les pollen tricolporés et héterocolpés" (Campos, 1964: 306). Here, as well as in the pollen grains of *Lafoënsia,* where the pseudocolpi are very faint, these could be interpreted either as incipient or reduced. A study of the lythraceous pollen morphology may indicate that (distinct or faint) pseudocolpi seem to occur in derived genera (A. Graham & S. Graham, pers. comm.), although this is not clear. In variation of occurrence and number of pseudocolpi (relative to apertures), Lythraceae are outstanding in the order, and it may be argued whether absence of pseudocolpi represents an original or (by secondary loss) an advanced state.

Sonneratia and *Duabanga* have angulo-aperturate pollen grains with short colpi (Muller, 1969, 1978). Distinct pseudocolpi are lacking, but in *Sonneratia* intercolpate depressions resembling pseudocolpi may occur. According to Erdtman (1952) the pollen grains resemble those in *Diplusodon* of the Lythraceae, and Muller (1981) reports a pollen type, *Florschuetzia trilobata,* from the Oligocene and Miocene of Borneo, that combines lythraceous and sonneratiaceous characteristics. Also the pollen grains in *Punica* resemble those in other Lythraceae. They are 3- (or rarely 4-) colporate and likewise lack pseudocolpi.

Whether the very characteristic pollen grains in Trapaceae, with three meridional crests of folded exinous material meeting at the poles, represent a heterocolpate type or rather a type with pronounced intercolpate depressions, needs to be verified.

The heterocolpate pollen grain types thus do not represent a distinct category. They include very peculiar shapes, such as that in Oliniaceae, where the pseudocolpi are restricted to one hemisphere (Patel et al., 1984).

Nevertheless, there is evidence from this attribute, as from others, that the families or subfamilies with clearly heterocolpate pollen grains form a coherent group, along with some others, where pseudocolpi are absent or at least very indistinct (Lythraceae subfam. Punicoideae, Duabangoideae, and Sonneratioideae, Combretaceae subfam. Strephonematoideae and Alzateaceae) or where pseudocolpi are missing or "doubled" in number (Lythraceae subfam. Lythroideae).

Pseudocolpi, aside from Myrtales, are known only in Ehretioideae (Boraginaceae pro parte) and a few Fabaceae (Leguminosae) (Skvarla, pers. comm.), and the tendency to have pseudocolpi is not likely to have evolved independently in more than one line within Myrtales.

Pseudocolpi are absent in Psiloxylaceae, Heteropyxidaceae, Myrtaceae, and Onagraceae. The first three families are fairly homogenous. They have (2–)3(–4) apertures and are mostly triangular, angulaperturate, very often syncolp(or)ate, with thin exine, and with a psilate to faintly patterned, scabrate surface (Schmid, 1980). The syncolp(or)ate pollen grains of *Psiloxylaceae* as well as *Heteropyxidaceae* strongly resemble those in many Myrtaceae (Schmid, 1980). We agree with Johnson and Briggs (1984) that this strongly supports the assumption that syncolp(or)ate pollen grains occurred in the common ancestor of these three families.

The Onagraceae are palynologically very distinct in the order. The pollen grains are noteworthy by the often triangular shape with three or more protruding, "papillose" apertures, the mechanism of tetrad cohesion (Skvarla et al., 1975), and the fine structure of the exine, in particular the ektexine, which is granular, "beaded," delicately branched, etc. (Skvarla et al., 1976), and especially by the constant presence of viscin threads (Skvarla et al., 1978), matched only in two other angiosperm families, viz., Ericaceae and Fabaceae. The relative number per pollen grain and the surface structure of these threads are variable in Onagraceae and supply some characters of interest for the division of the family. It can be claimed that the character-states associated with the pollen grains in Onagraceae along with many other distinctive features indicate that the family was differentiated early from ancestral Myrtales. At any rate, the exine structure as well as the pollen grain shape and apertures of the Onagraceae seem to have their closest resemblance in Myrtaceae (Nowicke, pers. comm.), Psiloxylaceae, and Heteropyxidaceae.

Muller (1981) in his review of fossil pollen of angiosperms noted that probably myrtaceous pollen (*Myrtaceidites*) is known from Santonian and Maestrichtian (Cretaceous) of Gabon and Colombia, and that onagraceous pollen (cf. *Epilobium* type) are also known from the Maestrichtian, whereas the earliest heterocolpate types so far known date from upper Eocene (Tertiary). The latter, *Heterocolpites*, are perhaps combretaceous, although similar ones have been claimed to be melastomataceous.

With due consideration given to the yet incomplete knowledge of fossil pollen and to the uncertainty of pollen identification, the above information may indicate an earlier differentiation of the Myrtaceae and Onagraceae pollen types than the heterocolpate ones (cf. the evolutionary discussion on pp. 680–681).

None of the families outside Myrtales, showing considerable similarities to them, possess pseudocolpi, but the tricolporate general pattern in Rhizophoraceae is of the basic type found in the Myrtales (Lythraceae pro parte, Alzateaceae), whereas the pollen grains in Lecythidaceae vary from colpate to colporate (via "colporoidate" transitions, Erdtman, 1952).

The porate pollen grains of Haloragaceae (see below) and Thymelaeaceae are different and indicate that these families are not allied with the Myrtales.

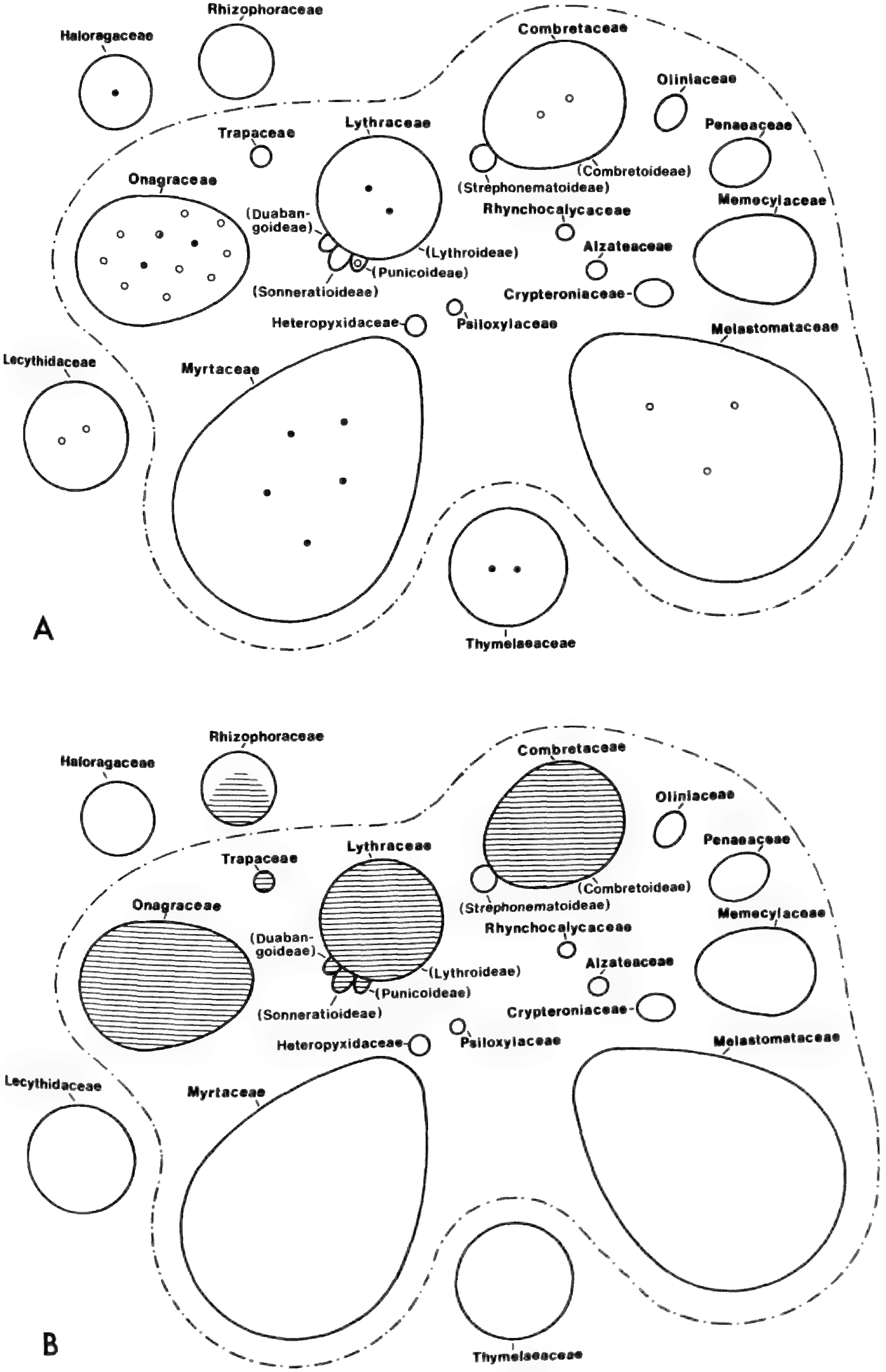
EMBRYOLOGICAL FEATURES

The main features of embryology of most of the core families of Myrtales, with a number of exceptions mentioned below, are rather uniform (Davis, 1966; Mauritzon, 1939; Schmid, 1984; Schnarf, 1931; Tobe & Raven, 1983a; Wunderlich, 1959). The most extensive presentation of myrtalean embryology is that of Mauritzon (1939). The basic pattern is as follows (see also Table 1 in Schmid, 1984; Tobe & Raven, 1983a):

The anthers are tetrasporangiate, the endothe-

→

FIGURE 7. Distribution, in the myrtalean and some other families, of:—A. dry (●) and wet (○) stigma types, according to Heslop-Harrison & Shivanna (1977).—B. seed coats with fibrous exotegmen (hatching) according to Corner (1976).


Haloragaceae
Rhizophoraceae
Combretaceae
Oliniaceae
Penaeaceae
Trapaceae
Lythraceae
Onagraceae
(Combretoideae)
(Strephonematoideae)
Memecylaceae
Rhynchocalycaceae
(Duaban-goideae)
(Lythroideae)
Alzateaceae
(Punicoideae)
(Sonneratioideae)
Crypteroniaceae
Heteropyxidaceae
Psiloxylaceae
Melastomataceae
Lecythidaceae
Myrtaceae
A
Thymelaeaceae
Haloragaceae
Rhizophoraceae
Combretaceae
Oliniaceae
Penaeaceae
Trapaceae
Lythraceae
(Combretoideae)
Onagraceae
(Strephonematoideae)
Memecylaceae
Rhynchocalycaceae
(Duaban-goideae)
(Lythroideae)
Alzateaceae
(Punicoideae)
Crypteroniaceae
(Sonneratioideae)
Heteropyxidaceae
Psiloxylaceae
Melastomataceae
Lecythidaceae
Myrtaceae
B
Thymelaeaceae

cium develops fibrous thickenings, the tapetum is glandular, cytokinesis is simultaneous, and the pollen grains are bicellular when shed.

The ovules are anatropous, or in various taxa hemianatropous or campylotropous. They are nearly always bitegmic and always crassinucellate. The micropyle is nearly always formed by both integuments.

Mauritzon (1939) noted a peculiarity, namely that in some species of *Combretum* and in *Trapa*, one or both integuments ceased to grow in certain parts, being then replaced by chalazal tissue; this was also observed in *Phaleria* of Thymelaeaceae and also occurs in Myristicaceae.

The integuments of most Myrtales are two-layered at the time of fertilization, but in Oliniaceae, Trapaceae, some Combretaceae, some Onagraceae, and *Cuphea* and *Punica* of Lythraceae, the outer integument consists of more layers. In contrast, both integuments of Lecythidaceae and Rhizophoraceae are made up of several cell layers (Mauritzon, 1939). Lecythidaceae are also peculiar in that the two integuments gradually fuse into one. In Myrtaceae, there may be total fusion into one single integument in a couple of genera.

A primary parietal cell is cut off from the archesporial cell in probably all Myrtales, a difference from the Lecythidaceae, where this is not the case. In addition, at the time of fertilization the nucellus is generally partly intact in the core families of Myrtales, whereas in the genera of Lecythidaceae and Rhizophoraceae studied, the whole nucellus between embryo sac and epidermis is destroyed at this stage. The epidermis may or may not divide periclinally to form a nucellar cap. Embryo-sac formation, with important exceptions (see below), conforms to the *Polygonum*-type. The synergids are usually hooked, and the antipodals are mostly ephemeral [a fact that according to Tischler (1917) implies a weakening of the basal part of the embryo sac, and thus perhaps a first step leading to the *Oenothera*-type of embryo-sac formation found in Onagraceae, which lack antipodals]. Endosperm formation is always initially nuclear. Embryogeny conforms to the Onagrad, Asterad (occasionally), or Solanad types. In the mature seed all or nearly all of the endosperm has been consumed and the embryo occupies most of the space.

The exceptions from the above pattern are notable:

Lythraceae conform well to the ordinal pattern of embryology. A uniseriate or, less commonly, a multiseriate suspensor is present in the embryo (Joshi & Venkateswarlu, 1935a, 1935b, 1936; Joshi, 1939). The occurrence of two nucelli within the same ovule has been reported in several cases (species of *Cuphea, Lagerstroemia,* and *Nesaea*). The archesporium is multicellular as noted by Joshi and Venkateswarlu (1936). Mauritzon (1934, 1939) found *Cuphea* to deviate from the other genera in the structure of ovule and nucellus; also *Lagerstroemia* was found to be peripheral; Mauritzon (1939) found *Punica* to be quite similar embryologically to *Lagerstroemia*. Also *Sonneratia* and *Duabanga* agree in the main features to other Lythraceae (Venkateswarlu, 1937; Mauritzon, 1939; Johri et al., 1967). The inner integument in *Duabanga* increases in thickness apically to form a considerable tissue, but this has not been reported in *Sonneratia*.

Trapaceae (Ram, 1956; Trela-Sawicka, 1978) are peculiar in their embryology. The ovule has a long nucellar beak and thus no ordinary micropyle. The endosperm may not be formed at all if the primary endosperm nucleus moves to the base of the embryo sac and degenerates (Ram, 1956), or it is very restricted if the primary endosperm nucleus undergoes only one or two divisions (Trela-Sawicka, 1978) to form a few free endosperm nuclei, which degenerate before development of the embryo starts. The nutritive function of the endosperm of *Trapa natans* L. is taken over by the suspensor and nucellus, which in early stages consist of cells with dense cytoplasm; later, suspensor and nucellus cells undergo endomitotic polyploidization (Trela-Sawicka, 1978). Embryogeny in *Trapa* conforms to the Solanad-type, and the embryo haustorium is long, coiled, and multiseriate. One cotyledon is also suppressed, the other being fleshy and filled with starch grains (starchy embryos also occur, for example, in some Myrtaceae). The anther tapetum becomes irregularly two-layered and its cells become multinucleate with frequent nuclear fusions.

Oliniaceae (Mauritzon, 1939; Rao & Dahlgren, 1969) have hemianatropous to campylotropous ovules but otherwise conform well with the myrtalean basic pattern, although data are not known for several embryological features.

In Combretaceae several genera, including *Combretum* and *Quisqualis*, have plasma-rich, papillate cells that connect the stylar canal with the micropyles of the ovules and seem to supply nutrients to the pollen tubes. Thus they function as an obturator and correspond to the obturator of Thymelaeaceae. Mauritzon (1939) found tetrasporic, 16-nucleate embryo sacs of the *Peperomia*-type, rather similar to those of the *Penaea*-type (see below), in two species of *Combretum,* but the studies by Fagerlind (1941) on *Quisqualis* and by Venkateswarlu and Prakasa Rao (1972) on several genera, including *Combretum,* showed only monosporic embryo sacs, and it is thus doubtful that tetrasporic embryo sacs occur in this family. The conditions are so interesting that a re-examination would be desirable.

Penaeaceae were studied by Stephens (1909) and consistently seem to have a 16-nucleate tetrasporic embryo sac of the so-called *Penaea*-type. Most often four nuclei fuse in the center and after fertilization result in a 5-ploid endosperm nucleus. The family is rather poorly known embryologically and modern studies are thus very desirable.

According to Tobe and Raven (1984a) the genus *Alzatea,* composing Alzateaceae, agrees with other Myrtales in the main embryological features, but has a bisporic, *Allium*-type, embryo sac. Like *Rhynchocalyx* (Rhynchocalycaceae) but unlike other Myrtales, the micropyle is formed by the inner integument alone. *Rhynchocalyx* (Tobe & Raven, 1984b) shows the *Polygonum*-type of embryo sac formation, differing in this characteristic from both Penaeaceae and Alzateaceae. In this respect it exhibits a more basic state than both of these families. *Rhynchocalyx* differs from the Lythraceae in some respects, including the ephemeral endothecium and the micropyle formed by the inner integument alone (see above), but it agrees with Lythraceae in having a multi-celled archesporium.

Within the three, rather divergent, genera of Crypteroniaceae, *Axinandra* has so far been studied (Tobe & Raven, 1983b). In this genus the micropyle is formed by both integuments, the archesporium in the ovule is one-celled, and the embryo sac formation is of the *Polygonum*-type. It is noteworthy, however, that the pollen grains in *Axinandra* are shed in the tricellular stage, as in the case in several Melastomataceae, and that—unlike all other Myrtaceae studied—it has an endothelium (i.e., an integumentary tapetum) (Tobe & Raven, 1983b).

Melastomataceae deviate from Memecylaceae in having a poorly developed (often crushed) endothecium, whereas Memecylaceae have a thickened, even fibrous endothecium (Davis, 1966; Eyde & Teeri, 1967). The tapetal cells in these families are uninucleate. Although Brewbaker (1967) reported trinucleate pollen grains in most genera of the family, Tobe and Raven (1984c) report that the grains are strictly 2-celled when dispersed, as is the case in all other families of Myrtales. The placental epidermis may consist of palisade-like cells with a large amount of protoplasm (Subramanyam, 1948), which has also been observed in certain Lythraceae. Subramanyam (1948) also observed that in mature seeds of *Melastoma malabathricum* L. the embryo was filled with starch grains, which is also the case with Trapaceae and some Myrtaceae. Otherwise, the ovular conditions conform well with the ordinal account given above.

Myrtaceae, and in particular 'Metrosiderineae,' agree with the last mentioned three families in embryological attributes (Mauritzon, 1939, and later references). The ovules vary with regard to their position and are often hemianatropous or campylotropous (Johnson & Briggs, pers. comm.). The presumed similarity in flower and fruit morphology between 'Myrtineae' and Lecythidaceae stated by, for example, Niedenzu (1893) was not supported by embryology, as Lecythidaceae are very divergent embryologically (see below). Within Myrtaceae, the micropyle may be formed only by the inner integument (*Angophora, Darwinia, Thryptomene, Wehlia*) (Davis, 1968, 1969; Prakash, 1969a, 1969b, 1969c), and unitegmic ovules occur in perhaps all species of *Syzygium.* The archesporial cell has rarely been observed to cut off a parietal cell, but Davis (1966; Prakash, 1969a) suspects that this happens so early that it has usually escaped observation. Adventive embryogeny is reported in the family, and polyembryony is common.

In Onagraceae (Johansen, 1929, 1934; Davis, 1966) the embryo sac formation follows the *Oenothera*-type and is 4-nucleate, the single polar nucleus fusing with a male gamete into a diploid endosperm. In this peculiarity, which seems to be consistent in the family, Onagraceae are well characterized.

Except for certain characteristic features occurring in particular families, of which the *Penaea*- and *Oenothera*-types of embryo-sac formation in Penaeaceae and Onagraceae respectively seem to be the most conspicuous, there is good conformity among the families of Myrtales in embryological characteristics. A most aberrant member is *Trapa,* which, however, seems adapted in its embryological syndrome characteristic of an aquatic life.

Among the families with dubious affinity to

Myrtales, Rhizophoraceae do not deviate considerably from the Myrtales pattern. The antipodals are not ephemeral as they usually are in Myrtales. Any specializations in embryo development (Corner, 1976) of the halophytic mangrove genera seem of little significance in discussing phylogenetic relationships.

Thymelaeaceae are very distinct from Myrtales in embryological respects (Fuchs, 1938; Davis, 1966; Corner, 1976; Tobe & Raven, 1983a). The pollen grains are tricellular when shed (a derived attribute found in Myrtales only in *Axinandra,* Tobe & Raven, 1984a). As in many Myrtales, however, a parietal cell is cut off from the archesporial cell and forms a parietal tissue, and also a nucellar cap is usually formed by periclinal divisions of the nucellus epidermis, which occurs in certain Myrtales. Unlike most Myrtales, however, the antipodals are persistent. An obturator of elongated cells from the base of the style is characteristic. Similar persistent and proliferated antipodals and a similar obturator occur in Combretaceae.

As regards Haloragaceae (embryological summary by Orchard, 1975), this family must be considered in the strict sense (i.e., excluding *Gunnera* and *Hippuris*). In this circumscription, the family yet deviates in embryological respect from Myrtales in some important features. The anther wall formation in both *Haloragis* and *Laurembergia* has, for example, proved to be of the monocotyledonous type, although this may not be the case in *Myriophyllum,* and the pollen grains of all three genera are shed in the tricellular stage. Cellular endosperm formation is recorded in *Haloragis* (Nijalingappa, 1975) and one species of *Myriophyllum* but nuclear endosperm formation in another species of *Myriophyllum* and in *Laurembergia.* In all three genera mentioned, the embryogeny conforms to the *Myriophyllum* variation of the Caryophyllad type, which has not yet been found in Myrtales. The combination of attributes does not support the inclusion of Haloragaceae in Myrtales.

Of other families occasionally referred to Myrtales, Hippuridaceae by virtue of the unitegmic ovules with cellular endosperm formation fall out of the pattern. Even more so do Callitrichaceae, which have unitegmic, tenuinucellate ovules, no parietal cell, cellular endosperm formation, and terminal endosperm haustoria (these are totally absent in Myrtales).

Elaeagnaceae are surprisingly poorly known embryologically, but the evidence known is in accord with the myrtalean pattern.

Lecythidaceae (Venkateswarlu, 1952) deviate strongly from Myrtales, and the pollen grains are sometimes reported to be tricellular when dispersed, which is rare in Myrtales. The ovule is tenuinucellate and no primary parietal cell is cut off from the archesporial cell, which is a difference from Myrtales. Also, the outer integument is thicker in Lecythidaceae than in nearly all Myrtales, and the nucellus becomes destroyed much earlier in the development. Some features, e.g., the ephemeral antipodials, agree with the myrtalean pattern.

The embryological evidence supports the myrtalean core families as related. The seven primary characteristics enumerated by Tobe and Raven (1983a) occur together only rarely in other plants, and in none of the other families that have been referred to Myrtales, with the possible exception of Elaeagnaceae.

SEED COAT STRUCTURES

The seed coat structures in a great number of representatives of dicotyledons were studied by Corner (1976). In a chapter called "Criticism of the arrangement of dicotyledonous families into orders," Corner stressed that the families here considered the core families of Myrtales fall into two groups as follows (Fig. 7B):

(1) seeds with a fibrous exotegmen composed of narrow pitted fibers or elongate tracheid fibers, often with sclerotic mesotesta: Combretaceae, Onagraceae, Lythraceae, Punicaceae, Sonneratiaceae (Punicaceae and Sonneratiaceae are here included in Lythraceae), Trapaceae, Legnotidaceae;

(2) seeds with sclerotic mesotesta but without a special exotegmen: Lecythidaceae, Memecylaceae, Melastomataceae, Myrtaceae, Penaeaceae, Rhizophoraceae (excl. Legnotidaceae).

Haloragaceae lack both sclerotic mesotesta and fibrous exotegmen and thus form a third group, to which also Callitrichaceae were referred (however, a position for Callitrichaceae in or near Myrtales is out of the question).

Corner (1976: 37) incorrectly stated that the first group has tenuinucellate ovules; actually, they are crassinucellate in all the families. The second group, with the exception of Lecythidaceae, likewise has crassinucellate ovules (Lecythidaceae being surely out of place in Myrtales).

Another difference between the groups created by Corner (1976) would be that in the first group the seeds are: "exalbuminous, exarillate and provided with straight or slightly curved embryos. *Punica* with epidermal sarcotesta seems to provide the least specialized and reduced seed." Starch grains often occur in the embryos of Myrtaceae, but this is not a general feature of the second group. Besides, starch grains occur in the seeds of Trapaceae in the first group. Arils are also generally absent in the second group except for Lecythidaceae, lacking in all Melastomataceae, Myrtaceae, and Penaeaceae and in most but not all genera of Rhizophoraceae. Thus, this is not a difference either. Also the curvature of the embryo comprises no considerable difference between the groups. The sarcostesta in *Punica* is no doubt a specialization.

Because the difference in seed coat structure was stressed by Corner as important and, together with Corner's other arguments, was used by Briggs and Johnson (1979) as the basis for a distinction between Lythrales and Myrtales, it needs some comment.

In group (1) there is similarity between taxa of the three subfamilies (Lythroideae, Sonneratioideae, and Punicoideae) of Lythraceae studied by Corner in the possession of a multiplicative outer integument ("testa sensu stricto"), the middle layers consisting of either a thin-walled mesophyll or a densely sclerotic part (in *Lawsonia* and *Lagerstroemia* with crystals in the cells) or both, or by sclerotic cells only. The innermost layer of the outer integument may contain crystals. The inner integument consists of two layers only, an outer layer of narrow longitudinal tracheids or of narrow thick-walled fibers, and an inner unspecialized layer with elongate thin-walled cells. These observations support the general conclusions that these subfamilies are closely related.

Onagraceae have a non-multiplicative outer integument ("testa") composed of large, often crushed cells, but rarely, as in *Oenothera,* of sclerotic cells. As in some members of the aforementioned families, the innermost layer of the outer integument consists of crystal-cells. The tegmen in Onagraceae, as in the previous families, also remains two-layered. The outer layer consists of longitudinal lignified fibers. Thus, it seems, Onagraceae belong to the first group of families, and in particular resemble some Lythraceae, in seed coat structure.

Combretaceae may or may not have a multiplicative outer integument, the mesophyll consisting of thin-walled cells with scattered sclerotic or tracheidal cells with more or less reticulate, in some cases spiral-annular, wall thickenings. The innermost layer of the outer integument is composed of sclerotic or tracheidal cells or is unspecialized. The inner integument consists of an outer layer of elongate, lignified fibers, while the other layers are unspecialized or crushed.

The conditions in group (2), above, are not much different. The outer integument is multiplicative in the large seeds (Memecylaceae) but not in the smaller seeds studied (Melastomataceae). The outer epidermis varies much, from a palisade-like layer of radially elongate cells, as in some families of the former group, to a layer of cuboid cells with thickened outer walls. The mesophyll is thin-walled or there may be groups of sclerotic cells (as in the previous group). The innermost layer of the outer epidermis is unspecialized or (as in some members of the previous group) may consist of crystal-cells. The tegmen is not multiplicative and consists of two cell-layers. Unlike the families of the first group the outer layer of the tegmen in the studied taxa does *not* consist of fibers but is more or less crushed.

In Myrtaceae, the outer integument in the seed may or may not be multiplicative and may or may not develop sclerotic tissue. The innermost layer may or may not consist of crystal-cells, the cell walls in this layer may be thin or thick and lignified, or may even be developed as radially elongate sclerotic cells at the micropylar end. As in group (1), the inner integument is not multiplicative, but mostly unspecialized and crushed; however in *Psidium* the outer layer may have slight, unlignified thickenings.

In the above variation Corner (1976) lays most stress on the occurrence of fibers or tracheids in the exotegmen, i.e., the outermost layer of the inner integument. However, tracheidal cells may be present in the endotesta, i.e., the innermost layer of the outer integument, as in Combretaceae, but not in Lythraceae studied. The presence of sclerotic cells to some extent seems to comprise a typical feature in Myrtales. The several-layered inner integument in Combretaceae is also notable, as is its few-layered outer integument. An evaluation of these differences can be made only in the light of a more complete knowledge of the variation in each family.

A division of Myrtales into two orders was suggested by Corner (1976), largely on the basis of seed coat structure. The seed coat structures in Myrtales are so divergent, however, that these can hardly be the main basis of such a rearrangement, although the occurrence of a fibrous exotegmen is perhaps important for relating some families to each other and contributes a piece of evidence for including Sonneratiaceae and Punicaceae into Lythraceae. However, the additional characteristics stated by Corner (see above) as differences between the orders have proved inaccurate or only partly true. To the former category belongs the statement that tenuinucellate ovules characterize the Lythraceae group (see above). Development of stamens, occurrence of starch in the embryos, etc., do not provide any differences between the suggested orders. Briggs and Johnson (1979), who accepted a division of Myrtales largely according to Corner's views, subsequently have abandoned this view.

CHLOROPHYLLOUS/ACHLOROPHYLLOUS STATES OF EMBRYO IN SEED

The occurrence of chlorophyllous embryos in seeds was presented by Yakovlev and Zhukova (1980) and discussed by Dahlgren (1980b). Chlorophyll formation in the embryo of seeds normally seems to be dependent on availability of light to the embryo in the course of its development and thus is generally absent in seeds with copious endosperm and in seeds enclosed in a thick testa or pericarp.

In Myrtales, the embryo is usually achlorophyllous despite lack of endosperm. The records in the order are few, however. Chlorophyllous embryos were found in the mangrove genus *Laguncularia* of Combretaceae, in two species of *Memecylon* of Memecylaceae, in *Sonneratia* of Lythraceae, and in two species of "*Eugenia*" (= *Syzygium*) of Myrtaceae. The records of achlorophyllous embryos are distributed through the order and include all families investigated except Memecylaceae. No taxonomic conclusions can as yet be drawn on the basis of this feature. The few studied taxa of Haloragaceae and Thymelaeaceae have achlorophyllous embryos, in which they agree with most Myrtales.

CHROMOSOME NUMBERS

Raven (1975) gives a summary of the chromosome numbers for the Myrtales. He concludes that as the base number is $X = 12$ in Trapaceae, Oliniaceae, and Combretaceae, and as this number has also been reported for both Psiloxylaceae and Heteropyxidaceae (Johnson & Briggs, 1984), it is likely to be the original basic number for the order as a whole (or, less plausibly, $X = 11$, which Raven assumed to be the original base number in Myrtaceae and Onagraceae).

Onagraceae (Raven, 1975) have $X = 11$, which is found in Fuchsieae and Circaeeae and in the more primitive taxa of Lopezieae and Onagreae. *Trapa* (Trapaceae) has $X = 12$.

Within the Lythraceae, *Lafoënsia* has a chromosome number of $n = 10$, *Lagerstroemia* $n = 22$–25, *Lythrum* $n = 5$, *Heimia* $n = 8$, *Nesaea* $n = 30$, *Peplis* $n = 5$, *Rotala* $n = 16$, *Woodfordia* $n = 8$, and *Cuphea* $n = 6$, 8, or 9, which suggests a basic number of the family of $X = 8$. This also seems to be the basic number in other genera not mentioned here (Graham, pers. comm. in Raven, 1975). *Punica,* as most other Lythraceae, has $n = 8$, while *Duabanga* has $X = 12$ and *Sonneratia* $X = 9$ or 11 (Muller & Hou-Lin, 1966).

Penaeaceae (Dahlgren, 1968, 1971) have $n = 10$, as in *Rhynchocalyx* (Goldblatt, 1976). The chromosome numbers in Crypteroniaceae, as circumscribed here, are not known. In Memecylaceae, *Memecylon* has $X = 7$ and *Mouriri* (one count only) $n = 12$, whereas several genera of Melastomataceae have basic numbers of $X = 14$, 12, and 9. Oliniaceae and Combretaceae, which show some other similarities, both are reported to have the basic chromosome number of $X = 12$.

Thymelaeaceae have a probable base number of $X = 9$. Finally, Haloragaceae (excl. *Gunnera* and *Hippuris*) have $X = 7$, Rhizophoraceae $n = 32$ (tribe Macarisieae) and $n = 18$ (tribe Rhizophoreae), suggesting base numbers of $X = 8$ and 9; whereas, the base number of Lecythidaceae may be difficult to establish, $n = 13$, 16, 17, and 18 being some numbers reported in that family. Chrysobalanaceae have $n = 10$ or (more often) 11. Finally, it may be mentioned that Rhamnaceae have a base number of $X = 12$, with $X = 11$ in the tribe Colletieae (Raven, 1975).

The chromosome base numbers of the Myrtales, as compared with those in other families, do not support inclusion of Lecythidaceae in the order (rather Lecythidaceae fit with the Theales), though Rhamnaceae agree better ($X = 12$ being, however, a base number in many complexes).

CHEMICAL CHARACTERISTICS

Myrtales, as circumscribed here, comprise a fairly homogenous complex in terms of chemical contents (Hegnauer, 1964, 1966, 1969, 1973).

Tannins. All families of Myrtales appear to contain tannin plants. In most of the families the tannins consist of the condensed type as well as of galli- and ellagi-tannins. Ellagic acid, according to Bate-Smith (1962), occurs in all studied taxa of Lythraceae (incl. Punicaceae), Combretaceae, Melastomataceae, Myrtaceae, and Onagraceae and, according to Lowry (1976), in Lythraceae subfam. Sonneratioideae; probably it is present in virtually all members of the Myrtales. Even a water plant like *Trapa* is known to be rich in tannins, the pericarp containing up to ten percent or more (Gnamm, 1949)! Species of Combretaceae, which are rich in gallyol- and ellagi-tannins as well as condensed tannins, are used for tanning.

Hegnauer (1969) concluded that "gallic and ellagic acids and tannins derived from these, as well as condensed tannins which are derived from flavon-3-oles and flavon-3,4-dioles, are characteristic of the order Myrtales."

Tannins are also present in rich quantities in Rhizophoraceae. Bate-Smith (1962) recorded small quantities of ellagic acid in *Cassipourea,* but not in *Rhizophora*; whereas Lowry (1976) reported ellagic acid in species of *Anisophyllea* and *Bruguiera* as well as in *Rhizophora.* In Haloragaceae ellagic acid has been reported (Bate-Smith, 1962) for *Haloragis* as well as *Myriophyllum,* in Elaeagnaceae for *Elaeagnus* and *Hippophaë,* and in Lecythidaceae for *Couropita, Eschweilera,* and *Lecythis.* All these groups are tannin plants in the wide sense. Thymelaeaceae, however, consistently seem to lack ellagic acid and accumulate no tannins, an important difference from all Myrtales.

Flavonoids. The flavonoid profile (Bate-Smith, 1962; Gornall et al., 1979) in Myrtales is based mainly on common flavonols and their O-methyl derivatives (e.g., delphinidin, cyanidin, pelargonidin, quercetin, kaempferol, O-methylated anthocyanins, and, quite often, proanthocyanidins). The methylated and oxygenated flavonols are especially common in Combretaceae. Myricetin occurs in some families (at least in certain genera of Combretaceae, Melastomataceae, Myrtaceae, and Onagraceae), but is of much rarer occurrence than are ellagic acid and quercetin. Glycoflavones are reported in at least single genera of each of the Lythraceae, Combretaceae, and Myrtaceae, and occur in all tribes except Onagreae and Epilobieae of the Onagraceae (Averett & Raven, 1983). In fact, glycoflavones may be widespread in Myrtales. Flavones are noticeably poor in the order. Caffeic acid is also rare in the order, except in Onagraceae (Bate-Smith, 1962).

The flavonoid pattern for Thymelaeaceae (Gornall et al., 1979) is different from that in Myrtales. Methylated flavones, C-glycoflavones, and luteolin/apigenin are reported, whereas delphinidin, cyanidin, pelargonidin, O-methylated anthocyanins, and myricetin are *not* recorded.

Rhizophoraceae are known to possess cyanidin/pelargonidin, myricetin, quercetin/kaempferol, and proanthocyanidins, and thus agree rather well with the myrtalean profile. Also Haloragaceae agree with Myrtales in flavonoid profile and, like Rhizophoraceae, seem to lack or be poor in flavones, as are Myrtales. In addition, Myrtales agree fairly well with Theales, Rosales, and other orders, such as Geraniales and Balsaminales, in flavonoid contents.

Essential oils. Myrtaceae are the only family in Myrtales with rich production of essential oils. The essential constituents of these (Penfold, 1948) in many cases are monoterpenes and, often to a considerable proportion, sesquiterpenes. Oils of phenyl-propane type are rarer. Characteristic of myrtaceous oils are phloroglusin derivatives of the baeckeol, eugenin, and tasmonol types.

Essential oils are also present in flowers of *Lawsonia* (henna plant) of Lythraceae.

Although Thymelaeaceae are not essential-oil plants, and lack ducts, the wood of some taxa contains essential oils.

Triterpenes; triterpene saponins. Triterpenes are widely distributed throughout the order Myrtales, and triterpene saponins are recorded from Combretaceae and Myrtaceae, although they are rare in the latter family. The occurrence of triterpene saponins in the other core families of Myrtales is uncertain or, at least, not common.

It is noticeable that the saponin barringtogenol has been recorded in Combretaceae and *Barringtonia* (of Lecythidaceae sensu lato) only, but the phylogenetic significance of this condition is uncertain.

Triterpene saponins are also known to occur in *Haloragis* of Haloragaceae, and richly so in the fruits of *Shepherdia* of Elaeagnaceae, but also in some Thymelaeaceae.

Cyanogenesis. Cyanogenic compounds occur in several families of the Myrtales, viz., in Memecylaceae (*Memecylon*), Myrtaceae (*Eucalyptus*), Lythraceae (*Lawsonia*), and Onagraceae (*Gaura, Oenothera*). Besides, wounded parts of *Olinia* (Oliniaceae) are reported to smell like "bitter almonds," indicating cyanogenic compounds related to prunasin.

Cyanogenic compounds are also known in Haloragaceae (*Haloragis* and *Myriophyllum*).

Alkaloids. Alkaloids are scattered in Myrtales and are reported in the families Combretaceae, Lythraceae (incl. *Punica*), Melastomataceae, and Myrtaceae. Although alkaloids have also been reported sporadically in Onagraceae, their presence has not been confirmed and the report is most likely incorrect.

Within Combretaceae the genus *Quisqualis* seems to contain a pyridin base. Lythraceae are richer in alkaloids and produce an interesting type of quinolizidine alkaloids not known from any other plants (Fujita et al., 1971; Seigler, 1977). *Punica* produces alkaloids similar to the better known tropane types, the chief being isopelletrierin, N-methylisopelletrierin, and pseudopelletrierin (Hegnauer, 1969), while others remain to be identified. Positive alkaloid reactions have been obtained for the genera *Memecylon* (Memecylaceae) and *Clidemia* and *Sonerila* (Melastomataceae), but these alkaloids have not been isolated. Alkaloids are rare in Myrtaceae, but alkaloid reactions have been obtained for a number of genera; they await further analysis.

Among other families associated with Myrtales, Rhizophoraceae are characterized by their alkaloids, which include hygrolintropine, and pyrrolizidin (necine) derivatives. Some of the alkaloids contain sulfur.

Haloragaceae seem to be alkaloid-free or almost so (Orchard, 1975), while Elaeagnaceae contain tryptofan derivatives (Boit, 1961) such as elaeagnin and serotonin. Alkaloids are rare and little known in Thymelaeaceae.

There does not seem to be a consistent tendency in the alkaloid contents of the myrtalean and "possibly-myrtalean" families; the alkaloid contents in several families still largely remain to be analyzed.

Quinones. Napthaquinones are known to occur in some taxa of Myrtales. The napthaquinone lawsone is known in *Lawsonia* of Lythraceae (also in *Impatiens* of Balsaminaceae). Lawsone accounts for the color in henna, which is used for dyeing hair and nails. Quinones (of unknown structure) are also known in *Dichaetanthera* of Melastomataceae (Hegnauer, 1969).

Anthraquinones are known in *Sonneratia* (Lythraceae). The occurrence of quinones thus offers no taxonomically useful information.

Aluminum accumulation. Aluminum accumulation (Chenery, 1948) is noticeable in Crypteroniaceae (*Crypteronia*) and especially in Melastomataceae and Memecylaceae (more than 10,000 p.p.m. in several genera). Aluminum accumulation occurs also in Rhizophoraceae subfam. Anisophylleoideae (*Anisophyllea, Combretocarpus,* and *Poga*), but not in the other rhizophoraceous subfamilies (Chenery, 1948; Chenery & Sporne, 1976).

Mucilage. Mucilage cells characterize some families of Myrtales, viz., Combretaceae, Lythraceae, and Melastomataceae (quite often, Hegnauer, 1969). The mucilage contains sugars and is often acid in reaction.

Storage substances in the seed. The seeds of myrtalean families mostly have a large and well-developed embryo, whereas the endosperm tissue is absorbed in the course of the seed development. Therefore, we are chiefly concerned here with the contents of the embryo. In most families, the embryo stores fatty oils and proteins, but it sometimes stores starch in Melastomataceae and Myrtaceae and always does in Trapaceae. Endosperm may be present or absent in Rhizophoraceae. If the latter, the embryo is large and stores fat and protein, which is also true in most Lecythidaceae, Thymelaeaceae, Elaeagnaceae, and Haloragaceae.

Phytochemical summary. Hegnauer (1969: 195), in a somewhat resigned comment, summarizes: "One must frankly admit that so far chemistry cannot give a decisive contribution to the problem of the descent of the Myrtales. Similar polyphenolic and triterpene spectra occur in the Cunoniales, Theales, Rosales, and Myrtales."

The families of Myrtales lack polyacetylenes, iridoid substances, and benzylisoquinolin alkaloids. The occurrence of such compounds in any taxon referred to the Myrtales indicates against inclusion of that group in the order.

The presence of tannins, both galli- and ellagitannins and tannins of the condensed type, is typical of the order, and the flavonoid spectrum is characterized by the presence of flavonols (including methylated flavonols), whereas, flavones (except glycoflavones) are absent or nearly so in the families studied. Triterpenes are characteristically present, and triterpene saponins are found in various representatives. Alkaloids occur sporadically in the order but show no consistent pattern. Napthaquinones are known in different subfamilies of Lythraceae. Mucilage cells with polysaccharide contents are common but not a criterion of Myrtales. Cyanogenesis occurs in several families, but again does not represent a typical attribute of the order. Considerable aluminum accumulation occurs in Crypteroniaceae, Memecylaceae, and Melastomataceae and may indicate affinity among these families, but this affinity is better shown by other attributes. The seeds have but little endosperm and their embryos usually accumulate fat and aleuron, exceptions being some Myrtaceae and Melastomataceae and the Trapaceae which store starch; this character is obviously of little phylogenetic significance. Myrtaceae, Heteropyxidaceae, and Psiloxylaceae deviate from the other families in their rich contents of essential oils.

The possession in Thymelaeaceae of poisonous compounds, coumarins of the daphnetic and daphnoretin type, and the lack of tannins and ellagic acid are strong indications that this family should *not* be associated with Myrtales, but that it may have close relationship with the Euphorbiaceae.

Rhizophoraceae agree rather well with Myrtales in the main chemical features, although the alkaloids present in subfam. Rhizophoroideae are absent from Myrtales. Otherwise the tannin content (incl. ellagi-tannins), flavonoid spectrum, mucilage cells, aluminum accumulation, and oil-rich seeds are in agreement with myrtalean families, and Rhizophoraceae cannot be separated from this order on chemical grounds.

Also Haloragaceae (excl. *Gunnera* and *Hippuris*) show a similar pattern; ellagic acid, quercetin, kaempferol, etc. are typical. Saponins and cyanogenic compounds found in the family are also present in Myrtales.

Lecythidaceae, which are often saponin-rich (triterpene saponins), agree fairly well with Myrtales in chemistry, but similar chemistry occurs in Theales; hence, the position of the family does not become obvious from chemistry.

Elaeagnaceae agree with the myrtalean families in general chemical features but the accumulation of L-quebrachite and the tendency for accumulation of indole bases and of sinapinic acid are *not* in accordance with Myrtales (Hegnauer, 1966).

By their possession of iridoids in at least some genera the families Escalloniaceae (or Escallonioideae of Saxifragaceae), Icacinaceae, Hippuridaceae, Loganiaceae, and Callitrichaceae are deemed distantly related to Myrtales.

THE CORE FAMILIES OF MYRTALES

Myrtales, like Caryophyllales (or Chenopodiales), are one of the few larger orders that have a rather uncontroversial circumscription as regards the "nucleus" or "core" families. These are the Onagraceae, Trapaceae, Lythraceae (incl. Punicaceae and Sonneratiaceae), Oliniaceae, Combretaceae, Alzateaceae, Penaeaceae, Rhynchocalycaceae, Crypteroniaceae, Memecylaceae, Melastomataceae, Psiloxylaceae, Heteropyxidaceae, and Myrtaceae. All of these entities may not necessarily be entitled to familial status, but in essential points this does not make a great difference. (See p. 635 for the preferred classifications of each of the two authors.)

ONAGRACEAE A. L. DE JUSSIEU (1789)

This family has 17 genera and ca. 675 species (Raven, 1964, 1976, 1979), ranging from the tropics to (especially in *Epilobium*) arctic-alpine habitats. Through the works of Munz, Raven, and associates, the family has become one of the most thoroughly investigated among the angiosperms. Although most genera are herbaceous, some are woody, and the leaves are opposite, alternate or, more rarely, verticillate, and in some tribes have minute stipules (Fig. 2A–E). The leaf teeth are of the fuchsioid (a variant of rosoid) kind (Hickey, 1981). The vegetative parts are rich in oxalate raphides, which is another unusual feature in the Myrtales. The flowers are epigynous, generally 4-merous, but 2-merous in *Circaea* and to 7-merous in species of *Ludwigia*, 5-mery occurring also within several genera (Eyde, 1977). The flowers are provided with a variably long hypanthium (lacking in *Ludwigia*, *Lopezia*, and sporadically in other genera). There are generally two staminal whorls or, by reduction, a single whorl in the flowers. By dislocation in the bud, these often appear to be in an obdiplostemonous position although the initials show a diplostemonous organization. Weak zygomorphy occurs in *Epilobium* (*Chamaenerion*), *Clarkia*, and *Heterogaura*, and strong zygomorphy in *Lopezia*. The reproductive biology (Raven, 1979) is varied, bird-pollination occurring in most species of *Fuchsia* and some species of *Lopezia*, *Oenothera*, and *Epilobium*. The pollen grains may cohere in tetrads (Skvarla et al., 1975) and are generally conspicuously triangular and angulo-aperturate. They have various patterns of exine stratification (Skvarla et al., 1976). Most conspicuously they have viscin threads in all but one species (*Circaea alpina* L.; Skvarla et al., 1978), the last mentioned feature matched only in certain Ericaceae and Fabaceae. Pseudocolpi are lacking. The carpels (and locules) are generally isomerous with the perianth whorls; in certain taxa the septa are incomplete in the upper part of the ovary. The ovules are usually numerous, and in most features have a myrtalean embryological pattern, although they are conspicuously distinct in having the monosporic, 4-nucleate *Oenothera*-type embryo sac formation. Antipodals are lacking, and the endosperm is diploid. The fruit in most genera is a loculicidal capsule, but may be a berry (*Fuchsia*) or an indehiscent dry fruit (*Circaea, Gaura,* etc.) with a variable number of seeds. The seeds in the tribe Epilobieae are generally provided with a tuft of trichomes and have a taxonomically useful surface sculpture. The embryo lacks starch grains.

Eyde (1981) provides strong evidence that epigyny has evolved separately in two lines within the onagraceous ancestors: in one line leading to *Ludwigia,* which has nectaries on the ovary summit, and one line leading to the other Onagraceae, which have nectaries on the tube side of the gynoecium-tube junction. Differences in vasculature and other details support this conclusion (Eyde, 1981).

The Onagraceae are a very distinctive family, and differ from other Myrtales in several features. The similarities to Lythraceae in teeth structure and marginal ciliation of leaves pointed out by Hickey (1981), and the fibrous exotegmen of the seeds and the similar petal venation are some other conspicuous attributes which may indicate a quite close connection between the Onagraceae and Lythraceae.

TRAPACEAE DUMORTIER (1829)

This family consists only of the genus *Trapa,* which, excluding introductions, currently has a temperate to tropical Old World distribution. The number of species is perhaps three, although as many as 30 self-pollinating races have sometimes been considered as species. The plants are floating aquatic herbs with decussate leaves, concentrated in rosettes on the branch ends; the leaves are caducous and replaced on the submersed stems by chlorophyllous roots. The stems have bicollateral vascular bundles and the leaves rudimentary stipules, supporting a myrtalean affinity. The floating leaves have marginal teeth with a unique double apex. The flowers are axillary, bisexual and perigynous to hemi-epigynous, with four valvate sepal lobes, four white petals, and four stamens alternating with the petals. The pollen grains are triangular, and have three meridional ridges. They can be interpreted as possessing intercolpate depressions. The ovary is bilocular with one pendulous ovule in each locule, but only one ovule develops into a seed. The family has a unique embryology: the embryo sac formation follows the normal type, but endosperm formation hardly takes place at all. The embryo sac becomes prolonged, and copious nutrient tissue including starch grains are accumulated in the embryo, which has one large and one rudimentary cotyledon.

The family has often been included in Onagraceae, but it lacks the viscin threads on the pollen grains, epigynous flowers, and the 4-nuclear *Oenothera*-type embryo sac of that family. Rather, it seems more closely related to the Lythraceae, although there is no obvious link between the two families.

LYTHRACEAE JAUME ST.-HILAIRE (1805)

This family, with ca. 29 genera and ca. 585 species (see Shaw, 1973; Schmid, 1980; Cronquist, 1981) is here more widely circumscribed, including Punicaceae Horan. as well as Sonneratiaceae Engl. & Gilg. It is widespread and occurs in various climatic zones of the New and Old World, with a concentration in the tropical and subtropical regions. Its new circumscription makes it rather vaguely defined, the newly included genera having epigynous flowers and stamens attached on the inside of the hypanthium or on its rim. With various of its genera it possesses a combination of features that are regarded as basic (plesiomorphic) in the order, in which it takes a central position. The amplitude of variation is considerable.

The family includes herbs and shrubs as well as fairly large trees (*Lagerstroemia, Lafoënsia, Sonneratia, Duabanga*). The leaves are opposite, more rarely disjunct-opposite, or verticillate, and the leaves are entire or sometimes indistinctly dentate ("cryptic teeth"). The stipules show advancement through their dissection into small trichome-like structures displaced into the leaf axil (see *Diplusodon,* Fig. 8C).

Branched foliar sclereids are absent in most Lythraceae; they are reported to occur only in *Sonneratia* and *Duabanga*. Unbranched sclereids occur rarely in other genera.

The flowers are usually actinomorphic, but in *Cuphea* and *Pleurophora* are zygomorphic; *Woodfordia* approaches this condition. Epigynous or hemi-epigynous flowers occur in *Sonneratia, Duabanga,* and *Punica,* but not in the subfamily Lythroideae. The flowers in Lythraceae exhibit a variety of merous conditions: 4-, 5-, or 6-mery being the most common (but to 16-mery occurs in *Lafoënsia,* to 9-mery in *Lagerstroemia,* and to 8-mery in *Punica* and *Sonneratia*). The flowers possess black glands in *Adenaria, Pehria, Pemphis,* and *Woodfordia.* The calyx-lobes are valvate. One pecularity that occurs in a considerable number of genera, incl. *Lythrum, Nesaea, Rotala,* and *Diplusodon* (Fig. 8G), is the presence of tooth- and spur-shaped structures isomerous and alternating with the often shorter calyx-lobes; these are nothing but extensions from the calyx-lobe base (and should not be confused with an outer whorl of perianth members), and no doubt can be regarded as a specialization (sometimes secondarily lost). The petals in Lythraceae have a peculiar, pinnate venation, a feature which Chrtek (1969) regarded as a derived attribute, but which has its counterpart in Onagraceae (and thus may be a synapomorphy for the two families). Petals are sometimes absent through reduction and vary widely in relative size and in color (though being usually crimson, pink, or white). When present they are often unguiculate and may be reminiscent of petals in Malpighiaceae in the crinkled, undulate structures.

Stamens more than double the number of sepals are found in *Punica* and *Sonneratia,* but also in *Lagerstroemia* and species of *Diplusodon, Ginoria, Heitia, Heimia, Nesaea,* and *Physocalymma.* In haplostemonous flowers the stamens may alternate with the sepals, as in *Tetrataxis* (Graham & Lorence, 1978) and species of *Nesaea* (Graham, 1977), or may be opposite to them, as in other species of *Nesaea* and in species of *Rotala, Peplis, Ammannia,* and *Lythrum.* Two stamens or only one are found in species of *Rotala* and two or four stamens in *Didiplis diandra* Wood. The filaments are straight or incurved (the long filaments in *Lafoënsia* inrolled) in bud, and are usually inserted on the inside of the receptacle between its base and middle, closer to the rim in *Lawsonia,* on the distal inner side of the hypanthium in *Punica,* and near or on the very rim in some advanced species of *Cuphea* and in *Sonneratia* and *Duabanga.* (The last condition is typical of nearly all other Myrtales except some Combretaceae.) The anthers generally lack strong specialization, and the connective is less developed than in Crypteroniaceae, Penaeaceae, Memecylaceae, or Melastomataceae, but have a broad connective in several woody genera (*Capuronia, Lawsonia, Orias,* and *Lagerstroemia*).

The pollen grains are exceptionally variable for the order and include heterocolpate types with pseudocolpi either isomerous to or double the number of the apertures as well as colporate or porate types without pseudocolpi. Porate pollen grains occur in *Cuphea* (Graham & Graham, 1971).

The common division of Lythraceae subfam. Lythroideae is according to whether the ovary is more or less completely septate (Nesaeeae) as is the case in subfam. Punicoideae and Sonneratioideae, or whether the septa are incomplete in the upper part of the ovary (Lythreae). The embryology of Lythraceae is of the common type compatible with the family's basic position in the order. The fruit is capsular or baccate, the seed of *Punica* deviating by its sarcotesta.

(Much of the above, detailed information has been received from A. Graham & S. Graham.)

Punicaceae Horaninow (1834) has been included here, as a subfamily of the Lythraceae. It consists of *Punica* with two species, *P. granatum* in southern Europe and western Asia, and *P. protopunica* Balf. f. on Socotra [this latter species has been placed in the segregate genus *Socotria* by Levin (1980)]. The fairly large, bright red flowers are epigynous, 5–8-merous in calyx and corolla, and provided with numerous stamens, the filaments of which are attached to the inner side of the hypanthial tube. The stamens develop in centrifugal succession as in *Lagerstroemia.* The carpels are 7–15 and in *P. granatum* are situated on two levels, but in *P. protopunica* form an ordinary syncarpous ovary. The fruit has a leathery pericarp and the seeds are pulpy from the edible sarcotesta. *Punica* is technically easy to separate as a family, Punicaceae, and is usually treated on the family level.

Also *Sonneratia* and *Duabanga* are generally separated, together, as the family Sonneratiaceae Engl. & Gilg, with perhaps ten species. *Sonneratia* consists of mangrove trees, *Duabanga* of lowland forest trees. They differ from the Lythraceae in having branched foliar sclereids, and the flowers are hemi-epigynous, relatively large, and have a carnose hypanthium and calyx. Unlike other Lythraceae with numerous stamens, those in *Sonneratia* seem to develop centripetally. The pollen grains (Muller, 1969) do not possess any distinct pseudocolpi (although their outline may approach a "heterocolpate" type);

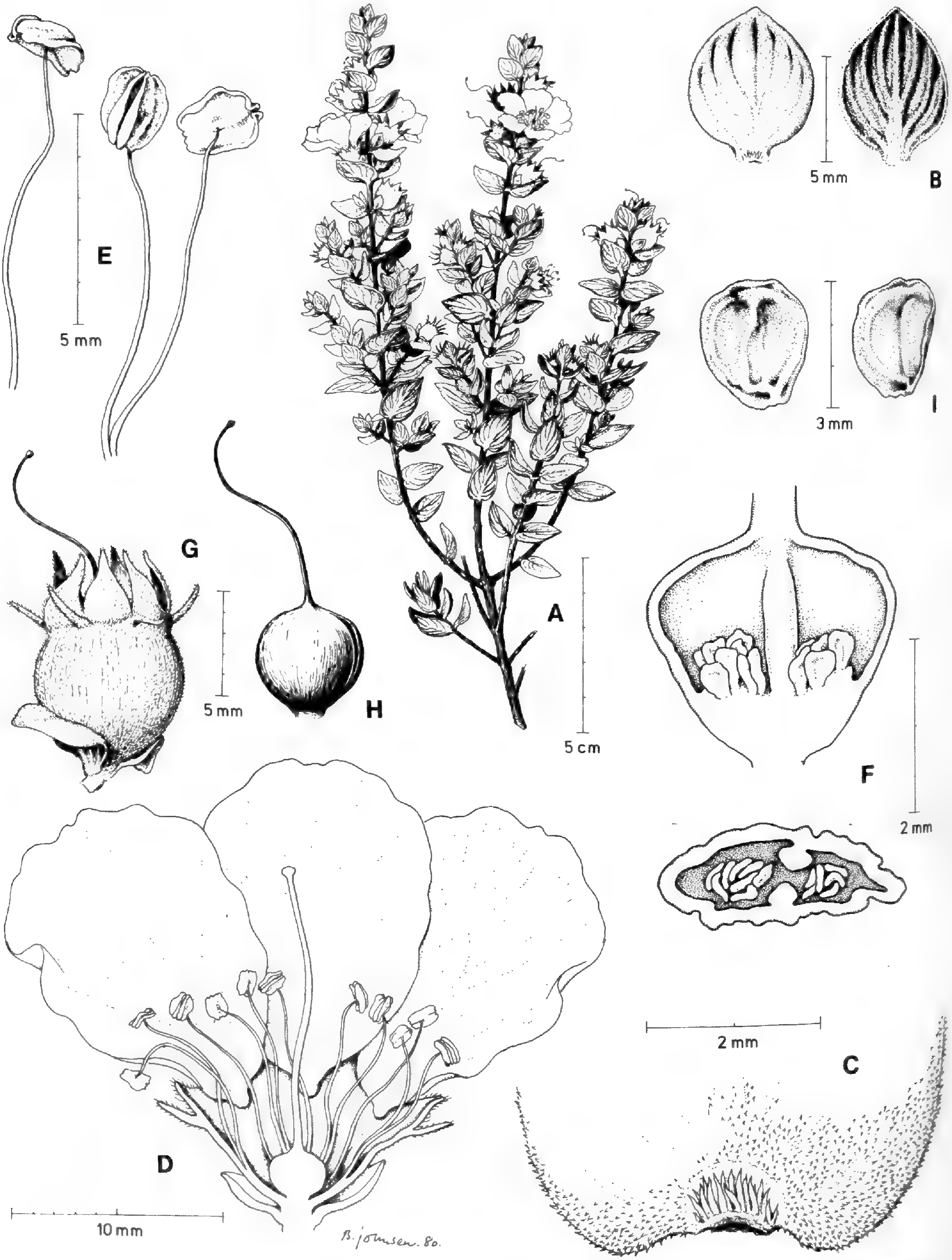


FIGURE 8. *Diplusodon sigillatus* Lourt. (*Irwin et al. 12447* from Brazil).—A. branch.—B. leaf, upper and lower side (left and right respectively).—C. leaf base showing axillary stipules.—D. flower, longitudinal section, note that the petals are inserted on hypanthium rim and have a basal adaxial "knee."—E. stamens in different views.—F. ovary in longitudinal and transversal section.—G. calyx in fruiting stage, showing processes from calyx lobe bases (see text).—H. fruit.—I. seeds. (Orig., del. B. Johnsen.)

they are porate, as in some other Lythraceae, e.g., *Diplusodon.*

The two genera differ from each other in a number of characters, and it seems questionable whether they are closely enough related to be treated together in the same subfamily. The difference in wood anatomy, demonstrated by van Vliet and Baas (1984); the different chromosome number; the different inflorescence type and fruit, etc., indicate that they are not particularly closely allied and some of the similarities that have been used to justify the previous family, Sonneratiaceae, are likely to depend on convergence. We suggest that each of them be treated as a subfamily (Sonneratioideae, Duabangoideae) under Lythraceae.

Also the genus *Rhynchocalyx,* treated below in the family Rhynchocalycaceae (see below), is often included in Lythraceae.

OLINIACEAE ARNOTT EX SONDER IN HARVEY & SONDER (1862)

This family consists of a single genus, *Olinia,* with perhaps eight or ten species (Rao & Dahlgren, 1969), of trees with opposite leaves, small stipules (Weberling, 1963), and unicellular hairs. The inflorescence is paniculate, with the branches ending as cymules of three flowers. Each flower is basally subtended by a short internode ending with some blunt teeth, a "calyculus," which is a stem structure. The flowers are epigynous, 4–5-merous (Fig. 9E), and have a tubular hypanthium continuing beyond the ovary. On the rim of this hypanthium are four or five elongate white lobes, which probably represent the calyx, and, inside these, and filling up most of the hypanthial mouth, are five thick, incurved, scale-like structures, which are best interpreted as petals. Below these, and inserted on the upper part of the hypanthial tube are the 4–5 isomerous stamens. The stamens, which are thus antepetalous, have a short filament and an anther with a carnose central connective and downwardly directed microsporangia (Fig. 9G). The pollen grains are heterocolpate, but the pseudocolpi are visible only on one hemisphere of the pollen grain (Patel et al., 1984). The inferior ovary is 2–5-locular with axile placentae. The style is short, and in our material the stigma reaches the level of the anthers.

Whether the flowers are self-pollinated or not deserves study. The embryology contributes no exceptional details, and the embryo sac, contrary to that in Penaeaceae, is monosporic and 8-nucleate. The fruit is drupaceous, and the cotyledons are spirally twisted.

The family approaches, in various respects, Combretaceae, Penaeaceae, Rhynchocalycaceae, Alzateaceae, and Lythraceae sensu lato, but is sufficiently different from all to be regarded as a distinct family. The interpretation of the "scales" as petals makes the flower correspond with Penaeaceae, where the stamens are alternisepalous, and Rhynchocalycaceae, where small petals alternate with the sepal lobes and are situated as hoods next to the stamens (in a fashion reminiscent of certain Rhamnaceae). Oliniaceae resemble the Combretaceae in chromosome number ($X = 12$), epigyny, and certain other details (see p. 682).

COMBRETACEAE R. BROWN (1810)

This family of ca. 20 genera and 400 species, occurring both in the Old and the New World, and particularly common in subtropical and tropical Africa, consists of trees, shrubs, and lianas, including mangroves, with alternate, opposite, or verticillate leaves lacking stipules or with minute stipules which are displaced into the leaf axils and dissected into multicellular glandular hairs (some species of *Terminalia* and *Buchenavia*). The stomata are anomocytic except in *Laguncularia* and *Lumnitzera,* where they are cyclocytic (Stace, pers. comm.). The trichomes consist of club-shaped or peltate glandular hairs and of nonglandular hairs which are of a distinctive type ("combretaceous hairs" of Stace, 1965, 1980). The inflorescences may be terminal on branchlets, as well as axillary, and consist of racemes, spikes, or heads with small or medium-sized, epigynous flowers with a usually fairly short hypanthium (sometimes absent or in *Quisqualis* to 8 cm long). This bears on its rim 4–5(–8) sepal lobes and equally many, mostly rather small petals, which are often lacking, as in *Pteleopsis* (Fig. 10). There are one or two staminal whorls, the outer sometimes having two or three times the normal number of stamens. The filaments are often long and colored, as may also be the whole flowers, and are inflexed in bud; and the anthers only rarely (*Thiloa*) have a "massive," fleshy connective. As in several related families, the pollen grains possess pseudocolpi (absent in *Strephonema*) and are tricolporate or triporate. A well-developed intrastaminal disc is very often

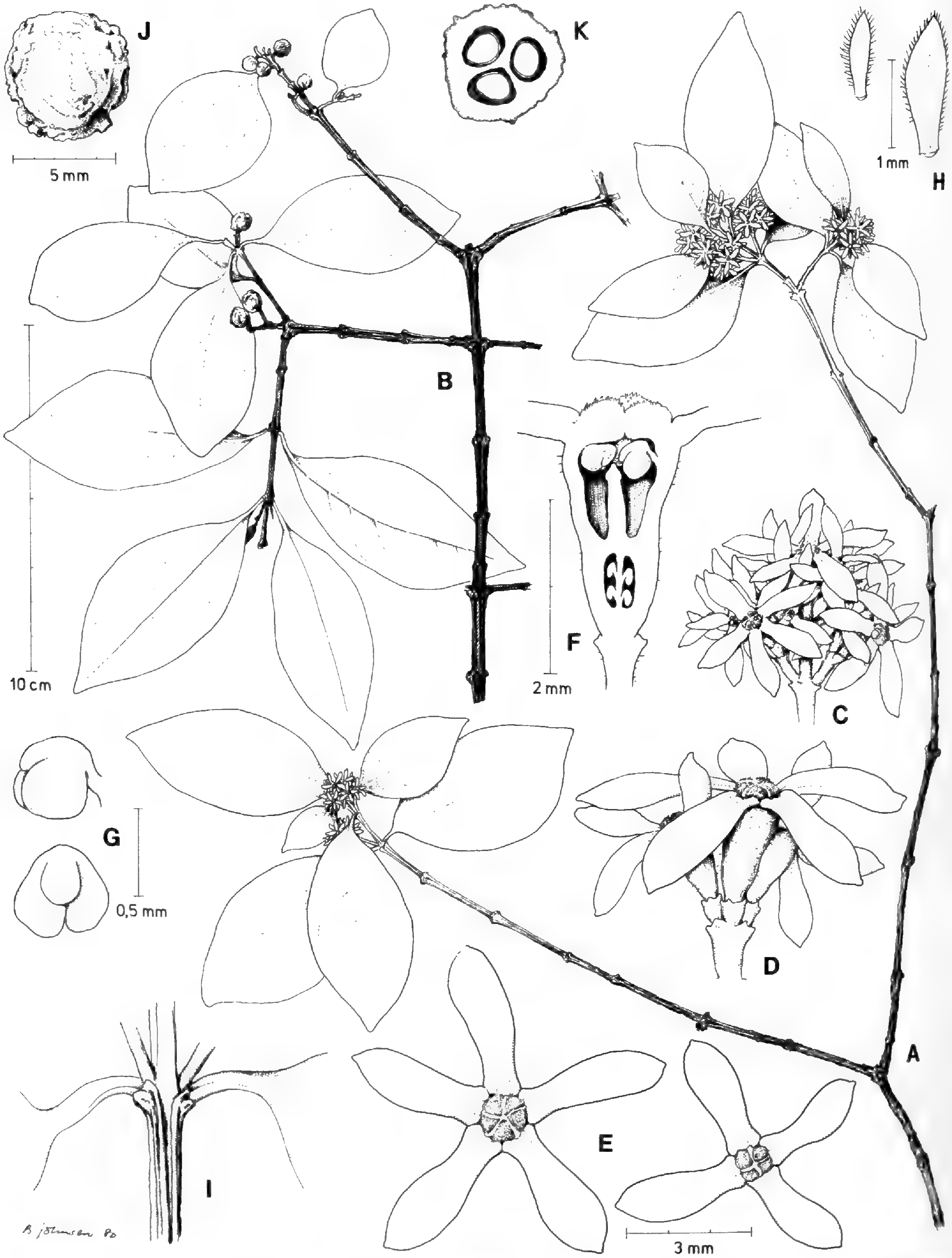


FIGURE 9. *Olinia aequipetala* (Delile) Cufad. (Oliniaceae), from collections made in Ethiopida: A, C–I. *Friis et al. 532*; B, J–K. *Friis et al. 1228*.—A. flowering branch.—B. fruiting branch.—C. inflorescence (panicle).—D. floral triad.—E. penta- and tetramerous flowers seen from above, showing elongate sepals and small papillate petals in hypanthial mouth.—F. flower, longitudinal section.—G. stamens, lateral and adaxial view.—H. caducous bracts.—I. leaf bases with auricles of stem lists.—J. drupe.—K. same in transverse section. (Orig., del. B. Johnsen.)

present. The mostly inferior ovary is 2–5-carpellate and unilocular, with 2(–6) pendulous ovules. An obturator tissue resembling that in Thymelaeaceae is sometimes present, which has been one reason for a suggested relationship between the two families. The embryology otherwise seems to be more or less of the basic myrtalean type [the occurrence of 4–sporic, 16-nucleate embryo sacs described by Mauritzon (1939) needs to be verified]. The fruit is generally one-seeded and indehiscent, rarely dehiscent; it is mostly leathery or drupaceous and often provided with conspicuous wings or ribs.

The family is dominated by the large genera *Combretum* and *Terminalia*; species of *Laguncularia* and *Lumnitzera* are mangrove trees; and *Quisqualis* species are creepers. The family is most closely related to those already described, but any close connections are not obvious.

This account of Combretaceae does not include *Strephonema,* which is a tropical, West African genus with three species. It was treated as a separate family, Strephonemataceae, by Venkateswarlu and Prakasa Rao (1971) on the basis of morphological, embryological (Tobe & Raven, pers. comm.), and anatomical differences from the other Combretaceae, but it is better treated as a subfamily of Combretaceae. The wood-anatomical differences include dimensions of vessels and fibers, the presence of fiber-tracheids, etc. (see also den Outer & Fundter, 1976, and van Vliet & Baas, 1984). The stomata are paracytic in *Strephonema* whereas they are anomocytic or cyclocytic in other Combretaceae (Stace, pers. comm.), but its species have the same type of characteristic ("combretaceous") hairs as have other Combretaceae. The flowers are actinomorphic, 5-merous, bisexual, petaliferous, and diplostemonous, and have a half-inferior ovary (inferior in other Combretaceae). The pollen grains lack pseudocolpi. The ovary is unilocular and has two pendulous ovules as in other family members. On the other hand, the massive, hemispheric cotyledons in the seeds of *Strephonema* contrast conspicuously with the folded, spirally twisted ones in other Combretaceae.

Thus, although fairly distinct, *Strephonema* is still considered a member of Combretaceae by most taxonomists, e.g., by Exell (1930), Exell and Stace (1966), and van Vliet (1979), who have a profound knowledge of the family. We agree with these authors that the genus should be placed in the Combretaceae family as a separate subfamily, Strephonematoideae.

ALZATEACEAE S. GRAHAM (1983)

Alzatea (Fig. 11) probably consists of two species. It was considered as lythraceous by Lourteig (1965), and was included in the widely circumscribed Crypteroniaceae by van Beusekom-Osinga and van Beusekom (1975). However, *Alzatea* is unique in several features. According to A. Graham and S. Graham, on whom we base part of this information, the species of *Alzatea* in Costa Rica "is almost epiphytic in habit, growing upwards via other trees in the cloud forests with only slender stem connections to the ground." It remains to be proven whether this is the case also with *A. verticillata* in South America. Baas (1979) and van Vliet and Baas (1975, 1984) in their anatomical evaluation found that *Alzatea* has different, trilacunar nodes, which they consider to be an ancestral rather than a derived feature (Baas, pers. comm.). In *Alzatea,* also, the arrangement of vascular tissue in petiole and midrib of leaves is different from that in Lythraceae, having a different ray type and possessing branched foliar sclereids, which are unknown in Lythraceae. Like the Lythraceae, rudimentary stipules are present, however (Weberling, 1968). Pentamerous apetalous flowers in a branched panicle are rare in Lythraceae. Stamen, connective, and microsporangium features are also different from those in Lythraceae; whereas, the pollen grains (Muller, 1975) lack any of the specializations, e.g., pseudocolpi, found in many Lythraceae and in all Crypteroniaceae and Melastomataceae. Unspecialized, similar pollen grains occur in some lythraceous genera, however. The placentation in *Alzatea* is parietal, thus differs from that in most Lythraceae. (*Ammannia microcarpa* DC., with parietal placentation, is aberrant within its genus and in Lythraceae; it exhibits reduced features, and does not approach *Alzatea.*) *Alzatea* according to Tobe and Raven (1984a) has a bisporic, *Allium*-type, embryo sac; as in *Rhynchocalyx* (Rhynchocalycaceae), but unlike all other Myrtales, the micropyle of the ovules is formed by the inner integument alone and the archesporium is multicellular. Also, according to S. Graham (1984; Tobe & Raven, 1984a), the seed shape and seed coat do not resemble those in Lythraceae.

Thus, it would seem justified to place *Alzatea* in a separate family, Alzateaceae. The family is formally described by A. Graham and S. Graham (Graham, 1984).

FIGURE 10. *Pteleopsis apetala* Vollesen from Tanzania; *Rodgers* coll.—A. leafy branchlet.—B. flowering branchlet with male and female flowers in the same inflorescence.—C. inflorescence.—D. female flowers.—E. same, longitudinal section.—F. fruits. (Orig., del B. Johnsen.)

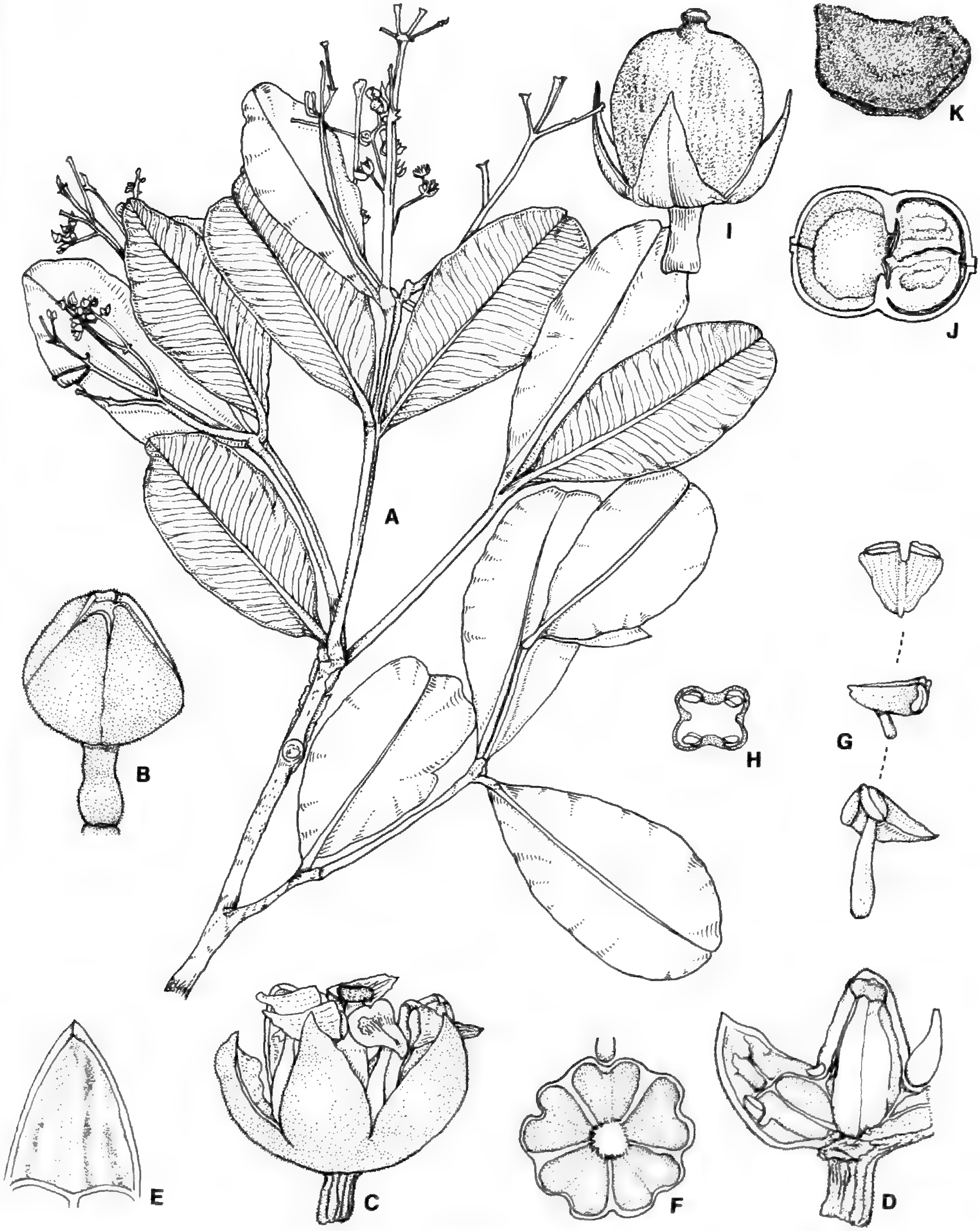


FIGURE 11. *Alzatea verticillata* Ruiz et Pav. (Alzateaceae), from Peru: A–H. *Klug 3349*; I–K. *Woykowsksi 6196*.—A. twig.—B. bud.—C. flower.—D. part of flower, interior.—E. interior of tepal.—F. disk.—G. stamen in different views.—H. transverse section of ovary.—I. fruit.—J. transverse section of fruit.—K. seed. (From Lourteig, 1965.)

PENAEACEAE GUILLEMIN (1828)

This is a fairly uniform family of ca. seven genera and 20 species restricted to the winter rainfall area of South Africa. The family consists of shrubs or shrublets with opposite, broad or narrow leaf blades, provided in their axils with small stipules dissected into rows of hair-like structures, which are usually glandular (but developed as relatively long hairs in *Stylapterus barbatus* A. Juss.; Dahlgren, 1967a). In this feature the family agrees with certain Lythraceae. The inflorescences vary between branched panicles and racemes, or may consist of a solitary terminal flower (*Saltera*). The flowers are consistently perigynous, 4-merous, apetalous, and haplostemonous, the four stamens alternating with the sepal lobes. The hypanthium is large and colored especially in *Glischrocolla* (Dahlgren, 1967b), *Endonema* (Fig. 12; Dahlgren, 1967c), and *Saltera* (Dahlgren, 1968), which are bird-pollinated. In *Endonema,* but not in the other genera, the stamens are inflexed in bud, in a way resembling that for *Mouriri* of Melastomataceae (Fig. 14C; see also Morley, 1953). The connective in all genera is massively carnose, and the introrse microsporangia sometimes, as in *Penaea* and *Stylapterus,* are only about half its length. The pollen grains are generally squarish or rectangular, 3–6-colporate, and always provided with pseudocolpi isomerous with the apertures. The four carpels form a 4-locular pistil with a narrow filiform to fairly stout style provided in *Stylapterus* and *Penaea* with four wings, in which case the stigmatic papillae are in commissural position between the apical lobes of the stylar wings, an indisputably derived condition. Whereas, in *Endonema* each locule has two lower pendulous and two upper ascending ovules, each locule in the other genera has only two ascending ovules. The embryo sac formation is peculiar, conforming to the 4-sporic, 16-nucleate *Penaea*-type (Stephens, 1909). The fruit is capsular.

Within Penaeaceae differentiation has taken place in two directions: (1) towards a large, rigid, and brightly colored hypanthium, in connection with ornithogamy, and (2) towards specializations of the style, with four prominent wings, and commissural stigmas in flowers of mediocre size and with yellowish (-purplish) color.

Penaeaceae show similarities to the Oliniaceae, Rhynchocalycaceae, Memecylaceae, Melastomataceae, and Lythraceae, most of which have perigynous flowers, minute stipular structures in axillary rows, pollen grains with pseudocolpi isomerous with the apertures, and prominently developed connectives.

The ancestors of Penaeaceae could have had common origin with Rhynchocalycaceae, in which the petals are somewhat reduced, the stamens alternate with the calyx lobes and are located on the rim of a receptacle, the connectives are well developed, the pollen grains are heterocolpate, the basic inflorescence type is paniculate, and the geographic distribution is close, though Rhynchocalycaceae are more subtropical in South Africa. There are several differences, however, e.g., the numerous ovules in the 2(–3)-carpellate pistil in Rhynchocalycaceae.

Penaeaceae are distinct enough to warrant separate familial status.

RHYNCHOCALYCACEAE JOHNSON & BRIGGS (1984)

This family consists of the genus *Rhynchocalyx* Oliv., with the single species *R. lawsonioides* Oliv., in the eastern parts of South Africa. *Rhynchocalyx* has previously been included in Lythraceae (Oliver, 1894; and several other authors) or Crypteroniaceae (van Beusekom-Osinga & van Beusekom, 1975) but is obviously out of place in both families.

It is a tree (Strey & Leistner, 1968) with decussate, opposite, entire leaves and fairly large paniculate inflorescences (Fig. 13) with small hexamerous flowers. These have an open hypanthium, which, with its six calyx lobes, has a stellate appearance. Six small, white, hood-like, lobate and unguiculate petals rise from the hypanthial rim. Below and opposite each of the petals is inserted a stamen, incurved in bud (as in *Endonema* of Penaeaceae and Memecylaceae) and with a basifixed anther having a somewhat broadened connective (as in the families mentioned). The pollen grains are 3-colporate-het-

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FIGURE 12. *Endonema lateriflora* (L. fil.) Gilg, an orthithogamous member of the South African family Penaeaceae: A–J. *Stokoe 2148*; K. *Zeyher 17.*—A. branch end with unifloral lateral inflorescences.—B. unifloral inflorescence ("flower").—C–E. leaves of lower, middle and upper pair in B.—F–H. stamen; adaxial, lateral, and abaxial view.—I. pistil.—J. capsule.—K. seed. (From Dahlgren, 1967c.)


A
B
C
D
E
F
G
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K

FIGURE 13. *Rhynchocalyx lawsonioides* Oliv. (Rhynchocalycaceae), from South Africa: A–H. *Wood 3124*; I–K. *Strey 6539*.—A. part of branch.—B. inflorescence.—C. flower bud.—D. flower.—E. two petals and two stamens on the hypanthial rim.—F. petal, flattened out.—G. stamen.—H. ovary in longitudinal section.—I. ripe fruit.—J. diagrammatic cross section of young fruit showing arrangement of seeds.—K. seed. (A–H from Oliver, 1894; I–K from Strey & Leistner, 1968.)

erocolpate, with three distinct pseudocolpi. The ovary is bi- (rarely tri-) carpellate and described by van Beusekom-Osinga and van Beusekom (1975) as unilocular, with two longitudinal placentae with numerous ovules, but it is partly bilocular. The style is simple and undivided. The fruit (Strey & Leistner, 1968) is a 2- (or 3-) locular capsule. It is cartilaginous, partly loculicidal, and contains 11–17 flat seeds per locule.

Unlike the Penaeaceae, *Rhynchocalyx* has the *Polygonum*-type embryo sac formation; it is peculiar in having a micropyle formed by the inner integument alone instead of both integuments; the nucellus, as in Lythraceae, has a multicelled archesporium, but there are several differences between *Rhynchocalyx* and Lythraceae that argue against a close relationship. (The embryological information according to Tobe & Raven, 1984b.) There are also embryological differences from *Alzatea* and *Axinandra* (Tobe & Raven, 1983b, 1984b), which support treating *Rhynchocalyx* as a family. The wood anatomy of *Rhynchocalyx* agrees well with that in Lythraceae, however (van Vliet & Baas, 1984). The chromosome number is $n = 10$ (Goldblatt, 1976), as is also the case in Penaeaceae, for example.

A comparison between Rhynchocalycaceae and other families is given by Tobe and Raven (1984b). The arguments for including the genus in Crypteroniaceae are weak, and it is also clear that the genus is best treated as distinct from the Lythraceae. A link with Penaeaceae (see under this family) is likely, but embryology does not support the inclusion of *Rhynchocalyx* in that family.

CRYPTERONIACEAE A. DE CANDOLLE (1868)

Crypteroniaceae (*Crypteronia*, Fig. 14; *Dactylocladus*, and *Axinandra* with perhaps a total of ten species; Shaw, 1973) are trees with opposite leaves, having a marked midrib and brochidodromous venation, the anastomoses of which are close to the leaf margin. Small stipules are present (note that such are seldom recorded for Melastomataceae). The inflorescences are profuse to poor racemules and the flowers small, often unisexual, 4–5-merous, and perigynous to epigynous, and may lack or have small petals, which in *Axinandra* are connate apically (and shed simultaneously as an umbrella). The stamens are alternisepalous and inserted on the margin of the receptacle, inflexed in bud, and with a wide connective, which is conduplicate in *Axinandra*. The pollen grains are 2- or 3-colporate, with apertures alternating with pseudocolpi. The ovary is 2–6-locular and develops into a chartaceous or woody capsule.

The embryology has been studied in *Axinandra* (Tobe & Raven, 1983b). It differs from all other Myrtales known in having an endothelium (i.e., integumentary tapetum).

This family has recently been circumscribed and redefined by van Beusekom-Osinga and van Beusekom (1975), who, in addition to the three southeastern Asiatic genera, *Crypteronia* (Fig. 15), *Dactylocladus*, and *Axinandra*, which we here refer to the family, also included the Central and South American genus *Alzatea* and the South African genus *Rhynchocalyx*, each with one species only. The two last-mentioned genera, according to these authors, make up Crypteroniaceae subfam. Alzateoideae with paniculate inflorescences, superior bicarpellate ovaries, numerous ovules, and chartaceous capsular fruits. However, they do not seem closely allied to the former genera, nor to each other, and are best treated as separate families, Alzateaceae and Rhynchocalycaceae.

The Asiatic genera (van Beusekom-Osinga, 1977) may form a monophyletic group, although even this is somewhat uncertain. Among them, *Axinandra* was considered by Meijer (1972) as particularly primitive due to its 5-merous flowers with 10(–12) stamens. The caducous petals fall off as a cap when the flower opens (as in *Eugenia*), and the capsular fruit opens with five valves. In these features the genus was said by Meijer to approach various other families, such as Lythraceae, Memecylaceae, and the tribe Macarisieae of Rhizophoraceae.

Morley (1953) comments on the relationship between *Axinandra* and *Dactylocladus* (Crypteroniaceae) and the genera of our Memecylaceae and Melastomataceae. He finds that the two genera differ from the Memecylaceae in lacking included phloem in the secondary xylem, in lacking terminal sclereids and anther glands, and in having anatropous rather than campylotropous ovules, antesepalous ovary locules, different floral vascularization, and capsular fruit. Thus, these genera should not be included among the Memecylaceae, but would require a separate subfamily. We believe they can, provisionally,

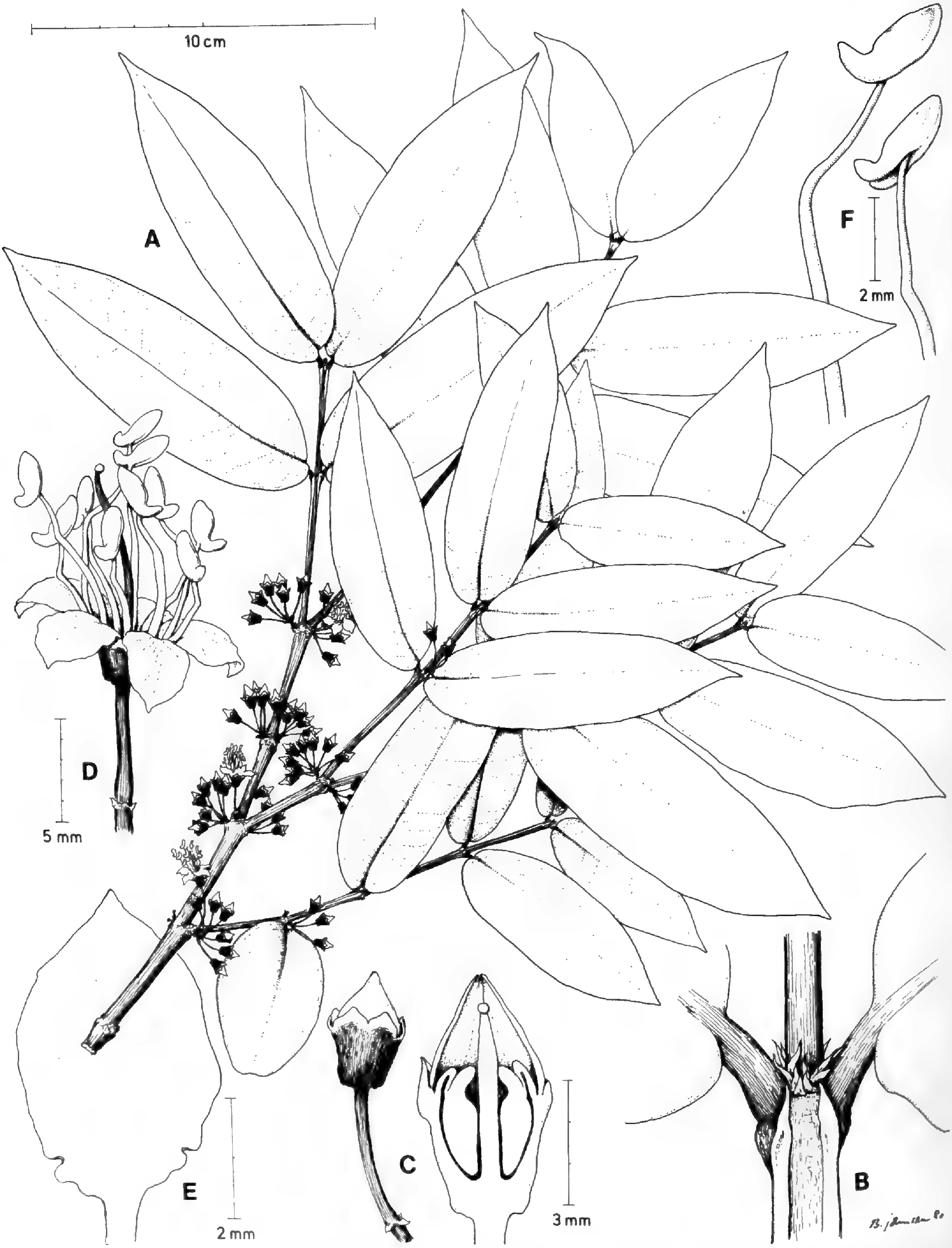

FIGURE 14. *Crypteronia paniculata* Kurz. (Crypteroniaceae), from collections made in Thailand: A–C. *Sangkachand et al. 1554*; D. *Larsen 8695*.—A. branch with spikes of male flowers.—B. branch tip showing auricles of stem lists.—C. male flower.—D. female flower. (Orig., del. B. Johnsen.)

be treated with *Crypteronia* in the family Crypteroniaceae.

MEMECYLACEAE DE CANDOLLE (1828)

Although there are still doubts about the distinctness of this family, it is recognized here by one of us (Dahlgren) in accordance with the conclusions by Johnson and Briggs (1984), the alternative being to treat it as a subfamily under Melastomataceae (Thorne). It consists of 6–8 genera, the New World *Mouriri* (Fig. 15) and *Votomita,* and the Old World *Lijndenia* (Bremer, 1982), *Memecylon, Spathandra,* and *Warneckea.* The distinctness of *Spathandra* is still in dispute. *Pternandra* is discussed below.

They are mainly large shrubs to huge trees with opposite leaves having mostly pinnate venation with indistinct lateral and intramarginal veins. Stipules are probably generally absent; but Figure 15B shows a species of *Mouriri* with a row of finger-like structures (dissected stipules), which agree with the stipules in various other families of Myrtales, e.g., Penaeaceae.

Anatomically the family stands out as distinct (van Vliet, 1981; van Vliet et al., 1981; van Vliet & Baas, 1984) in having included phloem of the foraminate type (lacking in Melastomataceae), diffuse and mostly solitary vessels (frequently in multiples in Melastomataceae), the fibers have distinctly bordered pits (in Melastomataceae the fibers are libriform). Fiber dimorphism occurs in many Melastomataceae but not in Memecylaceae.

The indumentum is much less developed than in Melastomataceae. The richness and variation of foliar sclereids (incl. terminal sclereids) is conspicuous. Stomata have been found to be paracytic (*Memecylon*) or occur in crypts (*Mouriri*). The leaf tissues contain crystal druses (Baas, 1981).

The flowers are generally small and less differentiated than in most members of Melastomataceae. The stamens are twice as many as the petals and have a carnose, compact connective generally provided with a gland, and the anthers are longitudinally dehiscent. As in Melastomataceae, Crypteroniaceae, and Penaeaceae, the pollen grains are consistently heterocolpate. The ovary is inferior and contains 1–5 locules, each with two to numerous ovules. The embryology largely coincides with that for Melastomataceae, except that the seeds are different. The fruit is baccate with large or (*Pternandra*) rather small seeds, generally with extensive, folded cotyledons (Bremer, 1981).

Morley (1953) defined this group by the presence of included phloem in the secondary xylem, pinnate leaf venation, occurrence of terminal sclereids on the vein endings in leaves and often in flowers, presence on the connectives of an elliptic or circular depressed gland, antepetalous ovary locules (when locules are isomerous with the petals), campylotropous ovules, relatively few and large seeds, and characteristic floral vascularization, all characteristics which do not apply to *Pternandra,* however. Morley (1953) considered the closest relatives of Memecylaceae sensu stricto to be the tribe Kibessieae, in which *Pternandra* (incl. *Kibessia*) has most of the memecylaceous features but leaf blades of the typical parallel, melastomataceous type. *Pternandra* also lacks terminal sclereids, it lacks a gland on the connective, and has numerous anatropous ovules and small seeds, but yet is probably best placed in Memecylaceae.

MELASTOMATACEAE A. L. DE JUSSIEU (1789)

The Melastomataceae consist of perhaps 195 genera and 3,500–4,000 species. These range from small, sometimes epiphytic herbs or shrublets to shrubs or, more rarely, lianas or trees. Nearly all have opposite leaves, which, characteristically, have 3–9(–19) main veins separate from the base of the blade. The leaves are entire in nearly all taxa, but have distinct, sometimes conspicuous teeth in *Sonerila tenuifolia* Bl., where the teeth seem to be an innovation and are different from those in Lythraceae and Onagraceae. Pellucid dots are generally absent, but occur in the genus *Microlicia,* where their presence and nature deserves attention. Stipules seem to be lacking. The nodes are unilacunar (van Vliet & Baas, 1984). Crystals occur as druses in all tribes except the Astronieae, where there are styloids instead; druses also occur in Memecylaceae and Crypteroniaceae where small styloids are also present (Baas, 1981). Interxylary (included) phloem appears to be lacking; libriform fibers are characteristic, and the fibers are often septate, these conditions representing differences from those in Memecylaceae (van Vliet & Baas, 1984). The stomata are generally anomocytic or polycytic (rarely diacytic, cyclocytic, or anisocytic), and the indumentum is extraordinarily differentiated, the trichomes being generally large, multi-

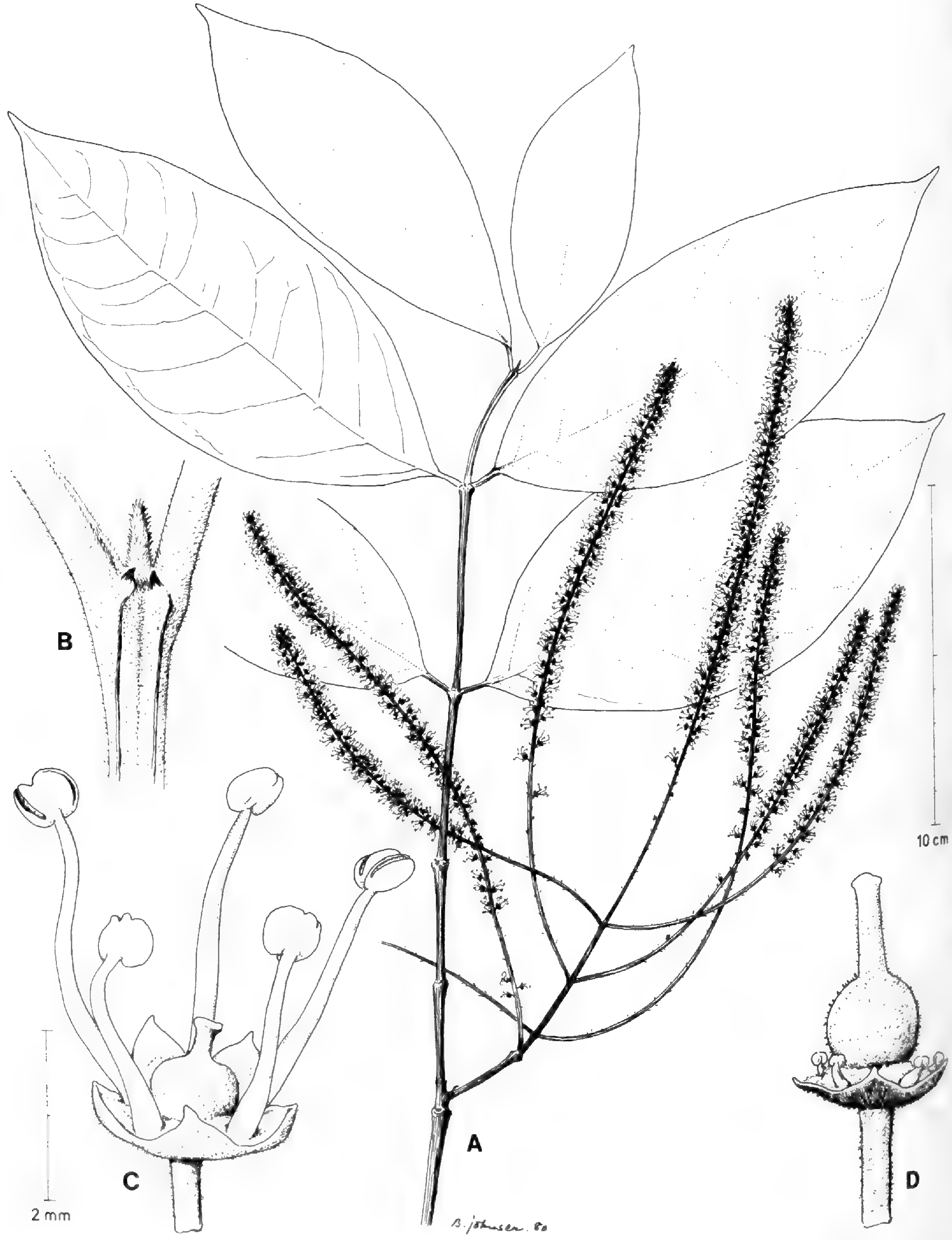

FIGURE 15. *Mouriri chamissoniana* Cogn., a Brazilian member of Memecylaceae; *Hatschbach 20223.*—A. branch.—B. bases of leaves showing axillary stipules as well as stem lists ending in "auricles."—C. floral bud, to the right in longitudinal section, showing inflexed filaments.—D. flower in full blossom.—E. petal.—F. stamens; note the difference in filament length within a flower. (Orig., del. B. Johnsen.)

cellular, and scale-like. The flowers vary in size from small and nearly actinomorphic to large, conspicuous, and distinctly zygomorphic, and are generally wholly or partly epigynous, the ovary generally densely beset with complex hairs. The petals, as in much of the order, are commonly pink to crimson or violet.

Stamens are in one or two whorls (diplo-, haplo-, and obhaplostemonous), with their filaments inflexed in bud and their connectives generally well developed, often prolonged or provided with appendages. The anthers are often poricidal but frequently open with longitudinal slits. The pollen grains as far as known (Patel et al., 1984; Carlo Hansen, pers. comm.) are consistently heterocolpate, being supplied with pseudocolpi or with intercolpate depressions isomerous with the usually three apertures.

The gynoecium is generally 3–5-carpellate, and the ovary 3–5-locular, only rarely unilocular where the partitions are dissolved, with axile or rarely basal placentation. The embryology is fairly typical of the order and shows no obvious specializations. The fruit is baccate or capsular with seeds smaller than in most genera of Memecylaceae. Its embryo also has smaller and less folded cotyledons, which may be equal or unequal (cf. Trapaceae). The seed coat lacks fibers in the exotegmen.

With this circumscription Melastomataceae becomes a rather homogeneous family. The genus *Pternandra* of Memecylaceae at least phenetically shows some features of Melastomataceae; some of these may be plesiomorphies (lack of connective gland, lack of terminal sclereids, small seeds), others convergences (leaf venation). It may be regarded as intermediate, which is an argument for including Memecylaceae as a subfamily in Melastomataceae, as preferred by one of us (Thorne).

PSILOXYLACEAE CROIZAT (1961)

This family is closely allied to Myrtaceae and, using a broad family concept, may well be included in that family (Schmid, 1980). It is monotypic, consisting of the genus *Psiloxylon* with the species *P. mauritianum* (Hook. f.) Baill. on the Mascarene Islands. The genus is a small tree with pseudo-alternate (disjunct-opposite), stipulate, glabrous, and gland-dotted leaves and small, axillary panicles. Divided myrtalean stipules are present at least in young plants (Johnson & Briggs, pers. comm.). The flowers are unisexual, 5(–6)-merous, and perigynous, with a nectariferous floral tube, free sepals and petals, and diplostemonous androecium. In the female and male flowers the stamen-like staminodia and a pistil-like pistillode, respectively, are present. The stamens are erect in bud, a rare feature in Myrtaceae, but the pollen grains are conspicuously similar to those in Myrtaceae. The tri- (bi-, quadri-) carpellate pistil is clearly superior and often has a (very) short stipe; it has an extremely short style and the (2–)3(–4) stigma-lobes are flat and reflexed. In these characteristics *Psiloxylon* differs from nearly all Myrtaceae. The ovary is trilocular and has axillary placentas, each with numerous anatropous ovules. The fruit is a berry. (Information mainly from Schmid, 1980.)

In anatomical respects (van Vliet & Baas, 1984), *Psiloxylon* shows a distinctive combination of features and has, for example, chambered, crystalliferous fibers, lacking in the Myrtaceae. *Psiloxylon* also has a cancellate testa, which is very rare in Myrtaceae.

In the light of a number of distinctive features it seems justifiable to treat *Psiloxylon* as a distinct family rather than as a member of Myrtaceae as treated by Schmid (1980). The presence of secretory cavities and sunken styles, and the pollen morphology are shared with the following two families and support the common evolution of Psiloxylaceae from the same ancestors as Myrtaceae and Heteropyxidaceae. With a broader family concept the three families could be treated as one (as preferred by Thorne).

HETEROPYXIDACEAE ENGLER & GILG (1919)

It is with doubt that this family is acknowledged here, by one of us (Dahlgren), in accordance with Johnson and Briggs (1984), the alternative being to include it in Myrtaceae either as a subfamily (as preferred by Thorne) or without discrimination at all (Schmid, 1980).

The single genus *Heteropyxis,* with three species in southeastern Africa, consists of shrubs or small trees with disjunct-opposite ("alternate"), entire leaves with minute stipules. The leaves, as in Myrtaceae and Psiloxylaceae, are gland-dotted. The anatomy seems to agree with that in Myrtaceae, although the cork is not stratified, as is usually the case in Myrtaceae; vasicentric tracheids are lacking (usually present in Myrtaceae) and axial parenchyma is lacking (rare in Myrtales) (data from Schmid, 1980). In some of these features Heteropyxidaceae agree with Psiloxylaceae. The inflorescence is a small panicle of unisexual, actinomorphic, perigynous, tetramerous or pentamerous flowers. Sepals and petals are imbricate and free, and the androecium, usually of (5–)8 stamens, are obdiplostemonous or rarely obhaplostemonous. The stamens are erect in bud, the anthers longitudinally dehiscent, and the pollen grains are triangular and syncolporate, similar to those in Myrtaceae, lacking pseudocolpi. The pistil is generally bicarpellate, with sunken style, much longer than in Psiloxylaceae, and with capitate stigma. The fruit is a dry loculicidal capsule with persistent style. The embryological information available is in accordance with the Myrtaceae.

Similarities between Heteropyxidaceae and Psiloxylaceae are the spiral phyllotaxy, the stamens that are erect in bud stage, and the reduced carpel number. Both are primitive in having perigynous flowers. On the other hand, Heteropyxidaceae differ from Psiloxylaceae as well as Myrtaceae in a number of respects (see Johnson & Briggs, 1984).

MYRTACEAE A. L. DE JUSSIEU (1789)

This is a large family of ca. 145 genera and more than 3,650 species (Schmid, 1980) with wide, chiefly tropical-subtropical distribution and a center in Australia, but also with many taxa in South America. As this family will be dealt with in more detail by other participants of this symposium, only a few remarks will be made here. Myrtaceae have generally been divided into two subfamilies, Myrtoideae and Leptospermoideae. Schmid (1980) reviewed the subfamilial history of the family and recognized two additional subfamilies: Chamaelaucioideae (formerly a tribe in Leptospermoideae) and Psiloxyloideae. For various reasons and in line with Johnson and Briggs' treatment of Myrtaceae (1984), we have excluded *Psiloxylon* and *Heteropyxis* as separate families (or subfamilies, Thorne), and abandoned the traditional division of Myrtaceae into (other) subfamilies.

The family is a fairly distinct one, characterized in particular by having gland-dotted leaves, stems, and floral parts (as do Psiloxylaceae and Heteropyxidaceae). In the presence of schizolysigneous secretory cavities filled with essential oils (monoterpenes, sesquiterpenes, phloroglucin derivatives of baeckerol, eugenin, and tasmonol types, etc.) Myrtaceae, Heteropyxidaceae, and Psiloxylaceae are distinctive in the order. The calyx and corolla are imbricate and the stamens are usually numerous, although very occasionally few. The inflorescences are basically paniculate. The evolutionary trends within Myrtaceae are presented in detail by Briggs and Johnson (1979). The flowers are nearly always epigynous and bisexual, nearly always actinomorphic, 4- or 5-merous (other merous conditions are not rare), with a floral tube of variable length often prolonged above the ovary, on the margin of which the sepals, petals, and normally numerous stamens are all inserted. The sepals or petals or both are occasionally fused, either into a cap (or operculum) that is shed at anthesis, or else the fused perianth ruptures irregularly. The androecium is usually polystemonous, very occasionally paucistaminal and then obdiplostemonous, diplostemonous, obhaplostemonous, or haplostemonous. When the stamens are numerous they may be evenly distributed or very occasionally appear in (basically five) fascicles (nearly always antepetalous); the fascicled condition is reminiscent of that in Hypericaceae, with the fascicles nearly always opposite the petals. The developmental succession of the polystemonous androecium is, however, centripetal. The connectives are only rarely enlarged although they usually have one or more apical secretory cavities (glands). The anthers dehisce by slits or (for example in certain sections of *Eucalyptus* and in the *Chamaelaucium*-group) by pores. The pollen grains are generally triangular, often syncolp(or)ate, and lack pseudocolpi. Staminodia are rarely present. There is great variation in number of loculi (carpels) of the pistil, which range from one to 16 per flower, three, four, five, and especially two being predominant (Schmid, 1980, tables 3, 4). The placentation is usually axile, occasionally subbasal, basal, or apical; the number of ovules per ovary is usually numerous, occasionally few, very rarely one. One feature of note is that the ovules are usually described as lacking a parietal cell. Davis (1966), however, suspects that the parietal cell is cut off so early that it has escaped notice, because parietal tissue is formed without periclinal divisions in the nucellar epidermis (except in *Psidium*).

The fruit is fleshy or dry, respectively a berry or loculicidal (very rarely circumscissile) capsule, very occasionally a drupe, schizocarp, or indehiscent, nutlike structure, and there is great variation in the shape of the embryo. Both fruit and embryo are useful in the division of the family. Each fruit usually contains one to few, though very occasionally many, fertile seeds. The endosperm is initially nuclear and is usually lost at seed maturity, occasionally a scant amount of endosperm being present. The embryo sometimes contains copious amounts of starch.

Except for Psiloxylaceae and Heteropyxidaceae, which Schmid (1980) included in Myrtaceae, the family shows no obvious connections with the other families of the order. *Punica,* in its polymerous androecium, lack of pseudocolpi, etc., is reminiscent of Myrtaceae (convergence), but the relationship is probably not close. A phylogenetic link with Lecythidaceae has been proposed but is not supported by detailed examination.

INTERRELATIONSHIPS OF FAMILIES AND EVOLUTION WITHIN MYRTALES

To approach the interrelations between families in Myrtales it may be profitable to deduce a probable original state for their common ancestors. This can best be done by comparing the character states of the myrtalean families inter se and by examining those of probably related orders, Rosales being chosen as the outgroup.

The myrtalean ancestors were probably woody plants with alternate or opposite leaves, the margins of which possibly had lateral teeth with a hollow, crater-like apex. Stipules were presumably present but minute, entire, and situated laterally. The stem had evolved bicollateral vascular strands and the vessel elements had alternate, vestured pits and end plates with entire perforation or scalariform perforation with few bars. Furthermore, the ground tissue of the wood consisted of fiber-tracheids, the wood parenchyma was paratracheal and apotracheally diffuse, and the rays were heterogenous (van Vliet & Baas, 1984). Crystals most likely occurred in the axial parenchyma and in the ray cells. The stomata probably were anomocytic, and no complicated trichomes were developed. The flowers, in determinate, paniculate inflorescences, were actinomorphic, perigynous, and diplostemonous, 5- or 4-merous, and petaliferous. The pistil was eusyncarpous with axile placentation, a simple style, and a lobate or branched stigma. The stamens did not have a particularly swollen or otherwise differentiated connective. The anthers dehisced longitudinally, the tapetum was glandular, and the pollen grains were binucleate at anthesis and most likely 3-colporate, lacking pseudocolpi; viscin threads were lacking. The ovules were anatropous, bitegmic, and crassinucellate with a parietal cell cut off from the archesporial cell in the nucellus. The embryo sac formation proceeded according to the *Polygonum*-type, endosperm formation was nuclear, and the ripe seeds had a very thin endosperm and a well-developed embryo probably containing protein and fat. The fruit was presumably capsular. In the seed coat, the exotegmen was probably not fibrous, and the mesotestal layer probably did not contain sclerotic cells.

The immediately ancestral forms were tannin plants with a flavonoid spectrum based on flavonols of the commoner types. Ellagic acid and ellagi-tannins were synthesized. Triterpenes likewise were presumably present, whereas triterpene saponins may or may not have occurred.

None of the extant families exhibits this combination of attributes, though the family approaching most closely the ancestral form of Myrtales would have been fairly similar to certain extant Lythraceae. In this family the leaves may have teeth of the kind mentioned above, although they are "cryptic," and the leaf margin can be ciliate. Pellucid dots with essential oils are lacking. The flowers are also generally perigynous and generally petaliferous, diplostemonous, and perfect; the pistil is basically eusyncarpous; and the embryology agrees closely with the general, unspecialized pattern in the order, with, for example, the *Polygonum*-type embryo sac formation.

However, in Lythraceae, the wood does not have fiber-tracheids but libriform fibers, which are generally septate. The stipules quite often are specialized and dissected, forming one or two groups of hair-like structures located in the leaf axils (Fig. 8c). The stamens are generally free from the hypanthial tube and inserted inside this, generally at or near its base. This condition is dubiously primitive in the order, and may be derived from the general condition where the stamens, like the petals, are inserted on the rim of the hypanthial tube. Furthermore, the pollen grains in at least nine of the 25 genera are heterocolpate, the heterocolpate condition being probably ancestral in the family but derived within the order. Finally, the seed coat with its fibrous exotegmen represents a specialized type.

Therefore, the Lythraceae should be excluded from consideration as wholly unspecialized. However, their position in the order is central, and they show close relationship with several of the families, including Penaeaceae, Rhynchocalycaceae, and Onagraceae.

A number of the supposedly primitive states are concentrated, perhaps to a higher degree than in Lythraceae, in Psiloxylaceae, Heteropyxidaceae, Myrtaceae, and Strephonematoideae, although each of the taxa is specialized in various respects. The varied rates of evolutionary specialization throughout the order are illustrated by *Psiloxylon,* which has retained the presumably ancestral condition of diplostemonous flowers with a wholly superior ovary but has libriform and septate fibers, which are presumably derived. Most Myrtaceae have numerous stamens and a more or less inferior ovary, but their wood is generally characterized by having fiber-tracheids.

We have refrained from giving a cladistic presentation of the probable evolution in Myrtales, as this is done elsewhere in this volume, by Johnson and Briggs (1984), on the basis of the same data. However, we find it appropriate to discuss the probable or at least possible evolutionary courses that might have taken place in the order, as our opinions may deviate in certain major as well as minor features from those of other authors.

An evolutionary line that probably diverged very early from the myrtalean ancestors is represented by Psiloxylaceae, Heteropyxidaceae, and Myrtaceae. These share some conspicuous features, such as the characteristic shape and aperture conditions (syncolpate) of the pollen grains (Schmid, 1980; Patel et al., 1984) and the presence of schizolysigenous cavities with essential oils visible as pellucid dots on the green parts. The first representative of this evolutionary line doubtless had diplostemonous flowers with superior ovary such as in present day Psiloxylaceae, but the latter are specialized in having, for example, unisexual flowers with an extremely short style and reflexed, flat and carnose stigma lobes. The great concordance in pollen morphology among Psiloxylaceae, Heteropyxidaceae, and many Myrtaceae indicates that this rather peculiar type evolved very early from proto-myrtaceous ancestors and later in many Myrtaceae gave rise to superficially simpler kinds. The fact that this kind of pollen is known already in the Cretaceous (ca. 72 million years ago), before any other certain Myrtales, also indicates that this group of families was differentiated from the myrtalean ancestors very early.

Also Onagraceae seem to deviate rather strongly from other Myrtales, and probably evolved as a lateral evolutionary line at an early stage. The evidence is somewhat contradictory in this respect. The family is an unusually distinct one in having the combination of epigynous flowers, pollen with viscin threads, *Oenothera*-type embryo sac formation, and tissues with calcium oxalate raphides. The latter three characteristics are absent from nearly all other Myrtales, and it is likely that all these character states are derived ones.

Thus, it is unlikely that other families, such as the Trapaceae, could have evolved from the onagraceous evolutionary line after these attributes had been acquired. In pollen-grain shape and pollen-wall structure Onagraceae show some general similarity to Myrtaceae, Heteropyxidaceae, and Psiloxylaceae (Nowicke, pers. comm.). But more conspicuous are a number of characteristics shared by Onagraceae and Lythraceae: wood with libriform and septate fibers; leaves with lateral teeth that have the same hollow and crater-like apex ("Fuchsioid" subtype, Hickey, pers. comm.), petals with similar, pinnate venation (Chrtek, 1969); and seed coat with fibrous exotegmen (Corner, 1976). With the probable exception of the leaf teeth, these attributes seem to represent derived states, and should be so considered. Convergent evolution of some of the derived states is not unlikely; though more likely is the alternative that Onagraceae diverged from proto-lythraceous ancestors after the wood and seed-coat structures had already evolved.

A probable appearance of epigyny in two independent lines of evolution in the onagraceous ancestors has been proposed by Eyde (1981) on the basis of the position of the nectaries on opposite sides of the ovary/hypanthium junction. In this feature the genus *Ludwigia* differs from all other Onagraceae.

The remaining families of the Myrtales form a somewhat coherent group, most families being characterized by so-called "heterocolpate" pollen grains, in which pseudocolpi are present between the true apertures. This feature is extremely rare in angiosperms outside the Myrtales, and it would be highly unlikely that pseudocolpi evolved independently in several phyletic lines within the order. Accordingly, we presume that the genetic constitution for pseudocolpi (whether expressed or not) evolved once in the common ancestors of these families, but that it may have "become lost," i.e., the attribute has not come to expression, in some lines. Thus, for example, in Lythraceae pseudocolpi occur in some but not in all genera (see above and in Patel et al., 1984); in some genera they are indistinct or inconsistently present. In Lythraceae at least *Lythrum* has pseudocolpi of the same number as the true apertures whereas in most lythraceous genera with pseudocolpi these are twice as many as the apertures.

Pseudocolpi are absent (or very indistinct) in the pollen grains of Alzateaceae and Lythraceae subfam. Punicoideae, Sonneratioideae, and Duabangoideae, in Combretaceae subfam. Strephonematoideae, and in Trapaceae, where the intercolpate depressions dubiously correspond to pseudocolpi. The first five taxa, which are all few in species, show strong affinity, as expressed by similarities in various respects, to families or subfamilies where the pollen grains possess pseudocolpi, and thus it is likely that their common ancestors had heterocolpate pollen grains.

Among the families where heterocolpate pollen grains are prevalent, some are characterized by having a seed coat with fibrous exotegmen and some lack fibers in this layer. A fibrous exotegmen was claimed by Corner (1976) to have great phylogenetic significance, and he suggested that this could serve as the basis for distinguishing a number of families from Myrtales sensu stricto as the order Lythrales. Although it is now obvious that this division would be unnatural, the fibrous exotegmen cannot be entirely ignored at the suprafamilial level.

A fibrous exotegmen occurs in Lythraceae with all its subfamilies, in Trapaceae, and Combretaceae (Oliniaceae remain to be investigated). Wood-anatomical, embryological, and other attributes strongly support close relationship between the subfamilies of Lythraceae, previously treated as several families, indicating thus considerable value for this seed coat attribute.

Trapaceae are often associated with Lythraceae (cf. Miki, 1959, who derives *Trapa* from *Lythrum* through *Hemitrapa*; but see also Vasil'ev, 1967, who disagrees with Miki). The family is unique in the order in many respects, however, as a specialized floating aquatic, the decussate leaves of which form a rosette. The leaf blades are provided with lateral teeth which deviate from those of other Myrtales in having a unique double apex (Hickey, 1981). The tetramerous, haplostemonous flowers are nearly perigynous; the fruit is dry, indehiscent, and provided with characteristic horns; the endosperm formation is arrested in the initial stage (as in orchids); one of the cotyledons is reduced; and the embryo is filled with starch. In these features *Trapa* has diverged strongly from other Myrtales and from any plausible ancestral type. The pollen morphology of Trapaceae may indicate affinity with the heterocolpate condition if the intercolpate areas between the meridional crests are homologous to intercolpate depressions and, hence, to pseudocolpi, but this is far from settled. (Intercolpate depressions substitute for pseudocolpi, for example, in various Melastomataceae.)

There is some variation within Lythraceae in the possession of sclereids. Thus, these are present in subfam. Sonneratioideae and Duabangoideae, whereas only few Lythroideae have unbranched sclereids restricted to the leaf petioles. The first two subfamilies also deviate from nearly all Lythroideae in having the stamens inserted on the rim of the hypanthial tube. Both these traits may be ancestral in the lythraceous line of evolution. In nearly all taxa of Lythroideae, the stamens are inserted inside the hypanthial tube or near its bottom and in subfam. Punicoideae the numerous stamens are inserted on the upper, inner part of the hypanthium. The flowers are generally diplostemonous in subfam. Lythroideae, but in certain genera (see p. 649) are haplo- or obhaplostemonous. In the relatively large flowers of subfam. Sonneratioideae, Duabangoideae, and Punicoideae, the stamens are numerous.

The different sequence of initiation of the androecium (centripetal in subfam. Sonneratioideae and Duabangoideae and centrifugal in subfam. Punicoideae and certain genera of subfam. Lythroideae) suggests that the multistaminate condition has evolved along several different lines in Lythraceae. Similarly, the haplo- and obhaplostemonous condition has certainly evolved along several separate lines in the family.

Within subfam. Lythroideae the polymerous, large-flowered genera, such as *Lafoënsia* and *Lagerstroemia* have numerous stamens (in the former only diplostemony, however) and unspecialized pollen grains, lacking pseudocolpi. In these features they are generally considered to be primitive, a view that we wish to challenge. More likely, an increase in floral size has involved increase in number of sepals, petals, and carpels and especially has favored an increase in stamen number. Lack of pseudocolpi is found in about half of the lythraceous genera studied, and does not seem to characterize natural groups of genera in subfam. Lythroideae (Graham & Graham, pers. comm.). The reasons for considering absence of pseudocolpi as derived in the family are mentioned elsewhere in this article. In contrast to all other myrtalean families the pseudocolpi, when present, tend to be double the aperture number, a condition which should be considered another derived character state.

How the first differentiation proceeded in the common ancestors of Lythraceae is perhaps impossible to deduce. As the insertion of stamens on the hypanthial rim is the normal state outside Lythraceae (some Combretaceae excepted), we presume that this was the ancestral state, and that their insertion inside the hypanthium is an apomorphy that arose in the ancestor of subfam. Lythroideae and, perhaps, Punicoideae. Punicoideae should have differentiated early from the latter line with its epigyny, increase in stamen number, indehiscence of fruit, acquisition of sarcotesta, etc. Alternatively, epigyny could have arisen in a common ancestor of the three small, unigeneric subfamilies. The discrepancy in anatomical details, in fruit, chromosome number, etc. suggest that *Duabanga* and *Sonneratia* differentiated early from each other, *Sonneratia* having possibly arisen at a later stage from the common lythraceous line.

A fibrous exotegmen is also found in the seeds of Combretaceae and, although not known in *Strephonema*, it is likely that it is the case in this genus, too. A considerable number of features are common to the subfamilies Combretoideae and Strephonematoideae, among them the combretaceous hair type (Stace, 1965), the racemose inflorescence type, obdiplostemony, at least some degree of epigyny (only partial in Strephonematoideae), and the unilocular ovary. *Strephonema* differs from other Combretaceae in the only hemi-epigynous flowers, in stomatal type and in several wood-anatomical features (van Vliet & Baas, 1984), which may justify separation at family level (see Venkateswarlu & Prakasa Rao, 1971), but as they are so obviously related, subfamily rank may be sufficient.

Oliniaceae agree with Combretaceae in several features, e.g., epigyny and the frequent occurrence of small petal scales, and also share the basic chromosome number ($X = 12$) and the geographical distribution, centered in Africa, but seem to belong rather to the following branch.

A number of families, mostly with heterocolpate pollen grains, have seeds without a fibrous exotegmen but often with sclerotic cells in the mesotestal layer. Although Oliniaceae are unknown in the latter respect, they probably belong in this group as is indicated by the number of features shared with Penaeaceae and Rhynchocalycaceae. These families are Melastomataceae, Memecylaceae, Crypteroniaceae, Rhynchocalycaceae, Penaeaceae, and Alzateaceae. Alzateaceae (*Alzatea*) probably belong to this group, although their pollen grains lack pseudocolpi. In all these families the leaves have a fixed, opposite phyllotaxy, and the stamens are inserted on the hypanthial rim, both features of which may, however, be ancestral (plesiomorphies). The connective is also frequently enlarged in these families.

The two unigeneric families Alzateaceae and Rhynchocalycaceae share a number of wood-anatomical characters (van Vliet & Baas, 1984), which makes it likely that they are closely allied, and in which they differ from especially Penaeaceae, which they otherwise resemble in floral characters. It is extraordinarily difficult to reveal whether wood-anatomical features have evolved by convergence here. Fiber-tracheids, which are considered primitive, are found in Penaeaceae, Memecylaceae, and Crypteroniaceae, whereas libriform and septate fibers have arisen in Melastomataceae and, probably independently, in Oliniaceae, Rhynchocalycaceae, and Alzateaceae; the last three families perhaps being rather closely allied.

Whereas Memecylaceae have fiber-tracheids and solitary vessels, they are derived in having included phloem and also epigynous flowers, and, as a rule, large seeds with curved embryos. The Crypteroniaceae, here restricted to the three Asiatic genera *Crypteronia, Dactylocladus*, and *Axinandra*, are a variable group which also has retained primitive wood features but adopted diverse specializations in the flowers of each genus. Whether all three genera have an integumentary tapetum, as in *Axinandra* (Tobe & Raven, 1983b), is uncertain. Parallel are the Melastomatoideae which are specialized both in the wood with libriform and septate fibers and aggregated vessels, in their more developed indumentum, and in their leaf venation.

It is conspicuous that the mentioned three families show very few synapomorphies, and thus may not be so intimately interrelated as has generally been presumed.

Penaeaceae, which have also retained a primitive wood anatomy, approaches the mentioned families, but are also closely connected with Oliniaceae, Rhynchocalycaceae, and Alzateaceae in various floral characters, e.g., in the obhaplostemonous condition. The bisporic *Allium*-type embryo sac in Alzateaceae (*Alzatea*) (Tobe & Raven, 1984a) may or may not be seen as a step in the direction toward the tetrasporic *Penaea*-type of Penaeaceae; at least the deviation from the *Polygonum*-type may have a common genetic basis. Both families have apetalous, perigynous flowers with prominent connectives. Alzateaceae are, however, very isolated by having trilacunar nodes and a different arrangement of vascular tissue in petiole and midrib of leaves (van Vliet & Baas, 1984), pollen grains lacking pseudocolpi (Muller, 1975), which we consider a derived state in this case, and a bicarpellate unilocular ovary with parietal placentation. In all this it appears as a distinct and isolated taxon, and the close connection with *Rhynchocalyx* indicated by the bicarpellary ovary and other details that caused the treatment of these genera in a subfamily of Crypteroniaceae, earlier, may largely be due to convergence.

Penaeaceae, Rhynchocalycaceae, and Oliniaceae, all with African distribution, may be closely interrelated, the last two more advanced in wood anatomy. Penaeaceae and Rhynchocalycaceae in particular resemble each other in the basically complex paniculate inflorescences, the obhaplostemonous flowers, the conspicuous connectives of the anthers, the heterocolpate pollen grains, and the basic chromosome number ($X = 10$), but the differences in wood anatomy, carpel and seed number, etc., still indicate some distance.

Oliniaceae and Penaeaceae each have a number of characteristic features (autapomorphies) but the two have rather few of their own synapomorphies.

We consider it very difficult to speculate about the interrelationships and evolutionary sequences for the Melastomataceae-Memecylaceae-Crypteroniaceae-Penaeaceae-Oliniaceae-Rhynchocalycaceae-Alzateaceae group, and refer to alternative interpretations presented by Johnson and Briggs (1984). Small differences in interpretation and small deviations from the most parsimonious evolutionary courses in this part may strongly change their evolutionary model.

Families Alledgedly Related to or in Various Respects Conspicuously Similar to Myrtales

Certain families have traditionally been linked with Myrtales, viz., Haloragaceae, Rhizophoraceae, Lecythidaceae, Thymelaeaceae, and, less often, Elaeagnaceae. In addition to these, there are a few families which have a combination of attributes similar enough to those of myrtalean families that they also deserve mention here. These include Elatinaceae, Coridaceae, and Chrysobalanaceae.

THYMELAEACEAE

Thymelaeaceae, with perhaps 500 species in 50 genera (Shaw, 1973; Cronquist, 1981), are sometimes included in Myrtales (and are still so placed by Cronquist, 1968, 1981, 1984), and the family indeed possesses a number of myrtalean attributes. Some of these are evaluated here.

The family consists mainly of shrubs (rarely trees, lianas, or herbs). Most, but not all genera (not the Gonystyloideae), agree with the myrtalean families in possessing intraxylary (and often interxylary) phloem, vestured pits, and presence of elongate crystals in the wood (van Vliet & Baas, 1984). The phloem is permeated by a network of tough fibers. The leaves are alternate, opposite, or verticillate, entire, and have mucilaginous epidermal cells. They lack stipules, representing a difference from most Myrtales. The flowers are frequently 4-merous and perigynous with sepals, petals, and two whorls of stamens (diplostemonous) located on a more or less well-developed, frequently cylindrical or campanulate and brightly colored hypanthium. The petals are generally lacking or are small or reduced to entire or 2-cleft scales (cf. Oliniaceae). The pollen grains are pantoporate and crotonoid, reticulate or rarely with no sculptural pattern and are wholly unlike those in the myrtalean families, without connection with wind pollination, and are dispersed in the trinucleate stage, which is rarely the case in Myrtales. The pistil consists of two or rarely up to 12 carpels and may have as many locules, but it is generally unilocular, with a single, often excentric style (considered pseudomonomerous), a condition not met with in Myrtales, where the most nearly similar condition is that found in Combretaceae. Thymelaeaceae, like a few Combretaceae, also have an obturator descending from the base of the stylar canal to the ovules, and, as in the latter family, the ovules are pendulous. The embryological features differ to a considerable degree from the basic pattern in Myrtales (Tobe & Raven, 1983a). The fruit in Thymelaeaceae is generally indehiscent, rarely a loculicidal capsule. As in Myrtales, the seed generally possesses little endosperm; its embryo is rich in fatty oils and, as in some Myrtales (e.g., in Melastomataceae), has expanded, flat cotyledons.

Whereas some of these attributes might indicate a position in Myrtales, the embryological and chemical evidence strongly argues against this. Among the chemical features of Thymelaeaceae that may be mentioned are a lack of tannins, lack of ellagic acid, a different flavonoid spectrum (cyanidin, pelargonidin, delphinidin, methylated anthocyanidins, and myricetin all lacking), and presence of coumarins like daphnin and daphnetin. The lack of bicollateral vascular strands in the relatively primitive Gonystyloideae indicates that the thymelaeaceous ancestors did not have internal phloem. A number of taxonomists believe that Thymelaeaceae approach most closely Euphorbiales and Malvales, although further evidence for this affinity would be desirable. The very distinctive pollen of Thymelaeaceae is totally distinct from that of any Myrtales and similar to that of most Euphorbiaceae. There is also similarity between Thymelaeaceae and Euphorbiaceae in seed wall structure (Corner, 1976), in which Thymelaeaceae differ from the myrtalean families. Both authors consider that Thymelaeaceae should be placed near Euphorbiaceae, and that these two families are related to Malvales.

It seems important, in this context, to reconsider the homogeneity of Thymelaeaceae. Some evidence suggests that the Gonystyloideae are out of place in this family, and may, moreover, not even be closely allied to it. If this is supported by further evidence, then some of the arguments, but by no means the most important ones, against an affinity with Myrtales are removed. Yet, chemical, embryological, pollen-morphological, and other evidence still argues strongly against placement of Thymelaeaceae in this order. On the basis of pollen, Gonystyloideae do resemble other Thymelaeaceae closely in their unique exine, and the family is probably natural (Nowicke, pers. comm.).

HALORAGACEAE

This family has often been placed in Myrtales by virtue of its often opposite leaves with minute stipules, its 4-merous, basically diplostemonous flowers with four carpels, its similar embryology, and its exendospermous seeds. The family has recently been studied in detail by Orchard (1975, and various other papers).

Many vegetative features are in accordance with those in Myrtales; however, internal phloem and vestured pitting are absent. According to Hickey and Wolfe (1975), who assigned Haloragaceae to Hippuridales, the leaf teeth are of the Rosoid type (similar teeth occur in some Onagraceae and Lythraceae; Hickey, 1981). Stipules (see above) are present and of a vestigial kind, as in Myrtales. Inflorescence characteristics provide little assistance in assigning Haloragaceae to any major complex. The floral anatomy of Haloragaceae (Orchard, 1975) shows similarity to that in Cornales and Araliales rather than to that in myrtalean families. Pollen morphology shows features connected with wind pollination, and comparisons with other groups (Orchard, 1975) give no clear indications of phylogenetic affinity. The pollen grains are shed in the tricellular stage as in Araliales, but unlike Myrtales. The gynoecium lacks a single style, and the stylodial parts are either very short, or there are separate stylodial branches, as in Araliales. The fact that the anther wall formation in certain taxa of Haloragaceae is of the monocotyledonous type may not be very informative because the dicotyledonous type also occurs in the family. More interesting, perhaps, is the fact that the endosperm formation in *Haloragis* and some species of *Myriophyllum* is of the possibly more basic cellular type, which is not known to occur at all in Myrtales. Embryo-sac formation is of the *Polygonum*-type, excluding any origin from within Onagraceae, and the embryogeny is of the *Myriophyllum* variant of the Caryophyllad type, in which the family differs from all Myrtales (Kapil, 1962; Kapil & Bala-Bawa, 1968). The seeds are often fairly rich in endosperm, which is not so in Myrtales; but in Araliales the endosperm is even more copious and the embryo proportionally smaller than in Haloragaceae.

Our conclusion is that Haloragaceae seem to comprise a fairly isolated family. They possess a number of myrtalean attributes but these are counterbalanced by several dissimilarities. One of us (Dahlgren) cannot support Orchard (1975) in his conclusion that Haloragaceae has its closest connection with Cornaceae, because the unitegmic, tenuinucellate ovules, lack of tannins, common presence of iridoids, and other details in Cornales (see below, p. 695) seem incompatible with the above-mentioned features of Haloragaceae. Orchard also found Haloragaceae to be similar in various respects to Rhizophoraceae and Combretaceae, the latter of which is clearly myrtalean. Thus Haloragaceae may better be treated in an order separate from, but near Myrtales. In accordance with Orchard's findings, Haloragaceae should be separated from Gunneraceae and Hippuridaceae. Its position is possibly closer to Araliales (near which it was placed in Engler & Prantl's "Die Natürlichen Pflanzenfamilien") than to Cornales. However, one of us (Thorne) agrees with Orchard in placing Haloragaceae in Cornales, and considers Gunneraceae and Hippuridaceae (see below) as related families in the Halorагineae.

RHIZOPHORACEAE

The homogeneity of Rhizophoraceae needs careful study. Such segregates have been described as Anisophylleaceae and Cassipoureaceae. Rhizophoraceae are trees or shrubs, tanniniferous as in myrtalean families, and with opposite or alternate leaves. The stipules in some mangrove genera (Rhizophoreae) are relatively large and entire, but in another generic group they are minute and even dissected into minute components situated in the leaf axils. Contrary to the Myrtales (except *Alzatea*), the nodes are trilacunar. The vessel elements in some Rhizophoraceae have scalariform or mixed scalariform/simple perforation plates, which are barely known in Myrtales. The flowers show similarities with those in myrtalean families (those in *Macarisia*, for example, with flowers as in Lythraceae). They vary from nearly hypogynous or perigynous (e.g., *Ceriops*) to hemi-epigynous (*Rhizophora*) or epigynous, and have variable merous conditions, including the tetramerous (cf. Sonneratiaceae). A hypanthium extending beyond the ovary occurs in some genera with epigynous flowers. Also the basically diplostemonous flower type is in agreement with Myrtales; in *Kandelia* the stamens are numerous (cf. *Lagerstroemia* in Lythraceae). An intrastaminal nectariferous disc is generally present in the flower (cf. Combretaceae). The pollen grains are tricolporate and comparable to the basic myrtalean type. There are two to six carpels forming a pistil with as many locules (rarely a single locule) and with a simple style. The ovules are bitegmic and crassinucellate although the integuments have more cell layers than is usual in myrtalean families and the nucellus is destroyed much earlier in development (Mauritzon, 1939). The baccate to capsular fruit contains one or few seeds, the seed coat of which Corner (1976) found to resemble that in some myrtalean families as well as that in Lecythidaceae. The seeds of several genera contain more endosperm than is found in myrtalean families.

Chemically there is hardly any conspicuous feature to distinguish Rhizophoraceae from Myrtales, but the combination of chemical attributes is not unusual. To one of us (Dahlgren) the lack of iridoid compounds and the richness of tannins argue strongly against a position of Rhizophoraceae in the Cornales, which is further supported by the embryological features: bitegmic, crassinucellate ovules, formation of parietal cells, and nuclear endosperm formation. The other of us (Thorne), however, prefers to place Rhizophoraceae in Rhizophorineae, near Halorагineae, in his Cornales (which constitute with Araliales his Corniflorae). He regards Corniflorae as having common ancestry with Rosiflorae and Myrtiflorae, and believes the probable common ancestors of these three superorders as being most nearly represented today by various members of the Saxifragaceae, in the broadest sense.

It is our conclusion that Rhizophoraceae should be excluded from Myrtales, but that they possess (in diverse genera) a combination of features likely to have occurred in pre-myrtalean ancestors, which could well indicate a fairly close common origin.

LECYTHIDACEAE

The family Lecythidaceae (incl. Asteranthaceae, Barringtoniaceae, Foetidiaceae, and Napoleonaceae; Prance & Mori, 1977, 1978) has frequently been placed in Myrtales, alternatives being its inclusion in Theales, as suggested independently by both of the present authors (Dahlgren, 1975a, 1980a; Thorne, 1976, 1981), or its treatment in a separate order (Cronquist, 1968, 1981).

Lecythidaceae are mainly trees, which, contrary to Myrtales, lack internal phloem and vestured pits. The vessels sometimes have scalariform, although more often simple, perforation plates. The leaves are consistently alternate and entire, and in certain genera, at least, are provided with minute stipules; for this last reason and other reasons the family is considered to be myrtalean by Weberling (pers. comm.). Stomata are anisocytic, a condition rather rare in Myrtales (but known within Onagraceae and Melastomataceae). The flowers have variable merous conditions, and are commonly large. They are hemi-epigynous or epigynous, often with connate sepals. The petals are broad and imbricate (rarely lacking). There are generally numerous stamens and staminodia, symmetrically or asymmetrically disposed and developing in centrifugal sequence, as in most Theales. The pollen grains, at least in certain genera, are trinucleate when dispersed, and the tapetum is reported to be amoeboid. In both of these features the family deviates strongly from the myrtalean pattern. The pollen grains are tricolpate, often syncolpate (the *Planchonia*-type; Erdtman, 1952) or tricolporoidate, whereas, the simply colpate condition is unknown in the Myrtales. The ovary is 2–6-carpellate, with as many locules, and has a simple style. Placentation is axile to basal, and the ovules bitegmic and tenuinucellate, with the integuments being thicker and the nucellus more rapidly destroyed during its development than is the case in myrtalean taxa (Mauritzon, 1939), *Axinandra* excepted (Tobe & Raven, 1983b). A parietal cell is not formed. In these latter attributes Lecythidaceae are thealean. The fruits are of various kinds and often very large (Prance & Mori, 1978), and also the seeds (as in *Bertholletia*) are sometimes conspicuously large. The endosperm is chiefly or entirely absorbed during seed development and the embryo is large and rich in fat, as in myrtalean families.

The chemical contents of Lecythidaceae largely agree with those of myrtalean families (see above), but also agree with those in Theales. Lack of internal phloem, relatively more primitive vessels without vestured pitting, presence of wedge-shaped phloem-rays, alternate leaf arrangement, polymerous, centrifugally developing androecium, and tenuinucellate ovules all indicate thealean affinity, as does the lack of endosperm in the ripe seeds. A funicular aril, as found in some Lecythidaceae, has its correspondence in the thealean Clusiaceae. We do not claim, here, that the position of Lecythidaceae in Theales is settled, but a position in that order, especially in its own suborder, seems most appropriate.

ELATINACEAE

The small aquatic family Elatinaceae is generally considered to be thealean, but deviates from most Theales in some features, such as in having stipules and in having crassinucellate ovules.

The family consists of *Elatine* and *Bergia*, which are herbaceous, with the exception of the partly suffrutescent *Bergia suffruticosa* Fenzl. The leaves are opposite or verticillate and possess small interpetiolar stipules. Neither internal phloem nor vestured pitting has been reported. The small flowers are solitary or aggregated in cymes in the leaf axils and possess six or fewer (sometimes four) sepals and an equal number of petals, and are diplostemonous or haplostemonous. Hypanthial as well as disc structures are lacking. The pollen grains are tricolporate, bi- or trinucleate when dispersed, and the 2–5 carpels form a syncarpous, 2–5-locular ovary with bitegmic, crassinucellate ovules and nuclear endosperm formation. The seeds have little endosperm (see also Tobe & Raven, 1983a), and the embryo varies from nearly straight to strongly curved. It is filled with protein and fat.

This little family exhibits a combination of fairly common attributes which are also found in many Myrtales and Theales. The lack of internal phloem and vestured pitting, the very different interpetiolar stipules, and the hypogynous rather than perigynous flower argue against a position in Myrtales.

CORIDACEAE

The monotypic family Coridaceae recognized by one of us (Dahlgren) is normally considered a comfortable member of Primulales and the single genus, *Coris*, is most often treated in Primulaceae. Sattler (1962) provoked new ideas in finding similarities between *Coris* and certain Lythraceae, for example in the differentiation of calyx. The following similarities between *Coris* and Lythraceae were mentioned by Sattler: (1) descending initiation of the sepal primordia in *Coris*, occurring also in *Cuphea*; (2) similar epicalyx-like structures; (3) valvate aestivation of calyx lobes in both groups; (4) strongly convex floral apical meristem in *Coris* and *Cuphea*; (5) the centrifugally initiated petals in *Coris* and in *Cuphea*, *Lythrum*, and *Ammannia*; (6) single antepetalous staminal whorl in *Coris* and in lythraceous taxa, such as *Diplusodon hexander* DC.; (7) carpel initiation, starting as an annular ridge in *Coris* and in *Cuphea*; (8) strongly reduced septa in the ovary in certain Lythraceae, reminiscent of the condition in *Coris*, where there is a free central placental column; (9) zygomorphic flowers in *Coris* and, although weakly, in some Lythraceae; (10) similar pale crimson petal color; and (11) secretorial cavities in *Coris* and *Cuphea*.

The ovules in *Coris* are bitegmic and tenuinucellate; in the latter respect they differ from those in Myrtales. In the genera of Lythraceae studied by Joshi and Venkateswarlu (1935a, 1935b, 1936) the ovules are crassinucellate and cut off a parietal cell, although in the smaller-flowered genera the nucelli tend to have fewer cells. The condition in *Coris* is at present being investigated by Bolt-Jørgensen (Copenhagen). It seems that many features of Lythraceae and *Coris* are held in common, and at the present point it not easy to establish whether these have mostly evolved by convergence, so that we can reject Airy-Shaw's and Sattler's hypothesis of an affinity. The overall pattern of placentation and embryology in *Coris* is primulaceous. Species of *Nesaea* in Lythraceae (Fernandes, 1978, 1980) are superficially quite similar to *Coris*.

Among the differences between *Coris* and Lythraceae thus remaining to be explained are the alternate exstipulate leaves, the lack of internal phloem, the wholly free-central placentation, and the tenuinucellate ovules of *Coris*, all non-myrtalean features.

Thus both of the authors reject (Thorne strongly so) placement of *Coris* in Myrtales.

CHRYSOBALANACEAE

The members of this family have alternate, simple, entire, and stipulate leaves, the stipules being small but not as minute as in myrtalean families. The stems lack internal phloem (Prance, pers. comm.) and vestured pits in the vessel elements. In flower construction Chrysobalanaceae show conspicuous similarities to myrtalean families, being, for example, perigynous with a frequently conspicuous hypanthium, on the rim of which sepals, (often small) petals, and stamens are inserted. The perianth whorls are 5-merous. Stamen number is variable, although a diplostemonous basic condition (as in *Licania*), is probable, from which secondarily oligo- and multistaminate conditions have evolved. When numerous, the stamens may be united in groups. The pollen grains are 3-colporate. Arguments against considering Chrysobalanaceae as rosaceous, are, for example, the occurrence of foliar sclereids and the syncarpous (although gynobasic and generally pseudomonomerous) character of the gynoecium when this is 2- or 3-carpellate. A reduction of carpel number to one (i.e., a secondary, truly monomerous condition) no doubt also occurs in part of the family (cf. the discussion under Elaeagnaceae). The embryology of the family is very similar to that in families of Theales (Tobe & Raven, 1984d), which favors inclusion of Chrysobalanaceae in that order.

Chrysobalanaceae contain ellagic acid and ellagi-tannins (Hegnauer, 1973) as do Myrtales (and some Theales and Rosaceae, but not Amygdalaceae or Malaceae). The embryo contains protein and fat, rarely (*Couepia*) some starch. In these features the family agrees with Myrtales.

In the light of the several conspicuous differences between Chrysobalanaceae and Rosales sensu stricto and similarities between Chrysobalanaceae and, for example, Ochnaceae of Theales, the family should not be considered as the link between Rosales and Myrtales as may be thought from some gross morphological features. Should there prove to be a connection between the Myrtales and the Theales (see p. 688), then Chrysobalanaceae come into the picture.

ELAEAGNACEAE

Elaeagnaceae have occasionally, but rather rarely of late, been associated with Myrtales. Some vegetative features argue against a myrtalean relationship, as the alternate exstipulate leaves, lack of internal phloem, and lack of vestured pitting in the vessel elements. The anomocytic stomata and peltate hairs are found also in Combretaceae of Myrtales, and the vessel elements have simple perforation plates as in Myrtales. The flowers, which are mostly unisexual, agree in several respects with those in Myrtales, being often tetramerous, the male flowers being haplo- or diplostemonous, and at least the female flowers being provided with a hypanthium. Petals are missing. Foreign to Myrtales is the monocarpellate pistil with a single erect ovule, but embryological features and the exendospermous seed of Elaeagnaceae agree well with the conditions in Myrtales. Chemically Elaeagnaceae agree also fairly well with Myrtales (p. 661), although their alkaloid contents, tryptophane derivatives, are special.

Eyde (1975) considers that Elaeagnaceae cannot be derived from Myrtales as it has a truly solitary carpel (which is evidently the case; Eyde, 1975, fig. 2), but we see no reason why the carpel number could not be reduced in a syncarpous as well as in an apocarpous gynoecium. However, there are other reasons why Elaeagnaceae cannot be considered of myrtalean origin, such as their lack of internal phloem. The pollen grains are tricolporate, being sometimes reminiscent of those in certain Myrtaceae.

Both authors (Thorne, 1981; Dahlgren, 1980a) believe that Elaeagnaceae are closely related to Rhamnaceae, which was also proposed by Hutchinson (1959). This is supported by similarity of seed coat (Corner, 1976) and by parasitizing fungi (Thorne, 1979). The position of both of these families in relation to the Myrtales is assumed to be distant, with some similarities explained by convergence (see Rhamnaceae, below), but these similarities clearly deserve further study.

FAMILIES SOMETIMES ASSOCIATED WITH, BUT APPARENTLY DISTANTLY RELATED TO MYRTALES

Rhamnaceae are among those families which only occasionally have been mentioned as possibly related to myrtalean families, but which exhibit some interesting similarities. They are woody and have simple, often opposite leaves with (or rarely without) small or moderate-sized stipules, which may be present as a row of small hair-like structures. Intraxylary phloem is lacking, and the vessels have no vestured pitting although their perforation plates are simple as in Myrtales. The flowers are actinomorphic, with inferior to superior ovary, and generally have small petals opposite a single whorl of stamens. A hypanthium occurs in several genera (cf. Elaeagnaceae), and there is usually a prominent disc. The pollen grains are mostly tricolporate and two-celled. The carpels are 2–5, forming a syncarpous 2–5-locular pistil with simple style, which agrees with myrtalean families, although the locules have but one ovule each. The embryology is largely as in Myrtales and the seeds have little endosperm and a relatively large, straight embryo. Chemically, the Rhamnaceae are peculiar in the production of benzylisoquinoline alkaloids, documented in several genera. Anthraquinones are common. Tannins are present, but ellagic acid or ellagi-tannins have not been recorded.

The family cannot be considered seriously for membership in Myrtales, especially because of vegetative anatomy and chemistry, although technically there are a number of obvious similarities.

Datiscaceae were recently thoroughly reviewed by Davidson (1973, 1976). Shaw (1973) suggested relationship with Haloragaceae, which are often placed in Myrtales. Therefore mention may be justified here. Datiscaceae consist of three genera, the herbaceous *Datisca* and the tree genera *Octomeles* and *Tetrameles*. The latter genera may represent the more nearly ancestral forms. Internal phloem is lacking in the stem. The leaves are alternate and exstipulate and bear multiseriate, peltate or glandular hairs. As in many Myrtales, these genera possess branched sclereid idioblasts. The flowers are 4- to 8-merous in calyx and (when present) corolla, and the pollen grains are 3-colporate. The stylodia are separate, not fused into a single style as in the Myrtales, and the placentation is parietal (to nearly central), which is rare in Myrtales. Davidson on the basis of an extensive survey of the family concluded that it was not allied to the Myrtales. Links to Flacourtiaceae and other families of Violales are apparently most likely.

Marcgraviaceae in their opposite leaves, flowers which may have numerous stamens, and the nearly exendospermous seeds show some superficial similarity to Myrtales. There is no internal phloem, no vestured pitting, stipules are lacking, androecial developmental sequence is centrifugal, and ovules are tenuinucellate and at least in some taxa have cellular endosperm formation. These features are all lacking in Myrtales (cellular endosperm also in Theales). From the evidence available Marcgraviaceae seem best placed in Theales.

Theaceae, as a representative family of the Theales, have some superficial similarities to myrtalean families. The leaves are simple and, as in several families of Myrtales, often are well supplied with branched sclereid idioblasts. Stipules, internal phloem, and vestured pitting are lacking. The flowers are mostly more open than in the Myrtales and lack the conspicuous hypanthium of this order. They have from five (*Pelliceria* and other genera) to numerous stamens. These, however, tend to develop in centrifugal succession. The anthers of a *Camellia* species, for example, also possess a laterally expanded connective reminiscent of that in some myrtalean members. The syncarpous pistil has a single style, and the ovules are anatropous and, with the exception of their tenuinucellate character (and lack of development of parietal cell), are somewhat similar in their embryology to those of Myrtales. Rarely are they unitegmic. The seeds also lack endosperm. The alkaloid content in many Theaceae consists of purin bases. Otherwise Theaceae resemble the myrtalean families in containing ellagi-tannins. The similarities between Theaceae (and other thealean families) and Myrtales are ambiguous but (in the view especially of one of us, Thorne) do not indicate a close phylogenetic affinity at all.

Clusiaceae (Hypericaceae) agree with Theaceae in showing certain similarities to Myrtales (see also above for Lecythidaceae), but do not have the internal phloem and usually lack stipules. The lack of hypanthium, the tenuinucellate ovules, and the frequent occurrence of an aril indicate strongly thealean rather than myrtalean affinity. In the schizogenous secretory ducts and the occurrence of branched sclereid idioblasts they may superficially resemble Myrtaceae, but the secretory ducts contain great amounts of yellow to red phenolic pigments consisting of anthraquinone and xanthone derivatives and coumarins, which are not matched in Myrtaceae. A close relationship to Myrtales thus cannot be seriously proposed.

Myrsinaceae consist of woody plants with alternate or opposite leaves without stipules. Internal phloem is lacking. The vegetative parts have schizogenous ducts with resinous contents. In contrast to Myrtales there is no hypanthium, although the corolla is more or less sympetalous. The stamens, in one whorl, are antepetalous, a condition rarely met with in Myrtales (but present for example in Lythraceae). The free-central placenta is not indicative of myrtalean affinity either, and the ovules in addition are tenuinucellate. Finally, the seeds are rich in endosperm, which they are not in Myrtales. These conditions indicate that Myrsinaceae are rather closely allied to Primulaceae rather than to families in Myrtales.

Geissolomataceae (see Dahlgren & Rao, 1969; Carlquist, 1975) are a monotypic South African family which has often been associated with Penaeaceae of Myrtales. It has opposite leaves with minute stipular teeth. The flowers have four basally connate sepals, a diplostemonous androecium and four carpels, which may suggest myrtalean affinity. However, internal phloem is lacking and the vessels lack vestured pitting and have scalariform perforation plates with numerous bars (indeed, there may hardly be perforations at all, see Fagerlind & Dunbar, 1973). In addition, the pollen grains lack pseudocolpi (which Penaeaceae have), the stylodial branches are free from each other, and the seeds have copious endosperm and a small embryo. Therefore, there are no reasons at all to include the genus in Myrtales. Rather, a position in or near Hamamelidales or in Cunoniales (proposed by Dahlgren) seems appropriate, which agrees well with the view of Thorne, who firmly believes that Geissolomataceae are closely related to Bruniaceae and places these in the suborder Bruniineae, along with Buxineae and Pittosporineae, in a widely circumscribed order, Pittosporales (Carlquist, 1975; Thorne, 1975, 1977, 1981).

Gunneraceae, with the single genus *Gunnera,* are herbaceous plants with a habit different from most Myrtales. The larger, lateral stipules, reduced flowers, separate, long stylodial branches, cellular endosperm formation, and seed with copious endosperm and a tiny embryo, comprise important differences from Myrtales. This family also seems to have no close relationship to Haloragaceae, though one of us (Thorne) still prefers to retain Gunneraceae in his suborder Halorageae of Cornales.

Proteaceae show certain superficial similarities to myrtalean families but lack internal phloem and have alternate leaves without stipules. The flowers are hypo- to perigynous and as in most Myrtales have a tetramerous perianth on a conspicuous hypanthium. Pollen grains morphologically have some resemblance to those in Onagraceae (but no viscin threads and a very different exine structure) but hardly to those in other myrtalean families. The pistil is monocarpellate. The embryology agrees with that of Myrtales in most features, and the ripe seed is almost devoid of endosperm. The chemical characters are similar to those of Myrtales (tannins, flavonols, occasional aluminum accumulation, cyanogenic compounds) except that ellagic acid is not recorded. Proteales are quite distinct from Myrtales.

Malpighiaceae resemble superficially Lythraceae in the often violet, unguiculate petals with wavy margins. They lack internal phloem, but the vessels have vestured pits as in Myrtales and the perforation plates are simple. The leaves are simple, alternate or more often opposite, and may or may not have stipules. The paracytic stomata and branched "malpighian" hairs would be, however, unusual in Myrtales, and papillae are frequently present on the lower surface of the leaves. The plane of symmetry of the flower, which is slightly zygomorphic, is oblique, the flowers are obdiplostemonous, and in contrast to all Myrtales, the stylodial branches are often separate to their base. Each of the 3–5 locules has one pendulous, hemi-anatropous ovule with an embryology similar to that of Myrtales; the embryo sac, at least in some cases, is tetrasporic and reputed to resemble that in Penaeaceae. The seeds are exendospermous. The fruits vary but tend to be schizocarps, quite dissimilar to any found in Myrtales. Chemically, the family resembles various Myrtales in having triterpene saponins, but ellagic acid is not reported and the tannins seem to be of the condensed type only.

Malpighiaceae do not seem to be very close to Myrtales, but a number of similarities suggest that a set of attributes occurring in Polygalales (or Polygalineae of Geraniales) are held in common with that in Myrtales.

Pittosporaceae lack stipules and have schizogenous secretory ducts with resinous contents. Their production of polyacetylenes, unitegmic, tenuinucellate ovules, and copious endosperm and very small embryo in the ripe seeds do not indicate myrtalean affinity.

Escalloniaceae and *Icacinaceae,* whether closely related to each other or not, both differ from Myrtales in similar ways. They lack stipules and a hypanthium, and they have unitegmic and sometimes tenuinucellate ovules with cellular endosperm formation. In addition, they occasionally contain iridoids, which have not been found in Myrtales.

Montiniaceae (*Montinia, Grevea,* and *Kaliphora*) agree in morphology and especially in embryology with the majority of Cornales and also contain iridoids, which are quite common in this order. *Griseliniaceae* are probably related here too, along with Escalloniaceae, but need to be studied further.

Columelliaceae in overall floral construction and embryology (unitegmic, tenuinucellate ovules with cellular endosperm formation and terminal endosperm haustoria) are typically cornalean and thus can safely be excluded from Myrtales.

Montinioideae, Griselinioideae, Escalloniaceae, and Columellaceae are treated by one of us (Thorne) in the Saxifragineae of the order Rosales, which he considers to have common origin with the Cornales.

Dialypetalanthaceae (Fig. 16), like Rubiaceae, have opposite leaves with interpetiolar stipules, but the petals are free, the stamens 8–12(–16), the ovules more numerous, and the seeds different. The pistil is bicarpellate, and the fruit, although capsule-like, opens up as a schizocarp. The flat seeds are numerous, flat, winged, and apparently have evolved from unitegmic ovules. The position of this family although not yet firmly placed in Gentianales certainly does not seem to fit into Myrtales. The stomata (H. Rasmussen, pers. comm.) are paracytic, indicating (albeit not definitively) affinity with the Rubiaceae. *Dialypetalanthus* is probably an aberrant early off-shoot of the Rubiaceae or a relict family closely related to the Rubiaceae in the Gentianales.

Loganiaceae and *Rubiaceae* are preferably placed in the same order, Gentianales, of sympetalous angiosperms. Like Myrtales they have opposite leaves, vestured pits, and many Loganiaceae also have bicollateral vascular bundles. Interpetiolar stipules of rubiaceous type are absent in typical Myrtales, and stipules are lacking in Loganiaceae.

Loganiaceae and several other families in Gentianales show a combination of intraxylary phloem and vestured pits, as do Myrtales, Thymelaeaceae (or most of its taxa according to its circumscription), part of Vochysiaceae, and one genus of Polygonaceae. Van Vliet and Baas (1984) stress the common occurrence in Myrtales and Gentianales, e.g., Loganiaceae sensu lato, of the combination of intraxylary phloem, vestured pits, fiber-tracheids, and diversity of crystal types (including raphides and styloids) as shown by Mennega (1980). This calls for a general survey of other features. The embryology of Loganiaceae [which in the sense of Leeuwenberg and Leenhouts (1980) is probably heterogeneous!] is characterized by unitegmic, tenuinucellate ovules with nuclear or rarely cellular endosperm formation (Dahlgren, 1975b). The seeds are also generally provided with copious endosperm. Chemically, Gentianales show little affinity with Myrtales (see Dahlgren et al., 1981), and in floral morphology the similarity may be superficial. Thus, in spite of the fact that Myrtales and Gentianales are adjacent in the diagram of Dahlgren (1980a; Dahlgren et al., 1981), one of us (Dahlgren) does not consider the two orders as closely allied. Rather, he thinks in this case that it is likely that the wood-anatomical similarities have evolved by convergence. This is probably also the case, independently, with Thymelaeaceae. The other author (Thorne) believes that these wood-anatomical and floral similarities may have been retained from common, proto-rosalean ancestors.

Hippuridaceae (= *Hippuris*) from Hegnauer's (1969) chemical account, also according to Dahl-

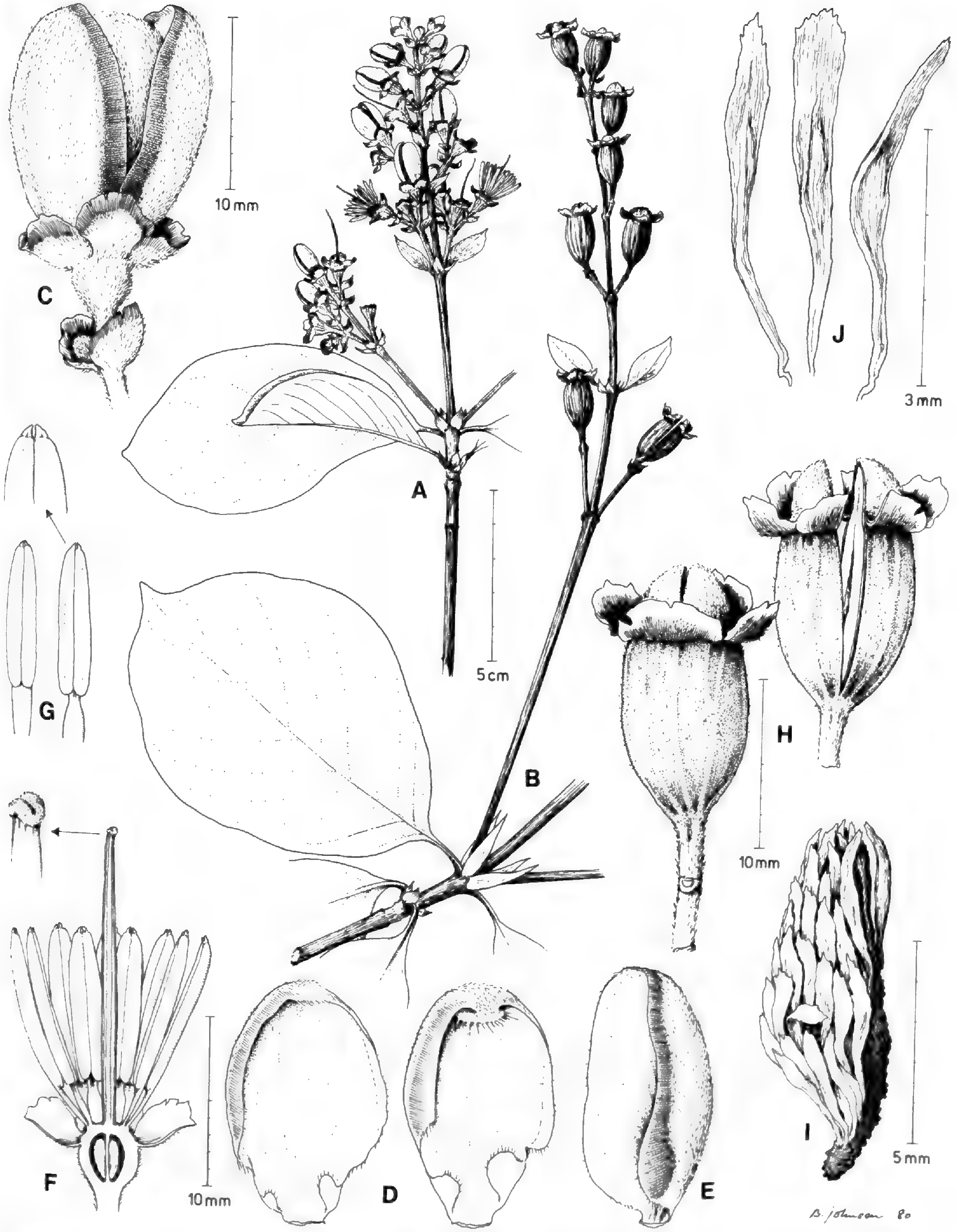

FIGURE 16. *Dialypetalanthus fuscescens* Kuhlm., forming the monotypic Brazilian Dialypetalanthaceae: A–G. *Prance et al. 8967*; H–J. *Prance et al. 6526*.—A. most part of inflorescence and upper leaf pairs of branch.—B. fruiting branch, note the variation of stipule size in successive leaves.—C. flower just before opening, showing decussate sepals and petals.—D. inner petals.—E. an outer petal.—F. flower in longitudinal section, petals removed; above: stigma in detail.—G. stamens; above: staminal tip in detail.—H. capsules in different views, the right opening along carpel commissures.—I. placenta with seeds.—J. seeds. (Orig., del. B. Johnsen.)

gren (1975a), Jensen et al. (1975), and Wagenitz (1975), seem to be best removed far from Haloragaceae, and show no discernible relationships to Myrtales either. Yet Cronquist (1968) and Thorne (1976, 1981) on the basis of other similarities prefer to retain Hippuridaceae in the same order Haloragales or suborder, Halorageae, with the Haloragaceae and Gunneraceae, though both agree that these families are not close relatives of Myrtales but probably have common ancestry with them and Rosales. The leaves are verticillate, and the small, epigynous flowers are so reduced as to give very little morphological indication of relationships. However, the unitegmic, tenuinucellate ovules with cellular endosperm formation, and the chemical spectrum, including the biosynthesis of carbocyclic iridoids, indicate scrophularialean or, alternately, cornalean affinity.

Callitrichaceae have now received an acceptable position near Verbenaceae and Lamiaceae on the basis of the 4-seeded schizocarps, unitegmic and tenuinucellate ovules, cellular endosperm formation, terminal endosperm haustoria, and carbocyclic iridoids, all characteristics that are foreign to Myrtales.

RELATIONSHIPS OF THE ORDER MYRTALES

The position of the order Myrtales has varied in different classifications and is still a matter of divergent opinions. Cronquist (1981) and Takhtajan (1980) in their recent classifications have been somewhat constrained by their division into the subclasses Dilleniidae and Rosidae of the majority of choripetalous orders of dicotyledons. Myrtales in both classifications are placed in the Rosidae, where they form the main order in Takhtajan's superorder Myrtanae. It is generally agreed that the order is more or less related to Rosiflorae, including Rosales, Saxifragales, and Cunoniales, although other, quite small, orders occasionally treated with Myrtanae are considered even more closely related, as Haloragales and Rhizophorales (and Lecythidales) when these are acknowledged. Other orders sometimes recognized and often associated with Myrtales are Elaeagnales and Thymelaeales. Theales and presumably closely related Primulales, being members of their Dilleniidae, have tended to be left out of comparison, although at one occasion or another the similarity has been pointed out, e.g., by Hickey and Wolfe (1975).

Several of these groups have been compared on the previous pages with myrtalean families, notably those representing monofamilial orders in some classifications, or have even been included as components in a more widely circumscribed Myrtales: Haloragaceae (Haloragales), Rhizophoraceae (Rhizophorales), Thymelaeaceae (Thymelaeales), Lecythidaceae (Lecythidales), and Elaeagnaceae (Elaeagnales). Some generalities will be discussed, and other orders compared with Myrtales.

Two attributes to which we have attached great importance above are the occurrence of internal phloem, i.e., the presence of bicollateral vascular strands, and of vestured pitting in the vessel elements. When the Myrtales are strictly circumscribed, these characteristics become critical.

Only one of the serious candidate families for myrtalean membership mentioned above possesses both bicollateral vascular strands and vestured pits, viz., Thymelaeaceae (these features being shared also with some Euphorbiaceae). Cronquist (1968, 1981, 1984) includes Thymelaeaceae in Myrtales, but, as pointed out previously, this meets with serious objections, especially with regard to phytochemical and embryological evidence.

Another order where opposite leaves are combined with internal phloem and vestured pits is Gentianales, within which especially Loganiaceae show some resemblance to Myrtales. Because floral morphology, embryology (unitegmic, tenuinucellate ovules), and chemistry (lack of ellagic acid and tannins on the whole, presence of iridoids and indole alkaloids) are vastly different, one of the authors (Dahlgren) does not consider the relationship between the Loganiaceae and Myrtales to be at all close.

Disregarding bicollateral vascular strands and vestured pitting, Haloragaceae, Rhizophoraceae, Elaeagnaceae, and Chrysobalanaceae provide combinations of attributes which are not seriously different from the myrtalean, although various peculiarities in each family would be aberrant or at least "untypical" in Myrtales. In the main phytochemical spectrum these families are in good agreement with the myrtalean pattern, and vegetative as well as floral details, also, are conspicuously similar in various respects. However, it is important to remember that most of the basic features of Myrtales are widespread in choripetalous dicotyledons. None of the families mentioned which lack internal phloem and vestured pitting seems to relate (in comparative-morphological terms) clearly to any of the "core families" of Myrtales. Thus it seems convenient and adequate to use the presence of these two attributes as significant diagnostic criteria for Myrtales.

MYRTALEAN VERSUS ROSALEAN ATTRIBUTES

One of the families mentioned above as particularly similar to many Myrtales is Chrysobalanaceae. This has been alternately referred to Rosales and Fabales (where these orders are not united); whereas, its position in Myrtales has hardly ever been suggested. Disregarding the lack of internal phloem and vestured pitting, the family seems to agree nearly as well with myrtalean as with rosalean attributes, thus justifying a comparison. Rosales sensu stricto normally include at least Rosaceae, Neuradaceae, Amygdalaceae, and Malaceae [all more often treated as subfamilies of Rosaceae sensu lato, whereas the Chrysobalanaceae are often treated separately, in the vicinity of Sapindaceae and Connaraceae (in Sapindales or Sapindineae of Rutales)].

Vegetatively Rosales sensu stricto are diversified: they are basically woody plants, the vessels of which generally have simple perforation plates. Stomata are mostly anomocytic, mucilage cells are common, and glandular hairs are common. The leaves are generally alternate, quite often compound, and in many species have well-developed stipules (never represented by rows of finger-like projections in the leaf axils as in many Myrtales). The leaf teeth in Rosales are of the Rosoid type (Hickey & Wolfe, 1975) and are slightly resembled by those in some genera of Onagraceae (Hickey, pers. comm.). The flowers are basically actinomorphic and the inflorescence determinate. A conspicuous similarity to the Myrtales is the prominently developed floral receptacle, which in several groups results in perigynous, urceolate types comparable to those in many Myrtales. A second trend, with elevated receptacle, has not evolved in the Myrtales. The tetramerous condition is rare in Rosales, but common (although, quite likely, secondary) in the Myrtales. The androecium of Rosales, although probably evolved from a diplostemonous basic type, has multiplied by the insertion of more whorls as well as by increase of initials in each whorl. A presumed primitive condition is the apocarpy of many Rosales. A syncarpous pistil occurs only in a few Chrysobalanaceae and in epigynous Malaceae (= Rosaceae subfam. Maloideae). Rosales sensu stricto and Myrtales agree essentially in pollen morphology, embryology, sparsity of endosperm in seed, and also in phytochemistry. Chrysobalanaceae deviate from the "typical" rosaceous pattern in several respects. In some of these, as syncarpy, single style, urceolate receptacle, and mode of stamen multiplication, they approach the Myrtales, although this may be by convergence. New embryological evidence (Tobe & Raven, 1984d) indicates great agreement with families of Theales, and Chrysobalanaceae may best be treated as a member of this order.

MYRTALEAN VERSUS CUNONIALEAN ATTRIBUTES

Cunoniales (Dahlgren, 1980a) can be variously circumscribed, but their delimitation from Saxifragales contributes difficulties. In some respects this group of families is more specialized than Rosales sensu stricto, e.g., in having more often syncarpous pistils, but in other features it shows much less specialization, as in wood-anatomical characteristics and abundance of endosperm in the seed. Stipules with various degrees of development occur in the order, thus agreeing with Myrtales, where they are mostly present but minute. The basically diplostemonous flowers, which are more often 5- than 4-merous, the general lack of a hypanthium, and the common presence of a well-developed disc are only partly in agreement with the myrtalean pattern. The gynoecium in Cunoniales ranges from nearly apocarpous to syncarpous, and the mature seeds differ from those in Myrtales by having, as a rule, copious endosperm, but embryological and phytochemical characteristics are not very different from those in Myrtales. As Cunoniales, which are dubiously homogeneous, show resemblance to Rosales and Saxifragales (Thorne treats all three as suborders of Rosales), they also approach a hypothetical ancestral myrtalean type. However, the similarity between families of the orders is not particularly impressive to some phylogenists.

MYRTALEAN VERSUS SAXIFRAGALEAN ATTRIBUTES

Saxifragales sensu stricto (Dahlgren, 1980a), include Crassulaceae, Saxifragaceae sensu stricto, and a few small families, e.g., Grossulariaceae (Saxifragaceae subfam. Ribesioideae), some often included in Saxifraceaeae sensu lato. The two principal families may not be as closely allied to each other as often stated. Each of them agrees in many respects with Myrtales, especially in floral construction and partly also in chemistry. Opposite leaves characterize many Crassulaceae, but stipules are lacking. The pentamerous or, especially in Crassulaceae, often tetramerous flowers are obdiplostemonous, but the significance of the difference between this and the diplostemonous condition is obscure. In Crassulaceae, the carpels are isomerous with the other floral whorls, as in many Myrtales, and the seeds are also exendospermous; whereas, in Saxifragaceae the seeds have copious endosperm. The tubular flowers of many Crassulaceae, e.g., *Kalanchoë,* should not be confused with the similar ones in many Myrtales, because in Myrtales the floral tube represents a true hypanthium. In Crassulaceae, however, it consists of the fused petals only (sympetaly!), to which the filaments are more or less adnate. The endosperm formation in Saxifragales is intermediate (helobial) or cellular, which is never the case in Myrtales.

In Saxifragales, the Grossulariaceae (*Ribes*), no doubt by a combination of parallel and convergent evolution, have developed a number of fascinating similarities to *Fuchsia* (Onagraceae), and exhibit a combination of epigyny, a simple (or cleft) style, an urceolate to tubular hypanthium, often brightly colored like the calyx lobes, frequently reduced petals, and a baccate fruit (*Ribes speciosum* is called "California-Fuchsia"). The seeds are, however, enclosed by a carnose, juicy arillus, the endosperm is copious, and the embryo is minute.

There are accordingly no close bonds between the Saxifragales sensu stricto and the Myrtales, although some basic features indicate that the groups may be derived from distant common ancestors.

MYRTALEAN VERSUS RUTIFLOREAN ATTRIBUTES

What has been said for the previous orders is partly valid also for various members of the orders Rutales sensu stricto, Sapindales, Geraniales, and Polygalales, where the general level of organization based on a pentacyclic, either diplostemonous or obdiplostemonous, floral plan partly corresponds to that in Myrtales. Odd families, such as Malpighiaceae and Erythroxylaceae, may strongly resemble myrtalean families but each exhibits important differences from them and lacks internal phloem and a hypanthium. In both aforementioned families there are, for example, separate stylodial branches instead of a single style. There is, however, within the rutiflorean complex a basic morphological, embryological, and phytochemical pattern of characteristics which approaches that of the Rosiflorae as well as the Myrtiflorae. However, any relationships between these groups must be fairly distant.

MYRTALEAN VERSUS THEALEAN ATTRIBUTES

The comparison between the orders Myrtales and Theales is justified because of certain shared attributes. Also, Lecythidaceae have quite often been included in Myrtales, and indeed some of their members are similar to such large-flowered, polyandrous tree genera as *Sonneratia, Duabanga, Punica,* and *Lafoënsia* within Myrtales. Also various details, such as the occurrence of minute stipules in some Lecythidaceae (Weberling, 1958) and the similar phytochemistry, could be taken to support the view that the Theales and Myrtales may be distantly related.

The members of Theales are mostly woody. They lack the internal phloem and vestured pitting of the Myrtales and often have more primitive vessel types; but they resemble many Myrtales frequently in having foliar sclereids, although possession of the latter is usually a feature of low phylogenetic significance at this level (Rao & Das, 1979). The flowers vary in merous conditions but are more rarely tetramerous and a typical hypanthium is rare. The petals are normally broad and imbricate. Typical of a great part of Theales are the numerous stamens with centrifugal developmental succession. Pollen morphology (see above, under Lecythidaceae), bitegmic ovules, nuclear endosperm formation, and sparsity or lack of endosperm in the ripe seed are in some, but not high level, agreement with conditions in Myrtales, but the ovules are generally tenuinucellate and dissimilar to those in Myrtales. In phytochemical characteristics the two orders are basically similar. Assuming that the numerous stamens are secondary to a diplostemonous state and that the tenuinucellate ovules are derived from crassinucellate ones, the distant ancestors of Theales should approach those of the Myrtales. Many taxonomists, on the basis of the clear differences mentioned, consider the orders very distant, which is reflected in the fact that they are placed in different subclasses, Theales in the Dilleniidae and Myrtales in the Rosidae in the classifications of Takhtajan (1980) and Cronquist (1981).

MYRTALEAN VERSUS CORNALEAN ATTRIBUTES

For Rhizophoraceae as well as Haloragaceae, alternative positions suggested in most literature are either in Myrtales or in Cornales. Therefore a short note on the differences between these two orders is justified. Crucial in this connection is the definition and circumscription of Cornales (see Huber, 1963). As defined by one of us (Dahlgren) Cornales include a number of families (among others, Cornaceae, Hydrangeaceae, Montiniaceae, Escalloniaceae, Icacinaceae, Symplocaceae, Adoxaceae, Sambucaceae), with variably opposite or alternate leaves, without internal phloem, with vessel elements having simple or scalariform perforation plates, and lacking vestured pitting. The flowers are sympetalous, and embryologically the families are fairly well defined by the generally unitegmic, tenuinucellate ovules and cellular endosperm formation (Philipson, 1974; Dahlgren, 1975b), which combine with the frequent occurrence of iridoid compounds (Jensen et al., 1975) but lack of ellagitannins. When so circumscribed, Dahlgren considers the order fairly homogeneous, and as having a quite distant relationship with the Myrtales.

In at least the wood-anatomical features, Haloragaceae and Rhizophoraceae agree better with Cornales than with Myrtales, but in other characteristics Dahlgren finds little to support such a relationship.

The second author, Thorne, gives a very different circumscription and definition for his Cornales, which permits inclusion of the abovementioned two families in the order.

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MYRTALES AND MYRTACEAE— A PHYLOGENETIC ANALYSIS[1]

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ABSTRACT

Phylogenetic analysis of 19 families or quasi-families of the Myrtales is carried out by CLAX, a new numerical technique, as well as by other methods, the comparative merits of which are discussed. The results establish some phylads as reliable, in particular Psiloxylaceae-Heteropyxidaceae-Myrtaceae and the Lythraceae sensu lato (including *Punica, Duabanga,* and *Sonneratia*). Onagraceae are very distinct, but may have an early link with Trapaceae. Memecylaceae and Crypteroniaceae are separated from Melastomataceae sensu stricto, a family Alzateaceae is recognized, and the new unigeneric family **Rhynchocalycaceae** is described. The earlier suggestion of the separate order Lythrales is not supported. Scenarios of phylogeny are given, with attention to phytogeography; the order seems to have originated and largely radiated (except for the predominantly Australasian Myrtaceae sensu stricto) in West Gondwana. Similar analysis of Myrtaceae depends particularly on features of androecium, trichomes, and wood anatomy; a complex set of changes in the androecium is hypothesized. The analysis implies a considerably altered picture of tribal and generic relationships; the formerly recognized subfamilies Myrtoideae and Leptospermoideae must be abandoned. The subfamily Chamelaucioideae, previously discarded by us, is shown to be a polyphyletic grade taxon, and cannot be sustained as an integrated suballiance, much less as a subfamily. Consideration is given to the status of *Kjellbergiodendron,* the (possibly combined) *Eucalyptopsis* and *Eucalyptus* alliances, the *Acmena* alliance, and *Osbornia.*

1. INTRODUCTION

Our task is twofold: to consider the place of Myrtaceae among other families, and to provide an analysis of the major subdivisions within the family. In this we adopt an explicitly phylogenetic approach, attempting to present a reconstruction of ancestral conditions and a set of possible scenarios of subsequent developments. An endeavor to view the Myrtaceae in context has required general consideration of the phylogeny of Myrtales. Indeed, as the study progressed, it became increasingly oriented towards these more general questions. This led to some overlap with the field covered in this symposium by Dahlgren and Thorne.

The data on which our analyses have been based were in part gathered independently of those presented by Dahlgren and Thorne, but these authors drew our attention to the significance of some taxa (particularly *Alzatea* and *Rhynchocalyx*) and enabled us to include additional characters. Our conclusions and theirs now agree in most respects.

2. METHOD OF PHYLOGENETIC ANALYSIS

2.1 APPROACHES

Phylogenetic analysis is not new, but in the last decade has been most vigorously promoted, especially in zoology, by the various schools of

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cladists. Unfortunately, this approach is becoming overwhelmed by methodological preoccupation. Hull (1979) gives a balanced account, which has been largely ignored by the enthusiastic practitioners of what he has called "Cladism with a capital C," just as Johnson's (1969, 1970) and other criticisms of Adansonian pheneticism were not refuted, but simply ignored, by its adherents.

We reject all forms of phenetic analysis for purposes of phylogenetic reconstruction at higher taxonomic levels. Johnson (1969, 1970) gave an exhaustive criticism of the unsound, or indeed biologically almost nonexistent, theoretical foundations of phenetics in such applications. Phenetics is moribund among zoologists, although discerning students of evolution such as Ernst Mayr (1981) find it necessary to reiterate its theoretical as well as practical deficiencies. In botany it lingers on, and new applications of hard-core phenetics (e.g., Barabé et al., 1982; Macfarlane & Watson, 1982) continue to appear, with no indication to their readers either that the foundations have been challenged or that a different approach exists and flourishes.

2.2 THE CLAX METHOD

One of us has been involved in the development (Johnson & Johnson, in prep.) of a cladistic ("small c") method, CLAX. Full exposition of this method must unfortunately await presentation elsewhere, but the results of hand-working data on Myrtales by CLAX and by the variant CLAXMIN are given and compared briefly with those from several other procedures. The CLAX results lead to several competing phylogenetic hypotheses but several groupings are robust under almost all methods of analysis, and the competing trees show substantial congruence.

Mayr (1981), reluctantly allowing the rigid Cladists to usurp the term "cladistic," would call our approach phylogenetic. We can perhaps accept this, and use his term "phylograms" for dendrograms generated by CLAX. These differ from strict neo-Hennigian cladograms in laying stress on length of internodes, including final branches to the terminal taxa (operational taxonomic units or OTU's of some authors), and not only on the branching sequence (i.e., the topology). Moreover, CLAX uses (or can use) autapomorphous character-states (see below, 3.1.2), as indeed can various other methods of numerical cladistic analysis. These do not contribute to the topological determination of generated trees, but do enable us to see something of the extent of evolutionary change. [Eldredge and Cracraft (1980) distinguish "trees" from cladograms, using the former term more or less for what we call phylograms. The term "tree," however, has an established meaning in graph theory. This mathematical meaning embraces both cladograms and phylograms, as pointed out by Rohlf and Sokal (1981). Such diagrams, with an "ancestral" point specified, fall into the subclass of "directed trees." Herein, we shall use "tree" in general to signify "directed tree."] "Pure" cladograms can be extracted from such phylograms, without change of topology. These phylograms in no way confound cladistic procedure by mixing in "phenetics," contrary to the largely unfounded allegations by Eldredge and Cracraft (1980) concerning Mayr's (and others') "evolutionary" approach to phylogeny.

CLAX is a much-refined development of a method of phylogenetic analysis outlined previously (Johnson & Briggs, 1975). It is a "top-down" procedure, and the core of its algorithm unites in pairs (or larger sets) those taxa with the highest score of derived states (apomorphies in common), continuing the process at each decreasing "advancement level." An important feature is that equal possibilities of minimal and subminimal length can all be followed through at all stages. The method assumes that we can usually assign polarity to character-state changes (variations in the polarity assumed are treated separately) and also, in general, that the greater the number of apparently synapomorphous (derived in common) character-states of any two or more taxa the greater the confidence we can have in the common derivation of the characters on the stem concerned.

In all methods of cladistic analysis, the user determines which characters to use, on the basis of the distribution of features in the taxa, his judgment as to what features are homologous, and what should be regarded as single characters or syndromes of several characters. In the same way it appears that there is a place for judgment in determining the extent of acceptable reversals. In its basic form, CLAX does not generate reversal of character-state changes, and consequently the position of the root of each tree is determined. The user may decide whether reversal of a particular character is acceptable, as we have done in our analyses. Such reversal is by explicit rescoring in data matrices or in the submatrices for parts of a tree. Additional computation is necessary, of course, where alternatives of this kind are invoked.

For comparison, and for those who insist on methods that generate reversals unrestrainedly in the search for shorter trees, CLAXMIN—a development from CLAX—has also been used (2.4.1), as have some existing methods. In contrast to CLAX, we do not recommend any such method as CLAXMIN as an approach to phylogenetic analysis.

CLAX acknowledges the methodological value of parsimony (but not any principle of evolutionary parsimony as such; see the excellent critique by Crisci, 1982) though not at the expense of accepting unrestrained reversals. Most cladistic procedures strive to obtain a "most parsimonious" solution, in the sense of a tree or "network" (= undirected tree) of minimal length for the characters and the scoring measures used.[3] However, it should be remembered that (1) they frequently fail to find a shortest tree, (2) there may be very many shortest trees of which they find one or two *at most,* (3) there may be an even greater number of supraminimal trees longer by only one to two steps, (4) variants, whether minimal or supraminimal, may differ greatly from each other in topology, (5) shortest trees in practice tend to involve numerous and often repeated reversals of character-state change, (6) shortest trees (and supraminimals) may involve postulating functionally impossible intermediate hypothetical ancestors and are therefore not necessarily parsimonious at all in the sense of minimizing assumptions necessary for "explanation" in a wider context.

CLAX was developed to avoid the pitfalls of (2) and (3) in a top-down method with user-control of character reversibility, as well as user-choice intervention at intermediate stages for large taxon- and character-sets where numbers of alternatives may be generated.

A top-down procedure does not necessarily find the shortest no-reversal trees, for reasons that will be detailed elsewhere (Johnson & Johnson, in prep.). In brief, in the *n*-dimensional lattice space (so-called Manhattan space; see Johnson, 1969, 1970; and Johnson & Johnson, in prep., for preferred terminology) representing the *n* attributes used, the unions established at points most distant from the origin (zero point for all co-ordinates) may channel the downward-developing tree structure into paths that exclude the possibility of finding a shorter overall set of paths, such as could result (later in the procedure) from joining the taxa (including the generated hypothetical taxa) in a different order. So, by allowing longer partial trees during computation, additional equal *or shorter* ultimate trees may be found by a catching-up process. Moreover, phylograms of greater than minimal length may be more believable on grounds external to the analysis (i.e., more parsimonious in a broader framework), although they involve a higher degree of homoplasy (parallelism, or even convergence if the user fails to discriminate convergent characters as "different" when scoring).

To overcome this difficulty, the procedure allows also for supraminimal joining (and thus supraminimal partial and eventual trees) in the computations, longer up to a fixed amount than the minimals (at each stage); the maximum value (P) of this extra length is preset as a user-determined constant in the program. We find empirically, and can glimpse the foundations of a mathematical demonstration, that the additional probability of finding shorter ultimate trees falls off very rapidly as the value of P increases. For CLAX analysis of Myrtales, with 19 taxa, P = 1 yielded some partial trees that caught up with minimals during the computation, but increasing the value to P = 2 generated no additional overall competing minimal tree. At P = 2 we obtained one phylogram that returned to minimal length at a lower stage in the processing but dropped off to a supraminimal level again before completion. This particular tree corresponds with the CAMIN-SOKAL result mentioned at 2.3.

Some supraminimal overall trees have been worth considering in their own right. It is important to recognize that marked differences in topology, at any level, may characterize not only competing minimals but also supraminimals worthy of serious consideration as phylogenetic hypotheses. Hence it should not be assumed that cladograms produced by methods with limited and often non-minimal output necessarily approximate to "most parsimonious" trees, or (*a fortiori*) to "true cladograms."

Unlike those extreme Cladists who divorce

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[3] Many authors (e.g., Farris, 1970) designate shortest trees as "optimal;" this implies that they are in some sense "best estimates" of the true phylogeny. We reject this implication: minimal, no more and no less, is what shortest trees are, in terms of the data and method used (including any user-set constraints).

their approach from evolutionary considerations, we *do* suggest that the junctions (dichotomous, trichotomous, or higher-order) may in acceptable trees represent an approximation to the relevant character-state sets of conceivable ancestors. If they merely represent some abstract set (see Hull, 1979; Mayr, 1981—but those authors report this notion, they do not espouse it), we cannot see that they are of any conceptual use to anyone. We do not, however, believe that it is valid to assign quantitative probability (perhaps more properly likelihood) values to such comparisons, nor can we see that assignment of numerical likelihood to character-state innovations (Felsenstein, 1981) is possible in any but a tiny minority of cases.

The hypothetical ancestors represented at each node of the tree are defined by their positions and by the character-state sets computed by the procedure. These sets should always be considered, so far as possible, for acceptability by criteria external to the analytical procedure itself. We have attempted this in the Myrtales, and the intermediate ancestors considered plausible are discussed below (3.2.3, 3.2.4, 3.2.5).

All CLAX computation for this study was carried out by hand, since the rather complex computer program in the language PASCAL (Johnson & Johnson, in prep.), allowing supraminimals and user intervention at various points, was not complete at the time of writing. Results of applying CLAX to the order Myrtales are given at 3.2 (Figs. 3–7).

2.3 CAMIN-SOKAL METHOD

Since it also assumes known polarity of character-state changes, the algorithm of Camin and Sokal (1965) may be compared with CLAX, though it does not operate on the same principle. We used the CAMIN-SOKAL PARSIMONY ALGORITHM program of Felsenstein, part of his package for inferring phylogeny (Felsenstein, 1979, 1981). The single tree produced for Myrtales was one step longer than the shortest CLAX results. This tree was, in fact, identical with one of the CLAX supraminimals (2.2). Thus this approach can yield a result included among those given by CLAX but is much less satisfactory in not allowing for the multiplicity of competing trees. Moreover, it does not possess a systematic procedure designed to give a high probability of capturing no-reversal minimals.

The phylogram obtained is discussed below (3.2.1).

2.4 MINIMAL-LENGTH METHODS ALLOWING CHARACTER-STATE REVERSALS

The results reported in this section were obtained from an earlier version of the data matrix lacking certain embryological characters (76 and 77) included in Table 1. They have not been recomputed since we have rejected these methods for reasons that would not be affected by including the additional characters. The lengths of trees given are comparable with each other but would need adjustment for comparison with Figures 3, 4, and 5. From inspection, it appears that the range of topologies would not be much affected and the lengths would increase by about five units. Figure 1, as presented, has been adjusted so that it is directly comparable with the CLAX phylograms.

2.4.1 CLAXMIN. For comparison, we have processed the Myrtales data (again by hand, but taking some short cuts) by CLAXMIN. This allows partially or completely unrestrained reversal of character-state polarity both initially and internally. It achieves this by minimization of the whole data matrix, in effect rescoring characters (except any predetermined by the user as non-reversible) by assuming an "original" state such that each column-total is minimized. This replaces the overall origin ("ancestor"), on which the tree is to converge downwards, with what might be called a quasi-centroid in the lattice ("Manhattan") metric with respect to the array of points representing the taxa in the *n*-dimensional character space. (By the nature of the metric and the existence only of points with integral or a limited set of fractional co-ordinates, such a quasi-centroid is not necessarily unique). Except in the no-restraint case, this is modified for the "reserved" characters in which reversal is not permitted; for these the original zero co-ordinate is retained in the dimension concerned. All equal temporary minimal, or allowed supraminimal, alternatives are held for later processing.

Setting the origin at a lattice centroid will in general decrease tree length but will not guarantee a shortest branching path convergent on the origin. The constellation of points may be such that *local* reversals of direction will yield shorter paths, i.e., the original monotonicity condition of the CLAX procedure must be relaxed. Accordingly, subsequent procedure involves a systematic minimization of partial matrices for the taxa and their differential characters on each forked-off portion of the tree, working upwards (backtracking) and combining all possibilities that satisfy a pre-set P level (see 2.2), meanwhile continually readjusting the temporary new origin. This in effect seeks the local quasi-centroids for all parts of the trees but does not necessarily *accept* them since shorter overall trees may result from not doing so. Any tree or partial tree that exceeds the pre-set P level is discarded (note that if P is set at zero or too low, some eventual minimals are likely to be lost). The procedure is complex, and a computer program for it has not been completed. We believe that, if carried through fully, it should yield all minimals provided that P is set high enough. For obvious combinatorial reasons, however, the computational load will increase rapidly as the data-set grows, and may become impractically high.

When, and only when, character-state reversal is completely unrestrained, each tree may be treated as undirected, i.e., as what Farris (1970) calls a network (wrongly, as pointed out by Rohlf & Sokal, 1981). These graphs may then be re-rooted at any chosen point to form directed trees, which are of equal length but involve different initial character-states.

For such attachment of the root point, one must remember that we adopt the convention of writing the character-state innovations on each internode of a tree in the numerical order of their listing in the data matrix; nevertheless they can be rearranged *in any order* within any internode. We have attached roots in such a way as to minimize the number of reversals from the "ancestral" state as originally assumed in the matrix, arranging characters as necessary on each portion of the internode intercepted by the attachment. Such minimization of change from the initial assumptions is, of course, not obligatory, and a vast number of directed trees may be consistent with any undirected-tree graph—many or even all of them will of course represent absurd phylogenetic hypotheses.

The initial result of CLAXMIN on Myrtales data yielded no less than 64 trees of length 135 (without the ancestor; equivalent to 142 if the stalk to the originally assumed ancestral state is included).

2.4.2 WAGNER-78. For further comparison we used the more conventionally cladistic and currently popular WAGNER-78 program of Farris. This is not fully documented in any publication by its author, or in the program in its available form, but rests on the foundation expounded by Farris (1970) and discussed by Jensen (1981). It is, we believe, an unacceptable method for all of the reasons given above (2.2), but especially because of point (5). Even if that is not considered relevant, the usual operation of WAGNER-78 results in failures on points (1) and (2). Jensen (1981) correctly points out the danger of relying on Farris's WAGNER procedure for reasons (1), (2), and (4). The reason for failure on (1) is that channeling very often precludes finding a minimum tree, even after the so-called optimizing procedure of the method is applied. Essentially the problem is similar to the one CLAX is designed to overcome (2.2), though the path-finding procedure and assumptions are different. It is a fundamental fault in WAGNER-78 and its predecessors.

We applied the method both including and excluding the ancestor implied by the original scoring (treating this as another taxon represented by a row of zeros in the data matrix). We used two different arrangements of the family sequence in the matrix in the without-ancestor case and five in the with-ancestor case. As Jensen (1981) points out, such rearrangements result in different sequences of processing by the program. As with the CLAXMIN Myrtales results, we have examined those from WAGNER-78, mostly after setting them out fully in a form comparable with the CLAX phylograms presented herein. They are not illustrated, but are all topologically different from the CLAXMIN trees and from each other, and differ also in numbers of reversals of direction in character-state changes (using root-attachment points as indicated above). WAGNER-78 trees obtained had lengths of 138 when processed without ancestor, and 143, 144, and 145 with ancestor (equivalent to a range from 137 to 139 with the ancestor-stalk removed). Characteristic examples of earlier CLAXMIN and these longer WAGNER-78 trees respectively had ten and 30 internal reversals (zero and eight multiple reversals!). None of these is identical with the tree shown in Figure 1, or its variants, derived by later application of CLAXMIN (see 2.4.3), although certain groups are robust (see 2.4.3, 3.2.6). Being in fact supraminimal, these trees are not illustrated. The probably minimal tree in Figure 1 does in fact have 18 internal reversals, including one multiple reversal (character 75, on the Combretaceous stem).

It will be seen that these applications of WAGNER-78 failed to yield minimal trees at all, while the results implied more character-state reversals than in shorter trees obtained by CLAXMIN.

Moreover, they tended to give "chained" trees, with most taxa coming off one by one. We would surmise that the frequency of such chained cladograms in cladistic studies in recent literature is partly an artificial consequence of the use of Farris's program.

2.4.3 Other minimal methods and comparisons. D. H. Colless (pers. comm.) has developed two programs, SWAG and RWAG, that generate and compare large numbers of Wagner-type trees. Runs of our Myrtales data by SWAG yielded (without ancestor) two trees of length 135 and (with ancestor) six trees of length 143. None was the same as either those obtained by WAGNER-78 or the initial 64 trees of length 135 obtained by CLAXMIN as hand-computed. Surprisingly, RWAG, out of 1,000 trees, produced one of shorter length (134).

Subsequent hand-reworking by an extended version of our original CLAXMIN yielded the same tree as the shortest RWAG tree, *together with variations* that in combination *amount to 30 or more different trees also of length 134*! These had been missed because, to reduce computation in hand-working the data, insufficient supraminimal partial trees had been considered. Some of these trees differ in topology, others only in length of internodes. We do not count the huge number of variants obtained by changing the root point. One version (topologically different from the RWAG minimal) is illustrated in Figure 1; it has there been extended (using CLAXMIN principles) by the addition of characters 76 and 77. It is *not* the basis of our phylogenetic hypotheses (see Figs. 3 and 4).

Felsenstein (1979, 1981) has produced a package of programs in PASCAL for inferring phylogeny, covering various approaches developed previously by other authors. One run of his WAGNER PARSIMONY ALGORITHM produced a tree of length 134, different in topology from any of the other cladograms considered and placing the Combretacean and Onagracean groups between the Myrtacean line and the remainder of the families. We did not obtain this tree from our hand-working of CLAXMIN, but believe that it would be obtained by a complete computerized application of this method. The program does not indicate the character-state changes but we have worked these out from the matrix to fit the tree—a process of considerable difficulty since the output gives no information on the lengths of internodes and the positions of reversals.

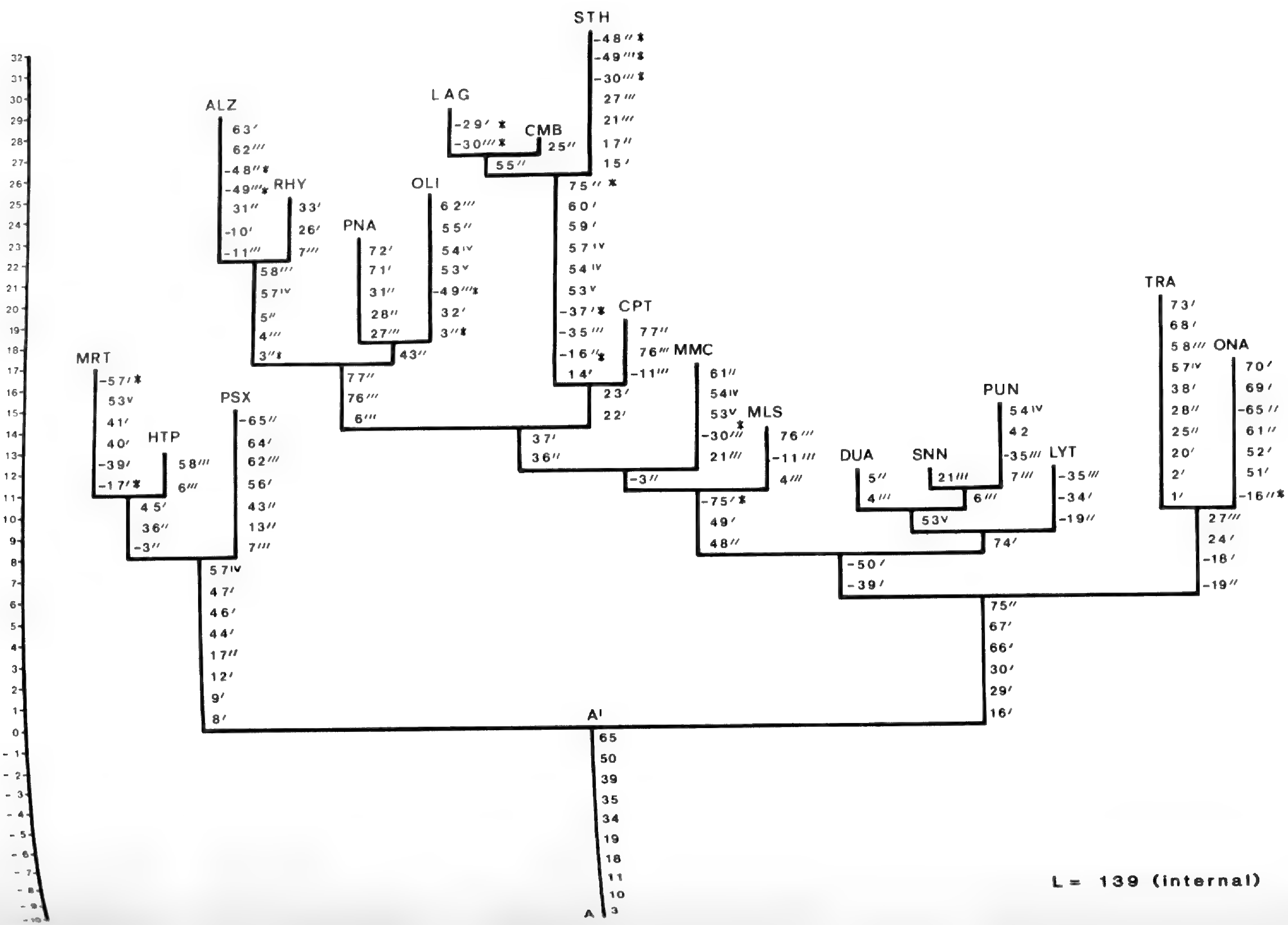
It is interesting that, from this limited sample, the Felsenstein program for the Wagner procedure seems to have been far more efficient than WAGNER-78. Not only was an apparently minimal tree produced from a single run (in contrast to longer trees from Farris's WAGNER-78 and a single tree of similar length out of 2,000 produced by runs of Colless's SWAG and RWAG), but both chaining and internal character-state reversals were less than in all WAGNER-78 results. This surprising result may be fortuitous, since, in analyses of Rutaceae tribe Boronieae (J. A. Armstrong, pers. comm.), the tree resulting from a single run of this Felsenstein procedure was longer than any of the trees of rather widely ranging length produced by WAGNER-78.

All of this heightens our confidence in CLAXMIN, especially against WAGNER-78 but also as against SWAG and RWAG, *as a method of seeking unrestrained minimals.* It emphatically underlines Jensen's warnings against accepting any single result of an application of such a procedure as WAGNER-78 as a basis for phylogenetic conclusions. The same applies, in part, to Felsenstein's WAGNER PARSIMONY ALGORITHM, since it produces a single result without any warning that this is far from unique.

However, we believe that unrestrained CLAXMIN results *are also unacceptable,* because they too involve biologically implausible reversals. *We would warn both phylogenists and formal taxonomists against all such unrestrained-reversal approaches, which are insidiously misleading.*

In essence, CLAX-type procedures, with more-or-less set polarity of character-state change, treat homoplasy (repeated innovation of the "same" or a similar character-state) as being more likely overall than evolutionary reversion. Unrestrained CLAXMIN, WAGNER-78, WAGNER PARSIMONY ALGORITHM, SWAG, and RWAG treat overall shortness of the tree as overriding any objection to reversion. WAGNER-78 seems to be particularly prone to yield multiple-reversal trees.

A few groupings in the Myrtales are robust under all analyses and the phylograms generated by CLAX and CLAXMIN show considerable congruence (see 3.2.6). For the same data, these groupings would probably tend to show up similarly (though subject to confounding by counting symplesiomorphous "matches"), not only in any reasonable (which may not mean *any*) phenetic analysis, but also in an "intuitive" analysis. This merely goes to show that a very strong and distinctive signal gets through a lot of noise!


STH
LAG
CMB
ALZ
RHY
OLI
PNA
CPT
MMC
MRT
HTP
PSX
MLS
PUN
DUA
SNN
LYT
TRA
ONA
A¹
A
L = 139 (internal)

We use the term "reversion" to indicate an actual evolutionary change back to a previous condition. This is in contrast to "reversal" which refers merely to a formal change of sign in the trees generated. It has been put to us (Vicki Funk, pers. comm.) that many reversals can be interpreted as instances of neoteny, i.e., a later development in *ontogeny* may fail to occur. We would add that there are two aspects in plants: (1) such failure of a stage in *ontogeny* of the whole plant (say retention of a juvenile leaf form or phyllotaxy into a reproductive phase; this is perhaps reasonably called paedomorphosis); (2) failure of a stage in *organogeny* (say in elongation of a style).

The expression of the character-state concerned is in both of these cases taken to have occurred regularly in ancestors but the development is suppressed or not realized (by any of a variety of mechanisms) in the taxon under consideration.

Naturally we are on the watch for neoteny of either of these kinds and we agree that neotenic loss (just as with loss by conversion to another state) is itself an apomorphy. Funk suggests that because neoteny is the loss of a character [-state] we are left with congruence (agreement with other characters) as "the only way we have of testing whether or not the absence of a character [-state] is a real absence (in the sense that it has never existed) and therefore plesiomorphic, or neoteny or reversal and therefore apomorphid." Congruence tests of the kind suggested by Funk have been done (3.2.6, Figs. 6, 7) but do not appear to bear particularly on neoteny or the assessment of homology.

Neoteny may be suspected, not on the basis of congruence between different cladograms, but on the basis of "agreement with other characters" as stated above. The agreement of characters is indeed expressed in the shortness of trees when change of sign (unrestrained or somewhat restrained) is permitted by the tree-generating algorithm. In other words, this procedure again appeals to parsimony, but excludes those aspects of parsimony external to the immediate scope of the analysis.

It is surely not an authoritarian "prior-knowledge" approach to consider that one can sometimes assess the likelihood of changes (neotenous or otherwise) on the basis of information and experience that are not formally expressed in the data set used in tree-generation. Some combinations of attributes will work biologically either in relation to the external environment or to the internal environment (which is involved in organogeny), some will not. The more complex an adaptive syndrome the less likely is "reversal" in structures or underlying systems on which the syndrome depends. We have discussed this briefly in relation to inflorescences in Myrtales (Briggs & Johnson, 1979).

Certainly all these things *tend* to show up in the patterns obtained in cladistic analysis, but there is also ample evidence in such analyses and in other biological experience that repeated innovation of "the same" character-state is very frequent. We therefore do not exclude external considerations in judging the likelihood of reversal (neotenous or "real"), and have indeed considered possible reversals in this way in the present study. A few are discussed in the text.

To take one or two particular examples, Figure 1 would require loss of leaf teeth to be followed by regaining of fully organized teeth of essentially rosoid form, reversion from a valvate to an imbricate calyx aestivation and loss of the specialized condition of fibrous seed exotegmen followed by its reappearance. Perhaps none of these is impossible but there seems no reason to prefer such hypotheses, with all that they imply developmentally and adaptively, over repeated in-

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FIGURE 1. A phylogram generated by CLAXMIN; *not* accepted as the basis of our phylogenetic hypotheses (see Figs. 3 and 4). Internal length = 139; length with basal stalk = 149; (respective lengths without characters 76 and 77 are 134 and 144). [There are several equal-length sequences (not shown, see text), some interdependent, some independent, involving combinations of variations in the regions ALZ-RHY-OLI-PNA and MRT-HTP-PSX. "Advancement level" is shown on the left. Character-state innovations are shown on each internode, the number of occurrences of each innovation in the tree (above A') is shown by the superscripts. Changes in reverse direction from those in the original scoring of Tables 1 and 2 are indicated by a minus (−) sign. The order on any internode is numerical and does not imply chronological sequence. * Indicates a reversal within the tree above A'. Abbreviations of the taxa are listed in Table 2. The character-states shown on the basal stalk are those that would have to be acquired by an ancestor of the group A' from an earlier ancestral condition (A) as postulated, as in the original scoring.]

novation of various other character-states simply on the grounds of the shortness of the resulting tree. The trees are, in any case, necessarily incomplete and arbitrary to some degree in choice, matching, and scoring of characters (Johnson 1969, 1970). The WAGNER-78 trees, as stated, involve more multiple reversals, and are not even minimal.

3. Phylogeny of Myrtales

3.1 THE DATA

3.1.1 The taxa. The families included in this study are those that formed the Myrtales and Lythrales of our previous account (Briggs & Johnson, 1979). Several families that have at times been placed in Myrtales by various authors were there considered to be of distant or doubtful affinity; our conclusions on their relevance to Myrtales are unchanged and are very similar to those of Dahlgren and Thorne (1984). Thymelaeaceae are retained in Myrtales by Cronquist (1981, 1984), but would certainly separate below the "ancestral" base in our analysis. For the reasons given by Dahlgren and Thorne, we believe that the family's affinities lie elsewhere. We cannot accept Elatinaceae as a member of Myrtales, despite some (not complete) embryological congruence of that family with the order (Tobe & Raven, 1983a). It would branch off below the ancestor in our phylograms by virtue of several characters, including the several-styled gynoecium. This is reinforced by the absence of intraxylary phloem and vestured pits (Dahlgren & Thorne, 1984), which are fundamental characters of Myrtales as here constituted.

We withdraw our former suggestion of upholding a distinct order Lythrales. The present study supports the views of other authors (e.g., Schmid, 1980) in completely rejecting the Lythrales concept. It was based in part on the erroneous report of a tenuinucellate condition in so-called Lythrales (Corner, 1976), which is discussed by Dahlgren and Thorne (1984). This error had been pointed out by Stafleu (1978) in a review that we overlooked; we erred also in not ourselves checking the standard embryological literature. In 1979 we also took into consideration seed-coat characters (see below), centripetal versus centrifugal development of the androecium, presence or absence of toothed leaves, and the chemical nature of seed reserves.

We do not discount direction of androecial development as a phylogenetic indicator as strongly as do Eyde (1975) and Schmid (1980), but now conclude, in agreement with Dahlgren and Thorne (1984), that polystemonous conditions are secondary in several distinct lines of the Myrtales and that the directions of stamen initiation in these are not significant for the oligostemonous basic groups in the order.

Our earlier comments on toothed leaves led to further studies by Hickey (1981), including the finding of cryptic teeth in some Lythraceae (e.g., *Cuphea*); these are in fact not difficult to observe once one knows about them. Our interpretation of the significance of leaf teeth and their loss is clear from our listing of characters and from the phylogenetic scenarios. The comments of Keating (1984) on leaf teeth in Onagraceae are also pertinent to the interpretation of this feature in Myrtales.

We have now examined seeds of a scatter of Myrtaceae and, contrary to the impression given by the literature (Corner, 1976; Hegnauer, 1969), find oil (presumably fatty) to be the most frequent and widespread storage material (e.g., in species of *Callistemon, Eucalyptus* sensu stricto, the eucalypt segregates "*Corymbia*" and *Symphyomyrtus, Fenzlia, Leptospermum, Lophostemon, Psidium,* and *Rhodomyrtus*). Two species of *Austromyrtus* differ: oil in *A. tenuifolia* (Sm.) Burret, starch in *A. bidwillii* (Benth.) Burret. Starch was also found in species of *Acmena* and *Syzygium* and appears to be mostly a secondary feature in species with large storage cotyledons and cryptocotylar germination [cf. our earlier remark (Briggs & Johnson, 1979: 164) on the starchy seeds of *Trapa*].

The terminal taxa in this analysis are families or "quasi-families." Wherever there seemed to be serious doubt about the placement or distinctiveness of a group we have treated it separately; this does not imply any necessary acceptance of family rank, and indeed we recommend sinking some commonly recognized families while elevating other groups not usually distinguished at family rank (see 3.3.2).

Where brief reference to the taxa is needed, as in the figures, we use the 3-letter abbreviations (they are not acronyms as he states) of Weber (1982). For groups not in his list we have used the following: Alzateaceae ALZ, *Duabanga* DUA, Laguncularieae LAG, Rhynchocalycaceae RHY (see 3.3.2), and *Strephonema* STH. Also, CMB is used for the tribe Combreteae (which is only part of the traditional Combretaceae), MLS refers to Melastomataceae sensu stricto with Memecylaceae kept distinct, and SNN covers only the genus *Sonneratia.*

3.1.2 The characters. The characters used in the phylogenetic analyses (Table 1) are those for which data are available to us and which present differences within the set of taxa. The state considered ancestral within each taxon is scored; differences developed subsequently *within* the taxa are not relevant to comparisons between taxa. Whether conscious or unconscious, weighting of characters is inevitable. This is because (1) it is both theoretically and practically impossible to define, even in terms of the genetic code, such a concept as equivalent unit attributes (see Johnson, 1969, 1970), and (2) "probability of evolutionary change" (a complex concept at best) is variable between as well as (temporally) within "characters" (serially transformable attribute sets), so that the methodological analyses of Felsenstein (1981) serve more as warnings than as useful recipes. In some cases we have assigned two serial binary characters, because the change involved is clearly complex, even though only extreme conditions are present. These are shown by brackets in the score column of Table 1. One can argue ad infinitum on all such matters, and we have simply adopted what seemed to be reasonable weighting.

For ease of representation and because it is necessary for the input of some other analyses used but not presented here (e.g., programs developed by Felsenstein, 1981) the characters are presented in binary form. Cases involving serial states are indicated by brackets in the character list. A pair of bracketed binary characters implies three states represented by the ordered pairs (0,0; 1,0; 1,1). By changing the initial assumptions, any one of these states can be taken as the starting point and the sequence can be read forwards, backwards, or from the middle in two directions. However, since the states are ordered, one cannot simultaneously assume both extremes as initial starting points and converge on the middle state. Thus the combination (0,1) is not admissible. This means that for characters *a* and *b,* with the possible scorings as indicated above, one can have, by partial reversal, $-a$ and $+b$ (i.e., middle condition primitive) or by complete reversal $-a$ with $-b$, but $+a$ with $-b$ is inconsistent.

Initial assumptions on the direction of characters are made on out-group comparison and "general principles," which usually amount to much the same thing. Our interpretations and assumptions correspond very generally with those of Dahlgren and Thorne (1984) and of van Vliet and Baas (1984), and will therefore not be justified here, although our reasoning sometimes differs. In a few cases we have no strong conviction about the polarity and the CLAX analyses have been done with alternative assumptions; these are marked in Table 1. Some other methods of analysis allow reversal of any character, and are rejected for that reason (see 2.4.3).

The taxa often include more than one state of a character among their constituent members. Our character-state sets do not cover those *internal* ranges, which are indicated broadly by Dahlgren and Thorne (1984). The state considered to be *ancestral within the group* is the appropriate one for comparison with other taxa. This is not necessarily the commonest state within the group and may not even be present among living members; it may be a state that it is necessary to postulate in order to account for divergent conditions within the taxon (Johnson & Briggs, 1975: 95). A striking example is the postulated superior ovary in the ancestor of Onagraceae (see 3.3.2 and Eyde, 1981). Clearly such assignment of an ancestral condition creates difficulties if character-state reversal is allowed in a phylogram; any phylogram involving such reversals should be re-examined with regard to the implications for taxa affected. If a taxon includes members with different states of a character, reversal of polarity would not necessarily change the numerical score but would lead to different members of the taxon being considered as exemplifying the ancestral state.

Within the Lythraceae, subsidiary colpi occur on the pollen grains of some genera. Our initial scoring assumes this to be an advanced condition developed within the family, which is therefore scored 0 for characters 48 and 49. In phylograms B and C (3.2.4, 3.2.5) we invoke an alternative hypothesis that the first stage of this condition (character 48) was attained in forerunners of the Lythracean group, but was not primitively present in the Myrtales as a whole. It must therefore be scored as 1 for the Lythraceae and for the three allied taxa, with an additional (reversed) character (−48) scored as 0 for (ancestral) Lythraceae but as 1 (representing loss of incipient subsidiary colpi) for *Duabanga, Sonneratia,* and *Punica,* this appearing as a synapomorphy on

TABLE 1. Characters used in phylogenetic analysis of Myrtales. Postulated primitive states with zero scores.[a]

1. Herbaceous habit	0 = woody; 1 = herbaceous
2. Aquatic herbs	0 = not aquatic herb; 1 = aquatic herb
3. Vessel aggregation	0 = mostly solitary; 1 = mostly grouped
4. Fibers: loss of bordered pits (change from fiber-tracheids to libriform fibers)	0 = bordered; 1 = reduced at least to intermediate state
5. Fibers: loss of bordered pits (change from fiber-tracheids to libriform fibers)	0 = bordered or intermediate; 1 = simple
6. Loss of apotracheal parenchyma	0 = present; 1 = absent or scanty
7. Crystalliferous septate fibers	0 = absent; 1 = present
8. Secretory cavities (oil glands containing terpenoids)	0 = absent; 1 = present
9. Secretory cavities (oil glands containing terpenoids)	0 = absent; 1 = present
10. Loss of trilacunar nodes	0 = trilacunar (3 gaps, 3 traces); 1 = at least some reduction[b]
11. Loss of trilacunar nodes	0 = trilacunar or intermediate; 1 = unilacunar (1 gap, 1 trace)
12. "Myrtaceous" hair-type	0 = not "myrtaceous" type; 1 = present
13. "*Psiloxylon*-type" modification (2-armed, thin-walled)	0 = absent; 1 = present
14. "Combretaceous" hair-type	0 = absent; 1 = present
15. Revolute domatia	0 = absent; 1 = present
16. Fixation of opposite phyllotaxy	0 = flexible[a]; 1 = opposite
17. Fixation of spiral phyllotaxy	0 = flexible[a]; 1 = spiral
18. Loss of leaf teeth	0 = leaves toothed; 1 = teeth reduced at least to vestiges
19. Loss of leaf teeth	0 = with leaf teeth or vestiges; 1 = teeth absent
20. Leaf teeth "trapaceous" (bifid)	0 = teeth simple (or lost); 1 = teeth bifid
21. Stomate type	0 = anomocytic; 1 = paracytic
22. Well-defined blastotelic[a] (anauxotelic) inflorescence	0 = anthotelic; 1 = blastotelic (anauxotelic)
23. Well-defined blastotelic[a] (anauxotelic) inflorescence	0 = anthotelic; 1 = blastotelic (anauxotelic)
24. Uniflorescence reduced to axillary monad on auxotelic[a] axis	0 = not reduced in this way; 1 = reduced
25. Loss of prophylls (bracteoles) in inflorescence	0 = prophylls present; 1 = absent
26. Increase in floral mery	0 = mery not regularly increased; 1 = regularly >5-merous
27. Reduction of floral mery	0 = not reduced; 1 = reduced at least to flexible 4–5
28. Reduction of floral mery	0 = not reduced or flexible 4–5; 1 = <5-merous
29. Loss of calyx imbrication	0 = imbricate; 1 = not or slightly imbricate
30. Loss of calyx imbrication	0 = some degree of imbrication; 1 = fully valvate
31. Loss of petals	0 = petals present; 1 = petals absent
32. Petals small and thick ("oliniaceous")	0 = petals "normal;" 1 = petals "oliniaceous"
33. Petals hooded (*Rhynchocalyx*-type)	0 = petals "normal;" 1 = petals hooded
34.[b] Staminal insertion	0 = stamens all below hypanthium[a] rim; 1 = not all below rim
35.[b] Staminal insertion	0 = at least some stamens below rim; 1 = all stamens on rim
36. Stamens "ob"	0 = not "ob" (i.e., diplostemonous or haplostemonous); 1 = stamens obdiplostemonous or obhaplostemonous
37. Obhaplostemony	0 = not obhaplostemonous; 1 = obhaplostemonous

TABLE 1. Continued.

38. Haplostemony	0 = not haplostemonous; 1 = haplostemonous
39. Loss of stamen inflexion	0 = inflexed; 1 = straight
40. Stamen proliferation (centripetal) in bundles	0 = absent; 1 = present
41. Stamen proliferation (centripetal) in bundles	0 = absent; 1 = present
42. Stamen proliferation (centrifugal)	0 = absent; 1 = present
43. Reduction of stamen filaments	0 = not reduced; 1 = reduced
44. Presence of connective gland[a]	0 = absent; 1 = present
45. Enlargement of terpenoid-containing connective gland ("myrtaceous" type)	0 = absent or small; 1 = well developed
46. Pollen syncolporate	0 = not syncolporate; 1 = syncolporate
47. Pollen syncolporate	0 = not syncolporate; 1 = syncolporate
48.[b] Subsidiary colpi on pollen[a]	0 = absent; 1 = present
49. Subsidiary colpi on pollen[a]	0 = absent, poorly developed or only at one pole; 1 = well developed
50. Pollen ± oblate[a]	0 = prolate or subprolate; 1 = ±oblate
51. Pollen with viscin threads	0 = threads absent; 1 = present
52. Pollen with "onagraceous" exine	0 = absent; 1 = present
53. Epigyny (fusion of ovary with hypanthium)	0 = gynoecium free; 1 = at least slightly fused
54. Epigyny (fusion of ovary with hypanthium)	0 = free or slight fusion; 1 = considerable fusion
55. Epigyny (fusion of ovary with hypanthium)	0 = not complete epigyny; 1 = complete epigyny
56. Ovary stipitate	0 = sessile; 1 = stipitate
57. Reduction of carpel number	0 = isomerous with perianth; 1 = reduced to 4 or 3 or fewer
58. Reduction of carpel number	0 = 3 or more carpels; 1 = reduced to 2 carpels
59. Ovary multicarpellate but unilocular ("combretaceous")	0 = condition absent; 1 = present
60. Ovary multicarpellate but unilocular ("combretaceous")	0 = condition absent; 1 = present
61. Carpels antepetalous	0 = antesepalous; 1 = antepetalous
62. Style reduction	0 = long or medium length; 1 = little or no elongation
63. Style reduction	0 = at least some elongation; 1 = not at all elongated (stigma sessile)
64. Exaggerated stigmatic lobing	0 = lobing or division no more than moderate; 1 = pronounced lobing
65. Reduction in stigmatic lobing	0 = lobing or division at least moderate; 1 = very little or no lobing
66. Style base not sunken[a,b]	0 = sunken; 1 = not sunken
67. Style base not sunken[a,b]	0 = sunken; 1 = not sunken
68. Very early loss of endosperm	0 = present; 1 = largely lost
69. *Oenothera*-type embryo sac	0 = not *Oenothera*-type; 1 = *Oenothera*-type
70. *Oenothera*-type embryo sac	0 = not *Oenothera*-type; 1 = *Oenothera*-type
71. *Penaea*-type embryo sac	0 = not *Penaea*-type; 1 = *Penaea*-type
72. *Penaea*-type embryo sac	0 = not *Penaea*-type; 1 = *Penaea*-type
73. Cotyledons unequal	0 = equal; 1 = one reduced
74. Outer integument multiplicative	0 = not multiplied; 1 = multiplied
75. Fibrous seed exotegmen	0 = absent; 1 = present
76. Loss of fibrous development of anther endothecium	0 = present; 1 = absent
77. Anther endothecium ephemeral	0 = persistent; 1 = ephemeral

[*] Brackets link serial or double-weighted (e.g. 8, 9) characters (see text).

[a] For explanation see text.

[b] Potentially reversible character.

TABLE 2. Data matrix (taxa and characters) used in analysis of Myrtales. Character-states are defined in Table 1.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Myrtaceae	MRT	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0
Heteropyxidaceae	HTP	0	0	0	0	0	1	0	1	1	1	1	1	0	0	0	0	1
Psiloxylaceae	PSX	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	0	1
Penaeaceae	PNA	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0
Alzateaceae	ALZ	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0
Oliniaceae	OLI	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0
Rhynchocalycaceae	RHY	0	0	1	1	1	1	1	0	0	1	1	0	0	0	0	1	0
Punicaceae	PUN	0	0	1	0	0	1	1	0	0	1	1	0	0	0	0	1	0
Sonneratia	SNN	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0
Duabanga	DUA	0	0	1	1	1	0	0	0	0	1	1	0	0	0	0	1	0
Lythraceae	LYT	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0
Strephonema	STH	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	1
Combreteae	CMB	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
Laguncularieae	LAG	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0
Crypteroniaceae	CPT	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Memecylaceae	MMC	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0
Melastomataceae sensu stricto	MLS	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1	0
Onagraceae	ONA	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Trapaceae	TRA	1	1	1?	0?	0?	0?	0?	0	0	1	1	0	0	0	0	1	0

the common stem of those taxa in the phylograms.

Our concept of the primitive states will be better understood by reference to 3.2.2, where a postulated ancestor of the order is described.

We are interested not only in branching sequence but also in some indication, however rough, of the differences accumulated along branches, i.e., in patristic change (cf. Mayr, 1981). Each terminal taxon is simply a point at which the tree is truncated. It could be extended into further branches by considering the constituent members of the taxa (which would then present many more autapomorphies, synapomorphies, and homoplasies). We therefore regard the "lengths" of the terminal branches to be of interest in assessing the degrees of divergence, and ultimately perhaps the assignment of taxonomic rank (for which the use of such a criterion lies outside Hennigian cladistics in the strictest sense, where only branching sequence is significant). Accordingly, we include a number of characters for which the presumed apomorphous state occurs in only one terminal taxon (autapomorphy). Since these do not affect the topology, anyone who does not like them can simply strike them out.

Notwithstanding claims to the contrary, no procedure can really "make allowance" for missing data; CLAX requires a numerical entry, which may be zero, for every character for each taxon. A few characters are not recorded for all taxa, and some taxa are not sufficiently well sampled for their most primitive character-state (on present assumptions of polarity) to be specified with reasonable certainty. Extrapolation has then been necessary; for example the non-woody Trapaceae have been scored similarly to Onagraceae in wood features, but inspection will show that the groupings do not depend on these characters.

A few characters need particular mention:

Characters 10, 11. Loss of trilacunar nodes. Baas (pers. comm.), while stating that trilacunar nodes are generally regarded as more primitive, points out that there can be considerable flexibility within genera in some families, and be-

TABLE 2. Continued. (Table 2 continues on pp. 714 and 715.)

18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1
1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1
1	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	1	1	1	0	0
1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	0	0
1	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	0
1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1	1	1	1	0	0
1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
1	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0
1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
1	1	0	1	1	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	0
1	1	0	0	1	1	0	1	0	0	0	1	1	0	0	0	1	0	1	0	0	0
1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
1	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	1	1	1	1	0	0
1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	1	1	0	0	0	1
0	0	1	0	0	0	1	1	0	1	1	1	1	0	0	0	1	1	0	0	1	1

lieves that the trilacunar nodes of *Alzatea* cannot be used in strong support of its isolated position. Intermediate conditions are described by van Vliet and Baas (1975) in the three genera of Crypteroniaceae sensu stricto and in a number of Melastomataceae ("Melastomatoideae"). These have three leaf traces, the lateral traces of the pairs of leaves sharing common gaps or alternatively simply girdling the node, which then has only the gaps corresponding to the median traces. This condition is possible only with opposite phyllotaxy. Since the general patterns in the order suggest that early members possessed spiral phyllotaxy at some stage in their individual life histories (see 3.2.2 "*Protomyrtalis*"), the girdling or common-gap condition could scarcely be plesiomorphous for the order. We therefore do not accept reversal of characters 10 and 11 (such as are shown in the CLAXMIN and WAGNER-78 trees, cf. Fig. 1), even though completely trilacunar nodes are recorded only in *Alzatea*. This non-reversal implies several independent losses of the trilacunar condition, either to the "intermediate stage" or to completely unilacunar states. Since the second stage of this has pretty obviously occurred in Melastomataceae, there seems no great difficulty in envisaging multiple acquisition of the unilacunar condition. Alternatively, trilacunar nodes in *Alzatea* may be a neotenous or paedomorphic condition (and thus appearing as a reversal in a phylogram); it would be interesting to examine juvenile stages of related families. Trilacunar nodes occur commonly in other families of the Rosiflorae, an out-group basis for our assumption.

16, 17. Phyllotaxy. Although it is conceivable that opposite phyllotaxy was primitive for the order or its predecessors, we believe that actual patterns indicate that ontogenetic change in this character was the primitive condition for both the Myrtales and Myrtaceae, with fixation to either opposite or spiral phyllotaxy in some families or parts of the families (see 4.1.3). Both opposite and disperse (spiral) conditions occur among the Rosiflorae. Lythraceae are taken here to have attained the fixed opposite condition;

TABLE 2. Continued.

		40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Myrtaceae	MRT	1	1	0	0	1	1	1	1	0	0	1	0	0	1	0	0	0
Heteropyxidaceae	HTP	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0
Psiloxylaceae	PSX	0	0	0	1	1	0	1	1	0	0	1	0	0	0	0	0	1
Penaeaceae	PNA	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0
Alzateaceae	ALZ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oliniaceae	OLI	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0
Rhynchocalycaceae	RHY	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Punicaceae	PUN	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Sonneratia	SNN	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Duabanga	DUA	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Lythraceae	LYT	0	0	0	0	0	0	0	0	0[a]	0	0	0	0	0	0	0	0
Strephonema	STH	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Combreteae	CMB	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0
Laguncularieae	LAG	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	0
Crypteroniaceae	CPT	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Memecylaceae	MMC	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0
Melastomataceae sensu stricto	MLS	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Onagraceae	ONA	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Trapaceae	TRA	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

[a] This score applies to some Lythraceae, others would be scored "1;" see text for relevance to phylograms B and C.

authors have stated that "alternate" arrangement occurs in some genera, but we find this to be in fact disjunct-opposite (Briggs & Johnson, 1979) in *Lagerstroemia* and *Lythrum*, for example, not truly disperse (spiral).

18–20. Leaf teeth. Characters 18 and 19 apply to the fuchsioid teeth as found in various Onagraceae and, in a reduced form, in some Lythraceae (3.2.3). Teeth of this kind are also interpreted as forerunners of the specialized bifid teeth of *Trapa* (character 20) (Briggs & Johnson, 1979; Hickey, 1981). Unvascularized tooth-like "*cilia*" (marginal projections of the epidermis) found in advanced Myrtaceae, such as *Baeckea*, are different in nature. They are almost certainly secondary developments, as are the variable teeth of some species of *Sonerila* (Melastomataceae). In the latter case, single vascular strands enter the teeth but these appear to have developed from the multicellular hairs characteristic of the family and present generally on most aerial organs of this genus. They have no glandular tip, are not always strictly marginal, and differ in underlying vascular pattern from the fuchsioid hair types (Dahlgren & Thorne, 1984). The features of *Sonerila* do not indicate any early divergence from the rest of Melastomataceae, and out-group comparison with neighboring genera therefore supports the interpretation of the teeth as secondary.

22, 23. Inflorescence. Inflorescences in Myrtales are discussed by Briggs and Johnson (1979), where the terminology used here is explained. In that paper we overlooked the presence of prophylls ("bracteoles") in *Ludwigia* of the Onagraceae and in the tribe Laguncularieae of the Combretaceae. Although the published descriptions are not clear in this regard, we have now found these structures to be present also in *Strephonema* and in some members of the Crypteroni-

TABLE 2. Continued.

57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	"Advancement level"
0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	19
1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	21
1	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	23
0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	0	1	1	25
1	1	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0	0	0	1	1	23
0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	25
1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	27
0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	19
0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	18
0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	18
0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	1	0	0	12
1	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	23
1	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	24
1	0	1	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	21
0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	19
0	0	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	17
0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	16
0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	0	19
1	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	1	0	0	26

aceae sensu stricto. In the latter family, prophyllar bracteoles occur in *Axinandra* and in some species only of *Crypteronia*. We have not found them in *Dactylocladus*.

29, 30. Calyx imbrication. On general out-group comparison, we take imbricate aestivation of the calyx as the original condition. We find some of the families generally described as having valvate aestivation to include some members that preserve a degree of imbrication. Cases are Memecylaceae, *Strephonema*, and the tribe Laguncularieae of Combretaceae.

34, 35. Staminal insertion. We cannot form any definite opinion as to the polarity of change in this character. Developmental studies will possibly shed some light upon it. We have reverted to the term "hypanthium" rather than "perigynium" as used in Briggs and Johnson (1979). The latter term is preferable in some ways, but confusion may result from its continuing use for a quite different structure in the Cyperaceae, in which it has priority of usage. Although "hypanthium" is etymologically misleading, its application seems now to be standardized.

44. Connective gland. Glands on the connective occur in some Melastomataceae and Memecylaceae but appear to be secondary acquisitions in these taxa. They do not appear to be of the same nature as the terpenoid-containing gland in the Myrtaceae, Heteropyxidaceae, and Psiloxylaceae.

48–50. Subsidiary colpi and pollen shape. We have preferred the term "subsidiary colpi" to "pseudocolpi," following Muller (1981a), who gave an excellent discussion of the evolution and dynamics of pollen grains in relation to shape, colpi, and exine structure. From this, and from out-group comparisons, we conclude with him that the more or less prolate condition with relatively little exine thickening is primitive for the order. A complete reversion from well-developed subsidiary colpi to their absence seems unlikely, but reversion from an incipient or weakly developed condition to apparent absence is regarded as a possible alternative (3.2.4). The effect of such an interpretation is mentioned under 3.2.5.

66, 67. Style-base. We have assumed that the sunken style-base is plesiomorphous, perhaps as a relict state deriving from a former apocarpous condition with the styles more or less running down the adaxial edge of the carpels, as in some Rosales. However, if it is not primitive the topology of Figures 3 and 4 is not affected, although the characters 66 and 67 disappear from their present positions, while −67 and −66 appear on the stem leading to the Myrtacean group (if we assume that the condition is primitive within the latter); alternatively these characters disappear altogether (the sunken style-base being then considered to have arisen independently in Psiloxylaceae, Heteropyxidaceae, and *within* the Myrtaceae) or appear only on the possible Psiloxylaceae-Heteropyxidaceae stem.

74, 75. Seed-coat structures. These are largely taken from Dahlgren and Thorne (1984), ignoring within-taxon (later) apomorphies. We have examined seeds of *Rhynchocalyx* and are indebted to S. A. Graham (pers. comm.) for information on *Alzatea* and confirmation of our observations on *Rhynchocalyx.* Neither genus shows a fibrous exotegmen or a multiplicative outer integument. In both, the seed coat is very simple, of only two cell-layers, whereas a multilayered seed coat is general in Lythraceae (Graham, pers. comm.)

76, 77. Embryological features. Information has been obtained from Tobe and Raven (pers. comm. and 1983a, 1983b, 1984a, 1984b).

3.1.3 Chromosomal features. Karyological characters have not been used in the analyses, and chromosomal evolution will need to be considered in relation to the various scenarios for the Myrtales and the different reliability of parts of these. Many details are still lacking. A base number of 12 seems quite likely, as suggested by Raven (1975), with dysploid reductions in various lines and within several families; $X = 11$ is of frequent occurrence, but chiefly in what we would consider to be somewhat advanced members.

Some further support for a base number of 12 comes from our finding of $2n = 24$ in *Psiloxylon* (Fig. 2). [*Psiloxylon mauritianum* (Hook. f.) Baill., cultivated Royal Botanic Gardens, Sydney, voucher *Briggs 7233* (NSW); seed source: Le Grand Brûlé, Réunion, *Guého* 14 June, 1979.] This number has previously been reported in *Heteropyxis* (Fernandes, 1971).

Such a base number may, of course, itself be derived by reduction after tetraploidy, or by tetraploidy after reduction from the often-suggested dicotyledonous base number of $X = 7$, but there is no particular evidence to support this. For plants in general, James (1981) challenges such common hypotheses of polyploidization followed by dysploidy, although he believes that descending dysploidy has happened frequently. His arguments rest on what he considers to be cytogenetically most likely, and are not absolute. Thus, in the light of correlations of chromosome number patterns and other features, we believe that polyploidy followed by decreasing dysploidy has in fact occurred in various orders and families. For instance in the Proteaceae (Johnson & Briggs, 1975) James's contention would lead to a very unparsimonious hypothesis indeed, in view of the phylogenetic pattern in the family as indicated by a mass of other evidence.

3.2 THE HYPOTHESES

3.2.1 Competing hypotheses. Arising from our analyses, we discuss three phylograms (each including some minor variants) representing hypotheses as to the evolutionary relationships and sequence of diversification.[4]

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[4] We do not discuss in detail the supraminimal tree produced by both CLAX and the Felsenstein program based on the Camin and Sokal algorithm (see 2.3). Its terminal groupings, with common stalks up to level 10 or higher, are MRT-HTP-PSX, LAG-CMB-STH-MMC, ALZ-RHY-PNA-OLI-CPT-MLS, DUA-SNN-PUN-LYT, TRA-ONA. The cores of these correspond with the robust groups as discussed below (3.2.6). MMC, CPT, and MLS do not come out in such robust groups, and both MMC and MLS attach at level 10 in this phylogram, i.e., below the other members of the groups listed. At a lower level this tree has a different branching pattern from the others discussed, since LAG-CMB-STH and MMC join at level 5 with MRT-HTP-PSX (the common characters being 10, 11, 18, 19, and 34). The remainder of the families have a common stalk to level 4 (characters 29, 30, 66, 67). All of the character-states concerned are of multiple innovation in this and other trees, and we see no reason to regard this slightly longer phylogram as competing very seriously with those discussed below. Nevertheless, it does illustrate that a multiple analysis of this kind points to uncertainty at the earlier ancestral stages.

These are founded respectively on: (1) our original scoring, i.e., our views of the likely primitive conditions, derived from internal and outgroup comparisons (3.2.2, Fig. 3)—phylogram A, (2) a variant of the above, allowing for an internal reversal; it is assumed that some degree of development of subsidiary colpi on the pollen grains is gained and subsequently lost (not illustrated) (3.2.4)—phylogram B, and (3) a further variant, with reversal of the character of subsidiary colpi as in (2) but making a different assumption as to the ancestral level of insertion of the stamens on the hypanthium (3.2.5, Figs. 4, 5)—phylogram C.

The character-state changes made in variants (2) and (3) result in shorter ("more parsimonious") trees. Moreover, these are characters in which it seems that reversal (in these cases not necessarily equivalent to actual evolutionary *reversion*) is not contra-indicated by structural impossibility. All these phylograms, and their minor variants as shown by alternatives on the diagrams, are conceivable sets of evolutionary relationships, unlike various phylograms discussed and rejected above (2.4).

To clothe the bones with some flesh, we present first a description of "*Protomyrtalis,*" the hypothetical common ancestor of the Myrtalian families, and then develop scenarios of diversification and geographic spread corresponding with the phylograms. These account for the characters taken as ancestral *within each of the taxa* adopted here as families or quasi-families, that is, each of the end-points of the phylograms. General conclusions will be discussed below, and the order of presentation of the phylograms and discussion does not necessarily imply an order of preference.

The fossil record of the Lythraceae has been reviewed by Graham and Graham (1971), and numerous additional records have been cited by Eyde (1972). Eyde and Morgan (1973) give a brief account of the record for Onagraceae. In general, however, the paleobotanical record for the order is extremely scanty (Muller, 1981b). Modern distribution patterns and their implications therefore form the basis of the historical phytogeographic suggestions. The techniques of vicariance biogeography as fervently advocated by such Cladists as Nelson and Platnick (1981) seem to us to be too formalistic and, equally importantly, subject to the same computational uncertainties as discussed above (2.2, 2.4). None the less, we suspect that they would *tend* to indicate a general pattern similar to that put forward below, though we are less dismissive than such authors of allegedly "untestable" dispersal hypotheses, less committed to their narrow view of acceptable scientific method, and much less convinced that allopatric speciation is a sufficient model upon which to base a rigid procedure. Moreover, we are conscious that fossils turn up in surprising places, and of the importance of extinction.

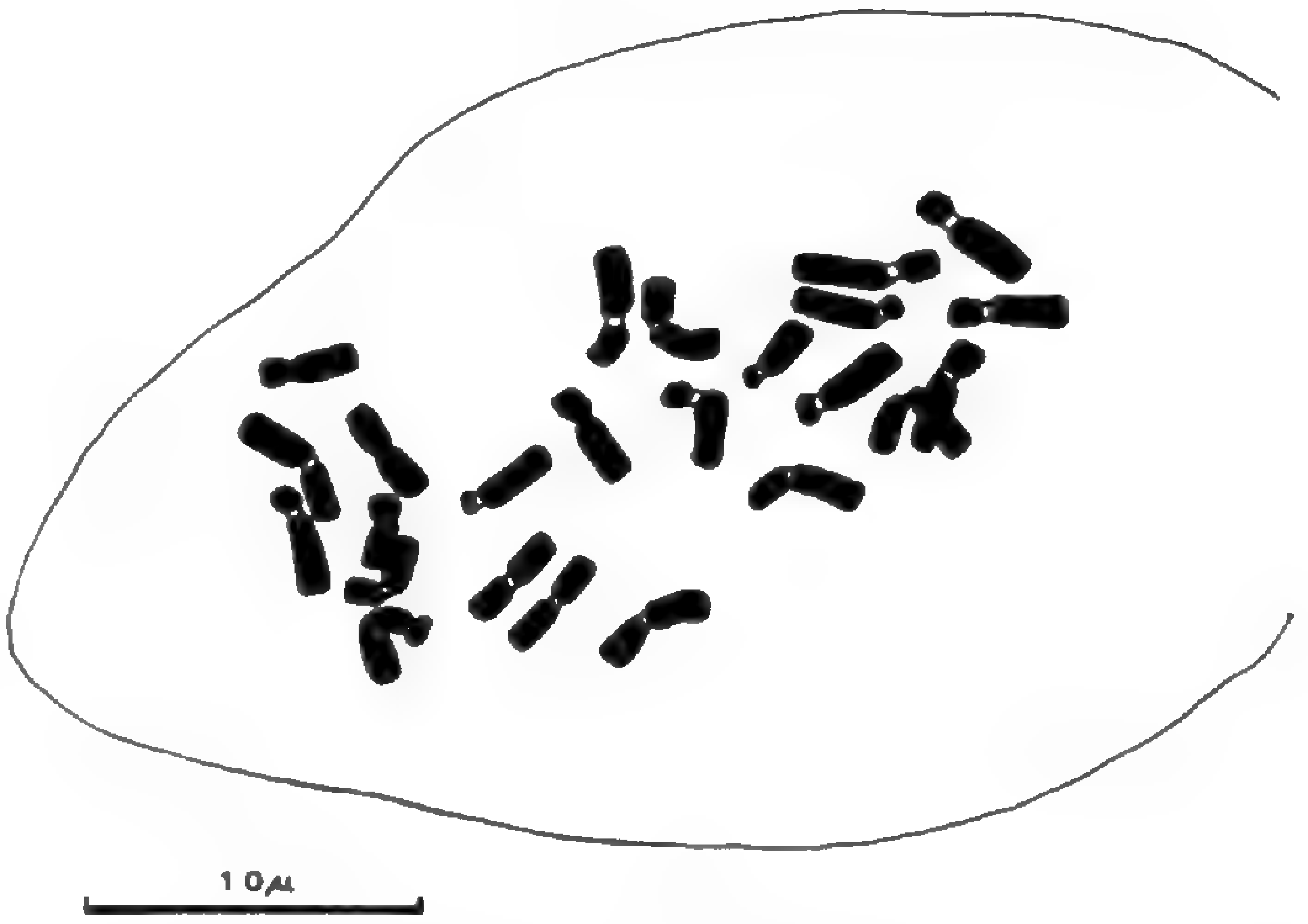

FIGURE 2. Mitotic chromosomes of *Psiloxylon mauritianum.* $2n = 24$.

3.2.2 "Protomyrtalis." Trees, evergreen, leptocaul, with sylleptic growth, of mesic habitats under equable climate. Bark of trunk and limbs probably with a tendency to shed in plates or strips. Without oil glands (secretory cavities) or laticifers; producing trihydroxylated flavonoids and tannin substances including ellagic acid; not producing iridoids or benzyl isoquinoline alkaloids. Endotrophic mycorrhiza probably present. Vascular bundles of primary stems and main bundles of leaves bicollateral and hence with intraxylary phloem in woody stems. Wood-anatomical characters as given by van Vliet and Baas (1984) for their "Protomyrtales." Sieve-tubes of the phloem with S-type (starch-containing) plastids, P-type plastids (with crystalline protein) absent (Behnke, 1984). Hairs unicellular and unbranched, just possibly some multicellular uniseriate hairs present, glandular hairs absent. Stomates anomocytic. Nodes trilacunar or potentially able to revert to trilacunar condition (e.g., by neoteny?). Phyllotaxy probably varying during ontogeny (opposite-decussate → spiral → opposite?). Stipules present, small, perhaps with a tendency to become divided. Leaves simple, petiolate but not articulate or pulvinate, moderately large, dorsiventral, hypostomatic, with pinnate-reticulate and ± brochidodromous venation, margins with modified rosoid ("fuchsioid") teeth. Inflorescence fundamentally anthotelic (determinate), paniculate (sensu Troll, 1964), but development of individual shoots flexible and inflorescence not sharply demarcated from the vegetative region (as in the primitive Myrtaceous inflorescence as postulated by Briggs & Johnson, 1979), prophylls present on ultimate branches but metaxyphylls probably absent. Flowers with a distinct anthopodium [i.e., a pedicel above any "bracteoles" (= prophylls) or other "bracts" present], bisexual, pentacyclic, pentamerous or flexibly 4–6-merous, somewhat perigynous, neither very large nor very small, actinomorphic, entomophilous, perianth members free. Calyx of broad-based, imbricate, herbaceous sepals. Corolla of white or cream or at least not highly colored petals; these ± spreading at anthesis, probably ± obovate and with stipule-like outgrowths at the base. Androecium diplostemonous; stamens perhaps borne somewhat below the rim of the hypanthium, filaments perhaps incurved in the bud. Anthers versatile, dorsifixed, introrse, connective narrow without a glandular protuberance, tetrasporangiate, bilocular at anthesis, dehiscing longitudinally; epidermis persistent; endothecium fibrous, tapetum glandular, becoming 2-nucleate. Pollen somewhat prolate, isopolar, 3-colporate and not syncolpate, lacking subsidiary colpi, 2-nucleate when shed, exine thin and probably with a granular infratectal layer (Gadek & Martin, 1982), not highly ornamented, without viscin threads. No strongly demarcated disk present but inner surface of hypanthium ± nectariferous. Gynoecium fully superior (quite free from the hypanthium), isomerous with the perianth, syncarpous (not coenocarpous). Style simple, only moderately elongated, base possibly ± sunken into top of ovary. Stigma probably of the Dry type, somewhat lobed. Ovary narrowed at base but not stipitate, locules antesepalous and as many as the carpels, septa complete except perhaps for a compitum below the style-base. Placentation axile, the placentas only moderately protruding and with axile vascular supply. Ovules several or numerous per carpel, anatropous or perhaps varying to hemitropous or campylotropous according to position on the placenta (as frequently in living Myrtaceae), crassinucellate and bitegmic, all potentially fertile (no ovulodes); embryo sac of *Polygonum*-type; endosperm formation Nuclear. Fruit a superior, loculicidal capsule, probably rather thin-walled. Seeds several or numerous in each loculus, wingless, without either a differentiated fibrous exotegmen or multiplicative outer integument; endosperm disappearing during development, very scanty or absent in ripe seeds; embryogeny of Onagrad type; suspensor short and small; embryo probably straight or slightly curved, storing fatty oil and aleurone, starch absent; cotyledons relatively thin. Germination phanerocotylar, cotyledons becoming herbaceous. Chromosome number perhaps $n = 12$.

3.2.3 Diversification and geographic spread—the implications of phylogram A. Among the descendants of the postulated ancestral population, "*Protomyrtalis,*" somewhere in west Gondwana [The second element in the word Gondwana means "forest" in Sanskrit. Thus "Gondwanaland" is not truly redundant as sometimes claimed, but the shorter form is used here.], two lines may have arisen (Fig. 3). One[5] (A1) differs[6] from the ancestor (phylogram C) in complete loss of teeth on the leaf margins and fixation of insertion on the hypanthium rim for at least one whorl of stamens (assuming that all stamens were inserted below the rim in the ancestral state). These characters marked the line that gave rise to the three Myrtacean families and the large central group of the phylogram.

The other line (A2), which became established in west Gondwana, showed grouping of vessels in the wood, and complete loss of trilacunar nodes (with fixation on the condition of one trace and one gap). Also, calyx aestivation became completely valvate, the style-base came to be apical on the ovary rather than sunken, and a fibrous exotegmen was developed in the seed coat. This was the line ancestral to the Onagracean and Lythracean families.

The next division (sequence of division differs in phylogram C) may have followed closely upon the first; and the surviving lines may, as always,

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[5] To facilitate cross-reference, the stems toward the base of the phylogram are numbered on the figure and are indicated in the text by phylogram symbol (A, B, or C) and stem number.

[6] Phylogram A differs from phylogram C at several important early divisions. Lest the first scenario presented appear to have greater validity than the evidence warrants, such comments are inserted at the main points of difference.

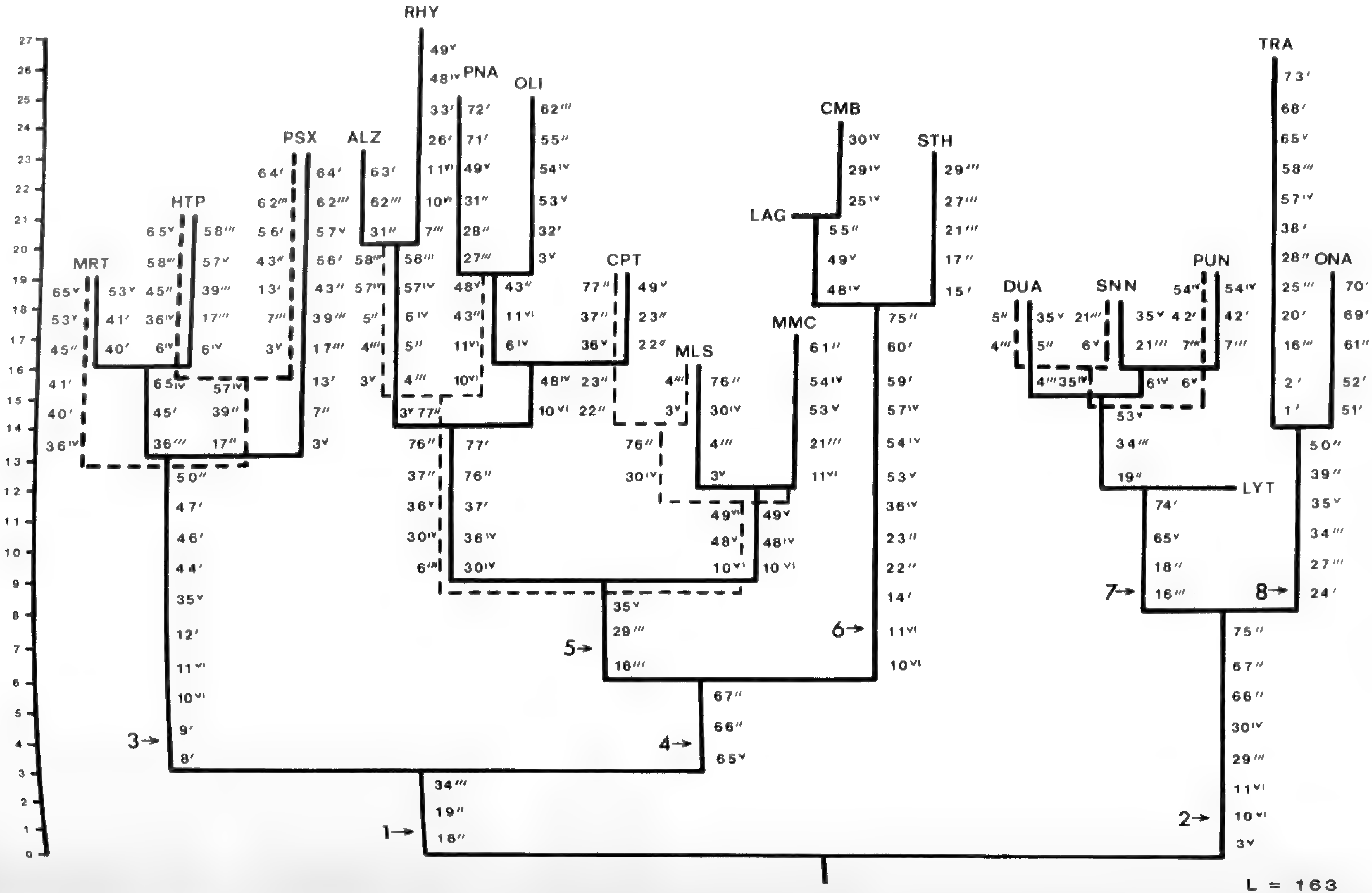
be only a sample of various lines most of which did not survive to the present. This separation marked the formation of the Myrtacean line (A3) which eventually, but not simultaneously, developed a substantial group of distinctive characters. These include: secretory cavities containing terpenoid substances in leaves, stems, and floral parts; loss of the trilacunar node; standardization of the myrtaceous hair-type; complete fixation of staminal insertion on the hypanthium rim; development of the connective gland; and shortening of the polar axis of the pollen grains to an oblate condition, with development of the syncolpate or parasyncolpate pollen-type and probably more elaborate thickening of the pollen exine. We cannot specify the likely region of occurrence of these plants within Gondwana, but perhaps it was at first still in the west.

Diverging from the Myrtacean line (not applicable in C) was a group (A4) marked by fewer character-state acquisitions; reduction of stigmatic lobing to very slight and loss of the sunken style-base condition, neither being unique to this group.

A further division followed, with the separation of the ancestors of the Penaeacean and Melastomatacean families from the Combretacean phylad. The first of these assemblages (A5) was marked by the fixation of opposite phyllotaxy throughout ontogeny, partial loss of calyx imbrication, and fixation of staminal insertion on the hypanthium rim (character-state changes differ in phylogram C). The second assemblage separating at this stage (A6) is a strongly marked line giving rise to Combretaceae sensu lato, with its unilacunar single-trace nodes, a characteristic hair-type, well-defined blastotelic anauxotelic inflorescences of generally racemose form (probably by reduction of lateral uniflorescences to monads, accompanied by anauxotely of conflorescence axes derived from portion of seasonal growth units) (see Briggs & Johnson, 1979), loss of anthopodium and adnation of bracteoles (floral prophylls) to the hypanthium, a shift in the levels of insertion of stamens in the mature bud so that the antepetalous whorl came to be inserted higher than the antesepalous stamens (apparent obdiplostemony), partial "fusion" or continuity [Sattler (1978) gives arguments for preferring the latter term] of the gynoecium with the hypanthium (i.e., incomplete epigyny), development of a unilocular but still multicarpellate ovary (i.e., loss of septa, with accompanying change in placentation), possibly a change to Asterad type embryogeny (Tobe & Raven, 1983a), and development of a fibrous exotegmen in the seed. The last-mentioned and fairly distinctive feature occurs also in the Lythraceae-Onagraceae group but, on the present hypothesis, would have been independently attained in the two cases. Not all the attributes indicated on this or on any other branch of the phylogram were necessarily acquired in a short period or in the order given; they do not appear to constitute such an obvious functional syndrome that one must believe that their acquisition was correlated as a marked "punctuation of equilibrium," and there may have been other divergences to now extinct lines along the way.

Also early in the history of the order, the Lythracean group of families diverged from the postulated common ancestor of Onagraceae and Trapaceae (a supraminimal alternative of C differs). The Lythraceans (A7) were marked by another, independent, fixation of opposite phyllotaxy (see 3.1.2) and a reduction of leaf toothing to a cryptic dentate condition (Hickey, 1981) still shown by the vascularization and by retention of the apical gland, as in modern *Cuphea,* reduction to little or no stigmatic lobing, and multiplication of the cell layers of the outer integument of the seed (Dahlgren & Thorne, 1984).

This hypothesis suggests a short common stem (A8) leading to Onagraceae and Trapaceae, despite the great differences between those families. At this stage they were still woody plants. This is supported by the wood anatomy of arborescent and shrubby members of the Onagraceae, which gives no evidence of an earlier herbaceous condition (Carlquist, 1975); similarities between the herbaceous aquatic Trapaceae and some herbaceous Onagraceae and Lythraceae are superficial. The suggested common stem would have been marked by reduction of the inflorescence to axillary monads on auxotelic axes (a character not shown elsewhere in the Myrtales except in individual genera in some families, e.g., in some Myrtaceae), possibly some reduction of floral mery to a flexible condition of 4- or 5-membered perianth and androecial whorls, fixation of the staminal insertion on the hypanthium rim, loss of staminal inflexion in the bud, and a tendency for the pollen grains to become oblate. The separation of Trapaceae and Onagraceae is discussed at 3.3.2.


RHY
PNA
OLI
PSX
ALZ
HTP
MRT
CPT
MLS
MMC
CMB
LAG
STH
DUA
SNN
PUN
LYT
TRA
ONA
1→
2→
3→
4→
5→
6→
7→
8→
L = 163

The distribution of their descendants suggests that all the divergent groups of Myrtales up to this point may have occurred in the parts of the west-Gondwanan region that formed Africa and/or South America.

Within the Myrtacean line, this analysis throws no light on the sequence of divergence, and Figure 3 shows two possibilities. The major descendant group is the family Myrtaceae, which exhibits much greater fundamental diversity in the east-Gondwanan region than in America or Africa. It is the only substantial Myrtalian group with this pattern. The unigeneric families Heteropyxidaceae and Psiloxylaceae are today found respectively in south-east Africa and in the Mascarene Islands of the Indian Ocean. The latter are volcanic and apparently not original Gondwanan fragments, so the distribution of Psiloxylaceae is probably secondary as well as relict. The existence of these two groups and their definite relationship with Myrtaceae indicate that the ultimate origins of the Myrtacean line may well have been west-Gondwanan also (at least in the African portion of that region), although the Myrtaceae themselves probably underwent their primary diversification in the Australasian region. At later stages the Myrtaceae extended to South and Central America but many major groups of the family, including some lines that must have diverged early, are absent from that region.

Since *Heteropyxis* and *Psiloxylon* are included with the subgroups of Myrtaceae in the analysis of the latter, Figure 9 also bears on the likelihood of each of the alternative hypotheses. The additional characters used in that case produce a tree that is one step shorter for the Heteropyxidaceae-Psiloxylaceae grouping than for a Heteropyxidaceae-Myrtaceae grouping. Although not conclusive, this favors the phylogeny shown by solid lines in Figure 3.

Returning to the diversification of the central group of families, the next division on this hypothesis was between the Penaeacean and Melastomatacean assemblages (with Crypteroniaceae included with the former in the minimal but with the latter in a supraminimal), at the time all still perhaps in the west-Gondwanan region. The first of these lines was marked by complete loss of calyx imbrication resulting in fully valvate calyx lobes, by obhaplostemony following the loss of the antesepalous stamens, moreover, the fibrous thickening of the anther endothecium was lost, with complete collapse at the time of dehiscence as a further development (Tobe & Raven, 1984b). The further diversification of this phylad was marked in a line leading to *Alzatea* and *Rhynchocalyx* by specializations of wood anatomy (loss of apotracheal parenchyma, vessel aggregation, loss of bordered pits), reduction in the number of carpels, and loss of participation of the outer integument in formation of the micropyle of the ovules. The last feature was reported by Tobe and Raven (1984a, 1984b), together with other embryological resemblances between these two genera. It is not included in Table 1 or our analyses.

Alzatea alone within the order has (retains?) fully trilacunar nodes; it is also distinguished by loss of petals and reduction of the style, as well as by a disporic *Allium*-type embryo-sac (Tobe & Raven, 1984b). The last feature is unique in the order and if included in the analyses would lengthen the *Alzatea* branch by one unit, comparably with the distinctive embryo-sac types included for Penaeaceae and Onagraceae. The single known species is a large shrub or small scrambling tree of cloud forests at middle elevations of the Cordillera in eastern Peru and Bolivia (Dahlgren & Thorne, 1984), and more recently discovered (Tobe & Raven, 1984b) in Panama and Costa Rica. *Rhynchocalyx*, a now rare tree of moist closed forests in south-eastern Africa (Strey & Leistner, 1968) shows unilacunar nodes, hexamerous flowers, a distinctive petal form, and subsidiary colpi on the pollen grains. We find that both of these genera retain branched anthotelic inflorescences (Trollian panicles; Troll, 1964), inadequately characterized by previous authors.

←

FIGURE 3. Phylogram A, based on data in Table 1 without (in the primary version) any reversal of direction of character-state change. Method of representation as in Figure 1. Reference in text to stems arising at the first four divisions is by phylogram symbol (A) and stem number as shown (with arrow). [Alternatives of equal length exist in the groupings MRT-HTP-PSX and DUA-SNN-PUN; a supraminimal (lighter broken line) places Crypteroniaceae (CPT) with Melastomataceae (MLS).]

If the origin of Crypteroniaceae was indeed as shown in the primary version of phylogram A (shown by solid lines in Fig. 3) then the next events would be the initial step in loss of trilacunar nodes and some degree of development of subsidiary colpi on the pollen grains (an additional variant occurs in phylogram C). This would be followed by separation of Crypteroniaceae, with its own peculiar characters. As well as the features just mentioned, Penaeaceae and Oliniaceae share loss of apotracheal parenchyma, complete attainment of unilacunar single-trace nodal anatomy, and reduction of stamen filaments. If Crypteroniaceae in fact arose from the Melastomatacean branch, as shown in a variant of this phylogram longer by only one unit, then the wood-parenchyma character-change would show on the common stem of PNA-OLI with the *Alzatea* line.

Crypteroniaceae are discussed below; both of the other families are endemic in Africa. The Penaeaceae are scleromorphic shrubs of the South African *fynbos* heathlands on infertile soils; Oliniaceae consist of one genus of shrubs and trees in forests of tropical and southern Africa. Features of Penaeaceae are the tetramerous flowers in which the sepals assume the function of the lost petals, the well-developed subsidiary colpi, and the unique type of embryo-sac (Stephens, 1909). The Oliniaceae have grouped vessels, small thick petals of distinctive type, and completely epigynous flowers; the style is very short, although the stigma is not quite sessile; the ovules are campylotropous, with a thick, vascularized outer integument (Tobe & Raven, 1983a).

The Melastomatacean line, as shown in the primary version (but also see below), is marked by acquisition of subsidiary colpi and modification of the presumedly ancestral trilacunar nodes. Three leaf-traces are retained, but the lateral traces of the two opposite leaves at the node share a common gap or, in some living members, a girdling trace replaces the lateral traces (van Vliet & Baas, 1975). A supraminimal variant of the tree shows Crypteroniaceae associated with Melastomataceae and Memecylaceae. In any case the possible synapomorphies linking these families provide rather weak evidence of their association, since, as shown in Figure 3, the characters concerned must have arisen independently a number of times in Myrtales as a whole. They may well have arisen in parallel twice or thrice within this group also.

Wherever the family Crypteroniaceae diverged, it is quite strongly distinct. It is here taken to comprise only *Crypteronia, Dactylocladus,* and *Axinandra,* in agreement with Dahlgren and Thorne (1984) and van Vliet and Baas (1984); inclusion of *Alzatea* and *Rhynchocalyx,* as for example by van Beusekom-Osinga and van Beusekom (1975), is strongly contra-indicated by the character-states possessed. These include the markedly dissimilar inflorescences (anthotelic and hence more plesiomorphous in the last two genera, blastotelic-anauxotelic in Crypteroniaceae sensu stricto); none of the authors cited clarified or stressed these differences.

Unlike van Vliet and Baas (1975, 1984), we are not wholly satisfied with the grouping CPT-MLS-MMC, nor are we convinced of the slightly shorter alternative shown, since the inflorescences within the groups are quite different in both cases. The blastotelic, anauxotelic systems of Crypteroniaceae contrast with anthotelic inflorescences in the other taxa (Briggs & Johnson, 1979: 181), but resemble those of Combretaceae (including Strephonemataceae). No phylograms that we accept show Crypteroniaceae linking with Combretaceae. Others were computed that do show that association but are either longer (CLAX cases) or have implausible character-state reversals (CLAXMIN and similar cases) and hence are less acceptable in other respects. Striking as it is, inflorescence similarity must probably be put down to remote parallelism or convergence, since a Crypteroniaceae-Combretaceae line is not supported by a majority of the characters considered.

In the supraminimal version of Figure 3, the Memecylaceae branch (equivalent to Melastomataceae-Memecyloideae as interpreted by Baas and co-authors), separates slightly before Crypteroniaceae, and no positive character in the phylogram links Melastomataceae and Memecylaceae in contrast to Crypteroniaceae. Whether the additional feature of uninucleate cells in the anther tapetum of Melastomataceae (Tobe & Raven, 1983a) also characterizes Memecylaceae we do not know. It is absent in *Axinandra* of the Crypteroniaceae (Tobe & Raven, 1983b). The attainment of a fully valvate calyx is shown as linking Melastomataceae sensu stricto with Crypteroniaceae, and differentiating these from Memecylaceae, but this is a weak indication and may perhaps be offset by other characters not included in the analyses. Loss of fibrous thickening of the anther endothecium occurs on the common stem of Melastomataceae and Crypteroniaceae and the second stage (complete collapse) has an additional innovation on the Crypteroniaceae stem, homoplastic with that on the stem leading to Alzateaceae, etc.

Melastomataceae and Memecylaceae are widespread in the tropics and in the western Gondwanan continents, but appear to be only recent (Miocene or later?) and scanty immigrants into the Australian region. The former is a large family, exceeding Myrtaceae in number of species, although it does not dominate extensive vegetational communities as do many members of the Myrtaceae. The three genera of Crypteroniaceae are endemic in south-eastern Asia and Malesia. This distribution is unique in the Myrtales, and may point to an early geographic separation of ancestors, unless it is a relict of a wider range.

In the well-marked Combretacean line, both the Laguncularieae and *Strephonema* are notable in having prophylls ("bracteoles") and an imbricate calyx. Both cases are probably retained from the primitive condition in the Myrtales; reversion to possession of such organs after complete disappearance seems unlikely. One branch is marked by acquisition of well-developed subsidiary colpi and complete epigyny. On this branch no distinctive synapomorphies mark the Laguncularieae, which would thus consist of three separate lines for the three genera, grouped only because of primitive features in common (symplesiomorphies, and therefore cladistically nonsignificant); however, Stace (fide Dahlgren & Thorne, 1984) reported the unusual condition of cyclocytic stomata in *Laguncularia* and *Lumnitzera*. The more advanced Combreteae are further marked by loss of prophyllar bracteoles and attainment of valvate calyx aestivation. We do not know whether the Asterad type of embryogeny recorded by Tobe and Raven (1983a) is basic to the whole Combretacean line, or is confined to Combreteae.

The second branch leads only to *Strephonema*. This is characterized by fixation of spiral phyllotaxis, distinctive revolute domatia (Stace, 1965b), paracytic stomates, and floral mery reduced to the 4–5 flexible condition (the last feature is seen also in some Combreteae). It differs from its associates in several wood and bark characters not used in the analysis, but these are considered by van Vliet (1979) to be primitive features. Patel et al. (1984) note that the pollen of *Strephonema* is distinctive in respects additional to the characters we have scored.

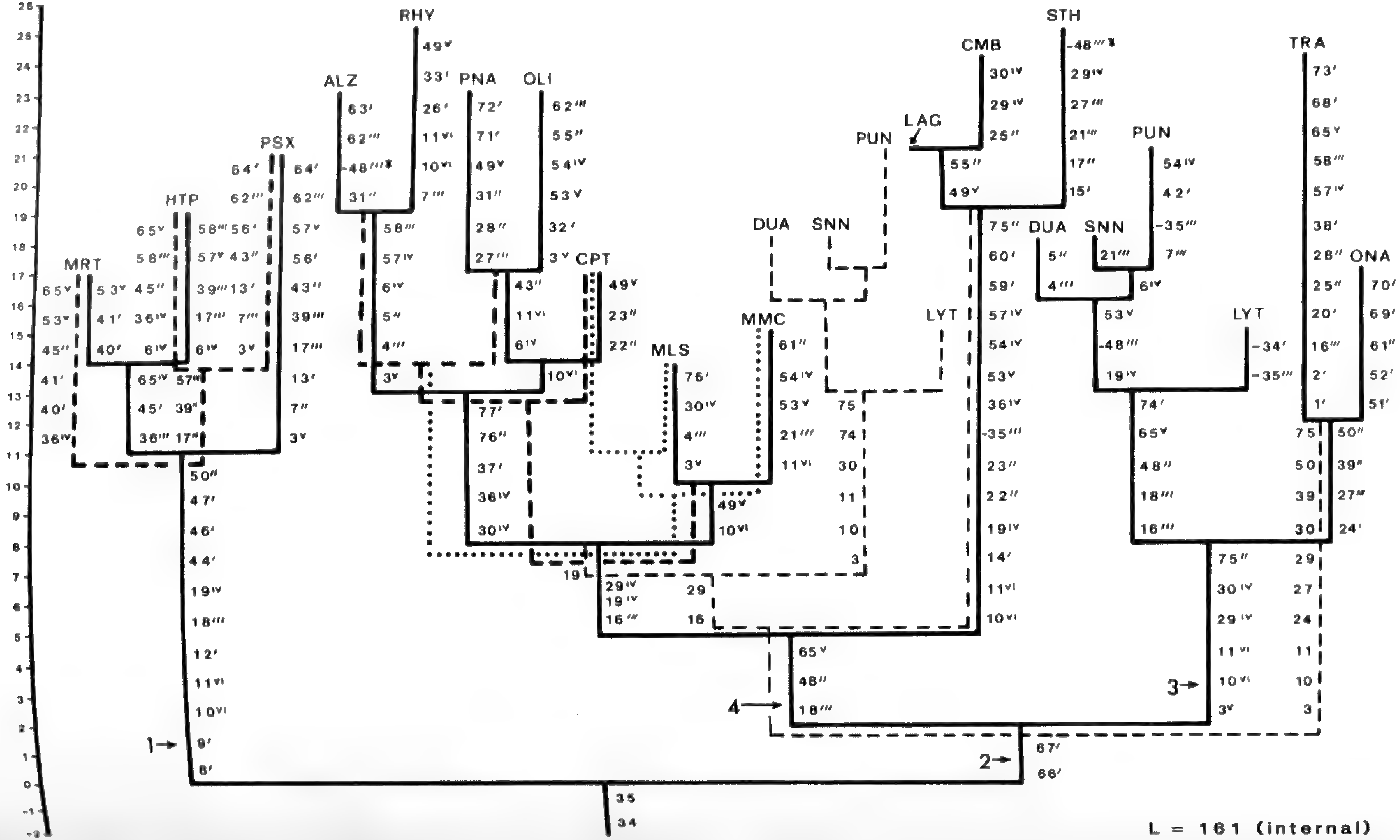
Strephonema has a probably relict distribution in tropical west Africa. The Combreteae are widespread, but best developed in the west-Gondwanan continents of Africa and South America. The Laguncularieae consist of three very distinct genera: *Laguncularia* and *Lumnitzera* are near-mangroves or mangroves, the former in tropical America and west Africa, the latter from east Africa to the Pacific. The dryland *Macropteranthes* is endemic in tropical Australia, but nothing postively suggests that it was a pre-Miocene inhabitant of that continent. Although considered by Stace (1965a) to be close to *Lumnitzera*, its characters point to ancestors different from living species of that (at present) more widespread mangrove genus.

Within the Lythracean group various possibilities exist as to the sequence of events. The common ancestor of the genera retained in Lythraceae sensu stricto could also be the common ancestor of the other members of the group. The terminal taxa are discussed below (3.3.2), as is *Rhynchocalyx*, which has often been included in the Lythraceae but which does not take that position in this analysis.

3.2.4 A variant hypothesis (phylogram B). Two variant hypotheses deserve consideration, involving different ancestral conditions and hence some character-state changes of reverse polarity from those in the scenario presented above. The relevant characters are 34 and 35 (stamen insertion on the hypanthium rim) and 48 (some degree of development of subsidiary pollen colpi). The effects of the respective rescoring of these on the CLAX processing can be considered jointly or separately: it will be convenient to consider the pollen feature first.

In the suggested phylogeny that results from reversal of character 48, the branching sequence is not changed and there is the same variant supraminimal position of Crypteroniaceae as in Figure 3. Character 48 appears as an innovation on the branch leading to the large middle group of taxa, before the separation of the Combretacean and Penaeacean lines. Reversals of the character (expressed as −48) would be inserted on the final stalks leading to ALZ and STH. The phylogram is thus one unit shorter than phylogram A, in which character 48 appeared on four internodes within the group.

Accordingly, the scenario changes only in that the initial stages of acquisition of subsidiary colpi are assumed to have taken place very early, in the ancestor of the middle group of families, and to have been secondarily lost within that group


RHY
ALZ
PNA
OLI
PSX
HTP
MRT
CPT
MLS
MMC
DUA
SNN
PUN
LAG
CMB
STH
LYT
DUA
SNN
PUN
LYT
TRA
ONA
1→
2→
3→
4→
L = 161 (internal)

only in *Alzatea* and *Strephonema.* If we were to assume further that some development of subsidiary colpi took place in the ancestor of the Lythracean group of families, this would imply loss of overt expression of this character-state in some lines within Lythraceae sensu stricto and in the line leading to the other three constituents of the group (see 3.1.2).

3.2.5 A further variant scenario (phylogram C). Phylogram C (Figs. 4, 5) also assumes internal change of the pollen character (some development of subsidiary colpi), but postulates additionally that, in the ancestor of the whole order, the stamens were inserted on the rim of the hypanthium. The first variant of this does not assume that subsidiary colpi were developed in the ancestor of the Lythracean group. The shortest phylogram then continues to place the Lythraceans with the Onagracean line, but there is a change at the base of the tree. The Myrtacean group (C1) is now seen as diverging first from the rest of the order, rather than having a short common stem with the central group of families.

The other important differences expressed in this tree are that (1) within the Lythracean group, the Lythraceae sensu stricto would be marked by a phylogenetic downward movement of the androecial insertion on the hypanthium, and there would be some parallel development in *Punica* (implying that *Duabanga, Sonneratia,* and *Punica* would have a common ancestor more primitive in some respects than could be assumed for the Lythraceae sensu stricto), and (2) some similar phylogenetic movement away from the rim would have occurred independently in the Combretacean line.

All versions of phylogram C imply the same alternative minimal and supraminimal positions of Crypteroniaceae as in A and B, as well as a third grouping in which Crypteroniaceae unite with the combined ALZ-RHY-PNA-OLI assemblage. Figure 5 shows the character-state innovations for these alternatives.

The situation within the Myrtacean line is unchanged from phylogram A.

Allowing alternative interpretations of the direction of change for particular characters leads to substantial re-grouping of taxa, particularly toward the base of the tree. The number of variant phylograms, one or two units longer than the minimum, is increased by combinations of these alternatives.

(a) In the primary version of phylogram C, the only synapomorphy (double-scored) marking a putative common ancestor for the non-Myrtacean part of the order (C2) is the complete loss of the sunken style-base condition. Thus, if our assumption about the base were reversed, taking the sunken style-base as apomorphous, there would be a trichotomy at the bottom of the phylogram, with the reversed characters (−67 and −66) showing on the Myrtacean stem. (Their inclusion on that stem would, of course, imply that the sunken style-base was considered an ancestral character in the Myrtacean group as a whole, and that it was subsequently secondarily lost in some members of the Myrtaceae. This is not the sole reasonable hypothesis; see 3.1.2, characters 66, 67.) In any event, the Myrtacean group remains highly distinctive.

(b) If the presence of subsidiary pollen colpi is taken as ancestral for the Lythracean line, the shortest tree still keeps (C3) that group with the Onagraceans but a supraminimal tree, which is only one unit longer, places the Lythraceans with the central group (C4) of families; this is also shown in Figure 4. If oblate pollen grains are considered primitive, as by Dahlgren and Thorne (1984) (see 3.1.2, character 50), then this alternative "catches-up" since character 50 disap-

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FIGURE 4. Phylogram C, based on data in Table 1 except for assumption of different ancestral staminal insertion and internal reversal of some degree of development of subsidiary pollen colpi. Method of representation as in Figure 1. [This tree assumes an ancestral condition in characters 34 and 35 in which stamens were inserted on the hypanthium rim. Character 48 (first stage of development of subsidiary colpi) is seen as gained in the line leading to the "middle group" of taxa, being subsequently lost in some members. The same equal-length alternatives as in phylogram A (Fig. 3) exist within MRT-HTP-PSX. CPT links with PNA-OLI or with the combined grouping LAZ-RHY-PNA-OLI (this alternative not generated in phylogram A), a supraminimal only one unit longer, places CPT with MLS (dotted line). The character-state innovations for these three alternatives are shown in Figure 5. Another supraminimal alternative (light broken line) links the Lythracean group (DUA-SNN-PUN-LYT) with the Penaeacean and Melastomatacean families rather than with ONA-TRA. Character-state innovations within the Lythracean group are identical in the two positions.]

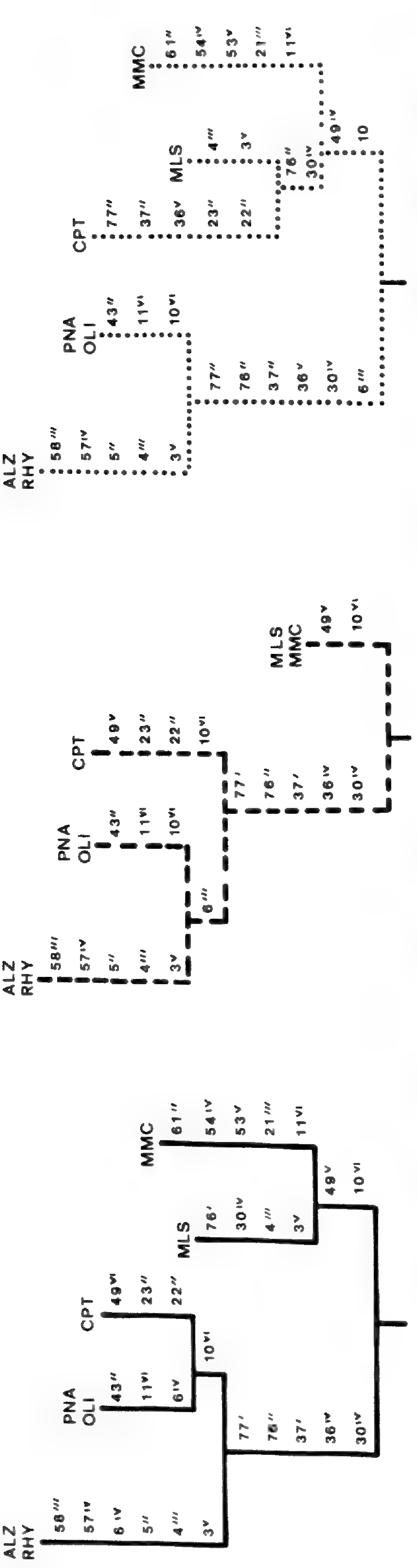

FIGURE 5. Two equal-length and one supraminimal alternative positions of Crypteroniaceae in phylogram C (as in Fig. 4) showing character-state innovations.

pears from two stalks and character −50 comes in on the stalk to the Lythraceans and the central group.

(c) Dahlgren and Thorne (1984 and pers. comm.) mention the possibility that the depressions between the colpi in the pollen grains of *Trapa* may represent incipient or reduced subsidiary colpi. Any hypothesis that character 48 was common to the ancestors of Trapaceae and other families, except for Onagraceae and the Myrtacean group, would lead to a phylogram several steps longer. The primary division in the order would then place Onagraceae on a stalk with the Myrtacean line, leaving Trapaceae on the other branch where it would share a subbranch with the Lythracean group. Assuming alternatively that character 48 occurred in the ancestor of Trapaceae, without any further assumption that it was common to that line and others, would yield a phylogram of intermediate length, identical in topology with Figure 4. In this case innovation of character 48 would be homoplastic, occurring in the ancestor of Trapaceae after its separation from the Onagracean line.

(d) There is another tree (not illustrated) only two units longer than the primary version of phylogram C, in which Memecylaceae are associated with the Combretacean group and the combination ONA-TRA links with MRT-HTP-PSX. We do not accept this, but it illustrates the considerable differences that can arise by slight relaxation of the length criterion. In these phylograms the Myrtacean group still diverges at the bottom of the order.

(e) Placing the Lythracean and "central" groups together, as in the supraminimal shown in Figure 4, implies an early divergence in which one line was marked by reduction of leaf teeth to a vestigial condition, a single initiation of subsidiary colpi, and reduction of stigmatic lobing. A second line would have eventually acquired the full set of common character-states of Onagraceae and Trapaceae. From the former line, one further development would be the fixation of opposite phyllotaxy and the first stage of loss of calyx imbrication; the other would be the Combretacean line with the characters as previously discussed. From the opposite-leaved line, the Lythracean group would be marked by acquisition of vessel clustering, unilacunar nodes, and the two specialized character-states in the seeds. The first of these seed features, multiplication of the outer integument, is unique to the

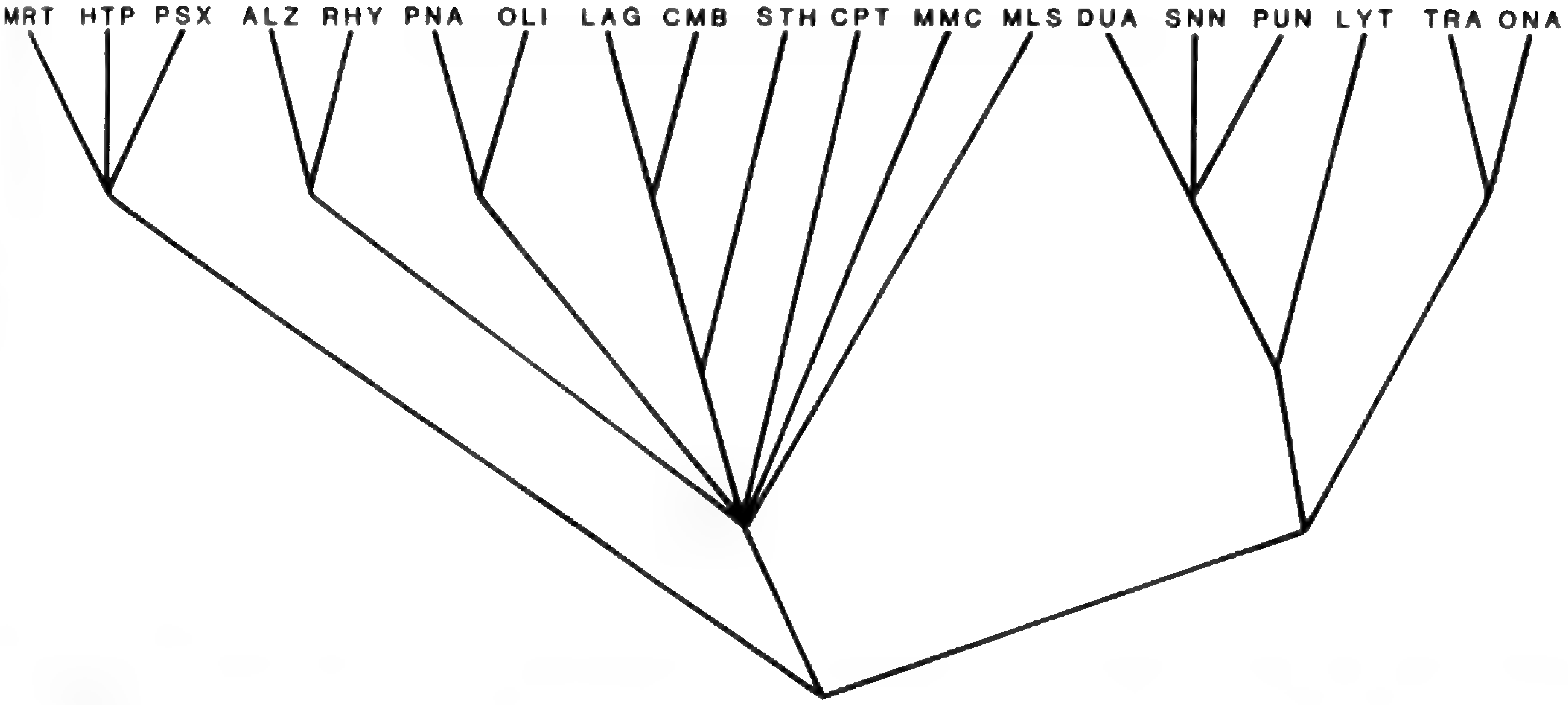

FIGURE 6. Congruence cladogram, expressing grouping common to minimal versions of CLAX phylograms A, B, and C and also the supraminimal CPT-MLS link (Fig. 3) but excluding supraminimal variant position of Lythracean families (Fig. 4).

Lythracean group, but this hypothesis requires the fibrous exotegmen to have been acquired separately three times (in the Lythracean, Combretacean, and Onagracean lines). The only common feature marking off the Penaeacean-Melastomatacean group from the Lythraceans would be the loss of all traces of leaf teeth.

3.2.6 A preferred hypothesis? The foregoing analyses pick out several competing preferred hypotheses from the very large number of theoretically possible phylogenetic trees which for 19 taxa could be of the order of 10^{22} (Felsenstein, 1978). That astronomical number is less daunting than it seems, since the vast majority of the possible trees are manifestly implausible, and many of the variants differ only slightly.

What degree of confidence can we have in the selected few? Clearly, the phylograms presented here have a great deal in common. This is partly a result of our assumptions as to the set of available and useful characters, our assumptions about the direction of character-state change, and the implicit or explicit weighting assigned. As discussed above (2.4.1), we have rejected shorter trees with initial character-states that are difficult to accept. Trees with numerous internal reversals of character-states are also rejected (2.4.3).

Confidence in the phylogenies or parts of them depends on (1) the total number of synapomorphies shared by terminal taxa (a fundamental principle of the CLAX method); (2) the lengths of internodes (equivalent to stalks) in the phylogram, which express both the number of synapomorphies grouping certain taxa and the patristic separateness of one group from another; (3) the degree of homoplasy both across the whole tree and in particular comparisons; and (4) the robustness of grouping, i.e., the invariance between trees. In accord with (1) and (2), our confidence in the topology is greater at high advancement levels than low in the phylogram.

Numerical or purportedly probabilistic measures could be devised to deal with all of these, separately or in combination, but such measures would themselves depend on so many arbitrary and subjective variables that we believe them to be a waste of time. Indeed, to apply any particular measure of this kind is dangerously misleading, because of the false confidence it engenders.

Nevertheless, we can say broadly that confidence increases with high levels of (1), (2), and (4) as expressed above, and decreases with high levels of (3).

All phylogenetic hypotheses are subject to "probable falsification" (see 4.1.3, characters 35–37); conversely, all may be supported by additional evidence. False rigor in these regards is undesirable, but these statements are still true in a general and useful sense (Hull, 1967; Johnson, 1969, 1970). Until additional hard data become available for the whole set of taxa, one can sometimes prefer or reject particular variants on grounds of biological or geographical likelihood or consistency. The danger of circularity can be offset by the usual process of reciprocal illumi-

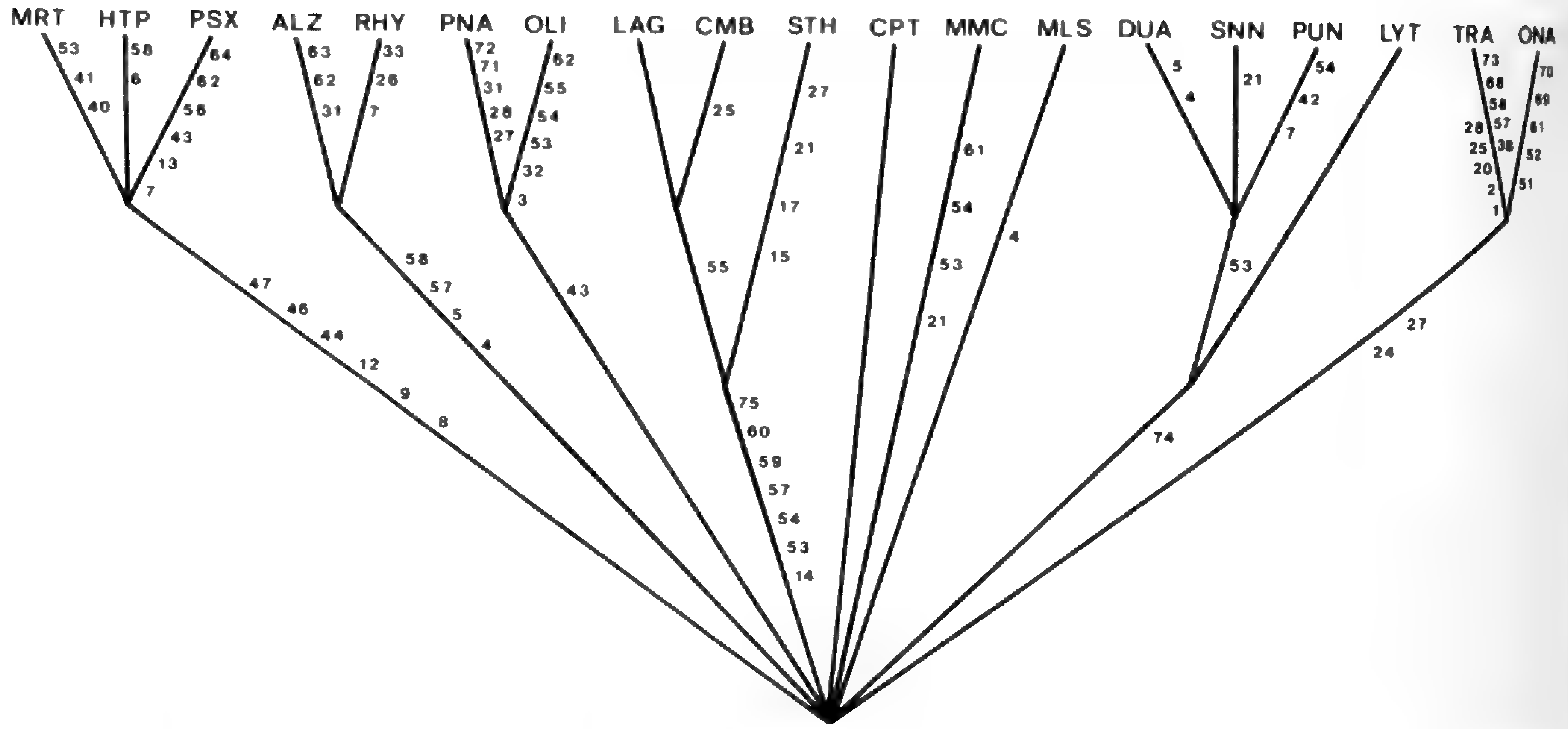

FIGURE 7. Congruence cladogram covering minimal CLAX phylograms A, B and C (including all versions illustrated in Figs. 3 and 4) and also a CLAXMIN cladogram (Fig. 1). See text for explanation of character-state numbers and limitations of the representation.

nation, as well as by progressive accumulation of information.

With respect to the scenarios given here, we have perceived no strong indications or contraindications as to the probable functional success of the hypothesized ancestors. We hope that other investigators may be able to do so, bearing in mind the probable physical and biotic conditions during the periods concerned. Such fossil evidence as exists is too scanty to help either in reconstruction or in timing of events.

The extent of congruence between the CLAX phylograms Figures 3 and 4 (excluding the supraminimal variant position of the Lythracean assemblage) is shown in Figure 6. If all illustrated supraminimals in Figure 4 and/or the CLAXMIN result shown in Figure 1 are incorporated, the congruence cladogram shows much less resolution of the branching sequence (Fig. 7).

Such "congruence cladograms" are not phylograms in our sense and are therefore given in cladogram form without a vertical scale ("advancement"). They present a visual indication of regions where one may have low confidence in particular branching sequences (the "unresolved" polychotomies) as against those where confidence is high. This would be more the case if one considered all the trees contributing to the confidence set to have comparable value, which may not be so, on other grounds. Character-state changes common to all the hypotheses considered may be written in on the internodes (as in Fig. 7) but the sum of these does *not* give the length of the tree or represent all the changes that must be taken into account. There are no constant characters on the stems immediately below Laguncularieae, Crypteroniaceae, and Lythraceae. One can conceive the phylogenetic history in the form of scenarios only by considering separately at least the favored contenders among more fully resolved trees (= hypotheses).

In the Myrtales, as in the Myrtaceae and other plant groups we have considered, the internodes are mostly short on the lower parts of the trees. This means that the ancestors were probably not very different through a sequence of levels of divergence, and possibly that many such rather small divergences took place early and over a relatively short period. It does not support a general theory of punctuated equilibrium.[7]

We believe (with Grant, 1982) that there is *a continuous range* of tempi and modes of evolution and that the processes leading to subspeciation and speciation are those by which, in the course of time and given appropriate circumstances, taxa of higher order—and grade evolu-

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[7] The currently vexed question (and vexatiously polemical dispute) of whether evolution proceeds by punctuated equilibrium or is gradualistic should scarcely affect the arguments as to the best methods of phylogenetic analysis, or the application of formal taxonomy to the findings of such analysis. The frequent association of ardent supporters of punctuated equilibrium with the more extreme philosophy of Cladism is unnecessary and fortuitous, as is the scientifically damaging association of political outlooks with evolutionary viewpoints.

tion—have their roots. Arguments for a different *kind* of macroevolutionary event, such as those given by van Waesberghe (1982) appear both specious and illogical. This is in no way to deny that hierarchical control is a vital part of genetic systems or that a systems-analytical approach (Riedl, 1977, 1979) is of value in understanding evolution; nor is it to deny that in certain groups (e.g., mammals) the evidence supports rapid evolution and fixation of new syndromes in small populations under circumstances of strongly selective environmental novelty (Stanley, 1979). It *is* to deny that this must *always* be the case, and it is to suggest that recognition of "higher" taxa is often psychologically and pragmatically influenced by the extinction, over a long period, of many branches of the relevant phylogenetic tree. When there has not been "enough" such extinction, the hypothetically reconstructed ancestors are often seen to differ in few characters and not in obvious highly co-ordinated syndromes, which often came later.

The most robust assemblage to emerge is Myrtaceae-Heteropyxidaceae-Psiloxylaceae. All the analyses (even the Wagner-type analyses rejected here) show this group as having a common stem of considerable length, made up of character-states showing few homoplasies, i.e., there is a high level of character-state congruence. Moreover, the group branches off before or soon after any other divergence.

The grouping Onagraceae-Trapaceae is also present in all phylograms presented, but is less strong in both respects. Some supraminimal phylograms not considered here would place Trapaceae elsewhere, though very weakly. Moreover, we have had to extrapolate to some extent in assigning characters to Trapaceae, in which there are no living woody members, though the common stem shown does not depend on extrapolations. Tobe and Raven (1983a) state that "Trapaceae are more distinctive in their embryology than any other member" of the order. This merely means that the family has autapomorphic pecularities, which have no effect on cladistic grouping. Raven (pers. comm.) does not consider the relationship between Onagraceae and Trapaceae to be close.

The Lythracean group hangs together robustly, but like Onagraceae-Trapaceae, together with which it may possibly constitute a holophyletic group, is not so clearly isolated as the Myrtacean line.

The Combretacean threesome has a long stem with some unique characteristics, despite the strong divergence of *Strephonema.* It associates fairly consistently (Fig. 6 although not Fig. 7) with the remaining complex of families discussed below, but not with a very long common stem. We have at times suspected that Crypteroniaceae may be associated with this group, partly because we are impressed by the inflorescence similarity, but other characters suggest that the blastotelic inflorescence is a convergent development in the two cases (3.2.3).

The remaining families are rather weakly held together in most analyses (Fig. 6) by a common stem without unique character-states. Variation in groupings leads to these appearing as six independent lines from the base in the more inclusive congruence cladogram (Fig. 7). Like the Lythracean and Combretacean groups (but with rare exceptions interpreted as secondary reversals in at least some of the phylograms), they show a pollen type marked by more or less prolate grains, primarily without a high degree of exine thickening or elaboration, and probably pre-adapted to the development of subsidiary colpi. However, Muller (1981b) considered this basic pollen type (without manifest subsidiary colpi) to be plesiomorphous for the order, and his reasons appear sound. Consequently, it is not a positive feature in a cladistic interpretation (but see 3.1.2 and 3.2.5 for a contrary view). The Lythracean phylad, on the results of the analysis, associates almost as closely with this weakly linked group of families as with Onagraceae-Trapaceae. We would regard the relationship of the Lythraceans as an open question.

As already mentioned, the position of Crypteroniaceae has been regarded as problematical. The analyses suggest that this family does not form a holophyletic group with Melastomataceae-Memecylaceae. Nevertheless, the latter pair separate only by a short string of markedly homoplastic characters from the Penaeaceae-Crypteroniaceae group.

The Penaeacean assemblage hangs together in the analyses with a shortish common stalk. On our scoring, the group divided into two parts, Alzateaceae-Rhynchocalycaceae and Penaeaceae-Oliniaceae(-Crypteroniaceae) respectively; all families are themselves well marked.

Thus we are not prepared to put forward any single more favored precise phylogeny; rather, we present several competing (but not highly dissimilar) hypotheses as a basis for thinking about the order Myrtales and its constituents, and for checking and refinement in the future. The individual terminal taxa are discussed below.

3.3 SYSTEMATIC IMPLICATIONS

3.3.1 Subordinal division. Because of the uncertainties at the base of the phylogenetic tree, it seems best not to recognize formal suborders, but one can refer informally to the Myrtacean, Lythracean, and other complexes if desired.

3.3.2 The families. Dahlgren in Dahlgren and Thorne (1984), has adopted family delimitations that coincide almost entirely with those we have reached from consideration of this analysis. The few cases where Thorne takes a more inclusive view are discussed below and also by those authors.

It would not be altogether unreasonable to accept as families all of the 19 terminal taxa of our analysis, especially if one took as a basis the traditional recognition of Sonneratiaceae and Punicaceae as families distinct from Lythraceae. However, the analysis suggests that these are "weak" families and their removal probably leaves Lythraceae as a paraphyletic taxon,[8] and moreover that there is no particular reason to place *Duabanga* and *Sonneratia* together in a single segregate family, or indeed as a subfamily, although they are still so associated, without any clear justification, e.g., as a family by Backer and van Steenis (1951) and Cronquist (1981), or as a subfamily by Thorne (1976, 1981). Tobe and Raven (1983a) acknowledge that there may be little reason to associate *Sonneratia* and *Duabanga.* We might then take these as a point of comparison, and suggest that Lythraceae be circumscribed in a moderately broad sense as by Dahlgren and Thorne (1984) and by Thorne (1981), but not Thorne (1976) where he included Crypteroniaceae also, as subfamily Crypteronioideae; inclusion of *Rhynchocalyx* and *Alzatea* has sometimes been suggested but is totally incompatible with our analysis. Our Lythraceae then include *Duabanga, Sonneratia,* and *Punica,* which represent particular specializations from the early Lythraceous stock, although Tobe and Raven (1983a) draw attention to embryological differences between *Punica* and the rest of Lythraceae sensu lato.

The second closely-linked group is the Combretacean complex, with three terminal taxa as fed into our analysis. The three genera of Laguncularieae differ considerably from each other and, being grouped chiefly by symplesiomorphy, may not constitute a clade. Some authors have recognized a family Strephonemataceae, despite its possession of a number of "Combretaceous" characters. *Strephonema* is peculiar in many respects and must have branched off early within the line. Pending the accumulation of more critical data, Combretaceae could perhaps be retained sensu lato, to embrace all three groups, with the present division (Exell & Stace, 1966) into only two subfamilies. However, the analysis provides no objection to recognizing Strephonemataceae as a family, and this may well emerge as the preferable treatment.

Crypteroniaceae have been discussed above (3.2.3). Accordingly, we would neither include the family in a broadened Melastomataceae nor, of course, in a very broad concept of Lythraceae as suggested at one time by Thorne (1976).

Melastomataceae-Memecylaceae separate only by a short string of markedly homoplastic characters from the Penaeaceae-Crypteroniaceae group. This last assemblage hangs together in the analyses with a shortish common stalk; on our scoring, it divides into two parts, Alzateaceae-Rhynchocalycaceae and Penaeaceae-Oliniaceae(-Crypteroniaceae) respectively. All its constituent families are themselves well marked.

A difficulty remains in the circumscription of Melastomataceae. The traditional arrangement (see, e.g., Melchior, 1964) in three subfamilies, Melastomatoideae, Astronioideae, and Memecyloideae, cannot stand. As pointed out by van Vliet et al. (1981), and van Vliet and Baas (1984),

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[8] The property of "convexity" (Estabrook, 1978) rather than strict Hennigian "monophyly," more unequivocally termed "holophyly" (Ashlock, 1971) has been claimed as a sufficient condition for recognition of a taxon in phylogenetic systems. Among others, Mitter (1981) has criticized this viewpoint. Some of his objections (like those of Eldredge & Cracraft, 1980) derive from adherence to strict Hennigian principles with which there are reasons to disagree, as indicated above. Others are formal and perhaps arise from some confusion in the wording of definitions of convexity, paraphyly, etc.; these can be overcome by re-definition (Johnson & Johnson, in prep.). Convexity (a concept adopted from point-set topology) embraces holophyly and paraphyly. The last does not depend on the definition of the group concerned alone, but on that of at least one other as well. It is dependent on the taxonomist and not solely on the cladogram for its distinction from polyphyly. Convexity can therefore be taken as a *necessary* condition for recognition in phylogenetic systematics. But whether it is a *sufficient* condition depends on point of view and the strength of arguments for recognizing grade-clade offshoots as worthy of individual recognition at the same rank as the paraphyletic residue.

the tribe Astronieae belongs in the Melastomatoideae whereas *Pternandra* (including *Kibessia*), constituting the tribe Kibessieae, is more closely related to *Memecylon* and its allies. Morley (1953) had indicated this affinity, mentioning also the antepetalous ovary locules as a difference from the Melastomatoideae. The feature of interxylary ("included") phloem (as distinct from the common Myrtalian feature of intraxylary phloem) in the Melastomatoideae, in its more recent circumscription, is not shown in the phylogram because it was difficult to assign a direction and therefore a primitive condition to the character in other families. It does stand as an important additional distinction between Melastomataceae and Memecylaceae.

At first sight, *Mouriri, Votomita* (*Coryphadenia*) (Morley, 1953, 1963; not mentioned by van Vliet et al., 1981), and the greater part of *Memecylon* appear very distinct from Melastomatoideae, by virtue of the absence of strongly acrodromous venation. However, this feature does appear in *Pternandra* and also in the genera *Spathandra* and *Warneckea* (Jacques-Félix, 1978a, 1978b; Jacques-Félix et al., 1978) and in the recently re-segregated *Lijndenia* (Bremer, 1982).

Jacques-Félix et al. (1978) present the view that acrodromous venation is fundamental in *Memecylon*, and presumably modified to a secondarily brochidodromiform condition in most of the genus. From the data in their paper and our examination of specimens, and by comparison with transitions in Myrtaceae (see also Hickey, 1981), we are not convinced of this. It seems equally possible on the internal evidence, and more likely from out-group comparison, that the original condition is brochidodromous as in most of the Myrtales, and that acrodromy has had separate origins in *Lijndenia, Spathandra, Warneckea*, and *Pternandra*, as well as in ancestral Melastomatoideae (becoming fixed throughout that group). Incidentally, van Vliet (1981) dismisses out of hand the claims to generic rank of *Spathandra* and *Warneckea*, apparently because they do not show differences from *Memecylon* within his field of study. This dismissal unjustly overlooks the sets of correlated characters carefully pointed out by Jacques-Félix, and segregation seems well justified for the genera recognized by him and probably for *Lijndenia*.

In discussion of the Melastomataceae, van Vliet (1981), van Vliet et al. (1981), ter Welle and Koek-Noorman (1981), Baas (1981), and van Vliet and Baas (1984), all propose a broadened concept of the family, comprising three tribes Melastomatoideae, Memecyloideae, and Crypteronioideae. Despite the number of papers cited, the arguments are not cumulative. From the characters used in our analysis, and without strong contra-indication from others mentioned by these authors, there are no unique synapomorphies to indicate that the three groups mentioned form a holophyletic assemblage. Crypteroniaceae, which we regard as a family, may appear intuitively to be the most distinctive member, but the features that might appear to hold *Memecylon* and its allies together with Melastomataceae sensu stricto do not appear to be ancestral in either group, or else are shared with other families. Consequently, it will cause less confusion and is more logical to regard Memecylaceae as a family, with the constitution indicated above. The congruence cladograms (Figs. 6, 7) emphasize the lack of association of these taxa vis-à-vis Crypteroniaceae. Some of the character-states discussed in the papers cited are plesiomorphous and have no significance in phylogenetic grouping. Of course, it is possible that future evidence may change this picture. Strongly advocated taxonomic conclusions founded almost entirely on particular subdisciplines, such as wood anatomy, embryology, chemistry, or pollen morphology, are always suspect, whether conservative or radical. It is no more of an upset of usage to recognize Memecylaceae than to sink Crypteroniaceae, and clarity will be served thereby.

Among the remaining families, Trapaceae and Onagraceae are very clearly separate, although they are associated consistently in our analysis. Onagraceae fairly clearly comprise two early-divergent lines, namely *Ludwigia* on the one hand and the rest of the genera on the other. This is recognized by other authors in this symposium, and is discussed by Eyde (1981). We have taken the ancestral floral condition as perigynous and not epigynous on the basis of the nectary position and Eyde's well-argued case. Our ancestral picture of the Onagraceae is of woody plants considerably different from some of the familiar modern herbaceous members, but there is no doubt of the unity of the family. The line leading to Trapaceae has clearly undergone great change since the ancestors of the Trapaceae separated from the proto-Onagrads, or from elsewhere among early Myrtales. Additional autapomorphic features characterizing Trapaceae are found in the embryology (Tobe & Raven, 1983a).

Alzatea does not fit in with anything else in the order, a conclusion in agreement with the views of Dahlgren and Thorne (1984) and with the findings of Graham (1984), who describes the family Alzateaceae. It comes out on a common stem with *Rhynchocalyx* in our analyses and Graham (pers. comm.) finds that both have trans-septal vascular supply to the placenta. She points out also that the placentation types (described by earlier authors as axile in *Rhynchocalyx* but parietal in *Alzatea*) differ in breadth of the placenta but are not as dissimilar as these terms might appear to indicate. However, trans-septal vascularization occurs in diverse families in the order (Schmid, 1984) and in scattered groups in Myrtaceae (Schmid, 1972a, 1972b, and our observations); it must have arisen several times. Moreover, the two genera are very different in anatomy, palynology, and general floral morphology. They do show embryological similarities, at least some of which could be synapomorphies (3.2.3), as well as differences (Tobe & Raven, 1984a, 1984b). For general accounts see Graham (1984), Lourteig (1965), Dahlgren and Thorne (1984), and references therein.

Rhynchocalyx was referred to Lythraceae when originally described (Oliver, 1894), a position upheld by Sprague and Metcalfe (1938), Baas and Zweypfenning (1979), and van Vliet and Baas (1984). None of our phylograms support this; they indicate that the common ancestors of *Rhynchocalyx, Alzatea,* and the Lythraceae would be common ancestors of several other justly recognized groups as well.

Some of the characters shown on the path leading to *Rhynchocalyx* are, of course, shared by Lythraceae; others do not occur at the base of Lythraceae but are found in several taxa within that family. Insertion of stamens on the rim of the hypanthium is found in *Duabanga* and *Sonneratia,* which we regard as offshoots from a Lythraceous base. The obhaplostemonous condition, trans-septal vascularization, micropyle formed by the inner integument only, and seed-coat type distinguish it from other Lythraceans. It may be argued that the first three could easily be homoplastically attained. The simple seed-coat structure may possibly be secondary, i.e., derived from the characteristic Lythraceous condition by evolutionary reversion. While all of these suppositions are conceivable, they imply a longer phylogram than those presented. Consequently, on the principles adopted in this analysis, to accept *Rhynchocalyx* as being on the Lythracean line would require additional evidence or cogent argument beyond that considered here.

It is not logically sufficient to point to resemblances with particular members of the Lythraceae that must, in part, be the results of homoplasy or be symplesiomorphic. To do so leads us back to the fallacies of phenetics or to intuition. On the characters used in our phylograms, we cannot accept that *Rhynchocalyx* should be placed in the Lythraceae; this opinion is strengthened by the evidence more recently available. Graham (1984) now supports this view. Raven and Tobe (1984a, 1984b) give embryological evidence, including the ephemeral anther endothecium, that *Rhynchocalyx* ought not be in Lythraceae.

In the context of the other taxa recognized herein as families, it should have a family to itself and it is therefore desirable to establish one formally.

RHYNCHOCALYCACEAE L. Johnson & B. Briggs, fam. nov. TYPE: *Rhynchocalyx* Oliv.

Arbores foliis integris decussato oppositis, inflorescentiis paniculatis (anthotelicis), floribus hexameris perigynis, lobis calycis valvatis, petalis unguiculato-cucullatis, staminibus in verticillo singulo antepetalis in summo hypanthii insertis, primo incurvatis, antheris bithecatis prope basin dorsifixis, granis pollinis colporatis colpis subsidiaribus instructis, ovario bicarpellato sed plus minusve uniloculari, stylo indiviso, ovulis in loculo unoquoque numerosis anatropis in placentis axilibus duabus longitudinalibusque, micropylo ex integumento interiore solo formato, fructibus loculicide capsularibus multispermis.

As indicated above (3.2.5), there is no certainty as to the position of the Lythracean line relative to the branch bearing Rhynchocalycaceae in the phylograms, and the wide separation of these lines is to some degree an artifact of the presentation in the phylograms. For instance, on one supraminimal tree the Lythracean line joins proximately with that leading to Penaeaceae, Rhynchocalycaceae, etc. Nevertheless, this does not invalidate what has been said above.

The Myrtacean assemblage remains. Formerly (Briggs & Johnson, 1979) we recognized Psiloxylaceae and placed that family near the Myrtaceae, but with some doubt as to its closest affinity. Schmid (1980) has argued for its inclusion in Myrtaceae. Scott (1980) recognized a tribe Psiloxyleae within Myrtoideae, while Baas and Zweypfenning (1979) pointed out resemblances in wood anatomy to the Lythraceae. We have now seen better material and young living plants of *Psiloxylon* and, if our interpretation of its characters is correct, the analysis shows it as clearly related to Myrtaceae but differing in a considerable suite of characters.

In our earlier paper we were impressed by the resemblances between *Heteropyxis* and some Myrtaceae and, in particular, interpreted the androecium of *Heteropyxis* as reduced from a condition of five staminal bundles (then considered by us to be primitive in the Myrtaceae). Reductions of that kind appear to have taken place in a number of Myrtaceous genera. Subsequent examination of better material, including living plants, indicates that there are fundamentally two whorls of stamens and that, unlike the condition in various oligostemonous Myrtaceae, the vascular traces of the stamens are separate, showing no indication of reduction from a fascicled condition. This would appear to be comparable with the condition in *Psiloxylon,* except that *Heteropyxis* shows apparent obdiplostemony. In Myrtaceae proper, on the other hand, it now seems that there were originally two whorls of staminal groups (see 4.1.3), but that the antesepalous whorl was lost early in most lines. There is no indication in the Myrtales at large that a polystemonous condition is an original character of the order; so it seems likely that this arose by *dédoublement* in the primitive Myrtaceae, and that the androecia of all members we admit to that family can be derived from such a condition. *Heteropyxis* and *Psiloxylon* appear to have diverged before this acquisition of staminal proliferation. Both genera, moreover, have a completely superior ovary contracted at the base, unlike Myrtaceae proper in which there is always some degree of union between the broad-based ovary and the hypanthium.

Schmid (1980) has provided very useful information on these genera, which has been used in our analysis where relevant. We can now confirm that *Psiloxylon* has anthotelic, though somewhat reduced, inflorescences.

The analysis indicates two competing hypotheses as to the divergence of *Heteropyxis*: one together with *Psiloxylon,* the other on the same line as the Myrtaceae proper. The further analysis of the Myrtaceae and these close allies (4.2) favors the former hypothesis, but only by one step. This does not provide sufficient grounds for placing *Heteropyxis* and *Psiloxylon* in a single family, and we recognize both Heteropyxidaceae and Psiloxylaceae as unigeneric families that separated early from the Myrtalian line. At an earlier stage of the present study (Johnson & Briggs, 1981b) we suggested that *Heteropyxis* might be treated as a subfamily of the Myrtaceae; more detailed analysis does not support the implied grouping.

The Myrtaceae constitute a large and diverse family, but one that is very well defined; the division advocated by Kausel (1956) into Myrtaceae sensu strictissimo and Leptospermaceae is untenable (see 4.4). Our delimitation of the family recognizes the Myrtaceous character-syndrome and the distinctiveness of the other two families from each other and from Myrtaceae proper, as well as pointing up the phytogeographic patterns.

4. PHYLOGENETIC ANALYSIS OF MYRTACEAE

4.1 THE METHOD AND ITS LIMITATIONS

4.1.1 The taxa. Our earlier treatment of Myrtaceae (Briggs & Johnson, 1979) listed the genera and assigned them to an informal system of alliances and suballiances, which may be regarded as roughly equivalent to tribes and subtribes in a formal system.

Phylogenetic analysis should ideally take small units as the taxa to be considered (the OTUs in the terminology of some authors), down at least to the level of the suballiances, but should treat problematical genera individually. We have not yet been able to do this for all taxa. Table 3 indicates the placement of taxa of the present analysis in the earlier system. Distributions are indicated and discussed, down to the suballiance level, in Johnson and Briggs (1981a) and given in more detail for the Australian members (Johnson & Briggs, 1983b).

In dividing the family into taxa for this analysis, our emphasis on problematical situations has led to units of unequal status. Three anomalous genera of the *Lophostemon* suballiance are treated separately but the *Myrcia, Myrtus, Cryptorhiza,* and *Eugenia* alliances are grouped into "Myrtoideae sensu stricto." The character-states scored for this group are those conditions that a common ancestor could have possessed consistently with the polarities assigned and the states in the constituent groups so far as we are able to determine them. This assumes that the group is monophyletic (= "convex," see 3.3.2) in the context of the other alliances. It does not assume that it is holophyletic (Ashlock, 1971), although the analysis would indicate that it is so.

We make similar assumptions at a lower taxo-

TABLE 3. Relation between taxa of present and earlier treatments.

Taxa of Present Analysis (and Names of Individual Genera Mentioned)	Previous Treatment (Briggs & Johnson, 1979)		
	Sub-family[a]	Alliance	Suballiance
Psiloxylon: excluded from Myrtaceae		Excluded from Myrtaceae	
Heteropyxis: excluded from Myrtaceae	L	*Heteropyxis*	
Metrosideros group (*Basisperma, Kania, Lophostemon, Mearnsia*, gen. aff. *Mearnsia, Metrosideros, Ristantia, Tepualia, Welchiodendron, Xanthostemon*)	L	*Metrosideros*	*Kania* *Metrosideros* *Xanthostemon* *Lophostemon* (pro parte)
Kjellbergiodendron	L	*Metrosideros*	*Lophostemon* (pro parte)
Whiteodendron	L	*Metrosideros*	*Lophostemon* (pro parte)
Lindsayomyrtus	L	*Metrosideros*	*Lophostemon* (pro parte)
Backhousia group (*Backhousia, Choricarpia*)	L	*Backhousia*	
Arillastrum group[b] (*Allosyncarpia, Arillastrum, Eucalyptopsis*, gen. nov.)	L	*Eucalyptopsis*	
Angophora group[b] (*Angophora, Corymbia*)	L	*Eucalyptus*	*Angophora*
Symphyomyrtus group (*Eudesmia*, "*Sebaria*," *Symphyomyrtus*)	L	*Eucalyptus*	*Symphyomyrtus*
Eucalyptus group (*Eucalyptus*, "*Idiogenes*," "*Gaubaea*")	L	*Eucalyptus*	*Eucalyptus*
Leptospermum group (*Beaufortia, Callistemon, Lamarchea, Leptospermum, Melaleuca, Phymatocarpus*)	L	*Leptospermum*	*Leptospermum* *Calothamnus*[c]
Chamelaucium group (*Astartea, Baeckea, Calytrix*, "*Catocalypta*," *Chamelaucium, Corynanthera, Malleostemon, Micromyrtus, Pileanthus, Scholtzia, Thryptomene, Verticordia*)	L	*Chamelaucium*	*Baeckea* *Chamelaucium*
"Myrtoideae sensu stricto" (*Austromyrtus, Eugenia, Fenzlia, Meteoromyrtus, Myrcia, Myrtella, Myrtus, Pilothecium, Psidium, Stereocaryum, Uromyrtus, Xanthomyrtus*)	M	*Myrcia* *Myrtus* *Cryptorhiza* *Eugenia*	
Osbornia	M	*Osbornia*	
Acmena group (*Syzygium*, gen. nov.)	M	*Acmena*	*Syzygium* *Acmena*

[a] L = Leptospermoideae; M = Myrtoideae.

[b] Some change in circumscription compared with earlier treatment. It is now clear that *Arillastrum* must be removed from the *Angophora* group to the affinity of *Eucalyptopsis* (see 4.4). Foreshadowing a future formal subtribal name, we have preferred *Arillastrum* as a basis, since the use of *Eucalyptopsis* may lead to confusion with the *Eucalyptus* group.

[c] Referred to as the *Beaufortia* suballiance in Johnson & Briggs (1983b).

nomic level for some of the other alliances, which are treated as a whole although it would be preferable to process suballiances as independent units. This applies particularly to what is here called the *Metrosideros* group, which comprises the *Kania, Metrosideros*, and *Xanthostemon* suballiances, together with the residue of the *Lophostemon* suballiance after the anomalous genera *Kjellbergiodendron, Whiteodendron*, and *Lindsayomyrtus* have been removed. We have seen material of several genera vaguely related to *Lophostemon*, some of them undescribed (Peter G. Wilson, pers. comm; B. P. M. Hyland, pers. comm.), that deserve special consideration, if only for the purpose of redefining the suballiances. As we pointed out previously, the *Lo*-

phostemon suballiance may not be a very natural group, even with the exclusions noted above. We discuss the *Chamelaucium* alliance separately (4.3), but hope to carry out a detailed analysis on this group and also on the constituents of the *Leptospermum* alliance, in which the suballiances may not fall out quite as simply as suggested in our previous paper.

Psiloxylon and *Heteropyxis,* though recognized herein as constituting separate families (3.3.2), have been included in the analysis for comparison.

Because of the deviations from our previous classification, we have designated each terminal taxon in the diagrams as a group (gr.) rather than as an alliance or suballiance, except for the genera treated individually and for "Myrtoideae sensu stricto." Taxonomic conclusions are discussed below (4.4).

4.1.2 The method. Since the completed CLAX program was not available for computer use, and hand processing of the data by the CLAX method was very time-consuming, we took some computational short-cuts for the analysis of Myrtaceae, in contrast to that for Myrtales. It is therefore less certain that a minimal tree (without reversals and on the initial assumptions) has been obtained; this will affect chiefly the portions of short internode-length, which are in any case very subject to variation according to character selection and scoring. We have not performed WAGNER-78 analyses or other procedures of that kind but, as discussed above (2.4), we do not find these practically useful in any case. More detailed studies are planned (but see 4.2.2).

4.1.3 The characters. The characters used (Table 4) include only those in which the primitive and derived states occur differentially as fundamental to taxa used in the analyses. Further derived states, and indeed further characters, are important in the evolutionary diversification of the family at large and mark many genera and species-groups. We have previously referred to many of them when listing vegetative and inflorescence features or when discussing adaptive syndromes (Briggs & Johnson, 1979); other features are mentioned by Schmid (1980).

In contrast to the treatment for the Myrtales, where some of the methods of analysis required binary coding, we have retained our original serial multistate coding, thus reducing the number of designated characters.

Many characters additional to those used for the order are significant at this level, but naturally the character-states taken to be ancestral for the *Psiloxylon-Heteropyxis*-Myrtaceae line are omitted.

The characters cannot be discussed at length in this paper. We have used all characters for which reasonable information has been available to us and which showed variation within the group, assigning polarity on the same principles as for Myrtales. Information has been derived from many sources, including Briggs and Johnson (1979), Carr and Carr (1969), Dawson (1970a, 1970b, 1970c, 1972a, 1972b, 1972c, 1972d, 1975a, 1975b, 1976, 1977, 1978a, 1978b), Gadek and Martin (1981), Gauba and Pryor (1958, 1959, 1961), Green (1979, 1980, 1983, and pers. comm.), Hyland (1983), Ingle and Dadswell (1953), Johnson (1972, 1976), McVaugh (1968), McWhae (1957), Pike (1956), Pryor and Johnson (1971), Schmid (1980), Thompson (1983), Wilson (1981), and Wilson and Waterhouse (1982, and pers. comm.), as well as our own observations in many fields. Useful characters undoubtedly exist in chemistry (e.g., Hegnauer, 1969; Hillis 1966, 1967a, 1967b, 1967c, 1967d, and pers. comm.; Lassak, pers. comm.) and bark anatomy (Bamber, 1962; Chattaway, 1953), and should ultimately be available from such fields as protein sequencing. Nothing could be incorporated from these fields into the overall analysis because of insufficient coverage of the taxa. Nevertheless, terpenoid and flavonoid chemistry as well as periderm anatomy have contributed to our general thinking in some of the Australian groups.

A few characters call for comment at this point:

Characters 1–12. Wood anatomy. Data are drawn largely from Ingle and Dadswell (1953) and our own observations, but van Vliet and Baas (1984) gave valuable suggestions as to directions of evolutionary change.

22–28. Phyllotaxy and inflorescence. Vegetative phyllotaxy and branching in the Myrtaceae were discussed by Briggs and Johnson (1979) but, as indicated above (3.1.2), it now seems probable that although the opposite-decussate condition occurred in some ontogenetic stages of primitive Myrtales and primitive Myrtaceae, it was part of an ontogenetic spectrum in which disperse (spiral or "alternate") arrangement also occurred. Within the Myrtaceae, the ultimate branches of uniflorescences usually revert to opposite in those cases where adult vegetative stages and conflorescence axes have spiral phyllotaxy. The sequences in the spectra are various; for instance,

TABLE 4. Characters used in the phylogenetic analysis of Myrtaceae. Postulated primitive states with zero scores.

1. Vessel aggregation	0 = mostly solitary; 1 = mostly grouped
2. Elongation of vessel-ray pits	0 = small + isodiametric; 1 = elongated
3. Elongation of vessel-ray pits	0 = isodiametric or moderately elongated; 1 = considerably elongated
4. Vessel-ray pits	0 = small; 1 = large simple
5. Loss of bordered pits from fibers	0 = pits present (i.e., fiber-tracheids); 1 = pits absent (i.e., fibers libriform)
6. Loss of vasicentric tracheids	0 = present; 1 = absent
7. Loss of apotracheal parenchyma	0 = present (often scanty); 1 = absent
8. Loss of paratracheal parenchyma	0 = present (sometimes scanty); 1 = absent
9. Increase in paratracheal parenchyma	0 = scanty; 1 = confluent or banded
10. Increase in ray heterogeneity	0 = type I[a]; 1 = heterogeneous type II[a]
11. Siliceous inclusions in rays	0 = absent; 1 = present
12. Crystalliferous fibers	0 = absent; 1 = present
13. Oil ducts (many small) in stem pith[b]	0 = absent; 1 = present
14. Oil ducts (few large) in stem pith[b]	0 = absent; 1 = present
15. Oil ducts in the petiole[b]	0 = absent; 1 = present
16. Loss of standard myrtaceous hairs (at least from vegetative body)	0 = present; 2 = absent
17. "*Psiloxylon*-type" modification of standard hair	0 = absent; 1 = present
18. "*Kjellbergiodendron*-type" modification of hair	0 = absent; 1 = present
19. "Angophoroid hairs"	0 = absent; 2 = present
20. "*Arillastrum*-type" hairs	0 = absent; 2 = present
21. Bristle-glands	0 = absent; 1 = incipient (papillate condition); 2 = present
22. Reduction of accessory buds	0 = frequent; 1 = infrequent; 2 = absent
23. Loss of stipules (excluding retention only at cotyledonary node)	0 = present (row of hair-like stipules); 1 = absent
24. Intramarginal vein	0 = absent; 1 = present
25. Fixation of opposite vegetative phyllotaxy	0 = ±opposite, switching ontogenetically to spiral; 1 = opposite throughout (incl. disjunct-opposite)
26. Fixation of spiral vegetative phyllotaxy	0 = ±opposite, switching ontogenetically to spiral; 1 = spiral throughout
27. Fixation of opposite phyllotaxy in inflorescence	0 = ±disperse; 1 = fully fixed
28. Fixation of spiral phyllotaxy in inflorescence	0 = ±opposite; 1 = disperse
29. Reduction of degree of inflorescence branching	0 = much branched; 1 = somewhat reduced; 2 = greater reduction; 3 = reduced to triads or monads (or single-flowered reduced botryoids)
30. Loss of recaulescence in inflorescence	0 = present; 1 = absent
31. Reduction of anthopodia	0 = developed; 1 = reduced; 2 = absent
32. Reduction of perianth mery	0 = 5-merous; 1 = 5–4-merous flexible; 2 = 4-merous fixed
33. Petal fusion into a calyptra	0 = free; 1 = fused
34. Herbaceous petals	0 = petaloid; 1 = sepaloid
35. Androecium	0 = diplostemonous; 1 = apparently obdiplostemonous; 2 = partial loss of antesepalous stamens; 3 = obhaplostemonous
36. Stamen proliferation	0 = absent; 2 = proliferated to cluster; 3 = well-developed phalange
37. Loss of stamen inflexion	0 = inflexed; 1 = straight
38. Well-developed connective gland	0 = poorly developed; 1 = well developed
39. Loss of syncolporate condition	0 = pollen syncolporate; 1 = apocolporate

TABLE 4. Continued.

40. Pollen with very large polar island	0 = absent; 1 = present
41. Reduction of carpel number	0 = isomerous with perianth; 1 = 4–3 carpels (1 or 2 less than perianth mery); 2 = 2 carpels
42. Epigyny	0 = gynoecium free; 1 = slightly adnate (broad-based); 2 = greater adnation; 3 = virtually completely adnate
43. Stipitate ovary	0 = not stipitate; 2 = stipitate
44. Exaggerated later growth of free portion of ovary above attached portion	0 = absent; 1 = present
45. Trans-septal ovary vascularization	0 = axile; 1 = mixed; 2 = trans-septal
46. Style reduction	0 = at least medium elongation; 1 = not at all elongated
47. Exaggerated stigmatic lobing	0 = slight or no lobing; 1 = exaggerated lobing
48. Reduced stigmatic lobing	0 = at least moderate lobing; 1 = little or no lobing
49. Loss of sunken style-base	0 = sunken; 1 = not sunken
50. Limitation of ovule attachment	0 = over most of axile area; 1 = near base of loculus only
51. Reduction of ovule rows on placenta	0 = many-rowed; 1 = few-rowed; 2 = 2-rowed
52. Peltate placenta	0 = not peltate; 1 = peltate; 2 = strongly peltate
53. Reduction of ovule number	0 = ovules numerous; 2 = ovules few
54. Modification of anatropous condition	0 = anatropous; 2 = hemitropous or campylotropous
55. Ovulodes[c]	0 = absent; 1 = present
56. Loss of fruit dehiscence	0 = dehiscent; 1 = tardily dehiscent; 2 = indehiscent
57. Hypanthium fleshiness in fruit	0 = dry; 1 = fleshy
58. Ovary-wall fleshiness in fruit	0 = dry; 1 = fleshy
59. Seeds fewer than ovules in multi-ovulate ovaries	0 = most ovules developing to seeds; 1 = seeds several but much fewer than ovules; 2 = seeds reduced to 1 or 2
60. Seeds fewer than ovules in 2- or few-ovulate ovaries	0 = most ovules developing; 1 = seeds fewer than ovules
61. Well-organized crystalliferous layer in testa	0 = absent; 2 = present
62. Embryo with hypocotyl much exceeding cotyledons	0 = absent; 1 = present
63. Embryo folded	0 = straight; 1 = folded or coiled
64. Cotyledons folded	0 = flat; 1 = folded

[a] Ray types of secondary xylem as in Ingle and Dadswell (1953).
[b] Records for oil ducts include unpublished data from Peter G. Wilson (pers. comm.).
[c] See Carr and Carr (1962).

as pointed out by Wilson (1981), in the *Xanthostemon* suballiance spiral phyllotaxy is characteristic of juvenile plants but is followed in some species by the opposite-decussate condition. In *Lophostemon* and *Welchiodendron* the reverse pattern is encountered while in *Tristaniopsis* and *Ristantia* the phyllotaxy is disperse throughout (Wilson & Waterhouse, 1982, unfortunately with an error for *Lophostemon* adults in their Table 1). Fixation in different directions has occurred in various groups. D. Carr and S. Carr (1981) and S. Carr and D. Carr (1981) point out that there are many variations of spiral phyllotaxy in the Myrtaceae and attach great importance to this. We (Johnson & Briggs, 1983a) would consider these as secondary to the essential ontogenetic sequence of opposite-decussate and spiral, in one or other of the usual Fibonacci-sequence arrangements.

The scoring of characters 27 and 28 (fixation of phyllotaxy in inflorescence) refers to the most plesiomorphous condition of the ultimate inflorescences attributable to the ancestor in each group. It frequently applies only within uniflorescences, which may be greatly reduced. This can be understood by reference to the analyses of inflorescences presented by Briggs and Johnson (1979). The many other changes and re-

TABLE 5. Data matrix (taxa and characters) used in analysis of Myrtaceae. Character-states are defined in Table 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Psiloxylon	1	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0
Heteropyxis	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucalyptopsis "alliance"	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	2	0	0
Angophora suballiance	1	1	0	1	0	0	0	0	1	0	0	1	0	1	1	2	0	0	2	0	2	0
Symphyomyrtus suballiance	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	1	0
Eucalyptus suballiance	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0
Acmena alliance	1	1	1	0	1	1	1	0	1	1	0	1	0	0	0	2	0	0	0	0	0	0
Kjellbergiodendron	0	1	1	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	0	0	0	0
Whiteodendron	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	0
Lindsayomyrtus	0	1	0	1	0	0	0	0	0	0	1	1	0	0	1	2	0	0	0	0	0	0
Metrosideros alliance	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Backhousia alliance	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptospermum alliance	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Chamelaucium alliance	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	2
Osbornia	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
"Myrtoideae" sensu stricto	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0

	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Psiloxylon	0	1	0	1	0	1	2	0	0	0	0	0	0	0	1	0	0	1	1	0	2	0
Heteropyxis	0	0	0	1	0	0	0	0	0	0	0	0	2	0	1	1	0	0	2	0	0	0
Eucalyptopsis "alliance"	1	0	1	0	0	0	0	1	2	0	0	0	2	2	0	1	0	0	2	2	0	0
Angophora suballiance	1	0	1	0	1	0	0	1	0	1	0	0	3	2	0	1	0	0	1	2	0	0
Symphyomyrtus suballiance	1	1	1	0	1	0	0	1	0	2	1	0	3	2	0	1	0	0	0	2	0	0
Eucalyptus suballiance	1	1	1	0	1	0	0	1	0	2	1	0	3	2	0	1	0	0	0	2	0	0
Acmena alliance	0	0	1	0	1	0	0	1	0	1	0	0	3	2	0	1	0	0	2	3	0	0
Kjellbergiodendron	1	0	0	1?	0	0	0	0	2	0	0	0	3	2	0	1	1	0	2	2	0	0
Whiteodendron	1	1	0	1?	0	0	0	0	1	0	0	0	3	3	0	1	0	0	1	2	0	1
Lindsayomyrtus	1	0	0	1?	0	0	0	1	1	0	0	0	3	2	0	1	0	0	2	2	0	1
Metrosideros alliance	0	0	0	0	0	0	0	0	0	0	0	0	3	2	0	1	0	0	1	1	0	0
Backhousia alliance	0	0	1	0	1	0	0	1	0	0	0	0	3	2	0	1	0	0	2	2	0	0
Leptospermum alliance	0	1	0	0	1	0	2	1	1	0	0	0	3	2	0	1	0	0	0	2	0	0
Chamelaucium alliance	0	1	0	0	1	0	2	1	1	0	0	0	3	2	0	1	0	0	1	2	0	0
Osbornia	0	0	1	0	1	0	3	1	2	2	0	1	2?	2	0	1	0	0	2	3	0	0
"Myrtoideae" sensu stricto	0	0	1	0	1	0	0	1	1	0	0	0	2	2	0	1	0	0	0	3	0	0

	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	"Advancement level"
Psiloxylon	0	1	1	0	0	0	0	1	0	0	0	2	0	1	0	0	0	0	0	0	22
Heteropyxis	0	0	0	1	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	15
Eucalyptopsis "alliance"	1	0	0	1	2	0	0	0	0	2	1	0	0	0	1	0	2	0	1	1	33
Angophora suballiance	1	0	0	1	2	0	0	0	0	2	1	0	0	0	1	0	2	0	1	0	38
Symphyomyrtus suballiance	1	0	0	1	2	0	0	0	0	2	1	0	0	0	1	0	2	0	1	0	33
Eucalyptus suballiance	0	0	0	1	2	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	27
Acmena alliance	0	0	0	1	2	0	1	0	0	0	0	2	1	1	2	0	0	0	1	1	38
Kjellbergiodendron	2	0	0	1	0	0	0	0	0	0	0	2	1	1	2	0	0	0	0?	1	32
Whiteodendron	2	0	0	1	0	1	0	0	0	0	0	1	0	1	2	0	0	0	0	1	30
Lindsayomyrtus	0	0	0	1	0	0	2	0	2	0	0	1	0	1	2	0	0	0	1	1	33
Metrosideros alliance	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12
Backhousia alliance	0	0	0	1	2	0	2	0	0	2	0	2	0	0	2	0	0	0	1	1	27
Leptospermum alliance	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
Chamelaucium alliance	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	22
Osbornia	0	0	0	1	2	1	2	0	2	2	0	2	0	0	0	1	0	0	0	0	37
"Myrtoideae" sensu stricto	2	0	0	1	1	0	0	0	0	0	0	2	1	1	0	0	0	0	1	1	23

peated trends in inflorescences there described are cladistically significant in the Myrtaceae chiefly at a finer level of analysis, as can be seen from Table 2 of that paper.

16–21. Trichomes are also discussed by Briggs and Johnson (1979: 172). We have considered the thin-walled unicellular hairs of the "*Corymbia*" group (equivalent to a genus) of eucalypts as a variant of the rather similar but multicellular hairs designated as "angophoroid." It is uncertain whether these are phylogenetically homologous with the *Arillastrum*-type branched hairs, the branched hairs found in a very few members of the *Acmena* alliance, or indeed the thick-walled acute hairs arising in groups on glandular protuberances in a minority of species of *Eucalyptus* sensu stricto (the assemblages incorrectly called "stellate hairs" by earlier authors and by Carr & Carr, 1980). Their differences and occurrence suggest that some of them at least are independent developments, and characters 19–21 are scored accordingly. S. Carr and D. Carr (1981) foreshadow further critical studies on Myrtaceous trichomes, which will be useful. We hope also to comment further on trichomes; for the present we merely draw attention (characters 17, 18) to what appear to be variants of the standard myrtaceous hairs in *Psiloxylon* (thin-walled, usually subacute, bulbous at the base or unequally 2-armed) and *Kjellbergiodendron* (very short, subacute).

Other variants, for example as described by Schmid (1972a) and observed by us in *Eugenia* spp. and some other Myrtoideae sensu stricto, are not basic characters to the taxonomic units treated in this analysis.

24. Intramarginal leaf vein. On the basis of out-group comparisons within and beyond the Myrtales, we have taken brochidodromy as the ancestral state. The strengthening of primary-lateral-vein arch connections, to produce an intramarginal vein (sometimes with a secondary but usually weaker outer one) and/or various degrees of tri- or multinerved acrodromy, appears to have developed from the brochidodromous condition in a number of lines, as it has in other Myrtales (see 3.3.2 and Hickey, 1981).

35–37. The androecium. Our general interpretation of the fundamental conditions in the Myrtales, and in Psiloxylaceae, Heteropyxidaceae, and Myrtaceae, has been discussed (3.2.2; 3.3.2). As briefly pointed out elsewhere (Briggs & Johnson, 1979; Johnson & Briggs, 1983a), the Myrtaceae, proper, display a wide variety of androecial conditions in mature flowers. Schmid (1980) has designated the staminal placement within the Myrtaceae in terms of diplostemony, haplostemony, obdiplostemony, and obhaplostemony, with considerable discussion. This is almost wholly descriptive of the condition in mature flowers, rather than interpretative. If we are to consider phylogenetic relationships, we are bound to make some interpretations and to reach at least some tentative conclusions on evolutionary changes and consequent equivalences and homologies. The dangers of partial circularity are obvious and have often been stressed. They may be averted or corrected by reciprocal illumination, successive approximation, and tests that potentially allow what might be called "probable falsification," as discussed by Hull (1967), Johnson (1969, 1970), and Mayr (1981).

We have formed an hypothesis of the sequences of androecial evolution in the Myrtaceae (Fig. 8) but cannot develop it fully here. According to this, the origin of the family more or less coincides with the proliferation of stamen initials within each of the ten primordia corresponding to an earlier ancestral 5-merous, 2-whorled condition. The evidence suggests that the original androecial condition in the Myrtales was diplostemonous, but that in a pre-Myrtaceous ancestor (perhaps common to Myrtaceae and Heteropyxidaceae, if a supraminimal tree were accepted, see 4.2.2), and indeed separately in some other Myrtalian families, this had given way to apparent obdiplostemony. This would be the result of a spatial shift in the levels of initiation at the rim of the hypanthium and/or differential early growth in this region of the hypanthium, not to suppression of whorls, hence the qualifier "apparent." The order of development within the resulting staminal groups or fascicles is centripetal with respect to the flower as a whole, i.e., the first-developed and often (but not always) longest stamens are in the radially outer median part of the bundle.

In accord with the studies of other authors (e.g., Mayr, 1969) and with the obvious condition in many genera with fasciculate stamens, we had previously thought that there were originally only five antepetalous primordia, i.e., that the family was fundamentally obhaplostemonous with proliferation. In *Arillastrum,* we have since found small antesepalous inner staminal fascicles to be present, though inconstantly; the additional fascicles were also described and illustrated by Dawson (1970a), though he made no comment on their significance.

Even if this were a reversion (failure of a sup-

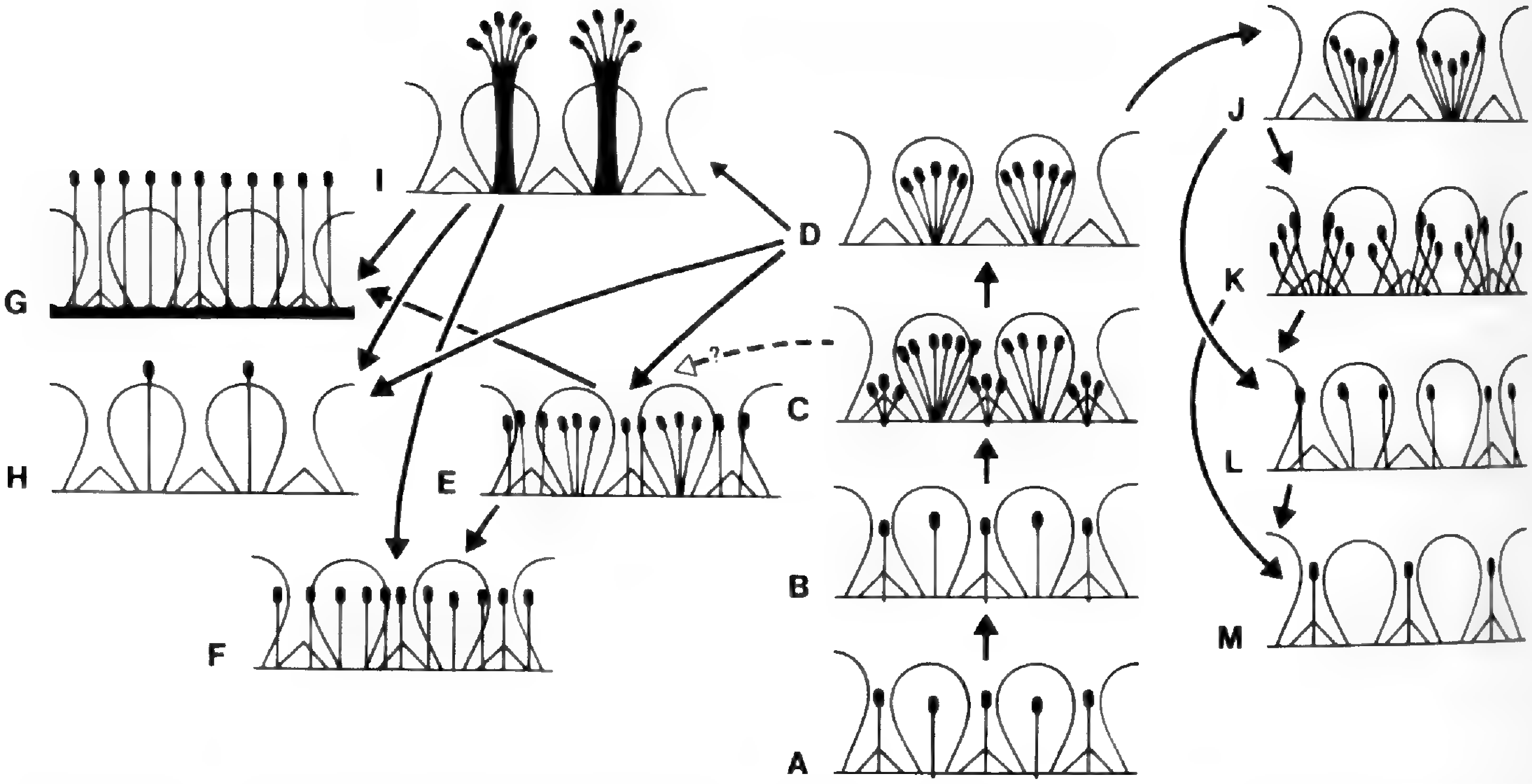

FIGURE 8. Trends in androecial evolution in the Myrtacean phylad. A–B. character-states in ancestors of the Myrtaceae; C–M. conditions in Myrtaceae, J–M occur in the *Baeckea* suballiance.—A. diplostemonous with 10 subequal stamens;—B. obdiplostemony;—C. 10 stamen fascicles, the antesepalous fascicles small (as postulated for "*Protomyrtalis*" and close to condition sometimes seen in *Arillastrum*);—D. antepetalous fascicles only;—E. irregular ring of stamens with some vestige of fasciculate condition;—F. ring of stamens;—G. ring fused at base;—H. stamens reduced to few or one in fascicle;—I. fascicles developed into long claws;—J. partial suppression of central stamens in fascicle;—K. complete suppression of central stamens in antepetalous fascicle, apparent antesepalous fascicles;—L. stamens few, irregularly spaced;—M. antesepalous stamens only. [The individual stamens are shown as if only one-deep in relation to the floral radius. In fact, the original Myrtaceous multistaminate fascicles show proliferation radially, as well as laterally, and this condition persists variously in many of the derived states. Thus the conditions shown in C, D, I, E, G, and (to some degree) F should be interpreted as including a range from a radially multiplied condition to a single ring. Many of the arrows indicate trends that have apparently been followed independently by several phylads. Possibly some additional or alternative paths exist, for instance from the I or I → G conditions to the J series.]

pressive mechanism), it would indicate an earlier obdiplostemonous condition. Developmental studies are necessary in the related genera of the *Arillastrum* group, and indeed in other assemblages such as the *Acmena* group and the four constituents of the Myrtoideae sensu stricto, to determine whether the antesepalous whorl persists elsewhere. Our preliminary examinations of young buds in *Eucalyptopsis, Allosyncarpia,* and gen. nov. aff. *Eucalyptopsis* have been inconclusive. It is clear that only the antepetalous whorl remains in many groups in the family, including *Eudesmia* and apparently in *Symphyomyrtus* and *Eucalyptus* sensu stricto. In the absence of positive evidence of the loss of the antesepalous staminal groups in Myrtoideae, *Backhousia,* and *Osbornia,* and in view of their persistence in *Arillastrum,* these three assemblages are conservatively scored without assuming such loss. In Myrtoideae, Bunniger (1972: 89) observed antesepalous ("episepalous") staminal-fascicle primordia, developed somewhat later than the petal-stamen complexes, in *Myrceugenella* (i.e., *Luma* in the usage of McVaugh, 1968). As he says, "Somit leigt im Prinzip ein diplostemones Androecium vor, das in beiden Kreisen polyandrisch ausgebildet ist." At least some Myrtoideae, however, do show suppression of the antesepalous whorl in organogeny (Payer, 1857; Mayr, 1969). Conditions in the mature flowers do not necessarily reveal the situation at the primordial stage and this needs to be examined in representatives of all groups throughout the families. In some cases it is clear that five (or four in tetramerous flowers) fascicle-primordia exist, even though the mature flowers have a ring of numerous stamens. This is the case, for example, in *Myrtus* sensu stricto (Mayr, 1969) and in at least some species of *Eucalyptus* sensu stricto and *Symphyomyrtus* (B. Knox, pers. comm.). In other cases it may well be that distinguishable fascicle-primordia are not found, and that there is an even distribution of stamen initials from a ring, which develops into a stemonophore (Johnson & Briggs, 1983a) in the mature flower (D. Carr & S. Carr, 1981, as "staminophore"). As discussed below, we see this as a derived condition, usually from five or four primordia, but just possibly in some cases from ten primordia in two whorls, as mentioned above.

The stamens are often described as pluriseriate or multiseriate (e.g., Bentham, 1867, as "several series"; D. Carr & S. Carr, 1981), but they do not usually form clearly defined separate series; rather, in these "multiseriate" cases the stamens are simply several deep on any radial sector.

As we see it, there have been several lines of departure, sometimes seen in combination, from the 5- (or 4-)fascicled condition (Fig. 8D):

(1) Lateral confluence of fascicle-bearing primordia in early or later stages of development to give a more or less uniform ring of stamens (Fig. 8E–G), as discussed above. Sometimes this is partial, so that the filaments are shorter opposite the sepals, giving a subfasciculate appearance.

(2) From ancestral stage direct, or from (1), reduction in stamen number (e.g., in *Myrrhinium*), at the ultimate to as few as five or four, e.g., in *Syzygium* pro parte ("*Tetraeugenia*" and "*Aphanomyrtus*") (Schmid, 1972b) (Fig. 8H). The last case implies a path from Figure 8F to 8H, not shown in the figure.

(3) Radial elongation of the united region to form a pronounced claw dividing into separate filaments on its edges, summit, and sometimes adaxial surface (Fig. 8I).

(4) Reduction from (3) by loss of the claw and/or reduction in number of individual stamens (Fig. 8H, alternative route, e.g., in *Lamarchea* sp.).

(5) Partial (Fig. 8J) or complete suppression of median stamens in each bundle, resulting, (a) as a penultimate stage, in apparently antesepalous bundles each of which is made up of two adjacent edges of antepetalous fascicles (Fig. 8K, e.g., *Astartea*), and (b) as an ultimate stage, in few rather irregularly spaced stamens (Fig. 8L) or, in the extreme, in five apparently regular antesepalous stamens (Fig. 8M, e.g., in *Thryptomene* spp.).

As well as these, there are of course considerable differences in filament length and color, as well as in the attachment, shape, and dehiscence of anthers.

We have applied these interpretations in postulating original conditions in the taxa, but many of the developments discussed appear to be later than the origins of the groups shown in the phylogram for the family. Hence, most of them do not appear in the character list for this level of analysis. Nevertheless, the androecial structures are vital to the interpretation of the family and to the groupings accepted by us.

4.2 PHYLOGENY OF MYRTACEAE

4.2.1 "Protomyrtacea." As with the Myrtales, using out-group comparisons and general morphological principles, we postulate an ancestral "*Protomyrtacea.*" This would represent a stage after the divergence of *Psiloxylon* and *Heteropyxis.* Some characters that are fundamental to the order, and appear in the "description" of "*Protomyrtalis,*" are not mentioned again.

Habit and bark as in "*Protomyrtalis.*" Schizolysigenous secretory cavities present in stems, leaves, flowers, and fruits, containing terpenoid substances (especially monoterpenes and sesquiterpenes) as essential oils. Habitat and wood-anatomical features much as in "*Protomyrtalis*" (3.2.2) and "Protomyrtales" (van Vliet & Baas, 1984), but perhaps with the vessels somewhat grouped. P-type plastids (with crystalline protein) perhaps present in phloem sieve-tube cells, as well as S-type. Without oil-ducts in the stem pith or petiole. Hairs present on vegetative parts at least when young and on the hypanthium and calyx, unicellular, acute, rather thick-walled, with narrow lumen and smooth wall. Nodes unilacunar, 1-traced. Phyllotaxy varying during ontogeny (opposite-decussate → spiral → opposite?). Stipules present, very small, divided, filiform. Leaves as in "*Protomyrtalis*" but entire, without vascularized teeth. Inflorescence as in "*Protomyrtalis.*" Flowers with a distinct anthopodium, bisexual, entomophilous, essentially pentacyclic (but see androecium below), 5-merous or flexibly 4- to 5-merous, perigynous, medium-sized or small, actinomorphic. Perianth members free; calyx and corolla as in "*Protomyrtalis.*" Androecium of two whorls, with the apparent outer and better-developed whorl antepetalous, each whorl consisting of staminal clusters developed by proliferation within the primordia. Stamen-clusters inserted on the hypanthium rim (or the antesepalous ones somewhat below the rim); filaments inflexed in bud. Anthers as in "*Protomyrtalis*" but with a well-developed terpenoid-containing connective gland. Pollen isopolar, oblate, syncolporate with three apertures, lacking subsidiary colpi and viscin threads, the tectate exine moderately thickened but not highly ornamented. Gynoecium broad-based (slightly united with the hypanthium), but otherwise gynoecium, placentation, ovules, fruit, seeds, and germination as in "*Protomyrtalis.*" Chromosome number $n = 11$.

4.2.2 Hypothesis and scenario. The historical picture that emerges if the phylogram[9] (Fig. 9) is approximately correct, taken in conjunction with the distribution of these families and of the order as a whole, suggests an origin of the Myrtacean line (see 3.2.3) in or near the African portion of west Gondwana. Psiloxylaceae probably included members now extinct; *Psiloxylon* itself is on the verge of extinction, and many of its character-states may have been acquired well after the initial divergence. As shown earlier, there is no reason to link *Psiloxylon* with the non-Myrtacean families. Of some 20 apomorphous features shown for it, seven are autapomorphous (i.e., unique to this line). The homoplasies of the other advanced states are widely scattered among the Myrtaceae. The shortest tree produced by the analysis shows a branch leading to *Heteropyxis* and *Psiloxylon,* but a tree one step longer would associate *Heteropyxis* with the branch leading to Myrtaceae. In any case, Table 5 and earlier discussion (3.3) show that *Heteropyxis* and *Psiloxylon* differ very considerably from each other and must have diverged early.

The most important new feature of the ancestor of the Myrtaceae proper (4.2.1) is the staminal proliferation (4.1.3), which is combined in this line with at least some degree of epigyny. We take the latter term (in agreement with Schmid, pers. comm.) as synonymous with adnation or continuity of the ovary wall with the hypanthium. Some authors have described the ovary in some Myrtaceous genera as fully superior. This is not the case; there is always considerable adnation, in contrast to the narrow-based ovary in the perigynous (but not at all epigynous) flowers of *Psiloxylon* and *Heteropyxis.* Differential growth during fruit development may modify the situation from that at the flowering stage.

We shall not narrate the suggested phylogenetic sequences here; they can be ascertained from Figure 9 and Table 5. The hypothesized ancestors of all main lines are not very different from one another. Two early internodes represent non-unique changes in single character-states, so that the sequential branching hypotheses at these points are weak. We suggest that the early divergences must have taken place at least by the Paleocene, although the macrofossil record does not yet appear to be useful in this regard and the microfossils are still not clearly assignable to groups. Internal analysis within the alliances and suballiances shows that many of the features commonly regarded as characteristic of particular groups are more recent acquisitions, and that parallelism and convergence have been rife. This applies to vegetative, floral, and fruit features.

All the lines of Myrtaceae shown in the phylogram are present in the Australasian region. Among them only *Kjellbergiodendron* and *Whiteodendron* are absent from the Australian continent, and the pollen of *Kjellbergiodendron* shows strong resemblance to the sporomorph *Myrtaceidites mesonesos* Cookson & Pike from the Oligocene of south-eastern Australia (McWhae, 1957). The distribution and possible phytogeographic history of the alliances and suballiances are discussed by Johnson and Briggs (1981a), although they are arranged therein under subfamily concepts to which we no longer adhere.

The "Myrtoideae sensu stricto" are best represented in South America, with a probably recent extension to the warmer parts of North America; but only the *Myrcia* alliance is endemic in the New World, though the *Eugenia* and *Cryptorhiza* alliances appear to be centered there. The *Myrtus* alliance is well represented by genera in the Old World (mainly in the Australasian region) as well as in the New. In contrast to some earlier views (e.g., Andrews, 1913; Beadle, 1981), our character-state polarity assumptions and analysis do not indicate the "Myrtoideae" as a base group for the family. In view of the occurrence in the Australasian region of the other main

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[9] Since acceptance of this paper, computerized CLAX analyses have produced a set of phylograms with alternative topologies, although the groupings discussed hereunder are mostly unaffected. The considerable uncertainty as to the early divergences within the Myrtaceae sensu stricto can be resolved only by further assessment of the existing data together with the accumulation of more data. Cladistic reprocessing of the present data set, by any method, will not produce a unique resolution in which we can have confidence.

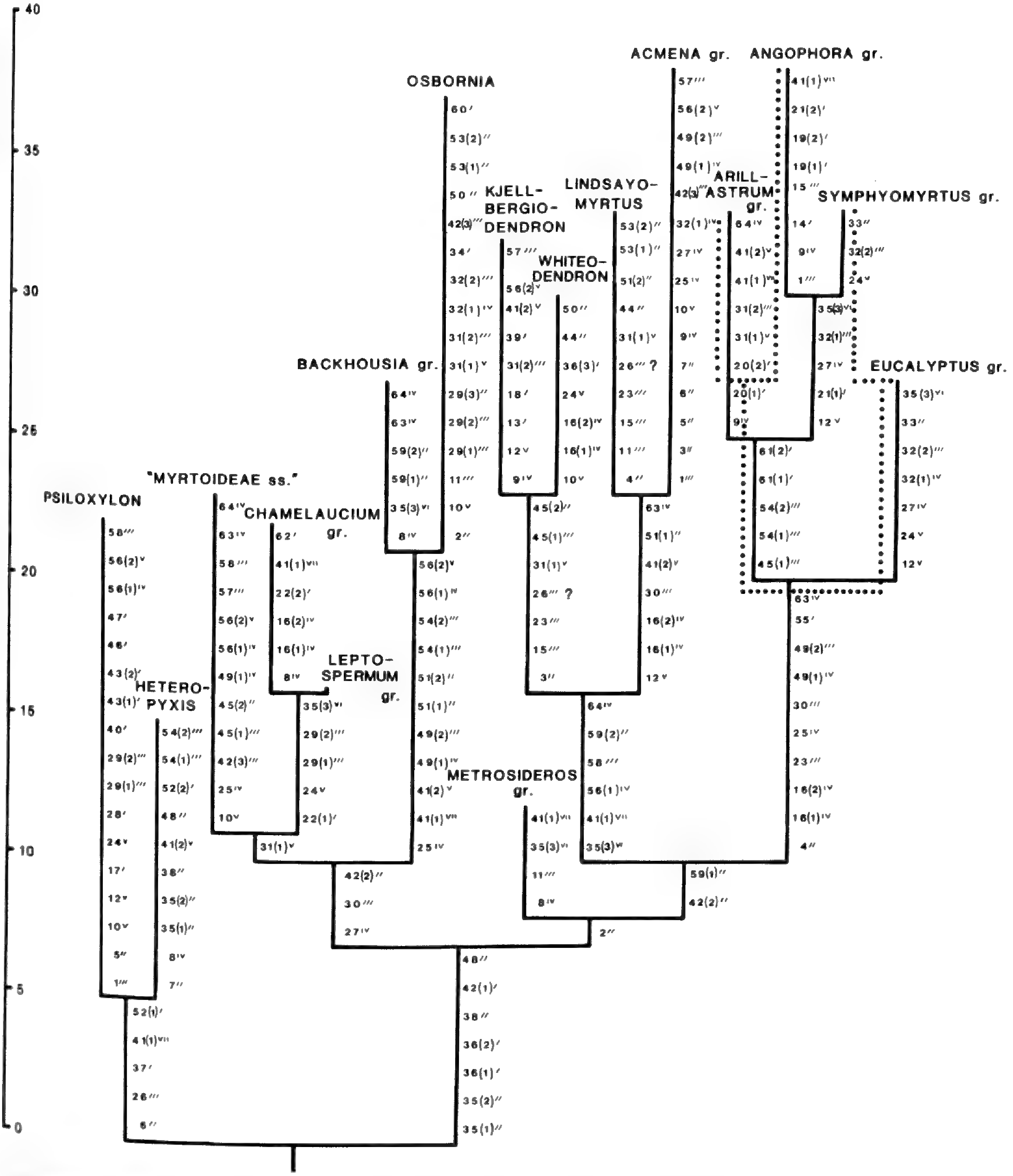

FIGURE 9. Phylogram of relationships in Myrtaceae. Representation as in Figure 1 but character numbers as given in Tables 4 and 5. [If *Myrtoideae, Backhousia,* and *Osbornia* were assumed to be derived from ancestors with a fully obhaplostemonous condition (character 35(3)), an equal alternative occurs with the *Metrosideros* group arising at level 8, above the base of the left-hand fork from level 7. The alternatives shown among *Eucalyptus* and its allies are discussed in the text (4.4).]

lines and at least some myrtoids with several endemic or near-endemic genera, it seems likely that much of the early diversification of the family took place in the east-Gondwanan region, although the earliest-known reliable fossils of Myrtaceae from Australia appear to be from the Paleocene (Lange, 1982, and references therein).

Probable later extensions from this region are listed and discussed by Johnson and Briggs (1981a). Some, notably the South American "leptospermoid" *Tepualia*[10] and perhaps some southern amphi-Pacific members of the *Myrtus* alliance (represented by allied but now distinct genera in the east and west), may result from connections or propinquity until mid-Tertiary in the Antarctic region; others, such as the East Asian outliers of the *Myrtus* and *Acmena* alliances and perhaps some "leptospermoids," may date from the Miocene approximation of the Australian Plate to that region. Others are almost certainly the result of dispersal over considerable distances, for instance, *Metrosideros* sensu stricto in much of the Pacific and perhaps the progenitor of "genus aff. *Mearnsia*" ("*Crystalla*") in southern Africa (Briggs & Johnson, 1979). Since "*Crystalla*" is much more closely related (by any criteria) to the west-Pacific *Mearnsia,* and indeed to the whole of the *Metrosideros* alliance, than *Heteropyxis* or *Psiloxylon* are to any Myrtaceae, it does not seem likely that the African-Australian disjunction in this case is particularly ancient.

After the exclusion of the unrelated *Syzygium* and its allies (the *Acmena* alliance, see below), *Eugenia* still remains a huge genus centered in South America with a scattering of species from Africa to the Pacific. We take it to include *Jossinia* (Schmid, 1980; Briggs & Johnson, 1979), at times used for the Old World species, and are unconvinced that Scott (1980) is justified in recognizing a small group of Mascarene species as a separate genus rather unfortunately named *Monimiastrum. Eugenia* needs a thorough reconsideration, in the context of such South American taxa as *Pilothecium* (Briggs & Johnson, 1979; Legrand, 1975).

A few odd cases remain unexplained, such as the occurrence of *Meteoromyrtus* in peninsular India and *Stereocaryum* in New Caledonia; these seem to belong to the *Eugenia* alliance, but *Stereocaryum,* at least, can hardly be a late derivative of *Eugenia* itself. The *Acmena* alliance is centered in the Australasian-Malesian region, but a few members of its largest genus, *Syzygium,* have reached Africa, perhaps through southern Asia (one species is still found in southern Arabia). The type genus of the family and order, *Myrtus,* has one of the most atypical distributions, being the only representative of Myrtaceae in the extended Mediterranean region. Scott (1979) considers that the Australasian-New Caledonian *Austromyrtus* should be included in *Myrtus;* Byrnes (1982) makes a similar recommendation, on the logically insufficient ground that the species referred to *Austromyrtus* display considerable heterogeneity. We are not disposed to accept this without critical reassessment of the affinities of *Myrtus* sensu stricto vis-à-vis the American *Psidium* group of genera. "*Austromyrtus*" and its western Pacific allies need critical phylogenetic re-evaluation; Byrnes' studies will yield useful information but traditional (phenetic though not numerical) approaches will not serve to clarify evolutionary taxonomy.

Common and wide occurrence of taxa familiar today is not necessary to the conclusion that the

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[10] Fossils (by courtesy of Edgardo Romero and Elsa Zardini) and photographs of fossils that we have seen of supposed *Eucalyptus* (sensu lato) from the Miocene of Patagonia (Frenguelli, 1953) are somewhat enigmatic. The illustrations of fruits of *Eucalyptus patagonica* ("*patagonicus*") Frenguelli, if we interpret them correctly, could conceivably belong among the more generalized members of *Symphyomyrtus.* Dr. Romero's specimens are similar in some respects but do not show a clearly capsular structure; it is also uncertain whether an associated bud-like piece shows a calyptra (operculum) of eucalypt type. On the whole they do not appear to us to belong to the *Eucalyptus* alliance, and probably not to "Leptospermoideae," although they may perhaps be Myrtoideae.

The leaves of *Myrcia chubutensis* Berry (1938), apparently from the same formation, are regarded by Frenguelli as possibly belonging to a eucalypt. The venation patterns do not particularly suggest this to us. The rich associated flora contains elements now characteristic of subtropical South America as well as some (e.g., *Embothrium*) still characteristic of moist southern parts of that continent. It is conceivable that species of *Symphyomyrtus* may have reached South America through the Australia-Antarctica connection but, if so, they have left no descendants there and the whole alliance appears to have its origins in East Gondwana. The situation may be comparable with that of *Gymnostoma* (Casuarinaceae) of which a fossil occurrence ("*Casuarina patagonica*" Frenguelli) is known from the same region (Johnson & Wilson, 1981). Though they are unfortunately very inadequate, occurrence of these supposed eucalypt fossils is at least plausible. This is much less so when the occurrence is geographically unsupported by other evidence, and far-reaching conclusions are drawn. Fossil pollen from the Paleocene of Canada, associated with north-temperate genera and boldly compared with *Metrosideros* by Jarzen (1982) is very far from being established as Myrtaceous. It was referred to the family on the strength of its general triangular shape in polar view and its being apparently "syncolpate." It is not hard to find pollen grains with these features in other families, and we would need much more solid evidence before accepting this glib "identification" and geographically unlikely occurrence.

ancestors of the lines concerned diverged early. It is often stated that "*Eucalyptus*" (referring indiscriminately to various members of the *Angophora, Symphyomyrtus,* and *Eucalyptus* suballiances) appears scarcely if at all in the fossil record before the Oligocene and became dominant over wide areas as late as the Pleistocene. Nevertheless, Lange (1978, 1982) has described fruits that look like advanced members of this group as "probably of early Neogene age." Phylogenetically it makes no sense to assert, as paleobotanists and paleogeographers are wont to do, that the eucalypts were a late development within "Leptospermoideae." Their characters are inconsistent with such an origin. Neither is it necessary to assume that the earlier members of the various eucalypt lines dominated large areas of vegetation or that they were associated with very open forest or woodland conditions. On the contrary, their indicated affinities suggest that they were adapted to conditions marginal to rainforest, intolerant certainly of suppression by shading, but possibly occupying quite small areas. The genus *Gymnostoma* in the Casuarinaceae, which dates at least from the Eocene, provides an ecological parallel (Johnson & Wilson, 1981; Johnson, 1982), expansion into more open habitats in that family being chiefly associated with the more "advanced" genera *Casuarina* and *Allocasuarina.*

The initial adaptational features marking the divergences, not only of the main lines shown, but of many genera of the family, will need further study and consideration. They have doubtless predetermined the later directions taken in the radiation of each group (see also Riedl, 1977, 1979). As a result, quite different habitats have remained characteristic of some genera, whereas others show parallelism from similar structural or other features, or convergence from dissimilar foundations, associated with the occupation of similar niches. We have discussed a number of such adaptations (Briggs & Johnson, 1979; Johnson & Briggs, 1981a).

4.3 THE *CHAMELAUCIUM* ALLIANCE

Before commenting on the systematic implications of the analysis within the family, we must look further at the *Chamelaucium* alliance.

4.3.1 A subfamily Chamelaucioideae—pro and contra. Various botanists (see Schmid, 1980) have recognized a subfamily Chamelaucioideae (usually misspelled as "Chamaelaucioideae" or even "Chamaelaucoideae"). We have pointed out (Briggs & Johnson, 1979) that this is untenable. More than a century ago, Bentham (1867), who treated the three subfamilies of such later authors as tribes, wrote, "The first two subtribes of *Chamaelaucieae* have a peculiar habit . . . but some of the third subtribe (*Thryptomeneae*) pass so gradually into the *Leptospermeae,* as only to be distinguishable from *Baeckea* by the examination of the ovary." Present-day workers on *Thryptomene* and its allies (e.g., J. W. Green, pers. comm.) are well aware of the affinities and difficulties of distinction in this area. Our own studies show that the connections are multiple and involve considerable parallelism.

Schmid (1980) retained Chamelaucioideae in the body of his paper. In the lengthy appendix, written after he had seen our treatment, he advocated its retention, claiming that "the distinctiveness of Chamelaucioideae sensu Schmid . . . as well as differences in inflorescence, fruit, and embryo structure between this taxon and Baeckeinae . . . strongly argue against including the latter in Chamelaucioideae sensu Schmid or '*Chamelaucium* alliance' sensu Briggs and Johnson." He also stated that "other than their probably correct belief that the '*Chamelaucium* suballiance' is 'an evolutionary grade' with its origins amongst early members of the *Baeckea* suballiance" we "present no rationale for this quite novel realignment."

In fact, the realignment is only formally novel, in that Bentham (1867) pointed out the lack of clear distinction. Bentham, of course, did not recognize a high-level distinction between his "Baeckeae" and what we call the *Leptospermum* alliance, and neither does Schmid.

To deal with Schmid's points as cited: (1) there *is* no consistent difference in inflorescence between our *Chamelaucium* alliance and quite a number of other "leptospermoids," as will be evident from Table 3 of our cited paper; (2) in *Scholtzia,* which is clearly related to *Baeckea,* fruits of some species approach closely the indehiscent fruits of the so-called Chamelaucioideae, and these latter differ considerably among themselves in detail (Green, 1980; and our own observations) suggesting homoplastic development. The embryos in fact do not differ greatly in the *Baeckea* and *Chamelaucium* suballiances, and we now doubt that even the small difference as quoted in our earlier paper and by other authors is consistent. All of these embryos do differ markedly, as indicated previously, from those in the *Leptospermum* alliance.

Schmid (1980) refers also to the diversity of chromosome numbers, quoting us on the contrast with the general stability in the family. As we had indicated, diversity in base numbers is in fact characteristic only of some genera within part of the so-called Chamelaucioideae, and is consequently cladistically irrelevant to the origins of the group as traditionally conceived. Smith-White (1959, and references therein) pioneered karyological study of the group, and he too stressed its supposed distinctiveness. He did make it clear that $X = 11$, the prevailing number in Myrtaceae as a whole, was general in *Calytrix, Thryptomene,* and their associated genera [i.e., Bentham's subtribes Calytrichinae ("Calythriceae") and Thryptomeninae ("Thryptomeneae")]. Moreover, it appears to be constant in *Pileanthus, Chamelaucium,* and section *Catocalypta* of the possibly diphyletic *Verticordia.* Rye (1979) has extended karyological studies, finding some additional base numbers, including $X = 10$ and $X = 9$ in individual species of *Thryptomene,* as well as $X = 10$ and $X = 8$ in *Beaufortia* and $X = 20$ in *Phymatocarpus.* The last two are undoubted members of what we have called the *Beaufortia* infra-alliance (Johnson & Briggs, 1983b) within the *Leptospermum* alliance (it is equivalent to the *Calothamnus* infra-alliance of Briggs & Johnson, 1979).

Combining the karyological and morphological evidence, we conclude that there have been quite a number of descending dysploid series, including two in the *Leptospermum* alliance, one or two in *Thryptomene,* and several in various genera of the *Chamelaucium* group as narrowly interpreted (i.e., the Chamelauciinae or "Euchamaelaucieae" in Bentham's sense). They appear to be associated with the mode of life of these habitally and reproductively very specialized genera. As stated, dysploidy gives no cladistic support to the concept of an integrated Chamelaucioideae in the traditional sense upheld by Schmid.

Schmid (1980) refers also to pollen morphology as differing markedly from that of the rest of the family, citing Pike (1956). In reading Pike's paper, one should refer to tables and text as well as illustrations, since these are not always consistent; but it is clear from her findings and even more so from the pollen we have ourselves examined in the *Chamelaucium* alliance and elsewhere in the family, that this also is not cladistically sustainable. We take it that a more or less oblate syncolporate or parasyncolporate condition is fundamental in the Myrtacean line, as a derived condition from the more or less prolate and apocolporate grains basic to the Myrtales (3.1.2).

Within the Myrtaceae, apocolporate (including "brevicolpate" and "longicolpate") grains are seen as a secondary development, and occur in genera scattered through several alliances. Certainly, such conditions, and particularly brevicolpate grains, are frequent in the *Chamelaucium* suballiance. But they are neither universal in the suballiance nor confined to it; they appear also in some members of the "*Baeckea* suballiance," and we have found series within some genera from syncolpate to brevicolpate. Again, the condition is not fundamental to the "chamelaucioids," except perhaps in the "Chamelauciinae." It must be seen as homoplastic within the group and is therefore irrelevant to its phylogenetic recognition.

As with the embryo character discussed above, the consistent absence of Myrtaceous trichomes from all vegetative parts also sharply distinguishes the whole of our *Chamelaucium* alliance from the *Leptospermum* alliance.

Phylogenetic analysis (Fig. 9) would place the origin of the "*Baeckea* suballiance," and that of such genera as *Calytrix* and its allies, alongside the very base of the *Leptospermum* alliance.

The above spells out part of our rationale. The remainder requires additional internal consideration of the *Chamelaucium* alliance.

4.3.2 Phylogeny within the Chamelaucium *alliance.* Our conclusions on probable phylogeny within the *Chamelaucium* alliance are summarized in Figure 10. This is not a rigorous numerical phylogram, but expresses the same mode of thought. It is largely based on our own observations, although naturally many of these have been suggested by statements in the literature (e.g., Bentham, 1867; Green, 1979, 1980, 1983; Rye, 1979; Schmid, 1980); and unpublished information from workers on particular groups, especially from J. W. Green.

Figure 10 does not attempt to specify order of branching at all points but, although additional characters exist that should be taken into account, we believe that the main phylogenetic groups shown are realistic. The chief characters used are indicated on the diagram or are mostly self-explanatory. The terms *dichasium, botryoid,*

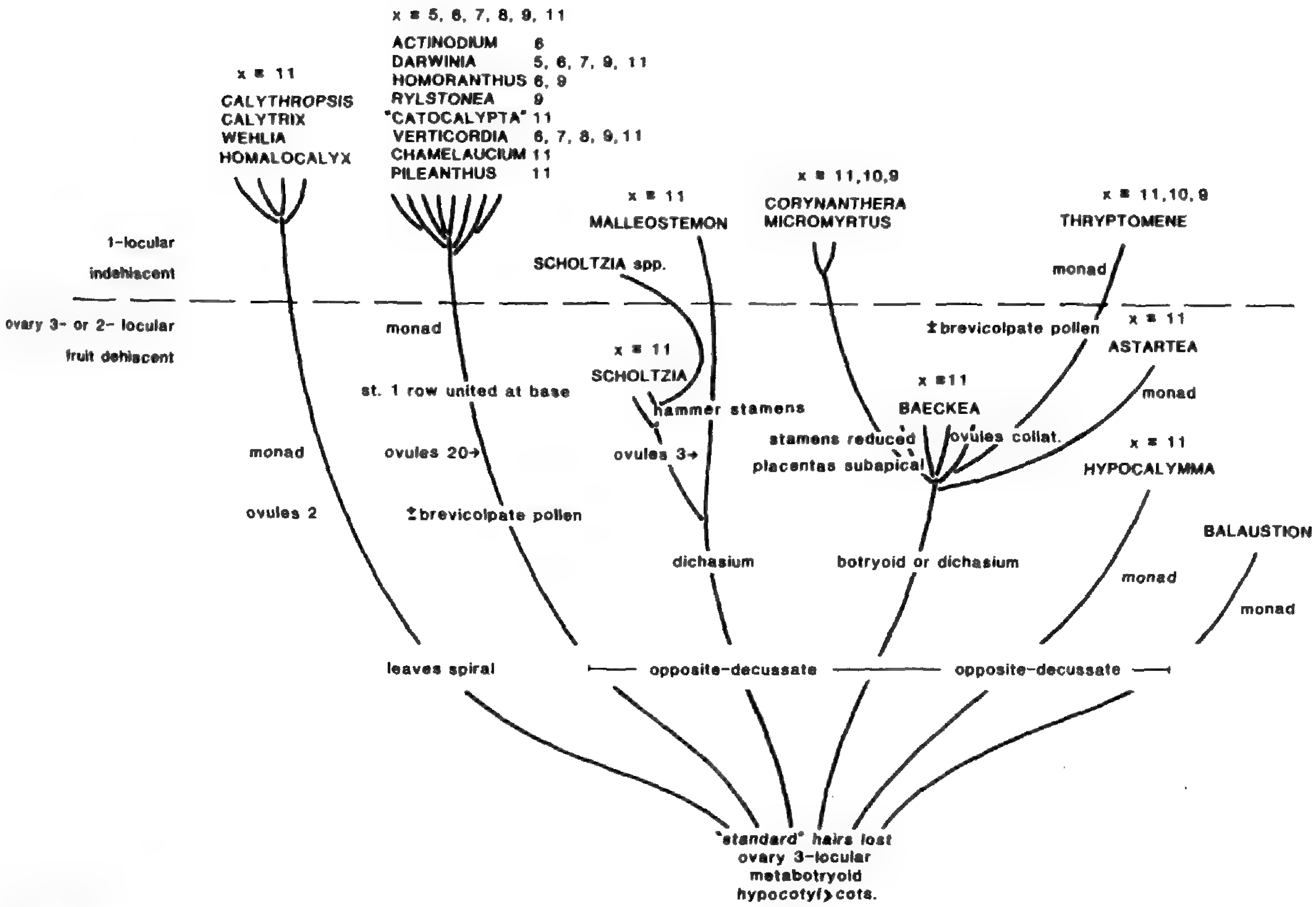

FIGURE 10. Sketch phylogram of relationships in *Chamelaucium* alliance (not a rigorous numerical phylogram). Five or six lineages are considered to have separately acquired the unilocular-ovary condition, the definitive feature of the traditional "Chamelaucioideae." Chromosome numbers are shown, and some of the more important features marking particular phylads. st. = stamens; cots. = cotyledons; collat. = collateral; monad refers to inflorescences. [*Baeckea* is almost certainly a paraphyletic group, as is the "*Baeckea* suballiance" (below the transverse broken line), whilst the now abandoned "*Chamelaucium* suballiance" above the line is highly polyphyletic.]

and *monad* are used in the sense of Briggs and Johnson (1979), where the structure of Myrtaceous inflorescences and the significance of their trends are treated in some detail.

"Hammer stamens" refers to a specialized shape in which the filaments are strongly bent at the tips and adnate to the connective of the anthers; in the extreme condition the anthers open by pores and may have more or less confluent loculi. Such stamens were mentioned by Bentham (1867) as occurring in part of *Scholtzia,* and J. W. Green (pers. comm.) pointed out to us that they are found in several species formerly referred to *Micromyrtus,* most of which are now placed in the new genus *Malleostemon* (Green, 1983).

We have closely examined most of the species of *Thryptomene, Micromyrtus,* and *Malleostemon,* as well as the single species of *Corynanthera* and some species of *Scholtzia.* Publications on some of these by Green (1979, 1980, 1983) have been most helpful. We confirm his observations, which are particularly useful in interpretation of the gynoecium. As yet, we have sampled the other genera much less intensively, and will need to pursue comparative studies. Some of the genera need redefinition. We have taken *Baeckea* in a broad sense, which will not hold. *Baeckea* sensu lato includes a variety of divergent lines with respect to androecial and gynoecial modification, and several states of inflorescence reduction, as well as some diversity in pollen type. We perceive *Micromyrtus* and *Corynanthera* as arising from a single line; this is not to deny the generic status (clade-grade leaving a paraphyletic residue) of *Corynanthera,* which is characterized by its highly modified trilocular anthers (Green, 1979). These genera are evidently most closely related phylogenetically to a different portion of *Baeckea* from those portions to which *Thryptomene* and *Astartea* are respectively allied. Other groups within *Baeckea* may be equally worthy of distinction (Briggs & Johnson, 1979; M. E. Trudgeon, pers. comm.)

and indeed were distinguished by the discerning nineteenth century botanist Schauer (1843). The formal taxonomy of the Australian Myrtaceae, in particular, has been largely fixed in the mold established by Bentham (1867) over a century ago. Subsequent authors have mostly simply used Bentham's classification and ignored his sage remarks; these indicate how tentative his decisions were in fact, as seen by himself. Bentham would probably do something quite different, in many cases, on today's evidence.

We also tentatively recognize "*Catocalypta*" as a distinct entity from *Verticordia,* though there are remarkable parallel developments in these, and some species may not be satisfactorily placed in either group.

Homoplasy must indeed be very widespread within the alliance. Even such a distinctive feature as the hammer stamens probably arose more than once, since it occurs only in part of *Scholtzia* and also in the two new genera, which would appear to have arisen near the base of *Scholtzia.* Doubtless the explanation lies in the prospectively adaptive previous condition of the anthers and in parallel evolution of pollination syndromes.

Figure 10 shows six separate lines crossing the boundary between the so-called Baeckeinae and the traditional "Chamelaucioideae." This stage is marked by the reduction of the ovary to a unilocular condition, developing into an indehiscent fruit. Each of these postulated phylads is supported not only by the characters shown on the diagram but by overall resemblance, much of which has been noted by previous authors. We have little doubt of the general affinities shown, although more detail will doubtless emerge.

Thus the so-called subfamily "Chamelaucioideae" is a highly polyphyletic grade taxon resting on one limited character syndrome. As such, it is not only unacceptable as a subfamily but we would not now uphold our equivalently circumscribed *Chamelaucium* suballiance (as distinct from our more inclusive *Chamelaucium* alliance); the situation calls for a new classification. Further comments are given below (4.4).

4.4 SYSTEMATIC IMPLICATIONS IN MYRTACEAE

The implications of this analysis for formal classification will be largely evident from Figures 9 and 10. More detailed study, down to lower taxonomic levels, is being pursued.

Psiloxylaceae and Heteropyxidaceae are recognized as families for reasons already advanced. Within the Myrtaceae proper, phytogeography and possible phytogeographic history have been briefly discussed (4.2.2; Johnson & Briggs, 1981a). They should be considered in relation to the suggested phylogeny.

It is clear from the analysis that our earlier acceptance of two of the traditional three subfamilies must be abandoned. We hinted at this at the time (Briggs & Johnson, 1979), but subsequent study of a wider range of features demonstrates that the *Acmena* group must have a separate origin from the remainder of the traditional Myrtoideae, and that the *Arillastrum* and *Eucalyptus* groups are likewise remote from other members of the traditional Leptospermoideae. These subfamilies have been recognized on the features of succulent and indehiscent versus dry and dehiscent fruits. Supposedly supporting characters show a correlation with these, as might indeed be expected since they often characterize subgroups that are numerous in genera and/or species. Statistics of numerical predominance, such as have been accumulated by Schmid (1980), may indeed show correlations with phylogeny, but they are not a logical basis for deducing it or for a systematic arrangement that attempts to reflect phylogeny. This is obvious from a consideration of the evolutionary process. In fact, the correlations in all these cases are imperfect, as again we should expect.

A fuller rationale for a revised system within the Myrtaceae must await further investigation and will have to be presented elsewhere, but the characters indicated in Figure 9 are among the most significant, although many of them have not been used in formal taxonomy of Myrtaceae up to the present. The internodes on the phylogram are short in the lower parts of the tree; the implications of such a tree form are discussed under the Myrtales (3.2.6).

Consequently, clear-cut sister-group hypotheses cannot be put forward with great confidence. Such situations should not be in the least surprising, and indeed seem to show up when many large groups are investigated phylogenetically. Polhill et al. (1981) give an excellent discussion of phenomena of this kind in the large and complex legume family (Fabaceae sensu lato). They are very evident in Proteaceae (Johnson & Briggs, 1975).

Before discussion of the overall taxonomy, few comments on the groups are necessary. We shall work from left to right across Figure 9.

However it may be ranked, the group here called Myrtoideae sensu stricto does seem to hold together, though we would like to analyze it more critically and a great deal of detailed revision and gathering of more morphological information are needed. Some of this is under way in North and South America and elsewhere. The Myrtoideae branch is shown as coming off among groups traditionally treated as Leptospermoideae. The three suballiances included here can be maintained for the present subject to the reservations we expressed in 1979, particularly in regard to the *Cryptorhiza* alliance. In the *Myrtus* alliance, which seems generally to be well defined, the Malesian and New Caledonian genus *Xanthomyrtus* shows some rather anomalous wood-anatomical characters (Ingle & Dadswell, 1953) and its pollen is also rather unusual (Pike, 1956). Nevertheless, it seems to conform in other respects with the alliance and we can, at present, see no other place where it might belong. Scott (1978) has united *Fenzlia* and *Myrtella*, but these seem clearly distinct, though closely related. Retention of both genera may require nomenclatural conservation or a new name for *Fenzlia*. We have not accepted all his conclusions, but Scott (1979) is certainly correct in pointing out that *Uromyrtus* occurs on the Australian mainland, for which it was not recorded in our earlier paper. Byrnes (1982) has since indicated that another Australian species is referable to *Uromyrtus*.

The phytogeographically enigmatic New Caledonian *Stereocaryum* shows a peculiar condition in that its tetramerous flowers, when open, show four apparently well-marked antesepalous bundles of numerous stamens. In fact, this appearance is caused by splitting of the hypanthium far below the intersepaline sinuses, thus mechanically dividing the formerly continuous "multiseriate" ring of stamens into four false bundles. Since the appearance of these conspicuous flowers is so like that of taxa with true fascicles, as in *Arillastrum* or *Eudesmia* spp., one suspects that the condition is an adaptive convergence. *Osbornia* is discussed below.

The *Chamelaucium* alliance appears to have its origins at the base of the perhaps paraphyletic *Leptospermum* group (see below) but is itself well marked. There seems little evidence to support the suggestion of Dawson (1978b) that *Baeckea* is closely allied to *Xanthostemon* (*Metrosideros* alliance); convergence in one or two features seems more likely. As stated above (4.3.2) we do not now uphold the two suballiances within the *Chamelaucium* alliance, and a different break-up will have to be devised in line with the pattern shown in Figure 10. Polyphyletic grade taxa are not tolerable in any attempt at rational systematics.

The *Leptospermum* alliance itself shows no common stalk separate from the *Chamelaucium* alliance, and we hope to give it further attention with a view to defining appropriate suprageneric taxa. It probably does not break up as clearly as we accepted in 1979 into the *Leptospermum* and *Beaufortia* suballiances (the latter equivalent to "*Calothamnus* suballiance") (Johnson & Briggs, 1983b).

The *Backhousia* group needs no comment beyond our remarks of 1979, but the position of the mangrove genus *Osbornia* is somewhat problematical. Figure 9 shows it as clearly on the same stem as the *Backhousia* alliance, in contrast to our earlier suggested placement in an alliance in the Myrtoideae sensu lato. Nevertheless, *Osbornia* differs from *Backhousia* and its ally *Choricarpia* in many respects, as pointed out also by Wilson (1981). Schmid (1980) discusses the position of *Osbornia* in terms of Myrtoideae and Leptospermoideae in their traditional senses, which is now irrelevant, but he is probably correct in disagreeing with our tentative placement in 1979. Its association with the *Backhousia* group is not as definitely established as the phylogram suggests, for some alternative trees, only slightly longer, tend to place it elsewhere. Its position is something of a mystery, but it is certainly very distinct.

The *Metrosideros* alliance comes out as something of a basal group, rather than as a well-defined sister-group to others in the family. Very useful studies by Dawson (1970b, 1970c, 1972a, 1972b, 1972c, 1972d, 1975a, 1975b, 1976, 1977, 1978b) contribute to our knowledge of it, but that author does not present his results in the context of phylogenetic analysis. Wilson (1981) and also Wilson and Waterhouse (1982) have studied some groups intensively, and Wilson is continuing this work. As with all basal groups, classification by Hennigian principles is difficult and practically unusable, so one may need to compromise rather than insist on holophylesis as a necessary condition for taxonomic entities. This applies both internally and with regard to better-defined groups that can be seen, in a sense, as arising from within the *Metrosideros* basal complex. This would imply that the *Metrosideros* alliance is a paraphyletic group in the sense of Ashlock (1971), though not necessarily in that of Nelson (1971).

The suballiances within the *Metrosideros* group do need reconsideration, especially in the light of several new genera from the northeast Australian rainforests, under study by Wilson and Hyland (pers. comm.).

We still consider it likely that *Basisperma* belongs phylogenetically with members of the *Kania* suballiance. Wilson and Waterhouse (1982) refer *Basisperma* to the affinity of *Ristantia*, a genus of very different facies that has been associated with the *Lophostemon* suballiance sensu lato but is rather anomalous there. In the light of other character-states, we suspect that the single large seed and placentation are convergent in these otherwise dissimilar genera. Single large seeds seem to be adaptations to vertebrate dispersal in tropical forest in diverse lines of the Myrtaceae. Wilson (1982) asserts simply that our placement of *Basisperma* with *Kania* and its allies "cannot be justified on morphological and anatomical grounds," but offers no further evidence.

We indicated in 1979 that the *Lophostemon* suballiance was unsatisfactory and tentative. Wilson and Waterhouse (1982) make this clearer, and possibly several suballiances should be recognized. Our analysis shows *Kjellbergiodendron, Whiteodendron,* and *Lindsayomyrtus* as excluded from the *Metrosideros* group, where they were formerly tentatively placed in the *Lophostemon* suballiance. They show relationships with the *Acmena* alliance, which is itself well defined. These three genera are not very close to each other and represent tag-ends that are barely surviving as phylads. The apparent former occurrence of something very like *Kjellbergiodendron* in southeastern Australia has been mentioned (4.2.2; McWhae, 1957). Schmid (1980) discusses *Kjellbergiodendron* in relation to the traditional subfamilies, and again this is scarcely relevant. *Kjellbergiodendron* would not fit in the Myrtoideae sensu stricto in inflorescence, phyllotaxis, indumentum, or floral details, including the staminal fascicles.

Schmid (1980) states that fasciculate stamens occur in the Myrtoideae, citing *Syzygium* pro parte (*Pareugenia*) but, as he says, those species have many fascicles showing no definite relation to the petals; this seems to be a secondary condition. In any case, *Syzygium* is a member of the *Acmena* alliance, which we show as somewhat more closely related phyletically to *Kjellbergiodendron* than to Myrtoideae proper. The false fascicles of *Stereocaryum*, which does fit in the Myrtoideae, have been mentioned above.

Schmid points out that the staminal fascicles of *Kjellbergiodendron* are "quite different" from those of *Whiteodendron*. They are indeed consistently different, but no more so than within groups of the *Lophostemon* alliance, for example. We do not claim that *Kjellbergiodendron* and *Whiteodendron* are as close as suggested by van Steenis (1952); quite a lot of their resemblances are probably either symplesiomorphic or habital parallelism. But Schmid's statement that "palynologically *Whiteodendron* is clearly leptospermoid," in contrast to the supposedly "myrtoid" pollen of *Kjellbergiodendron*, cannot be sustained in those terms. The syncolporate pollen condition shown in *Kjellbergiodendron* is probably ancestral within the family (4.2.1) and is seen in some members of almost all alliances. Apocolporate conditions, as in *Whiteodendron*, must have been multiply derived and also turn up in various groups. Again, use of weight of numbers or "prevailing conditions" as phylogenetic or taxonomic evidence is inconsistent with the rationale of phylogenetic taxonomy.

The *Acmena* alliance needs further attention at the generic level. *Waterhousea* (No. 123 "genus nov." of Briggs & Johnson, 1979), the distinctiveness of which was pointed out to us by J. T. Waterhouse (pers. comm.), has since been described by Hyland (1983). It is not monotypic, as we had thought. *Syzygium* itself may well include two or three rather distinct lines, though we agree that the forms with reduced flowers, included in *Syzygium* by Schmid (1972b), are not likely as such to have supportable claims for generic separation.

The phylogenetic picture and the mass of evidence, including wood-anatomical characters as well as the unitegmic ovular condition in *Syzygium* (Tobe & Raven, 1983a), argue very strongly against Schmid's continued association of "*Eugenia* sensu stricto and *Syzygium* sensu lato" as "more closely than distantly related in Myrtaceae." Schmid (1980) himself justifies this indefinite statement with the words "my conservatism still demands [it]." We cannot see how conservatism weighs against evidence.

Finally, we come to what we have previously called the *Eucalyptopsis* and *Eucalyptus* alliances. Further study and better material have convinced us that *Arillastrum* is not, as we previously thought (Pryor & Johnson, 1971, 1981; Johnson, 1972, 1976; Briggs & Johnson, 1979; Johnson & Briggs, 1981a) a member of the *Angophora* suballiance of the "*Eucalyptus* alliance." Rather it agrees in many ways, namely in leaf venation and hair-type as well as in flower, fruit, and seed features, with the other three monotypic genera previously referred to the *Eucalyptopsis* "alliance" (Johnson & Briggs, 1983b). Nonetheless, *Arillastrum* and its allies are now showing a fairly definite relationship to the three suballiances that constitute "the eucalypts," i.e., *Eucalyptus* of botanical tradition together with *Angophora,* and may be best included with them as a fourth suballiance (eventually subtribe) (Johnson & Blaxell, in prep.).

These eucalypt genera have been discussed elsewhere by one or both of us in the works cited above. We here reiterate that they fall into three groups, each showing considerable coherence but with some doubt as to the sequence of divergence of the groups themselves.

Three alternatives are shown in the phylogram (Fig. 9). The shorter of these on our character scoring shows a primary divergence that associates two of the "eucalypt" groups with the *Arillastrum* group on the one hand, while the *Eucalyptus* "suballiance" (consisting of *Eucalyptus* sensu stricto, "*Idiogenes,*" and "*Gaubaea*") is its sister-group. If this is correct then the "eucalypts" (if one excludes the *Arillastrum* group from that category) are polyphyletic. This may indeed be the case and the hypothesis calls for testing. On the other hand, the other two alternatives (one of which also implies polyphylesis for the "eucalypts") are longer by only one step. We may have given too much weight or the wrong polarity, at least locally in this portion of the phylogram, to the characters of ovular condition (character 54) and/or presence of crystalliferous layer in the testa (61). If these were altered, the relative lengths would change and a further alternative hypothesis would be favored in which the *Arillastrum* group separates first from the remainder, from which the *Eucalyptus* group is the next to diverge. On such variant scoring additional slightly longer trees exist, including those with the topologies shown in Figure 9. Two of the three distinct subgenera of the psyllid *Glycaspis* (see below) are respectively specific to the *Symphyomyrtus* and *Eucalyptus* groups, but this genus is not known to occur on members of the *Angophora* or *Arillastrum* groups. This might favor the alternative that associates the *Symphyomyrtus* and *Eucalyptus* groups, but one must bear in mind that the third subgenus of *Glycaspis* occurs on a variety of Myrtaceous hosts taxonomically remote from the "eucalypts" (K. Moore, pers. comm.; K. Taylor, pers. comm.).

The ten or eleven genera (segregating the distinctive section *Sebaria* from *Symphyomyrtus*; and see under "*Gaubaea,*" below) that we now recognize in principle among the "eucalypts" will be formally established elsewhere. They are more clearly distinguished than some traditional genera in the Myrtaceae, and indeed in other families, that no one challenges. Only in one case do we believe that there may be some doubt as to assignment to a "suballiance." The two species that we have placed in "*Gaubaea,*" endemic in Queensland, definitely do not fit in the *Angophora* suballiance of the *Symphyomyrtus* suballiance. They are very different from *Eudesmia,* despite their association with that group by Carr and Carr (1968). However, we have placed "*Gaubaea*" (which should perhaps constitute two genera) in the *Eucalyptus* suballiance chiefly because its species show less discrepancy there than elsewhere and because anatomy, ovules, and seeds have some features of that group. Supporting evidence from host-group-specific insects, especially *Glycaspis* of the Psyllidae (Hemiptera), such as exists for members of all other eucalypt genera, is as yet lacking for "*Gaubaea*" (K. Moore, pers. comm.) although a less host-specific psyllid group is recorded from *Symphyomyrtus,* "*Gaubaea,*" *Callistemon, Melaleuca,* and *Leptospermum* (K. Taylor, pers. comm.). Nor is there chemical evidence from flavonoids (W. E. Hillis, pers. comm.) to give definite support or otherwise to its suggested position. The terpenoid essential oils also remain to be studied (E. Lassak, pers. comm.). On the other hand, both insect associations (Moore, pers. comm.) and chemical evidence (Hillis, pers. comm.) do support a closer relationship of "*Idiogenes*" with *Eucalyptus* sensu stricto than with any other eucalypt genus.

4.4.1 The failure of the subfamilies. Since both the traditional three subfamilies and our later two subfamily divisions in Myrtaceae are untenable, what can be done about infrafamilial classification? We hope to formalize a system of tribes and subtribes, more or less equivalent to our informal scheme of alliances and suballiances. Such a scheme will have to differ from that put forward in 1979 in several ways upon which we are not yet ready to decide. By the very nature of phylogenetic divergence, and the persistence of various tag-ends, as well as by the ever-remaining uncertainties, no such system can be unequivocal. Nature does not comply with our classificatory desires.

It is doubtful that any new taxa at the level of subfamily will be satisfactory, and we strongly advocate the abandonment of the subfamilies hitherto recognized on the grounds that continued reference to them is misleading in setting a phylogenetic context and is phytogeographically irrelevant.

5. Conclusion

Phylogenetic analysis of the 19 taxa and 77 binary-coded characters used for the study of Myrtales reveals insufficiency and inappropriateness in currently-used techniques.

The CLAX approach, though designed to diminish such problems, does not yield a unique phylogenetic hypothesis in which we can have confidence. This is indeed to be expected. It does point up regions of comparative certainty and uncertainty and produces some trees upon which reasonable alternative scenarios (complex hypotheses in semi-narrative form) can be built. These scenarios provide a basis for more detailed phytogeographic and adaptational hypotheses, which are not carried far here.

Parallelism and convergence must have been rife at all levels (and consequently all periods) in the history of Myrtales and Myrtaceae, and a few possible apparent evolutionary reversals (not necessarily genetic reversions) have been brought to attention.

Formal taxonomic treatment is theoretically compatible with divergent phylogenetic tree structure, as indeed it is with *any* directed tree structure equivalent to an ultrametric (Rohlf & Sokal, 1981). In practice, the uncertainties of the tree structure, as well as the number of branching levels, render a complete formal hierarchic correspondence with phylogeny quite impracticable. Compromises are unavoidable, though they should not involve recognition of polyphyletic grades. The most notable such case in this study is the formerly recognized "subfamily Chamelaucioideae" of the Myrtaceae, but there are a number of others.

We agree with the majority of contributors to this symposium as to the constitution of the Myrtales and agree on many of the trends and lines of change and divergence. Efforts to resolve uncertainties have especially concerned Melastomataceae, Memecylaceae, Crypteroniaceae, *Alzatea*, and *Rhynchocalyx*; they have been discussed in the body of this paper.

We conclude that Myrtaceae form a coherent and holophyletic group, and that Heteropyxidaceae and Psiloxylaceae diverged from the ancestral lineage of Myrtaceae at an early stage. These relict groups can be reasonably treated as families. The family Myrtaceae sensu stricto is unique in the Myrtales in having its greatest fundamental diversity in the Australasian region.

Infrafamilial phylogeny in the Myrtaceae is becoming clearer, but needs more detailed study. As seen here, it is decidedly inconsistent with recognition of the two traditional subfamilies Myrtoideae and Leptospermoideae, not to mention Chamelaucioideae. A formal system of tribes and subtribes may be desirable but will be difficult to apply with both certainty and consistency. For the time being we recommend use of our informal "alliances" and "suballiances" (Briggs & Johnson, 1979; Johnson & Briggs, 1983b), subject to the caveats and modifications in section 4.4.

As phylogenetic and indeed general evolutionary understanding improves, change in formal taxonomy is inevitable. The present analysis and proposals will not be the last word, probably even on our own part.

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ALZATEACEAE, A NEW FAMILY OF MYRTALES IN THE AMERICAN TROPICS[1]

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ABSTRACT

The suggested affinities of the New World tropical genus *Alzatea* have included eight families in five orders since its discovery in the eighteenth century. Until recently, knowledge of the genus has been superficial, primarily limited to macromorphological features. Now evidence assembled from recently published and current research in anatomy, embryology, morphology, palynology, and cladistics of *Alzatea* and closely related genera allows a more accurate assessment of its relationships. Presence of internal phloem and vestured pitting place the genus in the order Myrtales, while stem and nodal anatomy suggest no close affinities to any one family of the order. Embryologically, *Alzatea* is unique in Myrtales in having a bisporic *Allium*-type embryo sac, and shares only with the related genus *Rhynchocalyx* micropylar development by the inner integument. Pollen features are very generalized, relegating the genus to an ancestral position with respect to the pollen of close associates. Parietal placentation and transeptal vascular supply of the ovary and anatomically simple seed relate *Alzatea* to *Rhynchocalyx* (Rhynchocalycaceae) and genera of the Crypteroniaceae sensu stricto, *Crypteronia, Axinandra,* and *Dactylocladus. Alzatea* is most similar to *Rhynchocalyx,* sharing 27 of 43 selected attributes, followed by *Crypteronia* with which it shares 18 of 43 listed features. Differences between *Alzatea* and *Rhynchocalyx* are deemed sufficient to justify establishment of the family **Alzateaceae.** Plants of *Alzatea* with large, sessile leaves from Central America are recognized as *A. verticillata* subsp. *amplifolia* S. A. Graham, subsp. nov.

Alzatea is an enigmatic genus of Central and South America whose suggested affinities, since its discovery in the eighteenth century, have included eight families in five orders. The genus is represented by the single species, *Alzatea verticillata* Ruiz & Pavón. It is a small tree of tropical cloud forests, distinguished by broad, oblong, coriaceous leaves and multi-flowered compound inflorescences of small, apetalous, leathery flowers. These produce compressed, conspicuously veined, bilocular capsules with many thin, winged seeds. A history of the systematic placement of *Alzatea* has been presented by Lourteig (1965), who succinctly reflected that most studies on the genus were as much justification for its exclusion from particular families as arguments for certainty of relationships. The past several years have seen no diminution in shuffling of *Alzatea* from one family to another (Table 1).

Most recently, there has been an increased interest in the genus stimulated by the collaborative reassessment of the Myrtales, the order to which *Alzatea* most certainly belongs. New observations and data of diverse types for *Alzatea* and related families now allow an evaluation of the phylogenetic and taxonomic position of the genus in the Dicotyledoneae in a more complete way than was possible previously. The evidence for *Alzatea*'s position as a monotypic family of the order Myrtales is assembled from personal observations and the extensive studies of several specialists, with much of the information generated since the Myrtales symposium of the XIII Botanical Congress in 1981. This paper summarizes the most pertinent contributions of macromorphology, palynology, embryology, anatomy, and cladistics as the basis for recognizing the new family Alzateaceae.

CHARACTERIZATION OF *ALZATEA*

Macromorphology. Hemi-epiphytic shrubs or small trees, 2–20 m tall, with stout, gray, roughened trunks or sometimes trunks slender and reaching the forest upper story supported by adjacent trees; branches glabrous, opposite or

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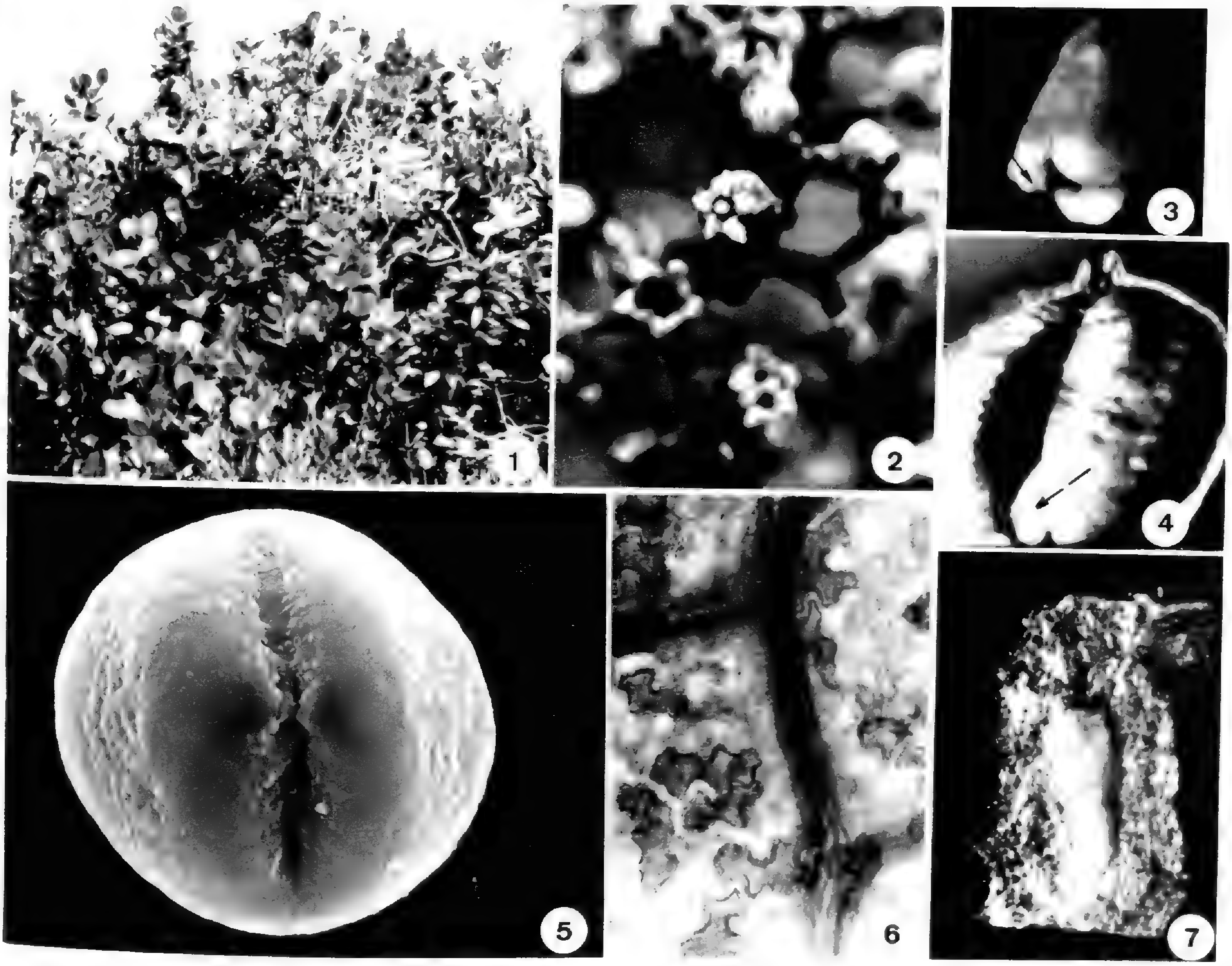
TABLE 1. Systematic placement of *Alzatea* by selected authors.

Year	Author	Classification
1794	Ruiz & Pavón	Santalaceae (Between genera of)
1825	Candolle, A. P. de	Celastraceae
1826	Blume	Celastraceae, near
1845	Planchon	Lythraceae
1862	Bentham & Hooker	Celastraceae
1868	Candolle, A. L. P. P. de	Crypteroniaceae
1872	Miers	Rhamnaceae
1892	Loesener	Celastraceae, doubtfully
1911	Hallier	Lythraceae sensu lato
1918	Hallier	Melastomataceae sensu lato
1942	Loesener	Flacourtiaceae
1955	Willis	Celastraceae
1956	MacBride	Rhamnaceae (or Clusiaceae or Icacinaceae)
1965	Lourteig	Lythraceae
1966	Airy Shaw	Lythraceae
1967	Hutchinson	Flacourtiaceae
1975	van Beusekom-Osinga & van Beusekom	Crypteroniaceae
1981	Cronquist	Lythraceae, questionably

verticillate, distinctively purple-red, peeling, becoming red-brown with age; stems of the inflorescence distinctly 4-angled to narrowly winged, the young branches scarcely 4-angled, the mature branches round in cross section; nodes enlarged, especially knobby when branches are verticillate; leaf scars half-round to nearly circular, the base slightly raised, the bundles forming a crescent, U-shaped, or nearly closed-circular scar. *Leaves* mostly clustered at the ends of the branches, opposite, less often verticillate, simple, entire, stipulate, the stipules axillary, 2 to a few in the axils at the base of the petiole, the stem wings of the inflorescence also extended at the nodes into stipule-like projections; petioles none or short, thick, deep purple-red, to 13 mm long; blades oblong-obovate, elliptical, or oblong-oval, thick, leathery, lustrous above, 50–145 mm long, 25–100 mm wide, with blades of terminal leaves smallest and mostly about 70 mm long, 40 mm wide, the bases variable, attenuate to acute or rounding, commonly acute, the apices rounding, occasionally retuse, the veination brochidodromous, the secondary vein pairs 16–22, parallel, oriented at 45° to the prominent midvein. *Inflorescences* anthotelic, basically paniculate (sensu Briggs & Johnson, 1979, traditionally termed cymose) with each axis terminating in a flower, axillary at the ends of branches, 10–30 flowered, the pedicels 1.5–2 mm long, lacking bracteoles (prophylls), articulated at the base, the lateral flowers of a cyme subtended at the base by small fugaceous fertile bracts, i.e., the bracts themselves subtending buds. *Flowers* actinomorphic, 5(–6)-merous, apetalous, bisexual, hemi-epigynous; floral tube leathery, green to yellow, conical in bud, open-campanulate at anthesis, 4–6 mm long, 4–7 mm wide, the thick, persistent, valvate lobes 3 mm long, extending nearly to the base of the floral tube, the interior surface of the lobes irregularly thickened and fleshy; nectary-disc 1 mm wide, lobed, extending from the ovary to the sinuses of the calyx lobes. *Stamens* 5, situated in the floral tube at the sinuses of the lobes, outside the nectary, alternating with the lobes; filaments green, stout, short, as long as the anthers; anthers dorsifixed, introrse, the connective broadly expanded, heart-shaped, pink with white edges, fleshy, at anthesis held at right angles to the filament with the distal apiculate apex extending out of the calyx between the lobes, thus simulating petals, the bisporangia positioned horizontally along the broad terminal end of the anther on each half of the connective, dehiscing longitudinally. *Gynoecium* slightly bilaterally flattened, with a capitate stigma and stout, short style 1 mm long; ovary bicarpellate, bilocular, placentation parietal, the placentae terminating shortly below the style on the inner ovary wall and septum; septum divided into 2 half-septa, the lower fourth provided with a circular opening; ovules horizontally imbricate in staggered



FIGURES 1–7. *Alzatea verticillata.*—1. Short-shrub (2–3 m) habit of *A. verticillata* subsp. *amplifolia, Knapp & Kress 4336,* on Cerro Tûte, Panama. Leafy branch in the lower right foreground belongs to the vegetatively similar *Clusia.*—2. Closeup of flower at anthesis displaying five petal-like fleshy anthers. Actual flower diameter, 5 mm.—3. Single stamen; line of microsporangial dehiscence indicated by arrow. Actual length, 1.75 mm.—4. Interior view of one valve of the bivalved capsule, with septal hole apparent at the base of the septum (arrow) and style remnants visible above the septum. Actual length, 8 mm.—5. Pollen of *A. verticillata* subsp. *verticillata, Woytkowski 8331* (F). Actual diameter, 22 µm.—6. Branched sclereids of the leaf palisade tissue. Actual lengths, 92–155 µm.—7. Fertile seed with central embryo. Actual length, 2 mm.

vertical rows. *Fruit* an indurated, loculicidally dehiscent, reddish brown capsule, obcordate, 2-valved, compressed-flattened, to 8 mm long, 9 mm wide, with raised horizontal venation extending outward from the central septal vein on each side, subtended by the persistent, erect to spreading calyx lobes; remnants of the style persistent at the apex of each valve above the central vein. Seeds numerous, crowded in the capsule, ca. 20–30 per locule, thin, flat, the sterile seeds reddish brown with roughened surface, the fertile seeds yellow-brown, obliquely oblong to lunate, 2–3 mm long, 1–1.5 mm wide, the embryo central in the fertile seed, straight, encircled by the membranous wing, the cotyledons oblong to slightly spathulate, the stalk conical, directed toward the micropyle; endosperm not apparent. Figures 1–7; see also Dahlgren and Thorne (1984, Fig. 11), for general habit and floral and fruit morphology.

Ovary morphology and anatomy. Ovary bicarpellate, bilocular, and bilateral, at anthesis 3 mm long, 1 mm wide, with suggestion of venation apparent on outer walls, particularly in the center of each slightly compressed side. Venation consisting of a dorsal and ventral supply; dorsal bundle one per carpel, with a few short branches only and independent of the ventral supply; ventral bundles of opposing carpels distinct, positioned laterally in the septum, two on each side of center in each half septum; ventral bundle branches traveling ± horizontally through the

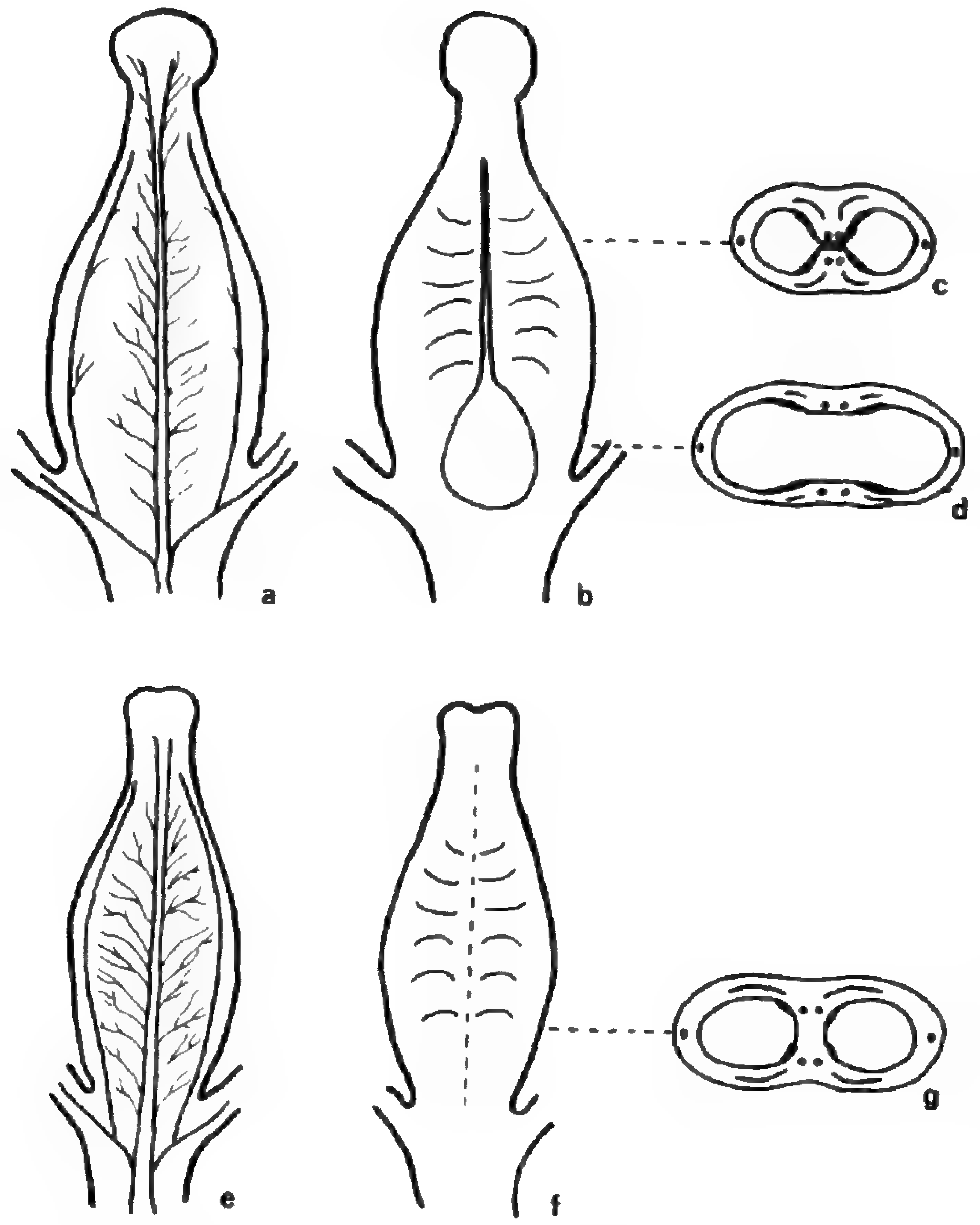


FIGURE 8. a–d. Diagrammatic ovary of *Alzatea verticillata.*—a. Loculicidal plane, with paired ventrals flanked by single dorsal veins.—b. Septal plane, with split septum and basal septal hole.—c. Cross-section at mid to upper ovary level; paired ventral veins and dorsals represented by dark circles, placental regions accentuated to indicate position on inner carpel walls.—d. Cross-section at level of basal opening. e–g. Diagrammatic ovary of *Rhynchocalyx lawsonioides.*—e. Loculicidal plane.—f. Septal plane with complete septum.—g. Cross-section; paired ventral veins and dorsals represented by dark circles, placental regions accentuated to indicate position on inner carpel walls.

septum to supply the ovules and carpel walls. Septum incomplete at the base due to the presence of a central opening in the basal fourth of the septum, septal margins meeting above the opening, but free, not fused at anthesis. Placental region spreading laterally on the carpellary walls, broad, to 1.5 mm wide, terminating ca. 1 mm from the apex of the ovary. Ovules stacked horizontally in vertically staggered rows and superposed in the locules. Figure 8a–d.

The capsule of *Alzatea* has been described elsewhere as unilocular with a false septum developing from the walls of the capsule inward as the fruit matures (Lourteig, 1965). The half septa with basal opening are, in fact, present in the young ovary, their free margins parallel and touching. They separate with dehiscence and subsequent opening of the capsule.

Seed morphology. Seeds bilaterally compressed, horizontally layered in the capsule. Fertile seeds yellowish brown when dry, irregularly rectangular to lunate, frequently with a tail at the chalazal end, 2–3 mm long, 1–1.5 mm wide; embryo central in the seed and winged all around, straight with plane, oblong to spathulate cotyledons, the stalk conical, 0.25–0.33 the length of the embryo, the raphe bundle ending at the chalaza. Outer integument (testa) two-layered, the cells reticulate-scalariform, the outermost layer of cells elongate with thin, undulating walls, composing most of the seed wing, the inner layer crushed. Inner integument (tegmen) two-layered, both layers crushed at seed maturity. Sterile seed (ca. ⅓ of total seed) reddish brown when dry, primarily crescent-shaped with curved tail, 2–3 mm long, 1–1.5 mm wide, 0.5–1 mm thick on the convex side; raphe bundle on concave side, ending at the chalaza. Testa of densely packed, radially elongate palisade cells with straight walls on the convex side, the remainder of seed coat composed of irregularly arranged, crowded, short, cuboidal or irregularly shaped cells. Central cavity present, no embryo development apparent. Figure 7.

Pollen morphology. Pollen prolate-spheroidal, amb circular; tricolporate, colpi meridionally elongated, equatorially arranged, equidistant, straight, ca. 14 μm long, extending within 4–5 μm of pole (PI 0.22), P/E 1.1, margins invaginated and slightly diffuse, tapering to acute apex with some sexine modification (granulations) extending to poles, ektexine bridge over pore, pore circular, diam. 3–4 μm, situated at midpoint of colpus; wall 1.5–2 μm thick, psilate bordering colpi, verrucate-areolate in elongated mesocolpal region suggesting faint subsidiary colpi; tectate; 18–22 μm by 16–20 μm. This description was provided by Alan Graham, Department of Biological Sciences, Kent State University, Kent, Ohio. Figure 5.

The above description is based on *Klug 3349* (F) and *Woytkowski 8331* (F), both of South American origin with fully developed pollen from functionally bisexual flowers. Pollen fertility in both collections is 97%, based on a count of 200 grains stained in cotton blue in lacto-phenol. In Central American plants pollen fertility is very low and few grains are well-formed. Pollen fertility does not exceed 36% in the Costa Rican collections examined by Tobe (unpubl. data). No fertile pollen has been observed in the Panama collection of *Knapp & Kress 4336* (MO).

Pollen of *Alzatea* has also been described and illustrated by Muller (1975) as part of a survey of the pollen of the Crypteroniaceae.

Anatomy. The following account is condensed from the detailed investigations of van Vliet (1975), Baas (1979), and Keating (1984). *Leaf:* Stomata abaxial only, anomocytic to nearly cyclocytic with subsidiary cells slightly submersed below guard cells. In transverse section, blade dorsi-ventral, 380–440 μm thick. Adaxial epidermal cells mainly square, larger than the abaxial ones. Adaxial, 1–2 layered hypodermis present, limited to each side of midrib or extending over midrib. Palisade tissue 2-layered with abundant large, short-branched asterosclereids. Spongy mesophyll compact, mostly sclerified. Midrib a flattened cylinder with abaxial and adaxial plates and a central lacuna, secondary veins circular in outline, collateral. Scattered druses present in lower mesophyll and near the veins. Figure 6. *Node:* Trilacunar with three traces. *Stem:* Epidermal cells square. Cortex of parenchyma interspersed with stone cells and 1–4 more or less centric cortical bundles in each corner of the 4-angled twig. Cork arising next to perivascular sclerenchyma, the phellem cells in late stages forming alternating layers of flat, thin-walled cells and square cells with unilateral wall thickenings. Primary phloem mostly sclerified in older material. Secondary phloem of sieve tubes, companion cells, chambered parenchyma and infrequent phloem fibers. Secondary xylem with faint growth rings. Vessels diffuse, 36/mm^2, solitary and in radial multiples of 2–4. Vessel members (330–)530 and 570(–750) μm long, mostly with long tails. Perforations simple in oblique end walls. Inter-vessel pits crowded, alternate, with vesturing abundant, spreading onto vessel walls to form diagonal bands. Vessel-ray pits large, simple, reticulate to scalariform. Thin-walled tyloses present in some vessels. Fibers (540–)960(–1240) μm long, walls thin, minutely bordered to simple pits, septate and/or gelatinous. Gelatinous fibers in tangential bands in young material. Parenchyma very scanty paratracheal. Rays heterogeneous I–II type, 1–3 seriate, usually with central portion of procumbent cells. Primary xylem and internal phloem in a continuous ring. Pith of lignified parenchyma. Druses abundant in chambered phloem parenchyma.

Chemistry. Leaves of *Alzatea* contain ellagic acid and flavonoid mono- and di-glycosides, including 3-OH flavonols. [Leaves of *Hammel 6247* (MO) were extracted using standard methods outlined by Bate-Smith (1962). A chromatographic R_f value of 0.32 was obtained in Forestal solvent, after ethyl acetate extraction. Additional leaf material extracted in 80% methanol was spotted on cellulose TLC plates. Plates were developed in two dimensions, (1) TBA (t-BuOH-HOAc-H_2O; 3:1:1) and (2) 15% HOAc. The TLC patterns suggest the presence of flavonoid mono- and di-glycosides. Two-dimensional plates, developed for the hydrolized material, showed the presence of 3-OL flavonoids. Contributed by B. Timmerman, Institute of Arid Land Studies, University of Arizona, Tucson, Arizona.] The chemistry is consistent with its position in the Myrtales, an order especially characterized by the presence of ellagic acid and tannins (Bate-Smith, 1962; Hegnauer, 1969).

PROPOSED RELATIONSHIPS

The relationships suggested for *Alzatea* encompass eight families in five orders of two subclasses (Table 2). Obviously this problematic genus displays a number of floral and vegetative characteristics widespread within the dicotyledons, especially in the subclass Rosidae. Such a diverse assortment of suggested affinities has been based primarily on either shared ancestral features which supply limited or no useful information about its near relationships, or have focused on one or two parallel or convergent specializations while ignoring a preponderance of dissimilarities. Most proposals of relationship were made prior to the availability of data from anatomical, palynological, embryological, and chemical information about *Alzatea.* When all current evidence is assembled, few taxa are serious contenders as close relatives of the genus.

DISTANT RELATIONSHIPS AND NON-RELATED FAMILIES

Placement of *Alzatea* in the Flacourtiaceae as a separate tribe or subfamily was first suggested by Loesener (1942), who excluded the genus from his monograph of the Celastraceae. Loesener's suggestion was followed by Hutchinson (1967) who established the monotypic tribe Alzateeae in the Flacourtiaceae to accommodate it. The Flacourtiaceae are generally considered ancestral in the Violales and are highly diversified (Cronquist, 1981), so that several *Alzatea* features can be found within this diversity. However, these are attributes of wide occurrence in flowering plants and even collectively are useless as indi-

TABLE 2. Summary of family placement previously suggested for *Alzatea*, following Cronquist's (1981) classification.

Subclass Dillenidae
  Violales—Flacourtiaceae
  Theales—Clusiaceae

Subclass Rosidae
  Celastrales—Celastraceae, Icacinaceae
  Rhamnales—Rhamnaceae
  Myrtales—Crypteroniaceae, Lythraceae, Melastomataceae

cators of close relationship. For example, in *Alzatea* and the Flacourtiaceae there are trilacunar nodes, vessel elements with simple perforation plates, tricolporate pollen, parietal placentation (probably the character most influencing Hutchinson's placement of *Alzatea* in the Flacourtiaceae), and bitegmic, crassinucellate ovules. On the other hand, the family lacks such important Alzatean (and Myrtalean) features as internal phloem, presence of ellagic acid and flavonols in the leaves, and in contrast to *Alzatea* primarily displays alternate leaves with paracytic stomates, imbricate sepals and petals, free styles and stigmas, and seeds with abundant fleshy endosperm. No alliance of *Alzatea* and the Flacourtiaceae is acceptable by reason of these major morphological, anatomical, and chemical differences.

Affinity to the Clusiaceae was postulated only because of similar vegetative morphology. Where *Alzatea* and *Clusia* grow side by side, as in Panama, the similarity in leaf form and general habit is striking (S. Knapp, pers. comm.). The family Clusiaceae differs from *Alzatea*, however, in an overwhelming number of characteristics of all types. Among them are lack of internal phloem and vestured pitting, presence of unilacunar nodes, leaves with resin cavities and paracytic stomates, numerous stamens, gynoecium of 3–5 carpels, mostly axile placentation, and tenuinucellar ovules.

The relationship of *Alzatea* to the hemi-parasitic Santalaceae was suggested by the placement of the protologue between two genera of the family. Links to the Santalaceae beyond the initial position in publication have not been proposed. As with the Clusiaceae, the Santalaceae lack internal phloem, have unilacunar nodes, and do not produce ellagic acid (Cronquist, 1981). They commonly have a 3-carpellate, unilocular ovary with few unitegmic, tenuinuellar ovules, and a solitary seed with abundant endosperm, features absent from *Alzatea*.

Alzatea was first associated with the Celastraceae by A. P. de Candolle (1825), followed by Bentham in Bentham and Hooker (1862), who chose to ignore Planchon's view (1845) that the genus ought to be in the Lythraceae, not the Celastraceae. In a later volume of the "Prodromous" (1868), A. L. P. P. de Candolle removed *Alzatea* to the Crypteroniaceae following Blume (1826–1827). Loesener (1892), regarded *Alzatea* of doubtful membership in the Celastraceae. In his later treatment of this family (1942), after reading Hallier's (1911) more extensive descriptions of the genus, he excluded *Alzatea* altogether, suggesting instead that it be accommodated in the Flacourtiaceae, as a new subfamily or tribe. Besides lack of internal phloem, the Celastraceae have axile placentation, a major reason Loesener excluded *Alzatea* from the family. In addition, the sepals and petals are mostly imbricate, and the seeds are often arillate with abundant endosperm. Anatomically, the family differs from *Alzatea* in the presence of unilacunar nodes and secretory canals in the phloem. Even though the Celastraceae is a rather diversified family with several highly distinctive genera, it diverges from *Alzatea* in too many major characters to be considered the appropriate family for the genus.

Possible association of *Alzatea* with the Icacinaceae was suggested by MacBride (1956), but no specific reason was given to support this view. As with the Celastraceae, the number of morphological and anatomical differences are too great for the family to merit serious consideration.

The family Rhamnaceae was thought a suitable, if perhaps temporary, repository for the genus by Miers (1872) by virtue of its antepetalous stamen condition. Miers regarded *Alzatea*, together with *Crypteronia*, and possibly also *Tetrataxis* (Lythraceae) as a "peculiar group" which could be positioned in the Rhamnaceae as a new tribe, the Crypteronieae. Floral morphology in the family exhibits some similarities to that of *Alzatea*, e.g., 5-merous flowers in axillary cymes, stamens alternating with sepals, the sepals often with a raised, fleshy, interior surface as occurs in *Alzatea*, a well-developed infrastaminal nectary disc adnate to the floral tube, and seeds lacking endosperm. There are, however, equally as many specialized features in which the family differs from *Alzatea*. Most distinctive of these are the

Rhamnaceous ovary with its single, basal, erect ovule in each locule; drupaceous fruits; and wingless seeds with stony, multiplicative walls. The family also lacks internal phloem and vestured pitting and produces no ellagic acid (Cronquist, 1981). Similarities may be attributed to their common distant ancestry in the Rosidae and parallel development of like structures in different lines of the subclass. Total evidence excludes *Alzatea* from the Rhamnaceae.

COMPARATIVE EVIDENCE FOR ORDINAL, FAMILY, AND GENERIC RELATIONSHIPS

Among the several orders suggested for *Alzatea,* the Myrtales offer the only comfortable fit. Two anatomical apomorphies of *Alzatea,* internal phloem and vestured pitting, are major definitive features of the Myrtales (Dahlgren & Thorne, 1984). Other characteristics of *Alzatea* prevail in the order. These include vessel elements with simple perforation plates, opposite and verticillate, simple, entire leaves with brochidodromous secondary venation, ellagic acid and flavonol glycoside leaf constituents, rudimentary axillary stipules (Weberling, 1968), anomocytic stomata, basically determinate inflorescences, floral tube with floral parts on the rim, bitegmic crassinucellar ovules, as well as several embryological features (Dahlgren & Thorne, 1984).

At the familial level, Myrtalean families to which *Alzatea* has been referred have been subject themselves to numerous interpretations, so that the varying familial placement of *Alzatea* in the order has depended in part on how the families were defined. Hallier (1911), for example, initially considered *Alzatea* a member of the Lythraceae. His concept of the family included *Sonneratia* and *Duabanga* (Sonneratiaceae, traditionally), *Crypteronia* (Crypteroniaceae), *Rhynchocalyx* (Rhynchocalycaceae), and *Punica* (Punicaceae, traditionally). After an "angry" letter from the monographer of the Lythraceae, Emil Koehne, disputing Hallier's delineation of Lythraceae, Hallier decided the same genera, questionably excluding *Punica,* were members of the Memecyloideae-Melastomataceae (Hallier, 1918). The change was due, not as much to Koehne's objection, since Hallier dismissed Koehne's argument as "pre-Darwinian," as to his new awareness of the genera *Dactylocladus* and *Axinandra,* which he found overwhelmingly similar to *Crypteronia* and *Alzatea* and which were considered Melastomataceous by their authors. Lourteig (1965), who regarded *Alzatea* as Lythraceous, extended her definition of Lythraceae to include *Crypteronia.* It has also been argued since that *Alzatea, Rhynchocalyx, Dactylocladus,* and *Axinandra,* with *Crypteronia* constitute a redefined Crypteroniaceae (van Beusekom-Osinga & van Beusekom, 1975). Most recently, *Alzatea* has been removed from that coalition of genera, with the latter three genera repositioned as a new subfamily of the Melastomataceae (van Vliet, 1981) and *Rhynchocalyx* comprising the monotypic Rhynchocalycaceae (Johnson & Briggs, 1984).

Several Alzatean characteristics occur repeatedly throughout the order in more than one family and must be regarded as having originated early in the evolution of the group or as instances of convergent or parallel evolution. Examples of the latter include foliar sclereids scattered throughout several families (Rao & Das, 1979); hemi-epigynous flowers seen also in the Crypteroniaceae (van Beusekom-Osinga & van Beusekom, 1975), Melastomataceae, and Myrtaceae (Dahlgren & Thorne, 1984); expanded fleshy anther connectives in the Crypteroniaceae; and transeptal vascular supply, which occurs in some Onagraceae, Myrtaceae, Oliniaceae, Punicaceae, and in *Rhynchocalyx* (Schmid, 1984). Combinations of these characteristics, together with the widely occurring plesiomorphic features of the order, have been used to infer relationship to the families Lythraceae and Crypteroniaceae (and the Melastomataceae via inclusion of Crypteroniaceae in that family).

The most recent arguments for the disposition of *Alzatea* in the Lythraceae have rested on such common Myrtalean characteristics as quadrat branches, subcoriaceous decussate leaves, 5–6-merous flowers, and capsular, bilocular fruit with loculicidal dehiscence (Lourteig, 1965). Apomorphic Alzatean features cited to support placement in the family, e.g., obhaplostemonous stamens with enlarged connective and apetaly are now believed to have evolved more than once in the order (Johnson & Briggs, 1984). Although the parietal placentation of *Ammannia microcarpa* DC. in Lythraceae has been cited in support of *Alzatea*'s placement in the family, the placentation is not homologous in these taxa. *Ammannia microcarpa* is a highly derived herbaceous species whose parietal placentation is unique in the Lythraceae. The species bears no other resemblance to *Alzatea.* Citation of this species as supporting evidence for inclusion of

TABLE 3. Comparison of *Alzatea* and associated genera.

Character	*Alzatea*	*Rhynchocalyx*	*Crypteronia*	*Dactylocladus*	*Axinandra*
No. of species	1	1	4	1	4
Habit	Small tree or shrub, hemi-epiphyte	Small tree	Tree	Tree	Tree
Habitat	Wet, submontane tropical forest	Moist, wooded, subtropical ravines	Wet, submontane tropical forests	Lowland peat swamps	Wet, submontane tropical forests
Distribution	Bolivia, Peru, Panama, Costa Rica	Natal & Transkei, South Africa	SE Asia, Phillippines, Malay Peninsula to New Guinea, esp. Borneo	Borneo	Malay Peninsula, Borneo, Sri Lanka
Branches					
Arrangement	Opposite or whorled	Opposite or whorled	Opposite	Opposite	Opposite
X-sect., young	Quadrangular	Terete to flattened	Terete to quadrangular	Flattened	Quadrangular ±
Leaves					
Phyllotaxy	Opposite or whorled	Opposite or whorled	Opposite	Opposite	Opposite
Stipules	Axillary, divided	Axillary, divided	Lateral, rudimentary	?	?
Venation	Brochidodromous	Eucamptodromous	Brochidodromous	Brochidodromous, indistinct	Brochidodromous
Inflorescence					
Type	Anthotelic, paniculate	Anthotelic, paniculate	Blastotelic, racemose	Blastotelic, racemose	Blastotelic, racemose
Position	Axillary, terminal	Axillary, terminal	Axillary, terminal	Axillary, terminal	Axillary, terminal
Flowers					
Sex	Bisexual (& func. unisexual?)	Bisexual	Bisexual & unisexual	Bisexual	Bisexual
Insertion	Hemi-epigynous, barely	Hemi-epigynous, barely	Perigynous	Hemi-epigynous, strongly	Epigynous
Nectary-disc	Present, broad	Absent	Absent	Absent	Absent
Merosity	5(–6)-merous	6-merous	4–5(–6)-merous	5(–4)-merous	5(–4)-merous
Floral bracts	Minute, fugaceous	Minute, fugaceous	Solitary, persistent (?)	Solitary, caducous	Three, persistent (?)
Calyx					
Lobes	Thick, adaxial surface raised, fleshy	Thin, membranous	Thin, membranous	Thin, membranous	Thin, membranous
Duration	Persistent	Persistent	Persistent	Persistent	Evanescent in fruit
Aestivation	Valvate	Valvate	Valvate	Valvate	Valvate

TABLE 3. Continued.

Character	*Alzatea*	*Rhynchocalyx*	*Crypteronia*	*Dactylocladus*	*Axinandra*
Petals					
Number	0	6	0	5	5
Shape	—	Hood-like, covering stamens in bud, clawed	—	Hood-like, covering stamens in bud, clawed	± Connate, broad-based
Deciduousness	—	Individually	—	Individually	As cone-shaped unit
Stamens					
Number	5	6	4–5	5	10
Position	Alternisepalous	Alternisepalous	Alternisepalous	Alternisepalous	Episepalous & epipetalous
Filaments	Thick, short, flattened	Thin, long, ± flattened	Thin, long, terete	? ± flattened	Thick, short, ± flattened
Connective	Conduplicate	Elliptical	Orbicular or nearly conduplicate	Orbicular	Conduplicate
Sporangia position	Terminal	Lateral	Lateral to subterminal	Lateral	Terminal
Pollen					
Aperatures	Tricolporate	Tricolporate	Bisyncolporate	Tricolporate	Tricolporate
Shape	Prolate-spheroidal	Prolate-spheroidal	Bilaterally flattened	Prolate-spheroidal	Prolate-spheroidal
Subsidiary colpi	3, indistinct	3, distinct	2, indistinct	3, distinct	3, distinct
Exine	Faintly verrucate to psilate	Faintly verrucate to psilate	Psilate	Psilate to irregularly verrucate	Psilate to finely verrucate
Nuclei at shedding	2	2	2	2	2
Style					
Length	Shorter than ovary, stout	Shorter than ovary, stout	Longer than ovary, filiform	Longer than ovary, filiform	Longer than ovary
In fruit	Base persistent	Base persistent	Entire style & stigma persistent	Entire style & stigma persistent	Non-persistent
Stigma	Capitate	Capitate, narrow	Punctate or capitate	Capitate	Punctate, minute
Ovary					
Shape	Bilateral, compressed	Bilateral, compressed	Bilateral & compressed or globose	Globose	Globose
Carpel No.	2	2	2 (3 or 4)	(3) 4 or 5	3 (2)
Locule No.	2	2	2 (3 or 4)	(3) 4 or 5	6 (4)

TABLE 3. Continued.

Character	*Alzatea*	*Rhynchocalyx*	*Crypteronia*	*Dactylocladus*	*Axinandra*
Placentation	Parietal	Axile	Parietal or basal	Basal	Basal
Septal Fusion	Not fused	Fused entirely	Not fused or fused basally (?)	Not fused	Fused slightly basally (?)
Ovule No./Capsule	Ca. 40–60	Ca. 40	Many 6(–12)	12–15	6–12
Ovule Position	Horizontal in staggered vertical rows	Horizontal in single vertical rows	Horizontal in staggered vertical rows or ± vertical & basal	Vertical & basal	Vertical & basal
Fruit	Indurated capsule	Indurated capsule	Indurated capsule	Indurated capsule	Woody, greatly enlarged capsule
Seed					
Shape	Irregularly oblong to lunate, flattened	Obliquely ovate, flattened	Ovoid-ellipsoid, flattened	Narrowly ellipsoid, flattened	Oblong, ellipsoid, flattened
Embryo Position	Central	Apical	Central	Central	Basal
Seed Wing	Encircling embryo	At micropylar end	At micropylar or chalazal end	?	At chalazal end
Seed Coat Cells	Specialized cell types absent	Specialized cell types absent	?	?	Specialized cell types absent
Testa Layers	2	2	?	?	2
Tegmen Layers	2	2	?	?	2 initially, becoming 3
Embryology					
Anther Wall Formation	Dicot Type	Basic Type	?	?	Dicot Type
Anther Endothecium	Ephemeral	Ephemeral	?	?	Ephemeral
Microsporangial Septum	Non-persistent	Persistent	?	?	Non-persistent
Ovule Archesporium	Multi-celled	Multi-celled	?	?	One-celled
Ovule Endothelium	Absent	Absent	?	?	Present
Micropyle Formation	Inner integument only	Inner integument only	?	?	Inner & Outer integuments
Embryo Sac Formation	Bisporic, *Allium*-type	Monosporic, *Polygonum*-type	?	?	Monosporic, *Polygonum*-type

TABLE 3. Continued.

Character	*Alzatea*	*Rhynchocalyx*	*Crypteronia*	*Dactylocladus*	*Axinandra*
Leaf Anatomy					
Cuticle	Granular	Smooth	Granular	Smooth	Granular
Stomate	Anomocytic	Anomocytic	Paracytic	Anomocytic	Paracytic
Petiole Bundle	Cylinder, ab- & adaxial portions with middle lacuna	Curved arc	Cylinder, ab- & adaxial portions with middle lacuna	Cylinder, ab- & adaxial portions with middle lacuna	Curved arc
Sclereids	Present, branched	Present, unbranched	Present, unbranched	Present, unbranched	Absent
Nodes	Trilacunar, 3 traces	Unilacunar, 1 trace	Common gap, 1 median bundle	Common gap, 1 median bundle	Complete girdling trace, 1 median bundle
Stem Anatomy					
Cork Origin	Pericycle	Cortex	Pericycle	Subepidermal	Pericycle
Vessel Aggregation	Mainly radial multiples	Mainly solitary	Mainly radial multiples	Mainly solitary	Mainly solitary
Vessel Member Length	530 & 570 μm	460 & 520 μm	650–900 μm	950–1120 μm	390–440 μm
Vessel-Ray Pits	Reticulate-scalariform, large	Alternate, small	Alternate, small	Reticulate-scalariform, large	Alternate, small
Vesturing	Spreading, forming bands on vessel wall	Spreading, forming bands on vessel wall	Within pit chamber & on pit margins	Within pit chamber only	Within pit chamber only
Septate Fibers	Present	Present	Absent	Absent	Absent
Fiber Pitting	Simple-minutely bordered	Simple-minutely bordered	Distinctly bordered	Distinctly bordered	Distinctly bordered
Axial Parenchyma	Very scanty paratracheal	Scanty paratracheal to vasicentric	Diffuse or scanty paratracheal to vasicentric	Aliform to confluent	Aliform to confluent
Rays	Heterogeneous I	Heterogeneous I	Heterogeneous I	Heterogeneous III	Heterogeneous I
Phloem Crystals	Clustered in chambered parenchyma	Solitary, prismatic in chambered parenchyma	Styloids in parenchyma	Crystal sand & druses in parenchyma	Styloids in parenchyma

Alzatea in Lythraceae (Lourteig, 1965) is an instructive example of how one or a few phenetic similarities can be emphasized to justify relationships of only remotely related or totally unrelated taxa. The relationship of *Alzatea* to the Lythraceae is clearly of a general nature, based on characteristics widely dispersed in the family. No Lythraceous genus shares a sufficient suite of characteristics to be considered directly or closely related to *Alzatea.*

Alzatea's closest relationships appear to center around the genera of the Crypteroniaceae, *Crypteronia, Dactylocladus,* and *Axinandra,* and the genus *Rhynchocalyx,* by virtue of their possession of more of the distinctive features which define *Alzatea.* Major similarities and differences among these genera, selected from recently published studies and personal observations of herbarium and fixed plant material, are compared in Table 3. Evidence of relationship based on these attributes is discussed in the following pages. In instances where variability occurs within the genus, as among the species of *Crypteronia,* the most common situation is recorded. The table is not meant to be all-inclusive; more complete characterizations may be found in the individual papers cited in the text. The reader is referred to these for further details not presented here.

Macromorphological evidence. Among the most strikingly similar, advanced characteristics uniting *Alzatea* with *Rhynchocalyx* and *Crypteronia* pro parte are those of ovule and seed morphology. The three taxa display hemi-epigynous, bilaterally compressed, bicarpellate ovaries in which numerous ovules are borne horizontally in one or more vertical rows. Placentation is parietal in *Alzatea* and *Crypteronia* (van Beusekom-Osinga & van Beusekom, 1975) and axile in *Rhynchocalyx* (Sprague & Metcalfe, 1937; Strey & Leistner, 1968) but the solid central axis in *Rhynchocalyx* (Fig. 8e–g) is only slightly less evolved than the divided septum of *Alzatea* (Fig. 8a–d) and *Crypteronia.* Additional ovarian features in *Rhynchocalyx,* the narrow (ca. 0.5 mm wide) placental region and uniseriate ovules, are similar to those of *Alzatea* but are regarded as evolutionarily somewhat more primitive (Puri, 1952). The shared characteristic of transeptal ovarian vascular supply enhances the similarity of *Alzatea* and *Rhynchocalyx.* The ovarian vascular system in *Crypteronia* is undescribed. However, free-hand sections of limited flower material of *C. paniculata* Planch. indicate that each fleshy half septum is free to the base and has its own ventral vascular system which supplies the ovules and adjacent carpel wall as in *Alzatea* and *Rhynchocalyx,* although probably differs from them in the major ventral vascular supply of each half septum consisting of a single, rather than double, major bundle. The remaining Crypteroniaceae display quite different features, such as a 4-locular ovary with central conical placenta (other spp. of *Crypteronia*) or a nearly inferior, 4–6-locular ovary with ovules basal between the septa (*Dactylocladus* and *Axinandra*).

Transeptal bundles have been described for other members of the Myrtales and occur infrequently in assorted families of other orders, e.g., in Cornaceae, Rubiaceae, Araceae, Umbelliferae, and Oleaceae (Schmid, 1972, 1984; Eyde, 1967, 1981; Puri, 1952). The condition is considered derived from the common axile system and appears most frequently in families with inferior ovaries (Schmid, 1972; Eyde, 1981). In Myrtales, transeptal bundles are recorded in one or more genera of the Myrtaceae, Oliniaceae, Punicaceae, Onagraceae, and Trapaceae, as well as in *Alzatea* and *Rhynchocalyx* (Schmid, 1984). The condition has most certainly arisen several times in the Myrtales and is not necessarily indicative of close phylogenetic relationship, although in *Alzatea* and *Rhynchocalyx* it is most parsimoniously considered to have been gained from their most recent common ancestor rather than independently evolved.

Fruit type in *Alzatea, Rhynchocalyx,* and *Crypteronia* pro parte is basically a dry, bilocular capsule in which the valves are crowned by the persistent base of the style. *Crypteronia* differs in retaining the entire style and stigma after dehiscence of the capsule. A persistent style characterizes *Dactylocladus* as well as *Alzatea* and *Crypteronia* pro parte, but the fruit of the first differs in shape, placentation, and seed number. *Axinandra* is even further differentiated from *Alzatea* by the epigynous, 6(–4)-locular ovary and large, globose capsule with basal, erect ovules. Compressed capsules and transeptal vascular supply are unknown in the Lythraceae.

In seed morphology, *Alzatea* appears to share a simple, anatomically much reduced, thin-winged seed type with *Rhynchocalyx* and Crypteroniaceae sensu stricto. Although the seeds are superficially similar, developmental sequences differ in *Alzatea, Rhynchocalyx,* and *Axinandra,* the only genera studied to date, and thus cannot be used to support a close relationship of the genera (Tobe & Raven, 1983, 1984a, 1984b).

The occurrence of a simplified seed in the Sonneratiaceae in *Duabanga,* but not in *Sonneratia,* indicates reduction in seed anatomy has occurred more than once within the Myrtales. The simple seed morphology of *Alzatea* is in marked contrast to the multiple-layered seed coats of core families of the Myrtales which are further specialized by the presence of fibrous and/or sclerotic cell layers (Corner, 1976). Simplicity of seed structure in *Alzatea* is regarded as derived for reasons that the more complex seed coat is the common condition both in the Myrtales and in the Rosiflorae generally, and the simple seed is associated with advanced ovary characteristics of parietal placentation, transeptal vascular bundles, and bilateral symmetry. According to Corner (1976), the main direction of seed evolution in Angiosperms has been toward reduction in complexity and size.

Few other derived macromorphological states are shared by *Alzatea* and any of the other four genera. The unusual anther connectives with terminal or apically placed sporangia (Fig. 3) appear in similar (homologous?) form in *Axinandra* but otherwise the genera hold no features in common other than those widespread in the order. The expanded connective of *Crypteronia* anthers could be taken as an evolutionary intermediate step toward the *Alzatea-Axinandra* type from the merely broadened form seen in *Rhynchocalyx* and *Dactylocladus.* The inflorescences of *Alzatea* and *Rhynchocalyx* are fundamentally the same, i.e., anthotelic, with the axes ending in a flower (Figs. 9, 11) but those of *Crypteronia, Dactylocladus,* and *Axinandra* are blastotelic, an evolutionarily more advanced type in which the inflorescence axes are not terminated by a flower (Briggs & Johnson, 1979; Johnson & Briggs, 1984). The well-developed nectary disc of *Alzatea* is an apomorphy not noted in these other genera.

Alzatea displays a total macromorphology which places it at a distance from even those genera considered most closely related or phenetically most similar. The isolation is probably more pronounced than even macromorphology suggests when one takes into account the liklihood that at least some of the phenetic similarities have independent phylogenetic origins.

Pollen morphological evidence. Pollen morphological differences among the putative generic relatives of *Alzatea* are considerable. *Alzatea* pollen has very generalized features, being binucleate, prolate-spheroidal, and tricolporate, with nearly psilate exine. Under the scanning electron microscope (SEM), mesocolpal depressions are apparent and have been interpreted as "incipient" subsidiary colpi (Muller, 1975, 1981). The presence of subsidiary colpi is a typical, although not constant, feature of Myrtalean pollen. It is the only pollen character of *Alzatea* which indicates relationship to the order, since other *Alzatea* pollen features appear in the dicotyledons in a number of unrelated families. There is no pollen characteristic of *Alzatea* which can be used to convincingly align *Alzatea* to any one Myrtalean family. It has been suggested that the pollen is comparable to that of *Physocalymma* in Lythraceae (van Campo in Lourteig, 1965). The characters they share, however, are generalized ones of shape, size, and possession of colporate aperatures. They differ in sculpture pattern, *Physocalymma* having a rugulate-striate exine, *Alzatea* a psilate one. No case can be made for a close relationship to *Physocalymma* or any other Lythraceae based on pollen (Graham et al., unpubl. data). In contrast to pollen of *Alzatea,* pollen of *Rhynchocalyx, Dactylocladus,* and *Axinandra* is tricolporate and distinctly 3-heterocolpate, falling within the range of Melastomataceous and Lythraceous pollen types. *Crypteronia* pollen, on the other hand, stands totally apart from both *Alzatea* and the preceding taxa by its unusual bisyncolpate, bilateral condition. Although a hypothetical scheme for transition from *Alzatea* to *Crypteronia* pollen has been postulated, no transitional pollen type is known (Muller, 1975). The generalized features of *Alzatea* pollen relegate the genus to an ancestral position with respect to the pollen of other genera discussed but indicate no special relationship to any one of the families or specific genera in the Myrtales with which it has been aligned.

Embryological evidence. Embryological comparisons confirm the Myrtalean position of *Alzatea* (Schmid, 1984; Tobe & Raven, 1984a). A comprehensive report of the embryology of the genus, from which this discussion is excerpted, is presented by Tobe and Raven (1984a). Of the seven ordinal distinctions listed by them, *Alzatea* differs only in one, having a micropyle formed by the inner integument alone, rather than by both inner and outer integuments. The formation of an inner integument micropyle is known elsewhere in Myrtales only in *Rhynchocalyx* (Tobe & Raven, 1984b). The micropyle in *Axinandra* and all embryologically known Lythraceous and Melastomataceous genera is

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FIGURE 9. *Alzatea verticillata* subsp. *verticillata*, *Woytkowski 8331* (MO) from Peru. FIGURE 10. *Alzatea verticillata* subsp. *amplifolia* S. A. Graham. *Knapp & Kress 4336* (MO) from Cerro Túte, Panama.

formed from both outer and inner integuments (Tobe & Raven, 1983). Unfortunately, comparisons cannot be made with *Crypteronia* and *Dactylocladus,* which are unstudied embryologically.

The most striking embryological feature of *Alzatea* is the bisporic *Allium*-type embryo sac, a type reported for no other Myrtalean taxa. The characteristic embryo sac type for the order is the monosporic *Polygonum*-type. Two exceptions, besides *Alzatea,* are known, however, in Peneaceae and Onagraceae, each of which has its own peculiar embryo sac type. *Rhynchocalyx* conforms to the general Myrtalean condition.

Alzatea is similar to *Rhynchocalyx* by virtue of the same micropylar formation and in having a multicelled ovule archesporium, ephemeral endothelium development, and binucleate pollen. It differs in several ways, in addition to the embryo sac character. In *Alzatea,* anther wall formation is of the Dicotyledonous type with the wall four cell layers thick and the epidermal outer cell walls of the anther flat. The septum between microsporangia is non-persistent. Cells of the nucellus develop normally. In the seed, the embryo is centrally positioned with straight cotyledons and the seed wing forms from the funiculus and outer integument. In *Rhynchocalyx,* anther wall formation is of the Basic type with wall layers five cells thick and epidermal outer cell walls of the anther papillate. The microsporangial septa persist after sporangial dehiscence. In the nucellus, subdermal cells elongate radially. In the seed the embryo is basally positioned with folded cotyledons and the seed wing develops from the funiculus only.

Axinandra, the only other putative close relative investigated embryologically, is more distantly separated from *Alzatea* than *Rhynchocalyx* by possession of two important distinctions: a one-celled ovule archesporium with endothelium present and the micropyle formed by outer and inner integuments.

Alzatea shares some generalized embryological features with Lythraceae, but differs in many. It can be excluded from the family foremost by the distinctive *Allium* embryo sac. Similarities to Melastomataceae are restricted to anther wall features only. Tobe and Raven have concluded that, embryologically, *Alzatea* takes an isolated position in Myrtales. The limited embryological similarities to *Rhynchocalyx* are attributed to parallel descendency from a common ancestor, from which Lythraceae are also derived.

Anatomical evidence. The recent series of anatomical studies in Myrtales offers a wealth of new information about *Alzatea* and associated taxa, as well as thorough assessments of relationships based on anatomical data (van Vliet, 1975, 1981; Baas & Zweypfennig, 1979; van Vliet & Baas, 1975, 1984; van Vliet et al., 1981; Keating, 1984). Major anatomical distinctions of *Alzatea* and the genera under discussion are extracted from these works and listed in Table 3 to facilitate comparison.

Anatomical evidence clearly places *Alzatea* in the Myrtales. Familial and generic affinites, however, are not clearly indicated by anatomical characters. *Alzatea*'s leaf anatomy is particularly distinctive in the order. The combination of anomocytic-cyclocytic stomates, midvein vascular system divided by a lacuna into abaxial and adaxial portions, abundant sclereids of two types, and small epidermal cells which are square in cross section, are unlike any other genus investigated in Myrtales (Keating, 1984). Other than the similar stomate condition shared by *Rhynchocalyx* and *Dactylocladus,* this synapomorphy isolates the genus in the order.

Nodal anatomy additionally supports the exclusiveness of *Alzatea* in Myrtales. The trilacunar node with three traces is presently unknown elsewhere in Myrtales, where the unilacunar condition prevails. Trilacunar nodes, regarded as primitive in Angiosperms, may be ancestral in the Myrtales and ancestral to the common gap-median trace seen in some Melastomataceae and Crypteroniaceae (van Vliet & Baas, 1975). Alternatively, the possibility has been raised that the trilacunar node in *Alzatea* is a neotenous condition (Johnson & Briggs, 1984). In either case, the genus is unique within the order for this attribute.

Wood anatomical details indicate *Alzatea* is linked in a general way to several Myrtalean families but is not a close fit to any of them. Within the order there is a wide range of wood anatomical diversity and much overlap in the families tentatively associated with *Alzatea,* i.e., Crypteroniaceae sensu stricto, Lythraceae, and Melastomataceae. This heterogeneity restricts use of the anatomical data as an indicator of family placement for *Alzatea.* At the generic level, there are major anatomical distinctions between *Alzatea* on the one hand and *Crypteronia, Dactylocladus, Axinandra,* and *Rhynchocalyx* on the other. *Alzatea* has branched foliar sclereids, trilacunar nodes with three traces, and clustered crystals in chambered phloem cells, character-

TABLE 4. Distribution of similar (homologous?) characteristics in genera and family associated with *Alzatea.* Key: + = shared with *Alzatea*; − = not occurring in the genus or family; ( ) = rarely, occasionally, or in part occurring in the genus or family; ? = unknown; * = evolutionarily advanced feature in *Alzatea.*

	Presence of a Similar State in:				
Selected *Alzatea* Characteristic	*Rhynchocalyx*	*Crypteronia*	*Dactylocladus*	*Axinandra*	Lythraceae
Leaves opposite and whorled	+	+	−	+	(+)
*Stipules axillary and divided	+	−	−	−	+
Inflorescence anthotelic (axes terminated by a flower)	+	−	−	−	+
*Flowers hemi-epigynous	+	+	+	−	−
*Nectary disc present	−	−	−	−	(+)
Flowers 5-merous	−	+	+	+	(+)
*Petals absent	−	+	−	−	(+)
*Calyx lobe thick, fleshy within	−	−	−	−	−
*Calyx lobes persistent	+	+	+	−	+
Stamen number five	−	+	+	−	(+)
*Filaments short, thick	−	−	−	+	−
*Connective expanded with terminal sporangia	−	+	−	+	−
Pollen tricolporate	+	−	+	+	(+)
*Subsidiary colpi indistinct, not prominent	−	+	−	−	(+)
Pollen bi-nucleate	+	+	+	+	+
*Style stout	+	−	−	−	(+)
Style base persistent	+	+	+	−	(+)
*Ovary bilateral, compressed	+	(+)	−	−	−
*Carpel number two	+	(+)	−	−	(+)
*Ovary vascular supply transeptal, lateral	+	(+)	?	?	−
*Placentation parietal	−	(+)	−	−	−
*Ovules numerous, ca. 40	+	(+)	−	−	(+)
Ovule position horizontal	+	(+)	−	−	(+)
Ovule archesporium multi-celled	+	?	?	−	+
Ovule endothelium absent	+	?	?	−	?
*Micropyle formed from inner integument only	+	?	?	−	−
*Embryo sac bisporic, *Allium*-type	−	?	?	−	−
*Seed wing present	+	+	+	+	(+)
*Seed testa 2-layered, unspecialized	+	+	+	+	−
*Seed tegmen 2-layered, unspecialized	+	+	+	+	−
Nodes trilacunar with three traces	−	−	−	−	−
Leaf stomates mainly anomocytic	+	−	+	−	+
Petiole bundle a closed ring	−	+	+	−	−
*Leaf sclereids present	+	+	+	−	−
*Branched leaf sclereids present	−	−	−	−	−
*Wood vessels mainly in radial multiples	−	+	−	−	+
*Vesturing forming surface bands	+	−	−	−	−
*Vessel-Ray pits coarse, large	−	−	+	−	−
*Septate fibers present	+	−	−	−	+
*Fiber pitting simple to minutely bordered	+	−	−	−	+
*Axial parenchyma scanty paratracheal	+	(+)	−	−	+
Rays heterogeneous I	+	+	−	+	(+)
*Clustered crystals in chambered phloem parenchyma	−	−	−	−	(+)

istics absent from the other genera. From *Crypteronia* and *Axinandra,* it also differs in having anomocytic rather than paracytic stomata and septate fibers with simple pits rather than nonseptate fibers with distinctly bordered pits. From *Dactylocladus,* in addition, it has pericyclic origin of cork and less advanced heterogeneous I-II ray types, while *Dactylocladus* has a subepidermal cork origin and heterogeneous III ray type. There are extensive differences from *Rhyncho-*

TABLE 5. Numerical summary of Table 4 listing of 43 characteristics of *Alzatea* shared with associates.

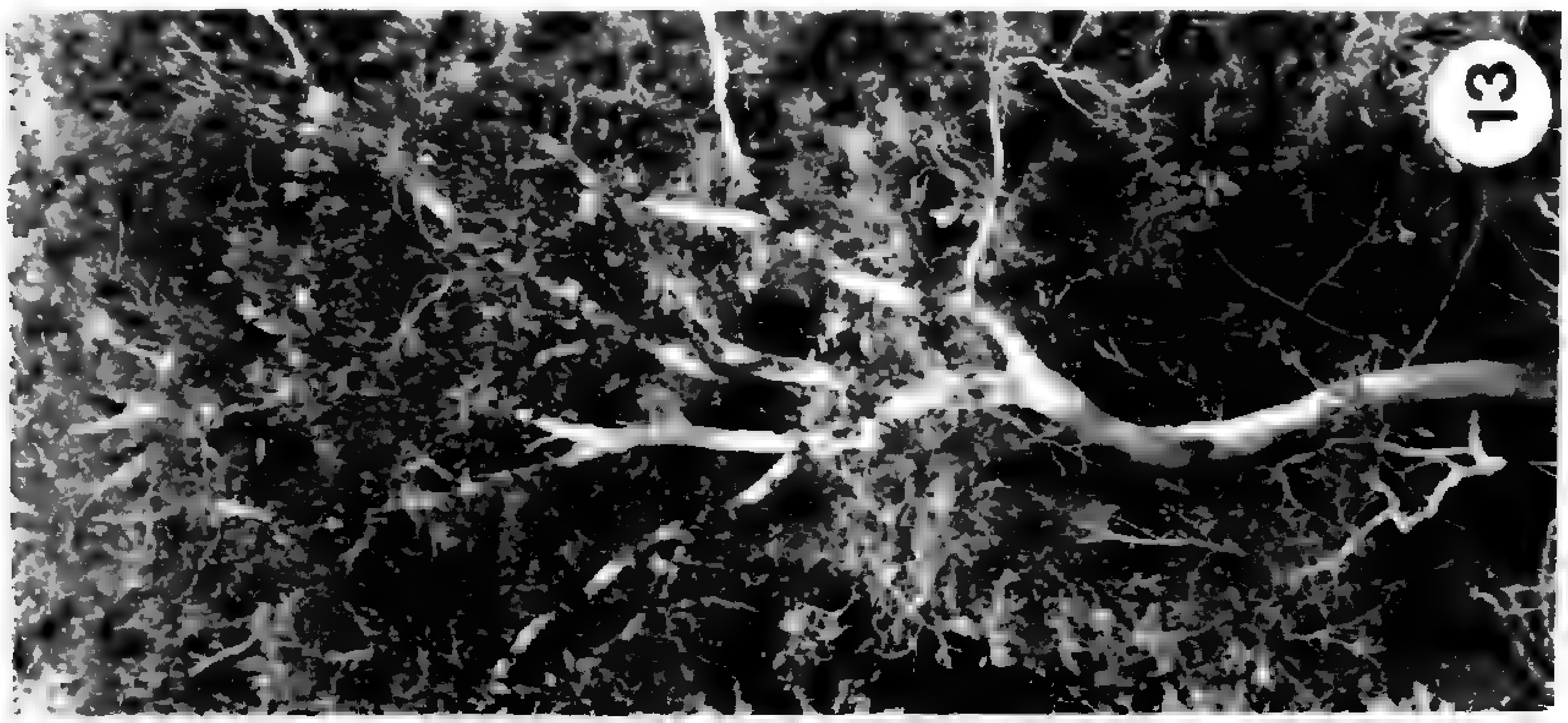
Genus	No. Shared Ancestral	No. Shared Derived	No. Shared in Part	Unknown	Total Wholly Shared	% Shared With *Alzatea*
Rhynchocalyx	10	17	0	0	27	63
Crypteronia	7	11	1—Ancestral 6—Derived	4	18	45
Dactylocladus	7	7	0	5	14	33
Axinandra	5	5	0	1	10	25
Lythraceae	4	6	7—Ancestral 8—Derived	1	10	25

calyx in cuticle texture, mechanical support of the veins, petiole anatomy, and vessel-ray pitting. The coarse, large, reticulate-scalariform vessel-ray pitting contrasts particularly with the small alternate pitting in *Rhynchocalyx*. The two genera are alike in having septate fibers with simple fiber pits, scanty paratracheal parenchyma, and peculiar vesturing of inter-vessel pits which extends beyond the pits in superficial bands. However, only the vesture condition can be considered highly derived; the other two features are typical of unspecialized "protolythraceous" wood (Baas, 1979).

Although there are similarities with Lythraceous anatomy, the trilacunar nodal condition, arrangement of vascular tissue of the petiole and midrib, and banded vesture type are not found in the Lythraceae. Three major features of *Alzatea* wood anatomy, scanty paratracheal parenchyma, heterogeneous rays, and septate fibers with simple pits recall unspecialized wood in Lythraceae. There are also wood anatomical agreements of *Alzatea* with Melastomataceae (e.g., coarse, simple vessel-ray pits), Sonneratiaceae and Oliniaceae, but no particularly close affinities to any one of them and no member of any of these families has most of the characters of *Alzatea*. Anatomical studies have led to the conclusion that *Alzatea* is an isolated remnant of the ancestral stock which gave rise to Lythraceae and Melastomataceae (van Vliet et al., 1981).

TAXONOMIC AND PHYLOGENETIC RELATIONSHIPS

Most recent taxonomic classifications associate *Alzatea* with the genus *Rhynchocalyx* and families Crypteroniaceae or Lythraceae, based on phenetic similarities. The extent of features shared with these associates is demonstrated by Table 4 where 43 selected characteristics of *Alzatea* are listed and their presence or absence in these associates is indicated. Twenty-nine characteristics are derived, 14 are regarded as ancestral. The list underlines the dispersed nature of *Alzatea* attributes in putative relatives and the heterogeneity of the Crypteroniaceae sensu lato. Among the associated genera, *Rhynchocalyx*, with 27 similarities, shares the greatest number of features (Table 5; Figs. 11–14). *Crypteronia*, with a maximum of 24 shared features in *C. paniculata*, but only 18 shared with other species of the genus, is less similar. Knowledge of the embryology of *Crypteronia* should contribute significantly to a more accurate assessment of relationships among the genera *Alzatea*, *Rhynchocalyx*, and *Crypteronia*. *Dactylocladus* and *Axinandra* are more distant, sharing, respectively, only 14 and ten of the 43 characteristics. Crypteroniaceae, as construed by van Beusekom-Osinga and van Beusekom (1975), thus groups a diverse assemblage of genera, with *Alzatea* and *Rhynchocalyx* especially separated by significant gaps from the others. At least 25 characteristics of *Alzatea* can be found in one or more genera of the Lythraceae, but no single genus has many and hence none approach *Alzatea* phenetically. With respect to the relationship of *Alzatea* to its most similar associate, *Rhynchocalyx*, *Alzatea* differs from that genus in 16 of the 43 character states listed. At least four of these are apomorphies unique to *Alzatea*. It is this prominent degree of divergence of *Alzatea* from even its nearest taxonomic neighbor which supports establishment of a new family to accommodate this distinctive taxon. On the same basis, *Rhynchocalyx* is also isolated by a substantial suite of specialized characters and is best treated as a separate family. I earlier stated in personal communications with Dahlgren, 1981 and Briggs, 1982 that the genus belonged to the Lythraceae based on evidence then available. It had been regarded, since first described, as most similar to *Lawsonia* in Lythraceae, primarily due to their superficially similar,



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floriferous, paniculate inflorescences of small white flowers (Strey & Leistner, 1968; Sprague & Metcalfe, 1937). Characters tying it to Lythraceae are now rightly regarded as ancestral ones shared by Melastomataceous and Lythraceous evolutionary lines. New contributions to our knowledge of the genus lead to the conclusion that *Rhynchocalyx* is another relic genus in the Myrtales, without close living relatives. This isolated position is best acknowledged by recognition of the monotypic Rhynchocalycaceae (Johnson & Briggs, 1984).

A phylogenetic study of Myrtales (Johnson & Briggs, 1984), including *Alzatea,* has recently been completed using cladistic methods based on many of the same characters cited in Table 4. In the phylogeny preferred by the authors (their Fig. 3), three major evolutionary groups emerge, the Lythraceae sensu lato–Onagraceae–Trapaceae line, the Myrtaceae–*Heteropyxis–Psiloxylon* line, and an assemblage now recognized as members of the Melastomataceae, Crypteroniaceae, Peneaceae, Oliniaceae, and *Rhynchocalyx* and *Alzatea.* Phylogenetic relationships among the members of this last group are uncertain and several alternative evolutionary schemes are proposed. However, in all phylograms of Johnson and Briggs, *Alzatea* and *Rhynchocalyx* share a common ancestral stem which is, in turn, related to Crypteroniaceae, Peneaceae, and Oliniaceae. Evolutionary relationships of *Alzatea* to modern Lythraceae in their preferred phylogram are seen as distant through ancient common ancestors.

Alzatea appears to have evolved along an independent course over a long period of time, retaining some generalized ancestral features, as in stem anatomy and pollen, while acquiring many specialized attributes. Ultimately, it has come to occupy an isolated position in the order, well separated from its nearest living relative, *Rhynchocalyx.* Its distribution in the wet forests of tropic Andean South America and in Central America further supports an early separation from the ancestral line which produced the East African *Rhynchocalyx* and the East Asian Crypteroniaceae. Homoplasy in taxa of shared ancestral lineage, especially with respect to macromorphological characters, has obscured the extensive divergence of *Alzatea* and is partly responsible, together with the incorrectly placed emphasis on synplesiomorphy, for misdirected ideas of relationship and questionable taxonomic placement. Carefully considered phenetic comparisons and phylogenetic studies concur that *Alzatea* is an isolated genus within the Myrtales, derived from the same ancestral pool which gave rise to the modern Lythraceae, Crypteroniaceae, and Rhynchocalycaceae, but now distinctly separated from them and consequently best treated as a monotypic family.

TAXONOMIC TREATMENT

ALZATEACEAE S. Graham, fam. nov. TYPE: *Alzatea* Ruiz & Pavón.

Arbor glaberrima, ramis verticillatis purpurascentibus. Folia integerrima, coriacea, opposita et verticillata. Inflorescentia paniculata, terminalia, multiflores. Flores bisexuales, 5-meri, apetala, hemi-epigyni. Discus conspicuus, lobatus. Stamina 5, antepetala, margini disci inserta, filamentis brevissimus; antherae cordatae connectivo late expansa ad basi et angustata usque ad apicem; pollinis grana oblata-sphaeroidea, tricolporata, sine colpiis subsidiariis, exinio fere psilato. Ovarium biloculare; dissepimentum incompletum, basi foramene; ovulis in quoque loculo multis, horizontalis, imbricatis. Fructus capsula indurata, lateraliter compressa, nervaturis conspicuis munitus. Semina oblonga ad lunata, plana, circumcirca ala tenui cincta.

This monotypic family of the New World tropics, represented by *Alzatea verticillata,* is distributed along the lower slopes of the Andean Cordillera in Peru and Bolivia in humid forests of the upper Amazonian basin and disjunctly in cloud forests of Costa Rica and Panama. Figure 15.

Alzatea verticillata Ruiz & Pavón, Syst. Veg. Fl. Peruv. Chil. 1: 72. 1798. Fl. Peruv. 3: 20, pl. 141, fig. a. 1802. TYPE: Peru. Huanaco: nemoribus ad Chinchao praeruptum prope Mesapata praeditum (holotype, MA, pho-

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FIGURES 11–14. *Rhynchocalyx lawsonioïdes* Oliv., Natal, South Africa, closest living relative of *Alzatea.*—11. Flowering specimen, *H.B. Nicholson s.n.* (MO).—12. Tree in bloom, edge of forest adjoining Table Mountain, Uvongo Nature Reserve.—13. Typical small tree habit with erect trunk to 6 m in height; bark pale gray, Uvongo Nature Reserve.—14. Inflorescence, flowers primarily in bud, actual bud length, 3–4 mm; actual leaf length, 25–75 mm.

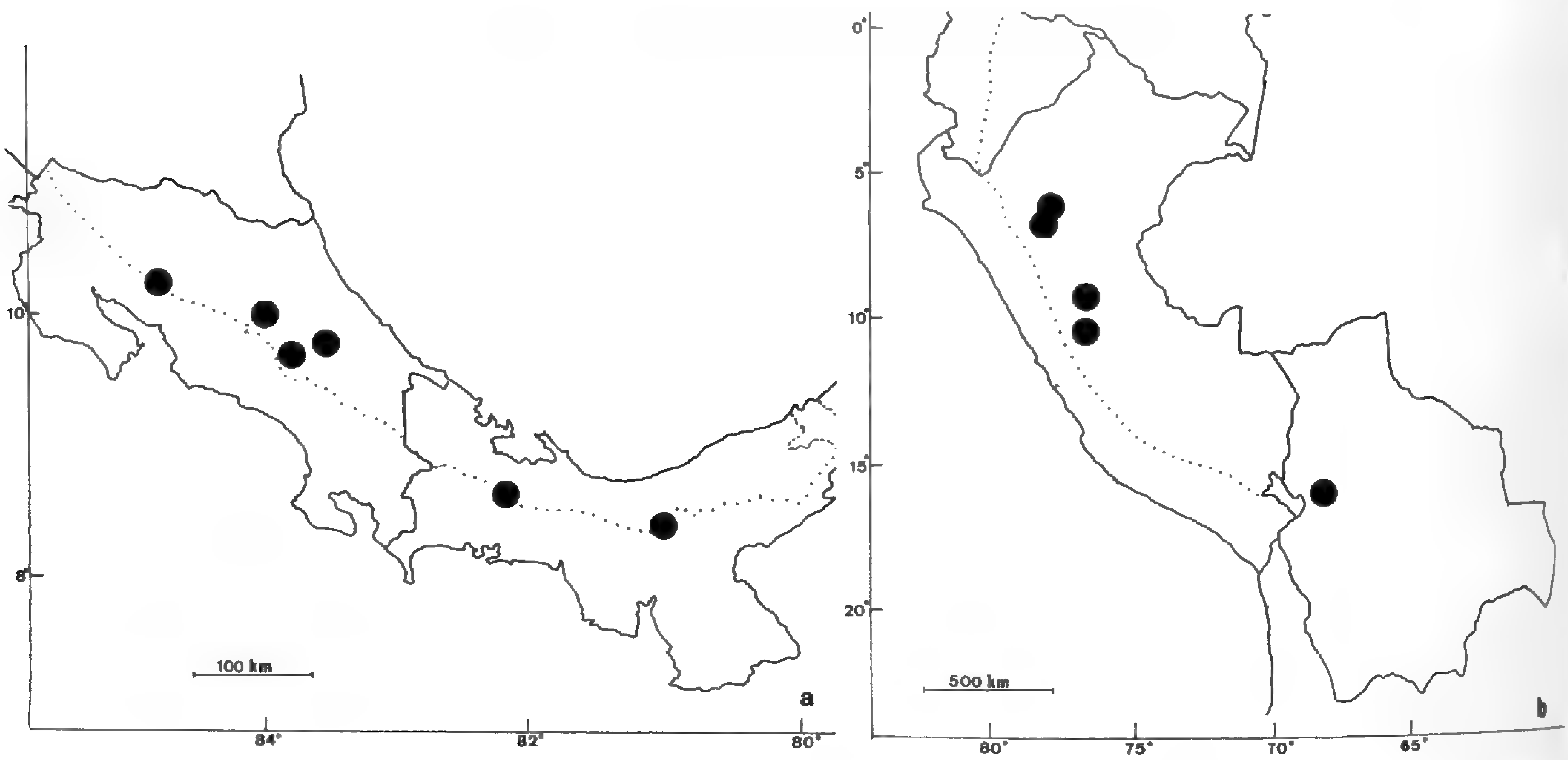

FIGURE 15. Distribution of *Alzatea verticillata*.—a. Subsp. *amplifolia* in Costa Rica and Panama.—b. Subsp. *verticillata* in Peru and Bolivia. Dotted line represents the continental divide.

tograph at F no. 91664!; isotypes, F no. 1573979!, F no. 843533!).

Alzalia mexicana F. G. Dietrich, Vollst. Lex. Gärtn. 1: 299. 1802. Nachtr. Vollst. Lex. Gärtn. 1: 199. 1815. Neu. Nachtrg. Vollst. Lex. Gärtn. 1: 187. 1825. TYPE: Based on *A. verticillata* Ruiz & Pavón.

1a. Alzatea verticillata subsp. verticillata.

Leaves elliptical or oblong-obovate, averaging 66 mm long, 35 mm wide, basally attenuate; petioles 2–13 mm long. Peru and Bolivia. Figures 9, 15a.

Additional specimens (those not mapped in Fig. 14 due to insufficient locality data are marked with an asterisk). BOLIVIA. Songo (= Zongo Valley), Nov. 1890, *Bang 829* (K, MO!, NY, US); PERU. AMAZONAS: *Cerro de Escalero, 1,300 m, Feb. 1903, *Ule 6750* (K); Mendoza, 1,600 m, 15 Aug. 1963, *Woytkowski 8331* (F!, MO!). PASCO: Oxapampa Alto Vaqueria, 2,200 m, 11 Aug. 1967, *Vasquez A. 114* (F!), 21 Nov. 1967, *Vasquez A. 136* (F!). SAN MARTÍN: Zepelacio, near Moyobamba, 1,100–1,200 m, Oct.–Nov. 1933, *Klug 3349* (GH, F!, K, MO!, S). UNKNOWN: *Santa Ana, Pitabamba, Nov. 1866, *Pearce s.n.* (K); *Río Negro, in the forest, 1,000 m, 15 Jan. 1961, *Woytkowski 6196* (MO!, P).

1b. Alzatea verticillata subsp. amplifolia S. A. Graham, subsp. nov. TYPE: Panama. Veraguas: Cerro Túte, 20 Mar. 1982, *Knapp & Kress 4336* (MO).

Folia oblonga-ovalia, ad 145 mm longa, 100 mm lata, saepe ca. 90 mm longa, 65 mm lata, basi pleraque rotundata, sessilia vel subsessilia, petioli 0–2 mm longi. Costa Rica et Panama. Figures 10, 15b.

Additional specimens (those not mapped in Fig. 14 due to insufficient locality data are marked with an asterisk). COSTA RICA. CARTAGO: 0.5 km W of Tapantí, 1,200 m, 14 May 1967, *Lent 966* (CR!, F!), 28 Jan. 1982, *Poveda et al. 3264* (CR!), Oct. 1982, *Gomez 18728* (CR!); Moravia de Chirripó, 28 Jan. 1977, *Poveda & Sieng 1523* (CR!). PUNTARENAS: Flora de Monteverde, cerro N of Pantano Chomogo, 1,620–1,690 m, 15 Jan. 1977, *Dryer 1133* (CR!, F!). SAN JOSÉ: Bajo La Hondura, above Río Hondura, 1,400 m, 22 Oct. 1967, *Lent 1443* (CR!, F!), 20 June 1973, *Poveda 566* (CR!), 24 Mar. 1977, *Poveda 1564* (CR!). UNKNOWN: *La Palma, 1,500 m, 31 July 1936, *Valerio 1403* (F!); *Quebrada Cuecha, 1,540–1,600 m, *Dryer 941* (CR!). PANAMA. CHIRIQUÍ: 15 km N of Hornito, 17 Feb. 1979, *Hammel 6247* (MO!), 12 km N of Hornito, 17 June 1982, *Knapp & Vodicka 5532* (MO!). VERAGUAS, N of Santa Fe, slopes and peaks of Cerro Arizona (= Cerro Túte), 11 Sept. 1978, *Hammel 4726* (MO!); Summit of Cerro Túte, 1,410 m, 5 June 1982, *Knapp & Dressler 5392* (MO!).

Comparison of the South American and Central American collections reveals two character differences consistent with geographical source and significant enough to deserve formal taxonomic recognition. Costa Rican and Panamanian plants have ample, broad, generally oblong to oval, sessile leaves and those of South America have smaller, narrower, generally more elliptic, petiolate ones. The mean size of Central American leaf specimens is 89 mm by 63 mm; leaves are sessile or subsessile with petioles 2 mm long or less. The mean size of South American leaves is 66 mm by 35 mm; leaves are basally attenuate, petiolate to subsessile with petioles varying from (0–)2–13 mm long, averaging 6 mm. Leaves of the type collection from Peru average 91 mm by 59 mm with petioles 10–12 mm long. On the Bolivian collection examined, leaves average only 57 mm by 33 mm and are mostly sessile. No floral morphological differences separate the Central and South American collections and Baas (1979) found no striking anatomical differences between Peruvian and Costa Rican samples. As more collections of the genus are gathered, perhaps even from the intervening areas of Ecuador, Colombia, and the Darien, it may well become more difficult to apply subspecific names. Based on present collections, however, recognition of subspecies *amplifolia* serves to point up the genetic divergence now expressed in the disjunctly distributed Central and South American plants.

It is possible that a discriminatory biological difference exists between Central and South American *Alzatea*. South American plants surveyed produce heterosexual flowers with pollen viability greater than 95%. In contrast, Central American plants appear to bear only functionally unisexual flowers. No fertile pollen has been found in flowers from Cerro Túte, Panama collections, although approximately 50% of the seed in each capsule appears fully formed. In Costa Rican collections studied, no more than 36% of the pollen appeared normal (Tobe, pers. comm.; Graham, unpubl. data). Investigations are in progress to determine the nature of reproduction in the Panama population (Raven, pers. comm.).

Description of the habit and habitat of the genus are known primarily from collectors' brief notations, mostly on herbarium labels. New observations, however, are rapidly accumulating on Central American *Alzatea* as a result of active research by members of the Missouri Botanical Garden currently working on the Central American flora. *Alzatea* is described in Ruiz's journal (1940) as a tall leafy tree with "a trunk divided into six thick props that formed an arbor underneath." Disparately, it is described as a slender, climbing epiphyte reaching the crowns of the largest trees of the lower montane rain forest in Costa Rica (R. Lawton, pers. comm.) or as isolated, small (ca. 7 m tall), much-branched trees (Poveda, pers. comm. to Raven). In Panama it occurs as a 2–3 m shrub of windswept elfin cloud forest in Veraguas Province (*Knapp & Kress 4336*, MO), as a stream-side epiphytic shrub in Chiriquí Province (*Hammel 6247*, MO), and has been observed also in Chiriquí Province growing epiphytically in tall trees of the forest (Knapp, pers. comm.). Height records vary from 2 m to 20 m and it is apparent that habit varies considerably with site conditions. The typical form is probably a much-branched hemi-epiphytic tree of 6–12 m which is capable of climbing to greater heights with support of surrounding trees when it occurs in tall tree forests. Trunk diameter ranges from 5 cm in high-climbing specimens to 20 cm (to 80 cm in Costa Rica, fide Poveda) on free-standing trees.

It occurs typically on steep slopes of the low montane rain forest at elevations of 1,000–2,200 m either as isolated individuals or, in at least two instances, at Cerro Túte, Panama and Tapantí, Costa Rica, as a locally common component of the flora. In South America the genus appears on the eastern escarpment of the Andean Mountains. In both Central and South America it occurs with and is easily mistaken for *Clusia*. The striking vegetative similarity between *Alzatea* and *Clusia* has led curators to file the unfamiliar *Alzatea* with the Clusiaceae (Guttiferae); curators of Latin American collections are advised to check that family as well as the Celastraceae for undetected specimens of *Alzatea*.

Flowering of the genus in Peru occurs from August to October; mature capsules occur from November onward. The single collection from Bolivia was in bud in November. Collections indicate that in Costa Rica, flowering begins in July and mature fruits are present from January to May, while in Panama buds have been collected in March and in August, suggesting less seasonally restricted flowering.

Production of nectar has not been observed (Knapp, pers. comm.) nor have insect visitors been reported. In the absence of petals, the showy pinkish white anthers may function to attract insects. The anthers are positioned, as petals would be, between the calyx lobes at anthesis and are sometimes mistaken by collectors for petals. The most recent observations of living plants have been on the Cerro Túte, Panama, a windy site with frequent cloud cover where conditions are not often conducive to insect visitation.

Seed containing embryos generally constitute less than half the seed produced. Lack of pollination may partially account for this, but in the Central American populations low pollen fertility is certainly a factor. Studies of the reproductive biology should lead to a better understanding of how *Alzatea* has managed to retain its place in the flora of the New World tropics.

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A COMMENTARY ON THE DEFINITION OF THE ORDER MYRTALES

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ABSTRACT

I concur in the delimitation of the order Myrtales proposed by Dahlgren and Thorne (this symposium), except for the position of the Thymelaeaceae, which they exclude. The Thymelaeaceae are chemically discordant with the Myrtales, but they cannot reasonably be attached to any other order as now constituted. The ancestors of the Thymelaeaceae, at some level, were probably tanniferous as are the modern Myrtales. Thus an evolutionary approach does not require that the Thymelaeaceae be dissociated from the Myrtales because of the chemical differences. Instead we face the question of how best to provide for the admitted differences within the framework of the taxonomic system. I find it more useful to retain the Thymelaeaceae in the Myrtales as a somewhat aberrant group than to establish a satellite order composed of a single family.

It appears that among the participants in this symposium there is substantial agreement on the limits of the Myrtales, with the single exception of the family Thymelaeaceae. The Combretaceae, Crypteroniaceae, Lythraceae, Melastomataceae, Myrtaceae, Oliniaceae, Onagraceae, Penaeaceae, Punicaceae, Sonneratiaceae, and Trapaceae, all of which have traditionally been referred to the Myrtales, are still kept there, although some of us would reduce some of these groups to less than familial status. The Cynomoriaceae, Dialypetalanthaceae, Haloragaceae, Hippuridaceae, Lecythidaceae, Rhizophoraceae, Theligonaceae, and other families that have been included by some authors in the past are properly to be excluded.

My esteemed colleague Academician Takhtajan would add only three families, the Haloragaceae, Lecythidaceae, and Rhizophoraceae, to the list of those included by Dahlgren and Thorne (1984). In his most recent system, Takhtajan (1980) puts each of these three families into a separate suborder, in contrast to the suborder Myrtinae for all the other families. Thus his suborder Myrtinae is functionally equivalent to the order Myrtales as discussed here.

It is interesting and perhaps significant that this degree of agreement has been achieved by several different individuals or groups working more or less independently of each other, although of course not in intellectual isolation. My own treatment was in the hands of the publisher before I saw the manuscript by Dahlgren and Thorne. As new information continues to accumulate, the range of taxonomic schemes that can reasonably be defended is progressively narrowed.

It is also interesting that two of the characters which have played a large role in reshaping the definition of the Myrtales are anatomical: internal phloem, and vestured pits in the vessels. It is only in the last several decades that enough information has become available about the taxonomic distribution of these features both within and without the Myrtales to permit any reliance to be placed on them. We cannot claim to be better taxonomists than our predecessors, but we do have more data to work with.

The position of the Thymelaeaceae remains debatable. On this issue I reluctantly part company with Dahlgren and Thorne. I include this family, somewhat doubtfully, in the Myrtales, whereas they exclude it, also somewhat doubtfully. The necessity to make a choice for purposes of a formal system magnifies the relatively small disagreement between us.

Dahlgren and Thorne (1984) present a considerable list of similarities between the Thymelaeaceae and typical Myrtales, including the usual presence of internal phloem. The vestured pits of the vessels should be added to their list. The evidently pseudomonomerous gynoecium of typical Thymelaeaceae sets the family apart from the rest of the Myrtales, but it does not argue against a relationship. Rather it directs our search for affinities (or at least for a plausible ancestry) to families with a compound pistil rather than to families with simple pistils.

There is a special problem here in that the Elaeagnaceae, with which the Thymelaeaceae

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ANN. MISSOURI BOT. GARD. 71: 780–782. 1984.

share some features, appear to have a simple pistil. Yet as Dahlgren and Thorne (1984) point out, there is no inherent reason why the number of carpels could not ultimately be reduced to one in a syncarpous as well as in an apocarpous gynoecium. Indeed that very thing seems to have happened in the Cucurbitaceae. If the Thymelaeaceae were to be associated with the Elaeagnaceae, then it would have to be assumed that the pistil of the Elaeagnaceae became monomerous by reduction. The two families would then have to form an order of their own; collectively they would spoil any other order into which they were put. It is possible that future evidence will support such an association of these two families, but in my opinion the balance is now against it.

The principal argument that Dahlgren and Thorne (1984) adduce against a position of the Thymelaeaceae in the Myrtales is chemical. There is no doubt that the Thymelaeaceae stand apart from the rest of the order in this regard. The question is what evolutionary and taxonomic significance to attach to the difference.

Unlike the other Myrtales, the Thymelaeaceae are not tanniferous, and they characteristically accumulate daphnin and allied compounds, which are simple coumarins. Simple coumarins are widespread among the angiosperms, but apparently not in the Myrtales. Daphnin and its immediate chemical allies are almost entirely restricted to the Thymelaeaceae, so far as present information shows. One species of *Euphorbia* has been reported to contain daphnetin (a daphnin-type compound), but it does not seem reasonable to lay great stress on such a single occurrence in an advanced genus of a family that is chemically so diversified. Furthermore, the Euphorbiaceae, like the Myrtales, are commonly tanniferous, and if this difference can be minimized in assessing a possible relationship to the Euphorbiaceae, it can also be minimized in assessing a possible relationship to the Myrtales. There are several other chemical and morphological features (e.g., phorbol-type diterpenoids, crotonoid pollen) that link some members of the Thymelaeaceae to some members of the Euphorbiaceae, but these similarities are taxonomically scattered rather than being pervasive.

Any attempt to associate the Thymelaeaceae with the Euphorbiaceae must confront the fact that these two families display different sets of advanced features, suggesting only a fairly remote common ancestry. Thus the Thymelaeaceae characteristically have internal phloem, vestured pits, daphnin, wedge-shaped phloem rays, more or less strongly perigynous, mostly perfect flowers, and well developed, often petaloid sepals, all of which are unusual or wanting in the Euphorbiaceae. The Euphorbiaceae, on the other hand, tend to be laticiferous and have mostly unisexual, more or less strongly reduced flowers with an obturator of different nature from that in the Thymelaeaceae. The Euphorbiaceae are so highly diversified, especially in chemical and vegetative features, that individual, ultimately meaningless links to many other families can be found in particular features of particular genera. I don't suppose that anyone wants to use the presence of mustard oils in *Drypetes* to warrant the inclusion of the Euphorbiaceae in the Capparales.

According to a hypothesis of chemical evolution that I proposed in 1977, the subclasses Hamamelidae, Dilleniidae, and Rosidae are all primitively tanniferous, producing ellagic acid and other tannins. Subsequent evolution within these subclasses and in the derived subclass Asteridae led to the substitution of other chemical repellents for tannins in many groups. A similar hypothesis was proposed at about the same time by Gardner (1977), who visualized a "gradual replacement of a defence based on tannins and crystals (primitive Rosidae) by defences based on a variety of toxic and repellent substances (advanced Asteridae)." Under this concept, the ancestors of the Thymelaeaceae, at some level, were tanniferous. Thus the chemical evidence alone does not preclude the origin of the Thymelaeaceae from within the Myrtales. The taxonomic level at which the Thymelaeaceae should be recognized is debatable, but their ultimate attachment to a tanniferous group is inevitable.

In a symposium concerned only with the limits of the Myrtales, I suppose it might be possible to exclude the Thymelaeaceae from the Myrtales as a discordant element. Being concerned with the general taxonomic system, I am not satisfied to exclude the Thymelaeaceae from the Myrtales unless I have a better place to put them. They would be an even more discordant element in any other order as presently constituted (at least in the Cronquist system, which is necessarily my frame of reference). The possibility of a future association with the Elaeagnaceae cannot be entirely discounted, but the Elaeagnaceae are just as strongly tanniferous as the Myrtales. Exclusion of the Thymelaeaceae from the Myrtales on chemical grounds would logically preclude association of the Thymelaeaceae with the Elaeagnaceae.

Thus, if the Thymelaeaceae are to be excluded from the Myrtales, they must form an order of their own. I cannot really argue with anyone who chooses that alternative, as Takhtajan (1980) has done. It is a matter of lumping or splitting, in which there is no objective right or wrong. Inclusion of the Thymelaeaceae in the Myrtales does not complicate the distinction of the Myrtales from other orders. Therefore I find it conceptually more useful to tolerate this somewhat discordant family in the Myrtales than to tolerate still another order consisting of a single family.

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WOOD ANATOMY AND CLASSIFICATION OF THE MYRTALES[1]

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ABSTRACT

The wood anatomical diversity of the woody Myrtales, comprising Combretaceae, Lythraceae (including Alzatea), Melastomataceae (including Crypteroniaceae), Myrtaceae, Oliniaceae, Onagraceae, Penaeaceae, Punicaceae (can also be included in Lythraceae), Psiloxylaceae, Sonneratiaceae and also Thymelaeaceae, is summarized. All these families share intraxylary phloem and vestured pits, and their other wood anatomical attributes represent parts of continuous, sometimes divergent, often parallel, specialization series. Rhizophoraceae, Lecythidaceae, Elatinaceae, Cordiaceae, Chrysobalanaceae and Dialypetalanthaceae are excluded because they lack this combination of characters. The phylogenetic relationships within Myrtales are discussed, and pictured in a two-dimensional diagram (Figs. 2–8). Most families are mutually closely related. The wider wood anatomical affinities of the order are with Gentianales.

Features from vegetative anatomy such as bicollateral bundles and vestured pits in the wood have entered discussions on the delimitation and classification of the order Myrtales for a long time. In this paper the entire evidence from wood anatomy will be applied to these taxonomic aspects. The knowledge of the wood anatomy of truly or putatively Myrtalean families has considerably increased in recent years (see references cited under the summarized wood anatomical descriptions) so that a discussion of its taxonomic implications can be meaningful. Our paper cannot, unfortunately, take wholly herbaceous families such as Haloragaceae and Trapaceae into consideration. For a survey of all families that have, from time to time, been assigned to the order Myrtales, the reader is referred to Dahlgren and Thorne (1984).

DELIMITATION OF THE ORDER MYRTALES

All families that have been and are currently regarded as indubitable members of the Myrtales are characterized by a combination of two anatomical features: vestures in the bordered pits of the secondary xylem, and bicollateral bundles in the primary stems (and leaves as far as major bundles are concerned), resulting in the presence of intraxylary or internal phloem in woody stems (not to be confused with interxylary or included phloem, which occurs in a restricted number of genera and families of the order only). Several authors have also used one or both of these characters in their delimitation of the order.

Vestured pits and intraxylary phloem are rather uncommon in the Dicotyledons, as can be seen in Figure 1, where the distribution of these characters is illustrated using Dahlgren's (1980) diagrammatic classification. The data are derived from Metcalfe and Chalk (1950), completed for recent records of vestured pits by Meylan and Butterfield (1974), Miller (1977), and Baas and Werker (1981).

The combined occurrence of vestured pits and intraxylary phloem appears to be very rare. Outside the Myrtales both features are found only in part of the Gentianiflorae (Apocynaceae, Asclepiadaceae, Loganiaceae pro parte) and in the Thymelaeales (Thymelaeaceae only) of Dahlgren's Malviflorae where the two characters are further only of very sporadic occurrence in the Euphorbiaceae, and then not even simultaneously present in the same genera (Bailey, 1933; Metcalfe & Chalk, 1950). Other combined occurrences are limited to Vochysiaceae (Polygalales) and the single genus *Centropodium* of the Polygonaceae (Polygonales).

The sporadic occurrence of the two features outside the Myrtales as understood by us and Dahlgren and Thorne (1984), and their very con-

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[1] Prof. Dr. C. Kalkman critically read the manuscript. Mr. J. van Os prepared the drawings. In connection with the research project on the wood anatomy of the Myrtales, concluded with this paper, the first author was over the years 1975–1977 financially supported by the Netherlands Organisation for the Advancement of Pure Research (Z.W.O.).

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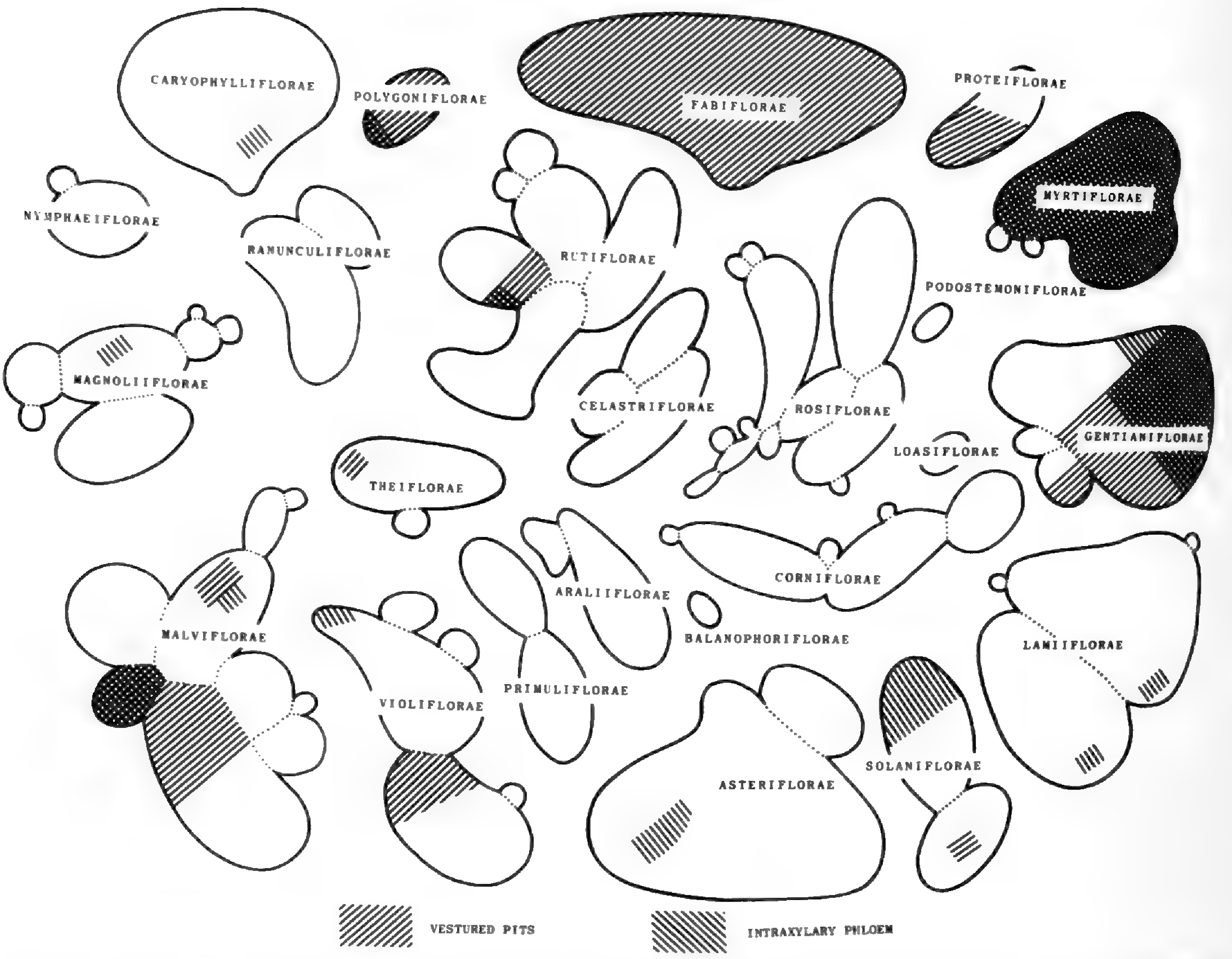

FIGURE 1. Distribution of vestured pits and intraxylary phloem in the Dicotyledons, projected on Dahlgren's classification system (1980). The cross-hatched part of the Malviflorae represents the Thymelaeaceae, in this paper referred to Myrtales.

stant presence within the order, strengthen the value of these characters for the delimitation of the Myrtales. Thus, Rhizophoraceae, Lecythidaceae, Elatinaceae, Cordiaceae, Chrysobalanaceae, Dialypetalanthaceae, Elaeagnaceae and Geissolomataceae, which lack intraxylary phloem and vestured pits, are not considered to belong to Myrtales. The record of vestured pits in Dialypetalanthus by Rizzini and Occhioni (1949) needs confirmation; in a wood sample we studied, vesturing is not obvious, but SEM studies should be carried out to verify this. These families also do not recall true Myrtales in other combinations of wood anatomical features (cf. van Vliet, 1976b, on Rhizophoraceae; Rizzini & Occhioni, 1949, on Dialypetalanthaceae; Carlquist, 1975a, on Geissolomataceae; and family descriptions in Metcalfe & Chalk, 1950, for other families). Thymelaeaceae, incorporated in Myrtales by Cronquist (1968, 1981) but treated in Malviflorae or Malvaneae as a separate order by Takhtajan (1980) and Dahlgren (1980), do share internal phloem and vestured pits with Myrtales and will later in this paper be compared with the 'core families' of the order. These are: Combretaceae, Lythraceae (including *Rhynchocalyx* and *Alzatea*), Melastomataceae (including *Crypteronia, Dactylocladus,* and *Axinandra*), Myrtaceae (including *Heteropyxis*), Oliniaceae, Onagraceae, Penaeaceae, Psiloxylaceae, Punicaceae (could also be included in Lythraceae, cf. Thorne, 1976; Baas & Zweypfenning, 1979), and Sonneratiaceae.

WOOD ANATOMICAL CHARACTERS OF THE MYRTALES

On the taxonomic level of the order one should not expect to be able to provide a concise wood anatomical diagnosis. Yet the major wood anatomical features will be reviewed in order to paint at least a sketchy portrait of the wood anatomy

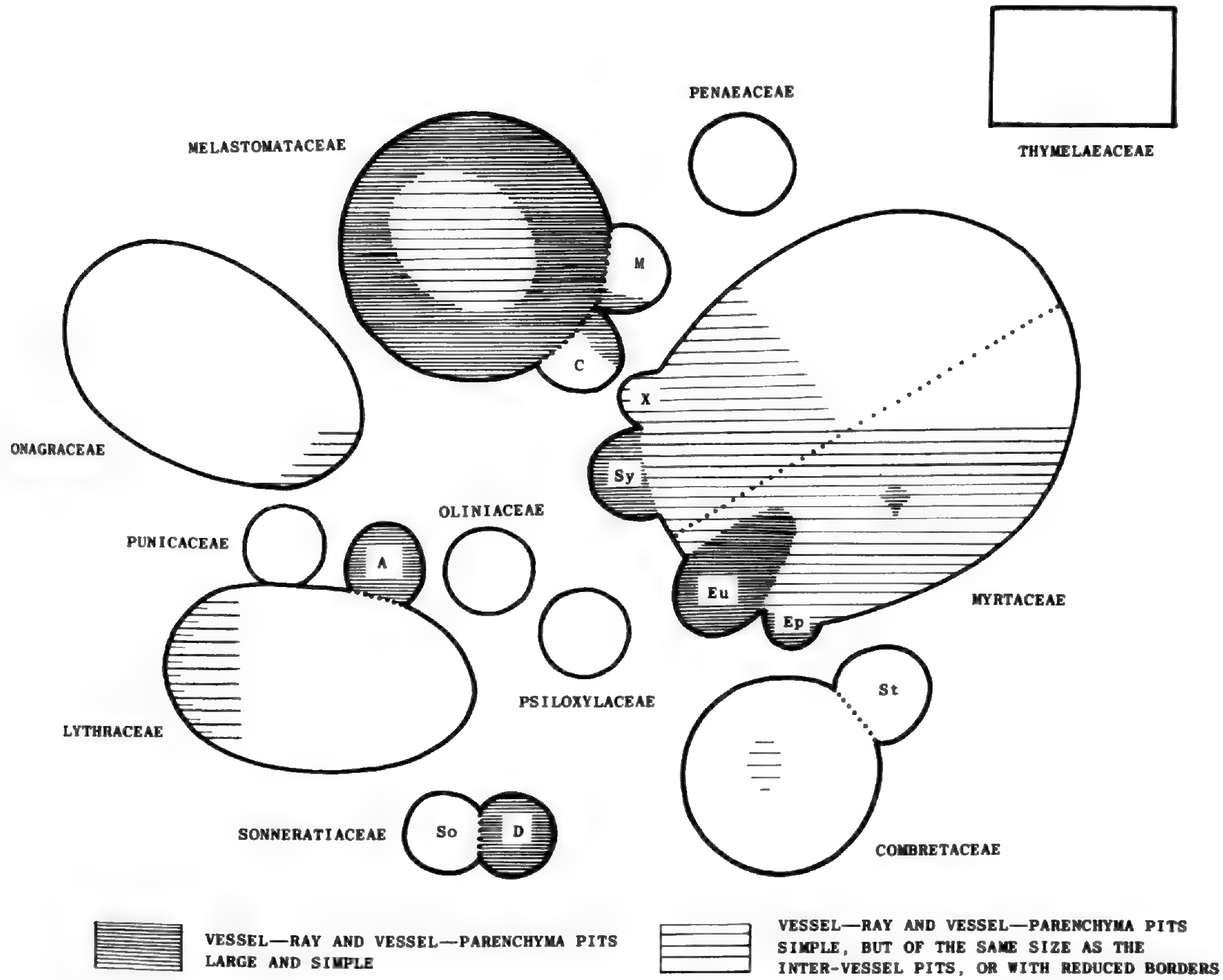

FIGURE 2. Diagram illustrating wood anatomical affinity patterns in the woody Myrtales. Entirely herbaceous families (Trapaceae and Haloragaceae) not considered. Position of Thymelaeaceae uncertain. Distribution of major types of vessel–ray and vessel–parenchyma pits (white areas represent half-bordered pits). A = *Alzatea*; C = Crypteronioideae; D = *Duabanga*; Ep = *Eucalyptopsis*; Eu = *Eucalyptus* pro parte; M = Memecyloideae; So = *Sonneratia*; St = Strephonematoideae; Sy = *Syzygium* sensu lato; X = *Xanthomyrtus*.

of the Myrtales. Thymelaeaceae will not be included in this survey. Constant for the whole order are vestured pits and intraxylary phloem as mentioned before. The other characters show various degrees of diversity.

Vessels. A number of Myrtales (most Myrtaceae, Penaeaceae, Memecyloideae of the Melastomataceae, Strephonematoideae of the Combretaceae) have almost exclusively solitary vessels; this feature is always associated with a ground tissue of fiber-tracheids. The other Myrtales have a mixture of vessels solitary and in radial multiples. Perforations are almost always simple except for very few Myrtaceae that have scalariform plates. Inter-vessel pitting is almost always alternate, and if deviating from this type (some Melastomatoideae and Onagraceae), the elongated pits must be considered derived from the isodiametric alternate pits (van Vliet, 1981; Carlquist, 1975b). Vessel–ray and vessel–parenchyma pits vary widely from half-bordered to large and simple. *Vasicentric tracheids* are typical for most Myrtaceae, and some Combretaceae and Lythraceae show vascular tracheids and/or narrow vessels associated with the normal vessels. *Fibers* either have distinctly bordered pits and are non-septate (fiber-tracheids; see list of Myrtales with solitary vessels above) or more commonly are often septate and have simple to minutely bordered pits confined to the radial walls (libriform fibers). Fiber dimorphism, presumably culminating in parenchyma development (i.e., phylogenetically, *not* ontogenetically) occurs in many Melastomatoideae, some Lythraceae, and weakly in Punicaceae. *Parenchyma* is most typically scanty paratracheal (this type oc-

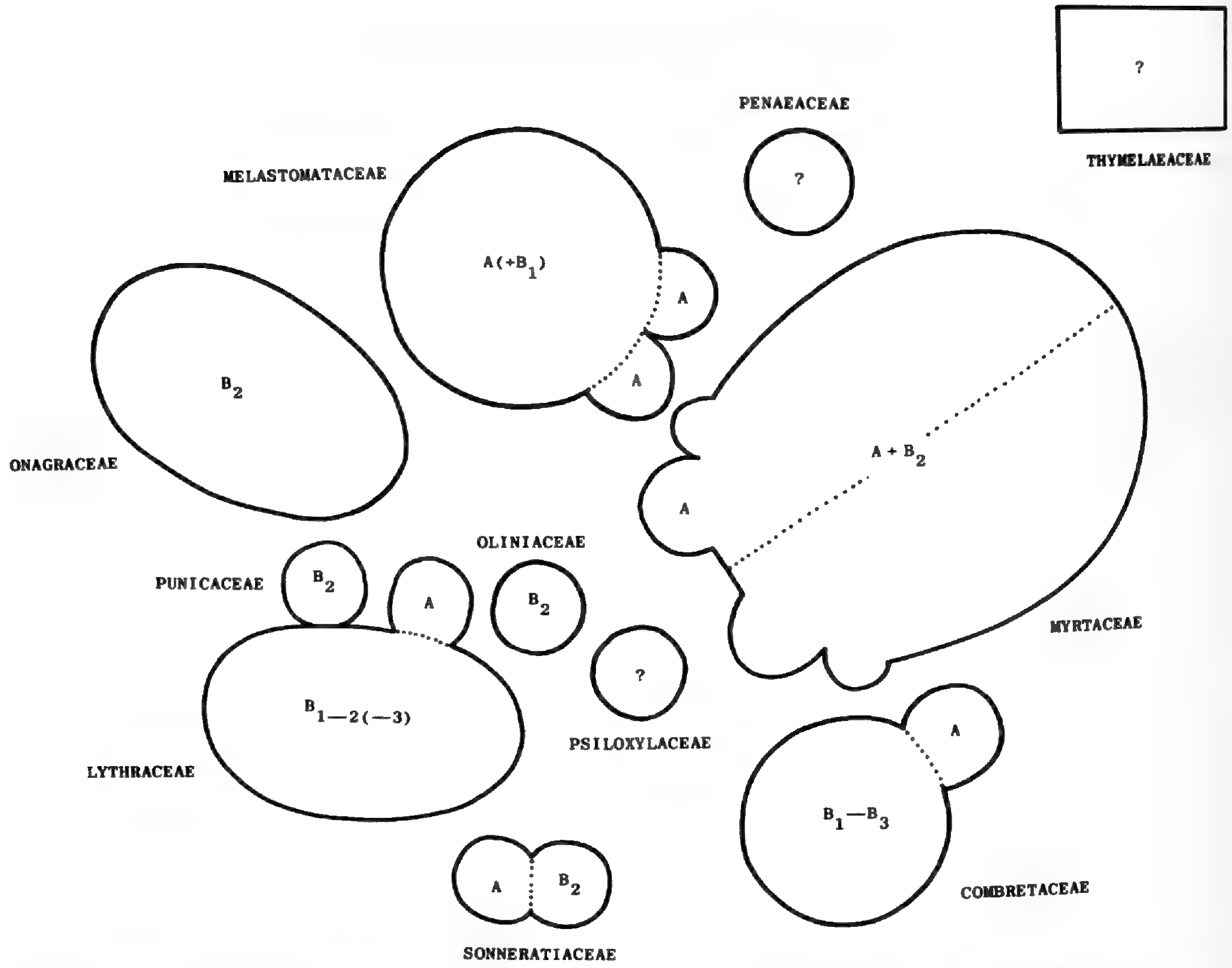

FIGURE 3. Distribution of various types of vestured pits according to van Vliet's classification (1978) in Myrtales. Families not studied are queried. See also legend to Figure 2; in the case of *Alzatea*, A stands for both the genus name and the type of vesturing.

curs in *all* families); in addition, it may be apotracheally diffuse or in narrow, short to continuous broad bands in some representatives; if more abundantly paratracheal it varies from vasicentric, aliform to confluent, to paratracheally banded; most families are heterogeneous with respect to parenchyma distribution. *Rays* also vary, and very often they do not fit into one of the types defined by Kribs (1968), but contain exclusively square to erect cells; in most taxa with heterogeneous ray tissue the central cells are only weakly procumbent. Heterogeneous rays, type I–III and homogeneous rays occur in a minority of genera. The unique feature of radial vessels is entirely restricted to tribe Combreteae sensu van Vliet (1979). Included or *interxylary phloem* occurs in part of the Onagraceae, Combretaceae (Combreteae pro parte) and Melastomataceae (all Memecyloideae sensu van Vliet, 1981). *Crystal types* and distribution are quite diverse in the order and include some unusual forms, which may be highly diagnostic for some restricted groups. Raphides occur in some Onagraceae and one species of the Melastomataceae. Small elongate to styloid-like crystals occur in some Myrtaceae, Combretaceae and Onagraceae; megastyloids occur in one tribe of the Melastomatoideae. Clustered crystals or druses are on record for some Combretaceae, Melastomatoideae, Myrtaceae and Penaeaceae. Rhomboidal crystals are fairly common either in the axial parenchyma or the ray cells; in some Combretaceae, Myrtaceae and Onagraceae they can be large and confined to enlarged idioblasts. Rhomboidal crystals in chambered fibers are typical for a number of Lythraceae, Punicaceae and Psiloxylaceae. Many Myrtales completely lack crystals in their wood. *Silica grains* are almost entirely restricted to part of the Myrtaceae, and are of very sporadic occurrence in the Combretaceae.

Carlquist and Debuhr (1977) included, besides

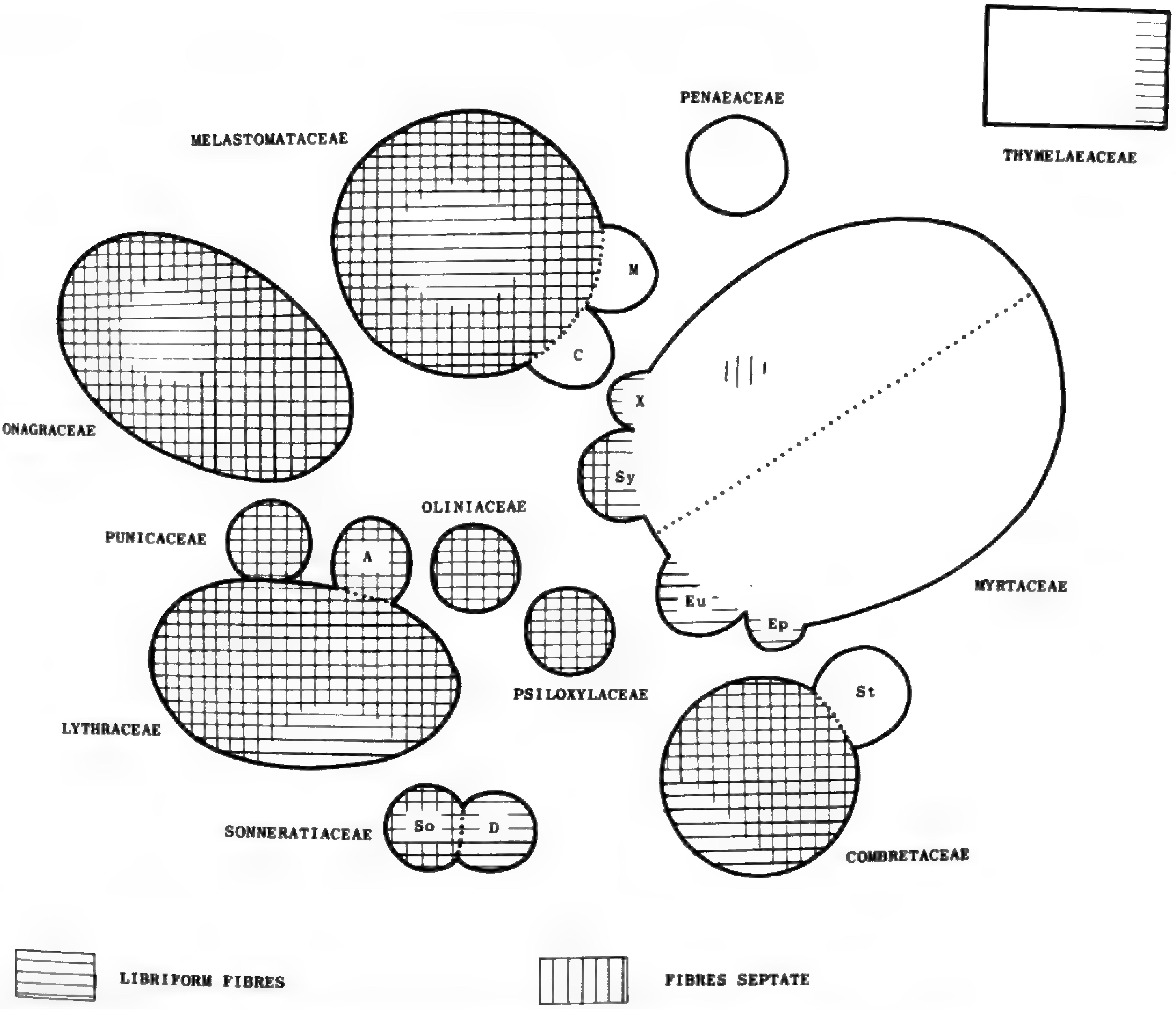

FIGURE 4. Distribution of libriform septate fibers in Myrtales. See also legend to Figure 2.

vestured pits and intraxylary phloem, the presence of crystalliferous strands in axial xylem, in their definition of the order Myrtales. We cannot support this, because so many genera entirely lack crystals, while in some taxa (e.g., *Sonneratia*) crystals are restricted to the ray system. Moreover, one should not equate such diverse types as raphides, styloids, druses and rhomboidal crystals. Presence of amorphous contents in ray cells also cited by Carlquist and Debuhr as a typically Myrtalean feature is probably too aspecific to be useful.

SUMMARIZED WOOD ANATOMICAL DESCRIPTIONS OF THE FAMILIES

(These do not include the common features such as vestured pits, or statements on the absence of unusual features. Type of vesturing is left out, because of incompleteness of data, but will be discussed in a later section.)

COMBRETACEAE

The two subfamilies Combretoideae and Strephonematoideae are wood anatomically very different, necessitating separate descriptions. For the tribal delimitation of Combreteae as followed here see van Vliet (1979). His Combreteae correspond to the subtribe Combretineae in Exell and Stace's classification (1966; van Vliet, 1976a, 1979).

Combretoideae. Included phloem of the foraminate type restricted to some genera of the tribe Combreteae. *Vessels* diffuse (wood rarely ring-porous or semi-ring-porous), solitary and/or in radial multiples (in Combreteae the normal vessels are mixed with very narrow vessels and

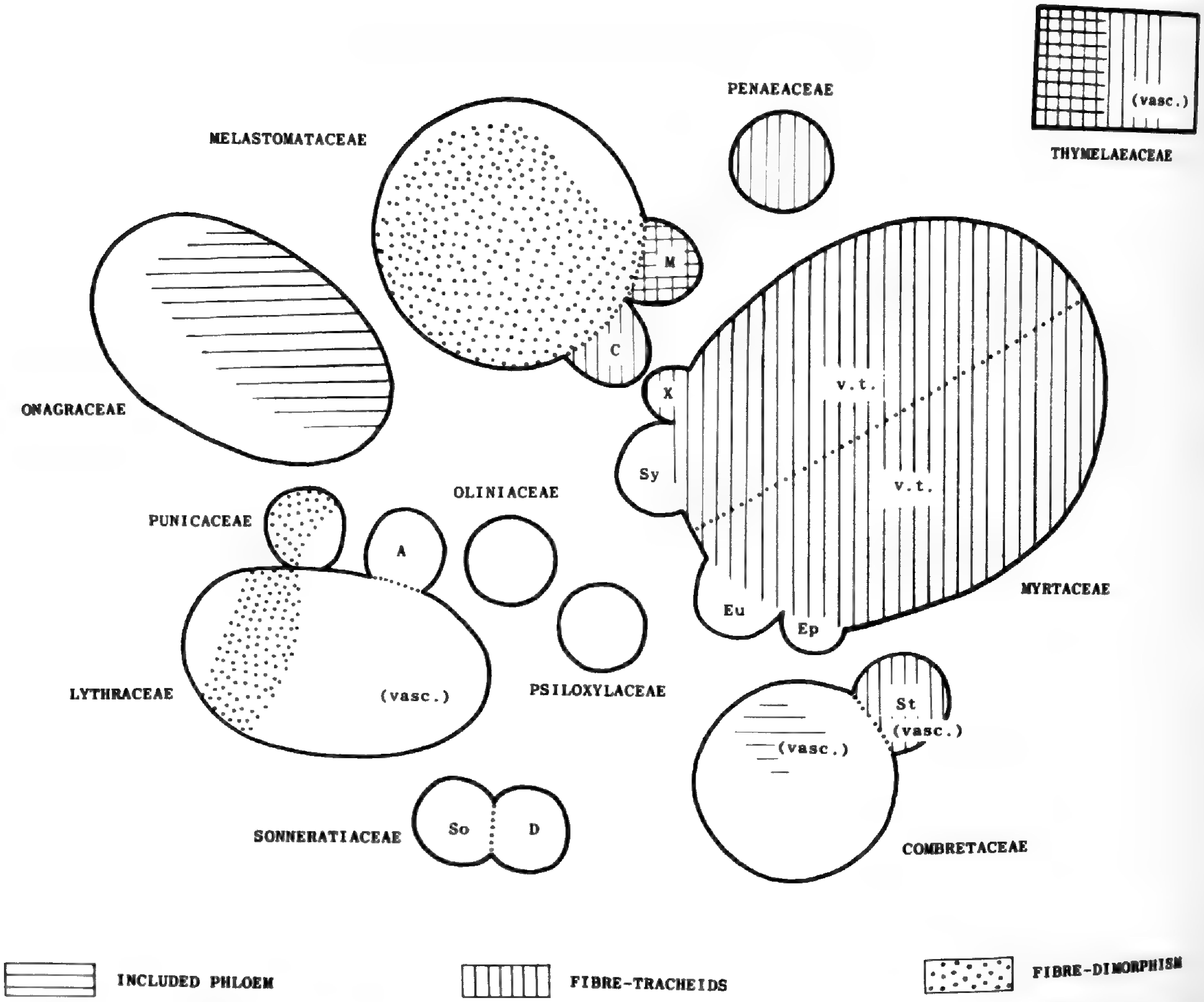

FIGURE 5. Included (interxylary) phloem and various fiber features in Myrtales (cf. Fig. 4). (vasc.) = vascular tracheids occasionally present; v.t. = vasicentric tracheids common. See also legend to Figure 2.

vascular tracheids); average diameter 45–280 μm, average vessel member length 200–650 μm; perforations simple; inter-vessel pits alternate; vessel–ray and vessel–parenchyma pits mostly half-bordered, but simple in a restricted number of species. Radial vessels (in rays) present in all Combreteae. *Fibers* 500–1,900 μm long, walls with simple pits (libriform), frequently septate. *Parenchyma* often scanty paratracheal only, in part of the genera aliform, confluent or banded and infrequently marginal. *Rays* mostly uniseriate, sometimes 1–3(–more)-seriate, weakly heterogeneous to homogeneous, composed of procumbent and infrequent square cells, infrequently composed of erect and square cells only. *Crystals* variable: small rhomboidal to elongate in axial and ray parenchyma; large rhomboidal completely filling the cells or in enlarged idioblasts of rays and axial parenchyma; rarely styloids; large or small clusters (the latter in idioblasts); rarely in fibers; absent from some genera. *Silica grains* very rare.

Strephonematoideae. Vessels diffuse, mostly solitary; average diameter 250–270 μm, average vessel member length 620–750 μm; perforations simple; inter-vessel pits alternate; vessel–ray and vessel–parenchyma pits half-bordered. *Vasicentric/vascular tracheids* very rare. *Fibers* 1,760–2,200 μm long, walls with distinctly bordered pits (fiber-tracheids). *Parenchyma* aliform to confluent and in short apotracheal bands or patches. *Rays* heterogeneous II–III. *Crystals* absent. Amorphous *silica* very rare.

LYTHRACEAE

Rhynchocalyx is included in the family description. *Alzatea,* which has been treated in Crypteroniaceae by van Beusekom-Osinga and van Beusekom (1975) but can be accommodated

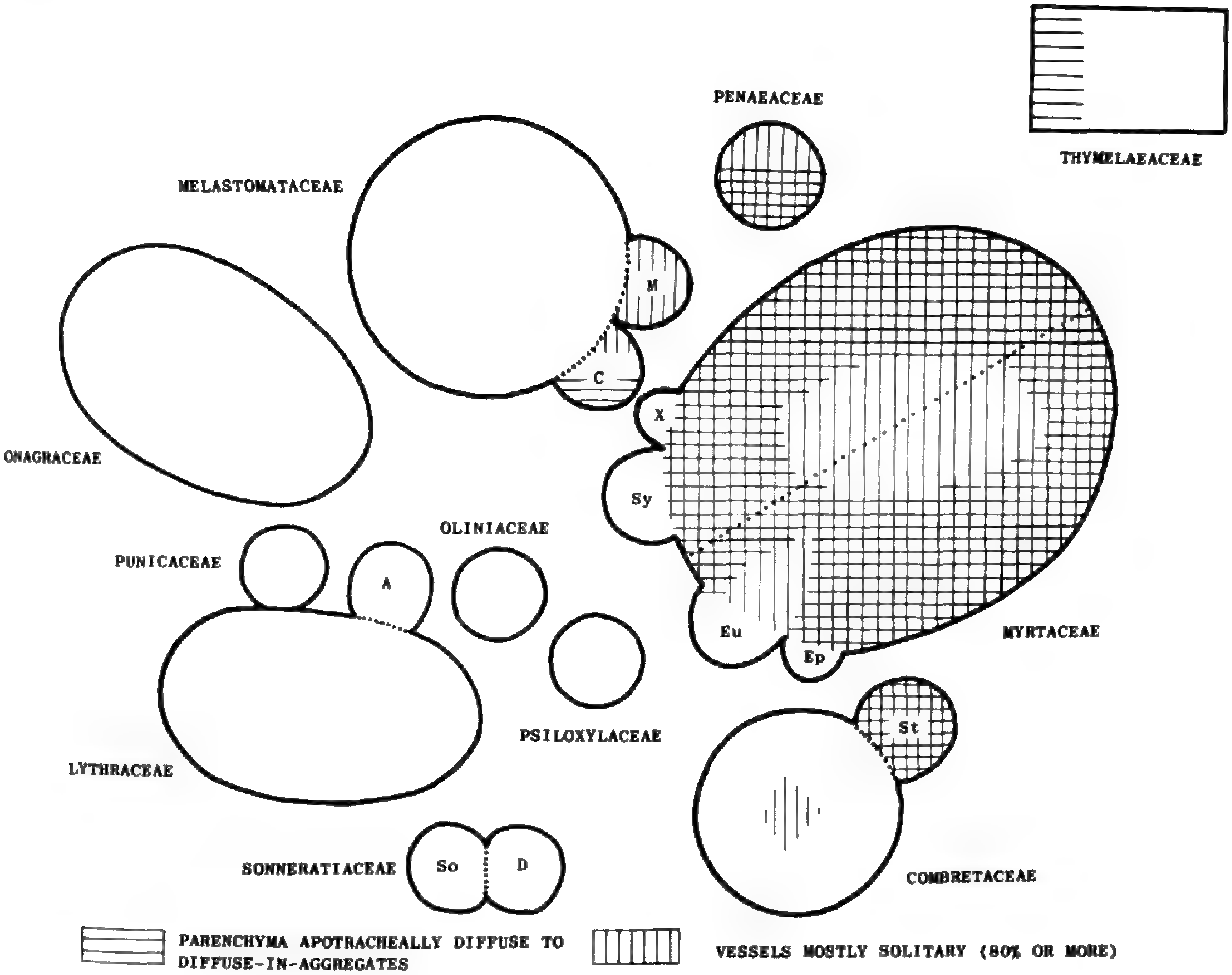

FIGURE 6. Distribution of primitive conditions of vessel grouping and parenchyma distribution in Myrtales. See also legend to Figure 2.

in Lythraceae (Lourteig, 1965; Baas, 1979), possibly merits subfamily status, and its wood anatomical characters are listed separately as far as they deviate from the remainder of the family (Baas & Zweypfenning, 1979; Baas, 1979).

Vessels diffuse (wood rarely ring-porous or semi-ring-porous), frequently in radial multiples; average diameter 30–220 μm, average vessel member length 200–580 μm; perforations simple; inter-vessel pits alternate; vessel–ray and vessel–parenchyma pits mostly half-bordered, but sometimes simple and fairly large. *Vascular tracheids* very rare. *Fibers* 380–1,350 μm long, walls with simple to minutely bordered pits, frequently septate; in some genera dimorphous with alternating bands or areas of normal and parenchyma-like fibers. *Parenchyma* mostly scanty paratracheal only, rarely apotracheally diffuse, vasicentric or aliform to confluent (and then derived via fiber-dimorphism). *Rays* mostly uniseriate (rarely 2–3-seriate), heterogeneous II or composed of erect cells only; rarely homogeneous. *Crystals* rhomboidal in chambered fibers or chambered axial parenchyma strands in part of the family, rarely in ray cells; often entirely absent.

Alzatea. Average vessel member length 730 μm; vessel–ray pits large and simple; rays 1–3-seriate, heterogeneous I–II.

MELASTOMATACEAE

Three subfamilies with distinctive wood anatomies are recognized: Melastomatoideae, Memecyloideae and Crypteronioideae. The traditionally recognized subfamily Astronioideae has been abolished: *Pternandra* (including *Kibessia*) is transferred to Memecyloideae as a separate tribe; Astronieae (four genera) are transferred to the Melastomatoideae (see van Vliet, 1981). The

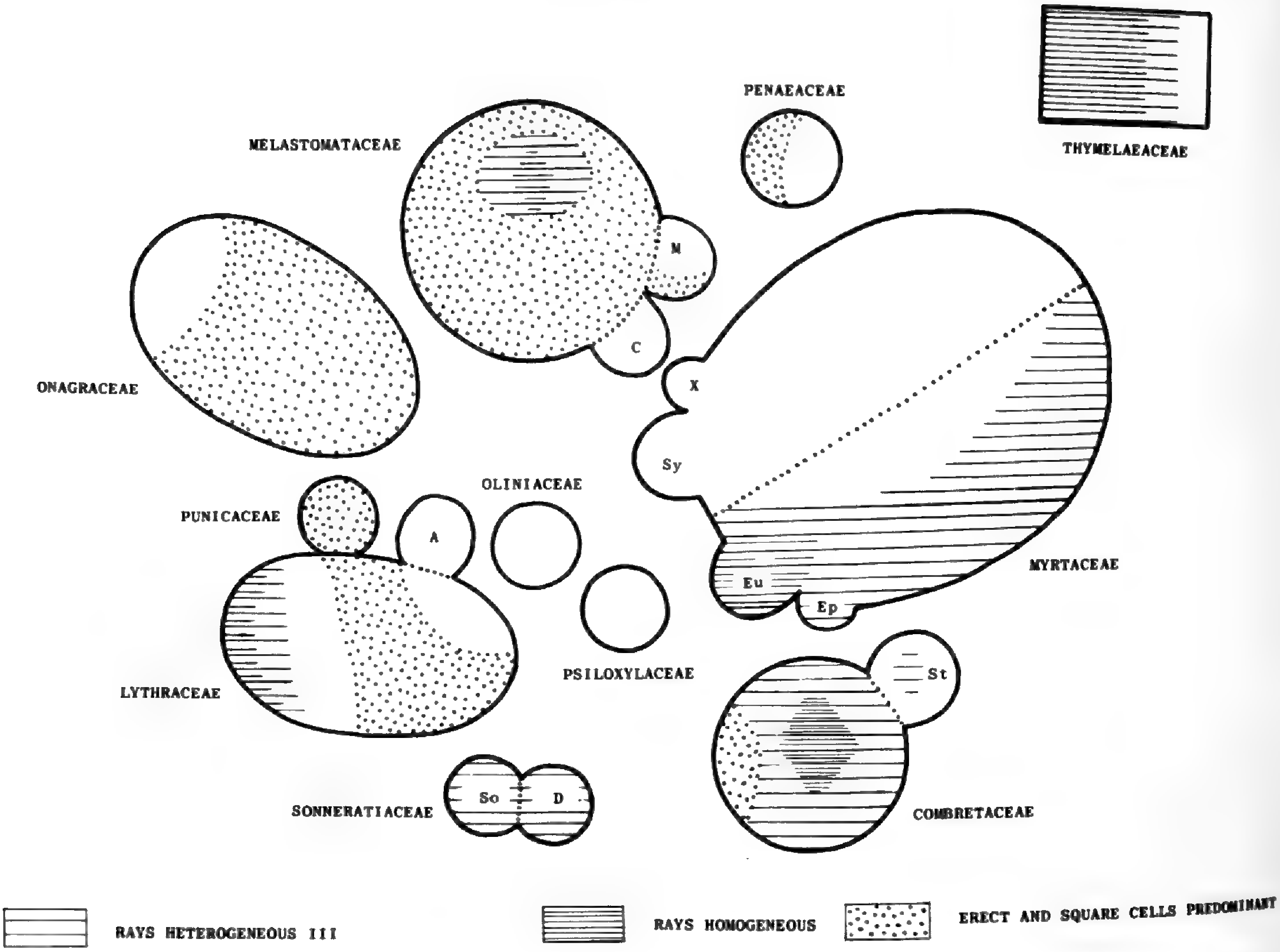

FIGURE 7. Distribution of variously specialized ray types in Myrtales. Krib's ray classification (1968) has been modified to include woods with exclusively uniseriate rays in his Heterogeneous III type. White areas represent more strongly heterogeneous (or heterocellular) rays. See also legend to Figure 2.

Crypteronioideae include *Axinandra, Crypteronia* and *Dactylocladus* (van Vliet, 1975, 1981; van Vliet et al., 1981; ter Welle & Koek-Noorman, 1979, 1981; ter Welle & Mennega, 1977).

Melastomatoideae. Vessels diffuse, frequently in multiples; average diameter 50–340 μm, average vessel member length 200–1,000 μm; perforations simple; inter-vessel pits alternate, alternate plus elongate and curved, or scalariform (and then as a derivation from alternate!); vessel–ray and vessel–parenchyma pits mostly simple and large, often in a reticulate or scalariform pattern. *Fibers* 300–1,500 μm long, walls with simple or very minutely bordered pits (libriform), frequently septate and dimorphous: i.e., with parenchyma-like fibers in narrow tangential arcs, or confluent and banded patterns. *Parenchyma* mostly scanty paratracheal, or also apotracheally diffuse within the bands of parenchyma-like fibers; infrequently in continuous bands (and then presumably derived via fiber dimorphism). *Rays* often uniseriate (also 1–7-seriate), mostly composed of erect, square and weakly procumbent cells, rarely homogeneous (i.e., entirely composed of procumbent cells). *Crystals* often absent; raphides present in one species; megastyloids infrequent in one tribe; clustered crystals in idioblasts restricted to species with banded parenchyma.

Memecyloideae. Included phloem of the foraminate type present. *Vessels* diffuse, mostly solitary; average tangential diameter 40–120 μm, average vessel member length 250–500 μm; perforations simple; inter-vessel pits (if present) alternate; vessel–ray and vessel–parenchyma pits half-bordered or simple. *Fibers* 350–1,200 μm long; walls with distinctly bordered pits (fiber-tracheids). *Parenchyma* scanty paratracheal or aliform to confluent and infrequently banded; also associated with included phloem. *Rays* 1–6-seriate, and heterogeneous II–III, or mostly uniseriate and composed of erect and weakly procumbent cells. *Crystals* often absent; large styloids in the included phloem of some species.

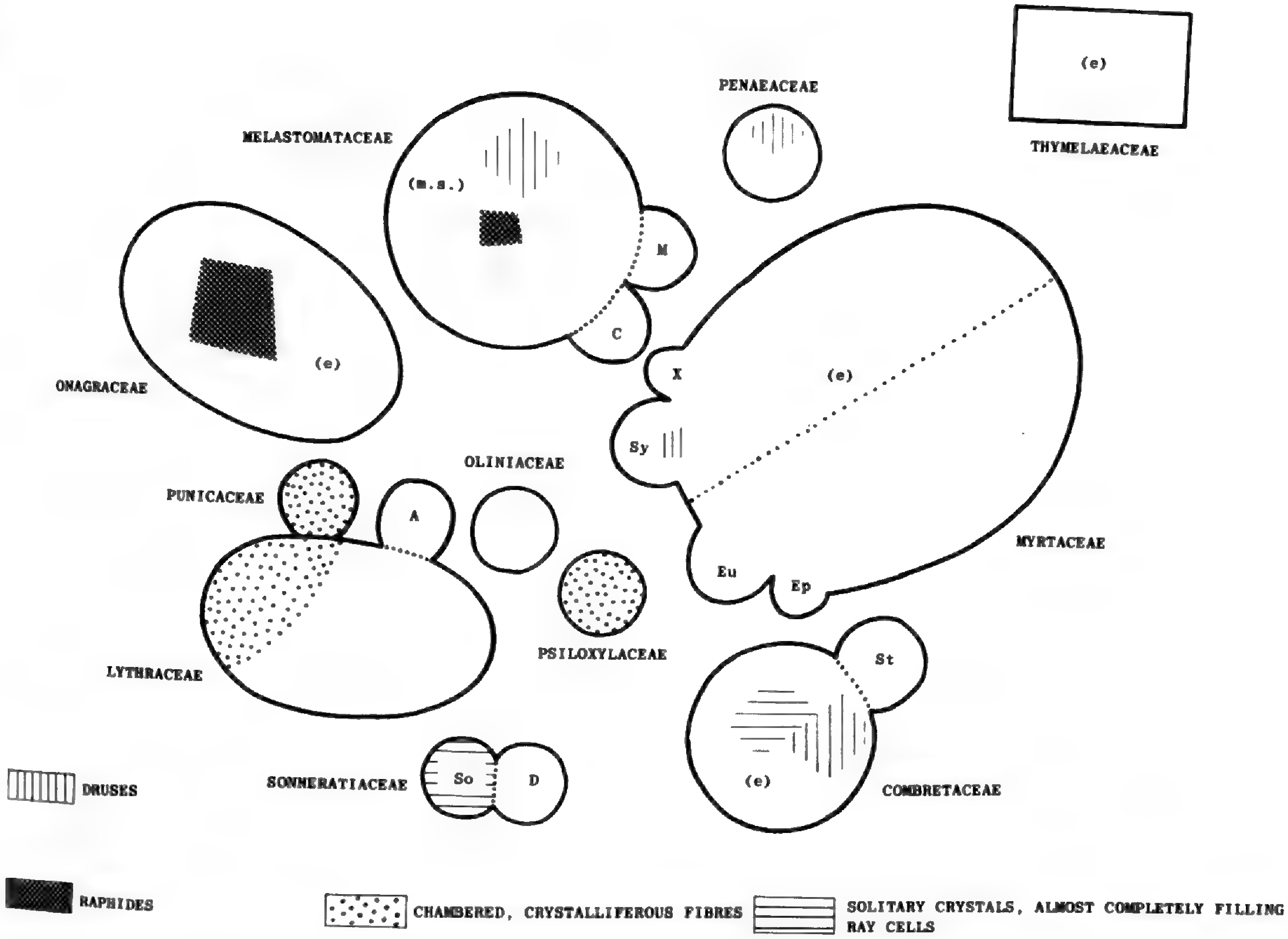

FIGURE 8. Distribution of different crystal types (excluding rhomboidal crystals in ordinary ray or parenchyma cells) in Myrtales. e = elongate crystals; m.s. = megastyloids. See also legend to Figure 2.

Crypteronioideae. *Vessels* diffuse, solitary and/or in radial multiples; average diameter 80–170 μm, average vessel member length 390–1,120 μm; perforations simple; inter-vessel pits alternate; vessel–ray and vessel–parenchyma pits half-bordered, rarely also simple. *Fibers* 600–1,550 μm long, walls with distinctly bordered pits (fiber-tracheids). *Parenchyma* diffuse in aggregates or aliform to confluent. *Rays* uniseriate or 1–3-seriate, heterogeneous I or III. *Crystals* absent.

MYRTACEAE

Combined description of the two traditionally accepted subfamilies Myrtoideae and Leptospermoideae. Schmid (1980) recognized two additional subfamilies: Chamaelaucioideae (formerly in Leptospermoideae) and Psiloxyloideae. For practical reasons the latter is still treated by us as a separate family: Psiloxylaceae (Ingle & Dadswell, 1953; Dadswell, 1972; Metcalfe & Chalk, 1950; supplemented with original observations on slides in the Rijksherbarium collection).

Vessels diffuse, often forming oblique patterns (wood rarely semi-ring-porous), predominantly solitary, but also in multiples in some genera (*Agonis*; *Angophora*; *Eucalyptopsis*; *Eucalyptus* section *Corymbosae* sensu Dadswell, 1972; *Leptospermum* pro parte; *Syzygium* sensu lato sensu Schmid, 1972, i.e., an alliance of genera including *Syzygium, Acmena, Cleistocalyx* and *Piliocalyx*, conforming to Ingle & Dadswell's *Eugenia* 'B' complex, 1953, or the *Acmena*-alliance sensu Briggs & Johnson, 1979; and *Xanthomyrtus*); average diameter 30–250 μm, average vessel member length 260–1,090 μm (mostly 400–800 μm); perforations simple, very rarely scalariform (*Neomyrtus*—Butterfield & Meylan, 1974, Meylan & Butterfield, 1978; *Myrceugenia*—Metcalfe & Chalk, 1950, Rudolf Schmid, unpubl. data; *Luma*—original observation, and Rudolf Schmid, unpubl. data; *Ugni, Myrteola,* and several other montane and cool temperate genera of Central and South America—Rudolf Schmid, unpubl. data; the record for *Myrtus communis* in Metcalfe & Chalk, 1950, is certainly incorrect); inter-vessel pits (if present) alternate; vessel–ray and vessel–parenchyma pits half-bordered or simple (sometimes large). *Vasicentric tracheids* mostly present, but absent from *Eucalyptopsis, Eucalyptus* pro parte, and *Syzygium* sensu lato (see above). *Fibers* 400–1,500 μm long, mostly with distinctly bordered pits (fiber-tracheids), but with simple to minutely bordered pits (libriform) in *Eucalyptopsis, Eucalpytus* pro parte, *Syzygium* sensu lato and *Xanthomyrtus*; very rarely septate (Metcalfe & Chalk, 1950; Meylan & Butterfield, 1978; Moll & Janssonius, 1918). *Parenchyma* typically apotracheally diffuse or diffuse-in-aggregates, in addition scanty paratracheal to vasicentric in many genera, more rarely confluent or even in wide or narrow paratracheal bands. *Rays* mostly 1–3-seriate, sometimes up to 8-seriate, rarely uniseriate; heterogeneous II in most Myrtoideae, more rarely heterogeneous I in this subfamily; in Leptospermoideae rays often more weakly heterogeneous to almost homogeneous (in *Eucalyptus* pro parte, *Leptospermum* pro parte, cf. Baas, 1977). *Crystals* if present, mostly small, rhomboidal in chambered axial parenchyma cells in both subfamilies; rarely elongate in slightly enlarged cells; solitary crystals in enlarged idioblasts infrequent in some genera (*Agonis, Calycorectes, Eugenia* pro parte, *Feijoa, Leptospermum* pro parte, *Lophomyrtus* pro parte, *Myrciaria,* and *Nothomyrcia*); druses rare in *Eugenia* (Chattaway, 1955). Crystals always absent from rays. *Silica grains* present in rays of at least 12 genera of the Leptospermoideae (in addition to ten genera mentioned by Ingle & Dadswell (1953), also in *Lindsayomyrtus,* original observation, and *Xanthostemon pachyspermum,* Amos, 1952, a gen. nov. according to Briggs & Johnson, 1979), and rare in two genera (rays of *Osbornia,* parenchyma of *Jambosa*; cf. Amos, 1952) of the Myrtoideae.

Note that within Myrtaceae, *Syzygium* sensu lato and *Xanthomyrtus* (Myrtoideae), together with *Eucalyptopsis* and *Eucalyptus* pro parte (Leptospermoideae), stand out on account of their much higher level of xylem specialization: libriform fibers, vessels in multiples, aliform to confluent parenchyma and large and simple vessel–ray and vessel–parenchyma pits all emphasize this (the two latter features also occur scattered in a few genera). Wood anatomical differences of this magnitude coincide in other Myrtalean families (Melastomataceae and Combretaceae) with subfamily boundaries, also marked by macromorphological differences.

Silica grains may appear to be of considerable taxonomic interest in the Leptospermoideae. They are present in all genera of the Metrosideros-alliance sensu Briggs and Johnson (1979) so far studied wood anatomically. The only exception is *Kjellbergiodendron.* Interestingly enough this genus has been transferred to the Myrtoideae by Schmid (1980) on the basis of both macromorphological and anatomical features. Outside the Metrosideros-alliance silica has only been found in one suballiance (*Calothamnus*) of the *Leptospermum*-alliance.

OLINIACEAE

Vessels diffuse, frequently in multiples; average diameter 50–70 μm, average vessel member length 500–600 μm; perforations simple; intervessel pits alternate; vessel–ray and vessel–parenchyma pits half-bordered. *Fibers* 900–1,000 μm long, walls with simple pits (libriform), septate. *Parenchyma* scanty paratracheal. *Rays* 1–3-seriate, heterogeneous I–II. *Crystals* rhomboidal in chambered axial parenchyma (Mujica & Cutler, 1974).

ONAGRACEAE

Combined description of the six tribes: Epilobieae, Fuchsieae, Hauyeae, Jussiaeeae, Lopezieae and Onagreae (Metcalfe & Chalk, 1950; Carlquist, 1975b, 1977).

Included phloem of the foraminate type often present. *Vessels* diffuse, frequently in radial multiples; average diameter 40–110 μm, vessel member length 110–550 μm; perforations simple; inter-vessel pits alternate, sometimes elongate and curved (in Epilobieae, Fuchsieae, Lopezieae, Onagreae pro parte); vessel–ray and vessel–parenchyma pits half-bordered, but sometimes with reduced borders. *Fibers* 240–820 μm long; walls with simple pits (libriform); often septate, or at least nucleate. *Parenchyma* mostly scantly paratracheal, apotracheal bands rare in Hauyeae, apotracheal parenchyma also associated with included phloem. *Rays* uni- to multiseriate, often predominantly of upright cells, or heterogeneous with mostly weakly procumbent and square cells. *Crystals* often as raphides, in axial parenchyma, rarely also in rays or fiber-like cells; sometimes rhomboidal to elongate in non-chambered fibers, and in rays, or absent.

PENAEACEAE

Vessels diffuse, predominantly solitary; average diameter 20–55 μm, average vessel member length 310–890 μm; perforations simple; inter-vessel pits alternate when present; vessel–ray and vessel–parenchyma pits half-bordered. *Fibers* 380–1,170 μm long, walls with distinctly bordered pits (fiber-tracheids). *Parenchyma* scanty paratracheal and scanty apotracheally diffuse. *Rays* mostly uniseriate and composed of erect and square cells, or 1–3-seriate and heterogeneous II. *Crystals* mostly absent, but present as druses or clusters in chambered parenchyma cells in one species, and as irregular aggregates in another (Carlquist & Debuhr, 1977).

PSILOXYLACEAE

Vessels diffuse, mostly in multiples; average diameter ca. 50 μm, average vessel member length 550–570 μm; perforations simple; inter-vessel pits alternate; vessel–ray and vessel–parenchyma pits half-bordered. *Fibers* with minutely bordered pits confined to radial walls (libriform), septate. *Parenchyma* typically scanty paratracheal. *Rays* 1–4-seriate, heterogeneous I. *Crystals* rhomboidal, in chambered fibers, very rarely also in ray cells (Schmid, 1980, and original observations; see also Baas & Zweypfenning, 1979).

Note that Schmid (1980) refers to distinctly bordered pits and apotracheal diffuse parenchyma for *Psiloxylon*; in the material at our disposal (*Lorence 1488*) the pit borders are very small (ca. 1.5–2 μm); apotracheal parenchyma has not been observed and can at most be very infrequent. Our observation of rhomboidal crystals in ray cells is new.

PUNICACEAE

This monotypic family could also be accommodated in Lythraceae (cf. Thorne, 1976; Baas & Zweypfenning, 1979) (Bridgwater & Baas, 1978).

Vessels diffuse, frequently in multiples; average diameter 40–70 μm, average vessel member length 250–330 μm; perforations simple; inter-vessel pits alternate; vessel–ray and vessel–parenchyma pits half-bordered. Fibers 460–540 μm long, walls with simple pits (libriform), septate; tendency to fiber dimorphism observed in several samples. *Parenchyma* scanty paratracheal to virtually absent. *Rays* mostly uniseriate (rarely up to 3-seriate), composed of erect to weakly procumbent cells. *Crystals* rhomboidal, frequent in chambered fibers.

SONNERATIACEAE

Vessels diffuse, frequently in multiples; average tangential diameter 120–160 μm in *Sonneratia,* 120–230 μm in *Duabanga,* average vessel member length 400–500 μm in *Sonneratia,* 600–800 μm in *Duabanga*; perforations simple; inter-vessel pits alternate; vessel–ray and vessel–parenchyma pits mostly half-bordered in *Sonneratia,* large and simple in *Duabanga. Fibers* 700–1,000 μm long in *Sonneratia,* 1,200–1,400 μm long in *Duabanga*; walls with simple pits (libriform); septate in *Sonneratia* only. *Parenchyma* absent in *Sonneratia,* aliform to confluent in *Duabanga. Rays* uni(-bi)-seriate, composed of weakly procumbent cells, with occasionally (*Sonneratia*) or commonly (*Duabanga*) square to erect marginal cells. *Crystals* rhomboidal; in *Sonneratia* large and almost completely filling the ray cells; in *Duabanga* smaller and sometimes accompanied by minute crystals in axial parenchyma and ray cells (Metcalfe & Chalk, 1950; Venkateswarlu & Rao, 1964, complemented with original observations).

Note that the above data deviate to some extent from those by Venkateswarlu and Rao (1964), which in our opinion is due to some erroneous observations by these authors. Moll and Janssonius (1918) described some form of fiber-dimorphism: around some of the vessels the fibers are more thin-walled and have small intercellular spaces between them. This weak form of fiber dimorphism, presumably due to the effect of enlarging vessels on fiber differentiation, should not be identified with fiber dimorphism as occurs in Melastomataceae and some Lythraceae.

THYMELAEACEAE

Included phloem (of the foraminate or concentric type) present in nine genera. *Vessels* diffuse, frequently in multiples, in part of the family in clusters or dendritic patterns; average diameter ca. 30–160 μm, average vessel member length 150–400 μm; perforations simple; inter-vessel pits alternate; vessel–ray pits half-bordered. *Tracheids* (vasicentric and/or vascular) present in some genera with clustered or dendritically arranged vessels. *Fibers* 300–900 μm long, mostly with distinctly bordered pits mainly confined to radial walls, but in some genera pits with strongly reduced to almost simple borders. *Parenchyma* scanty paratracheal to vasicentric, or aliform; sometimes also with apotracheal narrow bands or diffuse parenchyma. *Rays* 1–4(–9)-seriate, often almost or entirely homogeneous, sometimes heterogeneous, composed of weakly procumbent central cells and square to erect marginal cells. *Crystals* often absent, if present small, solitary, diamond-shaped, or elongate in ray cells and parenchyma cells; large styloids in included phloem of *Aquilaria*; crystalline masses or crystal sand doubtfully present in few genera (Metcalfe & Chalk, 1950; supplemented with original observations on a limited number of genera).

DISCUSSION

Although the previous descriptive sections, partly pictured in Figures 2–8, show a considerable diversity, the order Myrtales as delimited by Dahlgren and Thorne (1984) and us is wood anatomically a fairly closely knit assemblage. The possible inclusion of Thymelaeaceae, the relationship patterns within the order as evident from the wood anatomical variation patterns, and the wider affinities will be the subject of our further discussions.

POSITION OF THYMELAEACEAE

Although treated outside Myrtales by several authors (Takhtajan, 1980; Dahlgren, 1980; Dahlgren & Thorne, 1984), Cronquist (1968, 1981) has advanced arguments to treat Thymelaeaceae as an ordinary member of the order. Wood anatomy tends to support this opinion; apart from the shared intraxylary phloem and vestured pits, there are other similarities. In fact all wood anatomical characters of the Thymelaeaceae can be retraced in the order Myrtales, albeit not in a single family (Figs. 2–8). The occurrence of interxylary (included) phloem in a number of Thymelaeaceae as well as in a number of Onagraceae, Combretaceae and Melastomataceae, is especially significant, because this feature is rather uncommon in Dicotyledons as a whole. The fibers with distinctly bordered pits in Thymelaeaceae are a bit unlike the fiber-tracheids of Myrtaceae, Combretaceae pro parte, Penaeaceae and Melastomataceae pro parte, because the pits are largely confined to the radial walls. The slightly elongate crystals of some Thymelaeaceae recall certain Combretaceae and Myrtaceae. In view of the somewhat reticulate and faint wood anatomical affinities with the 'core' families of the Myrtales, we would advocate a fairly isolated position, also in view of its other deviating attributes (cf. Dahlgren & Thorne, 1984; Cronquist, 1981). The position of Thymelaeaceae near Euphorbiales and Malvales in the Dilleniideae (Takhtajan, 1980) or Malviflorae (Dahlgren, 1980; Thorne, 1981; Tan, 1980), finds no support in wood anatomy. Vestured pits and included phloem never occur together in the other families of this superorder: vestured pits occur in Dipterocarpaceae and some Cistaceae; their presence in Euphorbiaceae is restricted to Bridelieae (two genera); intraxylary phloem occurs sporadically in some other Euphorbiaceae and would merit further study to establish whether it is really comparable to the type of internal phloem occurring in Myrtales.

RELATIONSHIPS WITHIN THE MYRTALES

Ideally one would like to construct a phylogenetic system for the Myrtales, based on the occurrence of shared, uniquely derived specializations, as was attempted for Lythraceae (Baas & Zweypfenning, 1979) and Neotropical Melastomataceae (ter Welle & Koek-Noorman, 1981). At the ordinal level, most wood anatomical characters are, however, unsuitable for such a cladistic approach, because of the high probability of parallel specialization lines in individual families. Thus the occurrence of homogeneous rays in some Lythraceae, Melastomataceae, and Combretaceae does not point to mutual affinity across the family boundaries; likewise the specialization series from fiber-tracheids to libriform fibers has probably occurred more than once in the order; even within the family Myrtaceae the occurrence of libriform fibers in the minority of both subfamilies probably represents parallel specialization. The same applies to specialized patterns of parenchyma distribution.

Applying the chiefly unidirectional Baileyan trends for wood anatomical specialization it is, nevertheless, possible to reconstruct the wood anatomy of the putative common ancestor of the Myrtales (cf. Carlquist, 1961, 1962, 1975c, for summaries of and additions to these trends; and Carlquist, 1980; Baas, 1973, 1982, for a discussion of possible reversions). Most primitive character states hypothesized for this common ancestral stock are still represented in a number of extant Myrtales as well as in a fair number of Angiosperm families from other orders. The combination of ancestral characters can serve as a starting point to discuss the mutual affinities within the Myrtales, as well as the putative affinities with other orders. A wood anatomical diagnosis of 'Protomyrtales' would read as follows:

> *Vessels* mostly solitary, with scalariform perforations (only retained in a few genera of the Myrtaceae) and alternate, vestured pits, half-bordered where in contact with rays and axial parenchyma. Vestures of uniform thickness attached to the entire roof of the pit chamber (van Vliet's type A, 1978). Ground tissue of fiber-tracheids. *Parenchyma* scanty paratracheal and apotracheally diffuse. *Rays* heterogeneous I. *Crystals* in axial parenchyma and/or ray cells, probably of several types. *Intraxylary phloem* present.

The following specializations from this ancestral type are evident:

1. Vessels tending to be arranged in (mostly short) radial multiples (most families; cf. Fig. 6 all groups without vertical hatching). This common specialization within the Dicotyledons has probably occurred several times within the order.

2. Vessel–ray and vessel–parenchyma pits with reduced borders to simple, and ultimately large and mostly in a reticulate or scalariform pattern (Fig. 2). This specialization is most evident in Melastomataceae, Myrtaceae pro parte, *Alzatea* and *Lagerstroemia* of the Lythraceae, and *Duabanga* of the Sonneratiaceae; probably at least partly as a result of parallel development.

3. Concentration of vestures around the pit apertures and development of trunk-like bases (van Vliet's series of types A, B1, B2, B3). This hypothetical specialization trend occurs within a number of families and is based on the fact that type A mostly occurs in the representatives that have retained the highest number of primitive attributes in their wood (Strephonematoideae of Combretaceae; *Sonneratia* of Sonneratiaceae; *Alzatea* of Lythraceae; cf. Fig. 3). In Melastomataceae the vesturing is predominantly of type A, and the slightly more specialized type B1 is confined to a few Melastomatoideae—the wood anatomically most specialized subfamily. In Myrtaceae a range from types A–B2 has been encountered, but too few representatives have been studied submicroscopically to relate these types to classification.

4. Reduction of pit borders and limitation of pits to radial walls in fibers (i.e., shift from fiber-tracheids to libriform fibers) followed by or concomitant with septation of the fibers (Fig. 4). Lythraceae, Sonneratiaceae, Punicaceae, Psiloxylaceae, Onagraceae, Oliniaceae and the largest subfamilies of Melastomataceae and Combretaceae show this specialization; within Myrtaceae it occurs isolated in the two major subfamilies. Fiber dimorphism represents a further specialization, and is limited to part of the Lythraceae, Melastomatoideae and Punicaceae.

5. Parenchyma specialization (quite possibly reversible), presumably followed three different courses: a. *Reduction leading to exclusively very scanty paratracheal parenchyma, or total absence of parenchyma* (most families, notably Melastomataceae, Lythraceae, Onagraceae, Punicaceae, Psiloxylaceae, Oliniaceae, *Sonneratia* of Sonneratiaceae and Thymelaeaceae pro parte). b. *Increase of paratracheal parenchyma* (often paralleled by a decrease in apotracheal parenchyma). This specialization is evident in part of the Myrtaceae, Combretaceae, Crypteronioideae and Memecyloideae of the Melastomataceae, *Duabanga* of the Sonneratiaceae and to some extent in *Pemphis* and *Rhynchocalyx* of the Lythraceae, *Hauya* of the Onagraceae, and some Thymelaeaceae. c. *The presumed development of banded parenchyma through fiber dimorphism* in *Lagerstroemia* pro parte of the Lythraceae and some members of the Melastomatoideae.

6. Ray specialization also occurred along diverging lines: a. *Towards a higher proportion of procumbent cells, and greater procumbency of the marginal cells* (i.e., the classical specialization series according to Kribs, 1935, modified in 1968): Heterogeneous I–II–III–Homogeneous. The homogeneous (or rather homocellular) end station is represented by few Myrtales only, least infrequently in Myrtaceae and Combretaceae, abundant in Thymelaeaceae (Fig. 7). b. *Perpetuation of juvenile ray features* (i.e., composed of square to erect cells, or with only very weakly procumbent cells) *in mature xylem.* This phenomenon of paedomorphosis (Carlquist, 1962) is especially common in Melastomataceae, Onagraceae, Lythraceae and Punicaceae. Penaeaceae and Combretaceae also show this feature in some species but here it is not certain whether this should be ascribed to the truly juvenile nature of the material studied. In the former families many species also never develop substantial amounts of wood, but some representatives at least do show the juvenilistic tendencies in their

rays at the periphery of thick trunks. Carlquist (1962) developed the hypothesis of paedomorphosis to explain the wood anatomical syndromes in a number of woody plants such as giant lobelias and senecios that have probably evolved from a herbaceous ancestry. For the Myrtales involved, such 'secondary woodiness' is not necessarily indicated—the perpetuation of juvenile characters throughout the development of secondary xylem may also be hypothesized for basically woody plants (cf. Baas, 1982). c. *Reduction of ray width* of the originally 1–4-seriate rays to uniseriates (most families), *or sporadically phylogenetic increase in ray width* (partly recapitulated in ontogeny) in e.g., some scandent Melastomataceae.

7. Origin of interxylary (included) phloem in Memecyloideae, Combretoideae pro parte, Onagraceae pro parte and Thymelaeaceae pro parte probably independently of each other (Fig. 5).

8. Miscellaneous specializations: a. *Origin of radial vessels in the rays of* one tribe of the Combretoideae. b. *Development of vasicentric tracheids in Myrtaceae.* This possibility might be questioned. In view of the numerous primitive wood attributes of the Myrtaceae one might also hypothesize that vasicentric tracheids belong to the set of ancestral characters of the Myrtales, and that this feature (like scalariform perforation plates) was lost in all families except one. c. *Development of vascular tracheids* (reduction of very narrow vessels) in some Lythraceae, Combretaceae and Thymelaeaceae (Fig. 5). d. *Development of chambered crystalliferous fibers* (Psiloxylaceae, Lythraceae pro parte and Punicaceae) (Fig. 8). e. *Development of megastyloids in some Melastomataceae,* possibly from an ancestral type with rhomboidal to elongate crystals. It is very difficult to picture the other crystal types as primitive or specialized. Raphides, which represent a highly complex type of calcium oxalate deposition, are restricted in distribution in the Dicotyledons: among the 26 families listed by Metcalfe and Chalk (1950) are some primitive families (e.g., Dilleniaceae and Monimiaceae); in Monocotyledons raphides are more common. One can hardly imagine that in Onagraceae this feature evolved 'de novo' as a new specialization; it seems more likely that the expression of such a presumably old character in derived families is still triggered by unaltered genotypical information. The lack of raphides does not imply that the information is absent but that perhaps it is incomplete or blocked by other genes; such a hypothesis would also be compatible with the 'stray' occurrence of raphides in one *Bredia* species of the Melastomataceae (van Vliet, 1981). By the same token, the haphazard occurrence of elongate crystals or druses (Fig. 8—rare features in the wood of Dicotyledons) might still witness (ancient?) links between the families sharing them in some of their species.

The distribution of some of the primitive and derived character states discussed above over the different families of the Myrtales is given in Figures 2–8; in fact the arrangement of the families is the result of these wood anatomical distribution patterns. There appears to be a high degree of correlation of primitive characters in some of the families or subfamilies and of derived characters in the remaining ones. Primitive characters like solitary vessels, fiber-tracheids, and apotracheal parenchyma occur together in the majority of Myrtaceae, in Strephonematoideae of the Combretaceae, Memecyloideae, Crypteronioideae pro parte, and Penaeaceae. In all these groups, at least part of the species show heterogeneous rays with a clear distinction between the procumbent, central cells and square to erect marginal cells in one to several rows. The most primitive wood anatomical feature of the order, scalariform perforations (few Myrtaceae), coincides with these other primitive features. As far as is known, the presumed primitive type of vesturing also occurs relatively frequently in these taxa. Thymelaeaceae share primitive fibers, and to some extent parenchyma distribution, but are generally more specialized in vessel grouping and ray type.

Although the common retention of primitive features is not a sound basis for postulating close phylogenetic affinity, the above taxa still retain many of the ancestral characters of the Myrtales, and evince at least common ancestry.

From the above it automatically follows that the opposed, specialized character states (vessels in multiples, libriform fibers (mostly septate), reduced or abundant paratracheal parenchyma) also show a high degree of correlation in the remaining taxa: Combretoideae of the Combretaceae, Sonneratiaceae, Lythraceae, Punicaceae, Oliniaceae, Psiloxylaceae, Onagraceae and Melastomatoideae of the Melastomataceae. The incidence of specialized rays (heterogeneous III to homogeneous, and juvenilistic rays) is relatively high in these families, as is the occurrence of the more derived types of vesturing (types B1–3). Within the Myrtaceae, *Syzygium* sensu lato, *Xanthomyrtus, Eucalyptopsis* and *Eucalyptus* pro parte share the high specialization level of the above mentioned families.

Of these wood anatomically specialized core families of the Myrtales, Psiloxylaceae, Oliniaceae, and some Lythraceae (notably *Alzatea*) have retained a low level of specialization in their rays (heterogeneous I). Especially the wood of *Psiloxylon* and *Olinia* (half-bordered vessel-ray pits) probably resembles that of the ancestor that gave rise to the diversely specialized types in this part of the order (the 'Protolythraceae' type of Baas & Zweypfenning, 1979). Lythraceae and Punicaceae can be directly linked to this type, especially to *Psiloxylon,* through the shared crystalliferous fibers.

Of Sonneratiaceae, especially *Sonneratia* still retains many ancestral features but shows minor specializations in its uniseriate rays and (almost?) total absence of axial parenchyma; *Duabanga* diverged wood anatomically into another direction (aliform to confluent parenchyma, large and simple vessel–ray pits, homogeneous rays) and has a much higher specialization level. Onagraceae could also be derived from this type, but acquired (and/or retained) features that tend to underline a somewhat isolated position such as included phloem, rod-like crystals with one indented and one pointed end (Carlquist, 1975b), and raphides.

For Combretoideae and Melastomatoideae the story is more complex; these taxa belong to families that also have representatives with the primitive Protomyrtalean wood anatomical syndrome. If Combretaceae and Melastomataceae are monophyletic families, this implies that the specialized wood anatomies in the majority of their representatives arose independently from a more primitive type than that represented in the Protolythraceae type, and that the specialized Combretaceae and Melastomataceae are not so closely related to, for instance Sonneratiaceae and Lythraceae, respectively, as their wood structure would suggest. For Combretaceae this is quite acceptable, because the family does not resemble Sonneratiaceae so strongly. For Melastomataceae and Lythraceae it implies that many striking similarities are a result of parallel or convergent development (fiber dimorphism; large vessel–ray pits in most Melastomatoideae and part of the Lythraceae, notably in *Alzatea* and *Lagerstroemia* pro parte; juvenilistic rays; etc.). Parallel developments are more likely to occur in closely related (i.e., genetically similar) groups; the similarities in wood structure resulting from parallel or convergent evolution may thus still witness affinities: it seems therefore plausible to hypothesize a direct derivation of the 'Protolythraceae' type from the immediate precursor of Melastomataceae (which must have been very similar, if not identical, to the Protomyrtales type giving rise to Myrtaceae, Penaeaceae, and Combretaceae).

The arrangement of Myrtalean families in the diagrams of Figures 2–8 reflect our conclusions on natural affinity as far as is possible in a two-dimensional system. The deviating position and shape for Thymelaeaceae is not only a reflection of its presumed isolated position, but also of our more limited understanding of this family, simply because we did not study enough representatives in sufficient detail. The arrangement of the woody 'core' families is based on a combination of phenetic and phylogenetic classification principles; more emphasis on phenetic similarities, e.g., the shared possession of interxylary phloem, would put Combretaceae, Melastomataceae and Onagraceae much closer to each other, but, as explained above, the acquisition of this character presumably occurred more than once in the evolutionary history of the order. However, the great distance between Combretaceae and Melastomataceae in our diagram is primarily the result of our priority to put Strephonematoideae near Myrtaceae and Combretoideae near Sonneratiaceae; and not because we consider the two families as mutually remote. Although the diagram is inspired by wood anatomical characters, evidence of other characters (micro- and macromorphological) have also played a role. This is expressed in the adopted family delimitations for Combretaceae, Melastomataceae and Sonneratiaceae, for which wood anatomy could support the splitting of each into two or three separate families. Likewise, the perfect fit of *Psiloxylon* and *Olinia* wood with Lythraceae, has not resulted in the submerging of these genera in Lythraceae in view of evidence from other characters; e.g., the secretory cavities of Psiloxylon, which suggest Myrtaceae, as strongly advocated by Schmid (1980).

The splitting of the order Myrtales sensu lato into Lythrales and Myrtales as suggested by Briggs and Johnson (1979) cannot be supported by wood anatomy, but has also been withdrawn by these authors and thus needs no further comments (Johnson & Briggs, 1984).

We are aware that our arrangement of families can be opposed if emphasis is put on other character complexes, or if most known attributes are simultaneously employed (as attempted by Dahlgren & Thorne, 1984). In our opinion, any so-called conflicting evidence will only strengthen the tissue of intimate relationships between the core families of the Myrtales. If floral and leaf structure for instance point to a Myrtaceous nature of *Psiloxylon,* while the wood witnesses Lythraceous affinities, *Psiloxylon* only bridges a gap between Lythraceae and Myrtaceae; similarly presumed affinities of *Alzatea* with *Crypteronia* (van Beusekom-Osinga & van Beusekom, 1975) in combination with the Lythraceous wood anatomy of *Alzatea,* provides additional evidence of relationships between Melastomataceae and Lythraceae. The main conclusion can only be that whatever minor adjustments one wishes to make in the classification, the 10 core families of the Myrtales, possibly with the addition of Thymelaeaceae, are a very natural assemblage of closely related families.

POSITION OF MYRTALES IN THE DICOTYLEDONS

The hypothesized wood structure of Protomyrtales is a very generalized, primitive type, except for its vestured pits and intraxylary phloem. Among the (super)orders suggested as related to Myrtales in recent systems of classification (Dahlgren, 1980; Takhtajan, 1980; Thorne, 1976; Cronquist, 1981) these two features are absent or very rare and hardly ever occur in combination in Rosiflorae (Rosales, Cunoniales), Corniflorae, Rutiflorae, Theiflorae as shown in Figure 1 (see Dahlgren & Thorne, 1984, for a review of putative relatives and comparison of various attributes of these taxa with Myrtales). Of these only Vochysiaceae pro parte combine vestured pits and intraxylary phloem. This family is wood anatomically specialized (cf. Quirk, 1980) and any affinities to Myrtales can at most be very remote. In Dahlgren's (1980) and Thorne's (1976) system the Myrtiflorae are positioned next to Gentianiflorae in their pictorial "transverse sections through the phylogenetic shrub," but these authors do not comment on mutual affinities between these orders. The anatomical evidence would support a common derivation because the combination of vestured pits and intraxylary phloem is well represented in the order Gentianales. Moreover, primitive features like scalariform perforations occur sporadically in some representatives, fiber-tracheids also occur, and even the diversity of crystal types including raphides and styloids is matched (cf. Metcalfe & Chalk, 1950); the single family Loganiaceae, if taken in a broad sense, covers much of the wood anatomical diversity also encountered in Myrtales (cf. Mennega, 1980).

If less weight is attached to intraxylary phloem and vestured pits, the primitive Protomyrtalean wood anatomy could be used to argue in favor of affinities with a majority of the larger orders of Dicotyledons, because in most of them there are at least some representatives with scalariform perforations, fiber-tracheids and primitive parenchyma distribution and ray type. In that case the Rhizophoraceae would also be a candidate for affinity (cf. van Vliet's reconstruction of Protorhizophoraceae wood), but it should be stressed here that Rhizophoraceae are not more similar to Myrtales than to many other, unrelated woody Dicotyledons.

With these vague conclusions on the ordinal and supraordinal level we have stretched the possibilities of systematic wood anatomy. With abounding parallelisms partly directed or counteracted by ecological trends (cf. Baas, 1976, 1982; Carlquist, 1975c, 1980), further interpretation of extant wood anatomical diversity patterns with a bearing on events, that must have taken place in early Cretaceous times (cf. Muller, 1981, for the earliest pollen records of Myrtaceae), would be indulging in very wild speculation indeed.

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LEAF HISTOLOGY AND ITS CONTRIBUTION TO RELATIONSHIPS IN THE MYRTALES[1]

Richard C. Keating[2]

Abstract

An examination of the leaf histology of a wide array of families thought at one time to be included in the Myrtales has led to a restricted circumscription of the order as follows: Lythraceae, Rhynchocalycaceae, Trapaceae, Oliniaceae, Combretaceae, Alzateaceae, Penaeaceae, Melastomataceae, Crypteroniaceae, Psiloxylaceae, Myrtaceae, and Onagraceae. Data used in testing this concept were obtained from lamina transsections cut to include the midrib. Observations on midrib shape, venation configuration, shape and extent of extraxylary fibers, sclereids, dermal and mesophyll features were most discriminating when examining taxa with the most elaborate and/or generalized anatomy. While leaf histological trends of specialization are not independently producible from this data, correlation with information from leaf architecture should eventually make this possible. Seldom recorded features which have proven useful in this systematic context include length/width ratios of palisade cells and the shape of the boundary between the mesophyll and the midrib ground tissue. The sharpness of tissue differentiation also appears often to be a family characteristic.

In most respects, plant families comprising the core of the Myrtales form a coherent group and the recognition of the order has not been particularly controversial (Dahlgren & Thorne, 1984). At the same time, many of the included taxa pose problems as to their level of recognition as well as to which higher taxon they should be assigned within the order. In addition, more than 30 other families have been assigned to the Myrtales at some time in the recent past (Dahlgren & Thorne, 1984) demonstrating insufficient knowledge of the boundaries of the order as well as its evolutionary background.

A review of the general literature on the circumscription of the order and the evidence used in its definition has been ably dealt with in the other papers from this symposium from the standpoint of general systematic review (Dahlgren & Thorne, 1984; Johnson & Briggs, 1984), wood anatomy (van Vliet & Baas, 1984), leaf architecture (Hickey, 1981), pollen (Patel et al., 1984), and sieve element plastids (Behnke, 1984). I will restrict my comments to the contribution to be made by leaf histology, recognizing that a clear understanding will depend upon a synthesis of all of the above plus data yet to be obtained.

Some formidable problems must be faced when one attempts to use features from young vegetative anatomy in a systematic investigation. First is the insufficient number of studies of this sort to provide any reliable trends of specialization. I am convinced, however, that leaf histology contains not only valuable diagnostic characters, but that these characters will eventually demonstrate great utility in evolutionary studies. Much of the value will be based on both an increasing number of systematic studies of leaf histology, as well as character correlation with studies of leaf architecture (cf. Hickey, 1981). Leaf structure studies of both types should continue to accumulate rapidly. Leaves are obviously the most easily obtained of all plant materials both from the field and from herbarium collections. While leaves respond readily to evolutionary pressures toward xeromorphy or other modifications, their endomorphic characters commonly retain the ground plan of the phylad to which they belong (Keating, 1984; Dickison, 1970).

In this study a particular problem concerns the interpretation of the data from my sample. The sample appears comprehensive in that 176 species were examined representing 55 genera from 19 families. Actually, the specimens at hand amount to a very small sample of many of the families. Even though attempts were made to choose specimens representing geographic and taxonomic diversity within each family, obviously the family samples most likely do not include the total spectrum of characters to be found in them. The absence of a character from one group does not

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TABLE 1. Selected histological features of leaf transections of families of Myrtales.

	Histological Features																							
	Structure		Trichomes			Cuticle					Epidermis				Stomata						Chlorenchyma			
	Dorsiventral	Isobilateral	Simple 1-celled	Simple > 1-celled	Complex	Thin	Medium	Thick	Smooth	Ornamented	Adaxial = Abaxial	Adaxial > Abaxial	Adaxial 2× > Abaxial	Adaxial Cells Enlarged	Level	Sunken	Adaxial Only	Abaxial Only	Adaxial & Abaxial	Hypoderm	# Palisade Layers	Palisade % Lamina	Length/Width Ratio	# Spongy Layers
LYTHRACEAE																								
Ammannia coccinia	+					+			+			+		+	+				+		1	50	6 : 1	3
Cuphea spectabilis	+					+			+		+				+				+		1	30	5 : 1	5
Heimia salicifolia	+					+				+		+			+						1	50	4 : 1	3
Lafoensia speciosa	+					+			+			+			+			+			1	25	5 : 1	8
Lagerstroemia speciosa	+					+			+			≥			+			+			2	45	5 : 1	5
Lawsonia inermis	+					+			+		+				+			+			1(–2)	40	6 : 1	5
Lythrum alatum var. *lanceolatum*	+					+				+	+				+				+		1(–2)	50	5 : 1	3
Nesaea longipes	+					+				+	+			+	+				+		1	30	5–6 : 1	5
Punica granatum	+					+			+			±					+				2	50	4 : 1	3
Punica protopunica	+						+			+			+		+			+			2(–3)	40	5–8 : 1	5
Duabanga moluccana	+					+			+				+	+	+			+			2(–3)	50	5–6 : 1	4
D. grandiflora	+							+		+			+	+		±					2	50	5 : 1	4
D. grandiflora	+							+		+			+			±		+			2(–3)	50	5–6 : 1	9
D. moluccana	+					+			+				+		+			+			2	50	4–5 : 1	4
Sonneratia sp.	+	±						+		+	+					+			+		3–4	30	4 : 1	11
S. apetala		+						+		+	+					+			+		3 + 3	60	3–4 : 1	6
RYNCHOCALYCACEAE																								
Rhynchocalyx lawsonioïdes	+					+			+				+		+			+		+	2	60	4 : 1	5
TRAPACEAE																								
Trapa sp.	+					+			+			±			+		+				2	50	4 : 1	8
OLINIACEAE																								
Olinia emarginata	+						+	+	+			±			+			+		±	2–3	50	8 : 1	8

TABLE 1. **Continued.**

	Histological Features																						
	Structure		Trichomes			Cuticle					Epidermis				Stomata						Chlorenchyma			
	Dorsiventral	Isobilateral	Simple 1-celled	Simple > 1-celled	Complex	Thin	Medium	Thick	Smooth	Ornamented	Adaxial = Abaxial	Adaxial > Abaxial	Adaxial 2× > Abaxial	Adaxial Cells Enlarged	Level	Sunken	Adaxial Only	Abaxial Only	Adaxial & Abaxial	Hypoderm	# Palisade Layers	Palisade % Lamina	Length/Width Ratio	# Spongy Layers
COMBRETACEAE																								
Anogeissus leiocarpus		+	+			+			+		+				+			±			1 + 1	50	6:1	3
Buchenavia capitata	+							+	+				+	±	+						1	30	15:1	7
Bucida buceras	+						+		+				+		+			+			1	50	5–10:1	5
Combretum grandiflorum	+						+		+				+		+			+			1	50	8–10:1	5
Conocarpus erectus	±	±						+	+		+			+	+				+	+	3 + 2	50	4:1	5
Guiera senegalensis	+		+		±			+	+			+				±		+			2	50	8:1	5
Lumnitzera racemosa		+						+	+		+				+				+		2 + 2	40	8:1	8
Quisqualis indica	+		+			+			+		+				+			+			1	30	3:1	3
Strephonema pseudocola	+							+	+		+				+			+			1	25	12–15:1	9
Terminalia sp.	+						+		+		+				+			+			1	45	15–20:1	7
ALZATEACEAE																								
Alzatea verticillata	+							+	+	±	+				+			+		+	2	25	6:1	20
PENAEACEAE																								
Endonema lateriflora	+							+		±		+			+			+			2	30	8:1	8
Penaea mucronata	+							+		±	+				+			+			1	45	10:1	5
MELASTOMATACEAE																								
Tibouchina semidecandra	+				+	+			+		+				+			+			1	60	10–12:1	4
Heterocentron subtriplinervum	+				+	+			+				+	+	+			+			1	30	4:1	6
Memecylon blakeoïdes	+						+			+			+	+	+			+			1(–2)	40	2–3:1	3
M. guineense	+						+		+			+			+			+			2	15	1–2:1	4
M. parviflorum	+							+	+	+			+		+			+		±	3–4	40	2–4:1	8

TABLE 1. Continued.

	Histological Features																							
	Structure		Trichomes			Cuticle					Epidermis				Stomata						Chlorenchyma			
	Dorsiventral	Isobilateral	Simple 1-celled	Simple > 1-celled	Complex	Thin	Medium	Thick	Smooth	Ornamented	Adaxial = Abaxial	Adaxial > Abaxial	Adaxial 2 × > Abaxial	Adaxial Cells Enlarged	Level	Sunken	Adaxial Only	Abaxial Only	Adaxial & Abaxial	Hypoderm	# Palisade Layers	Palisade % Lamina	Length/Width Ratio	# Spongy Layers
M. afzelii	+							+	+				+		+			+			1	15	5:1	12
M. aylmeri	+					+			+			+			+			+			1	10	1–5:1	8
M. lateriflorum	+							+	+				+	+	+			+			1	10	4:1	12
M. sp.	+							+	+				+	+	+			+			2	20	2–3:1	7
Mouriri sp.		±						+	+	±	+				+			+		+	4 + 2	90	5:1	4
M. myrtilloïdes	+							+	+		+				+			+			2	30	1–2:1	4
CRYPTERONIACEAE																								
Axinandra zeylanica	+					+			+				+		+			+			1	10	2:1	9
Crypteronia paniculata	+			+			+		+	+			+		+			+			1(–2)	30	3:1	9
PSILOXYLACEAE																								
Psiloxylon mauritianum	+							+	+				+		+			+			1	20	12:1	15
MYRTACEAE																								
Tristania laurina	+							+	+				+		+			+			2	25	8:1	13
T. conferta	+							+	+		+				+			+		+	1	25	12:1	8
Eucalyptus micranthra		+						+		+	+				+				+		3 + 3	80	6:1	3
Syzygium paniculatum	+						+		+					+	+			+			2	40	6:1	7
Acmena smithii	+							+	+		+				+			+			1–2	15	12:1	11
Heteropyxis sp.	+					+			+			+			+			+			1	45	8–10:1	4
ONAGRACEAE	+	+	+			+			+		+	+			+			+	+		1–2	15–25	2–5:1	3–7

preclude a relationship between the two groups being compared. In spite of this, samples of many families demonstrate unique combinations of characters which will be commented on, often as negating relationships between taxa. The available anatomical literature on each family was consulted in order to record the known structural variability.

MATERIALS AND METHODS

All specimens available for this study were liquid preserved in either FAA or FPA at 50% alcoholic strength. Collection data follows each family description and vouchers are maintained at MO unless otherwise noted. Leaf specimens were removed for sectioning from the midrib and the margin, approximately equidistant between the lamina base and apex. The specimens were paraffin-embedded and sectioned at 10 μm on a rotary microtome (Sass, 1958). Most preparations were stained in Safranin-O, Fast Green FCF.

After a preliminary survey of the genera, the features discussed below (cf. Table 1) were selected for thorough observation. Studies by Dickison (1970), Böcher (1979), Pyykkö (1966), and Dahlgren (1968) were useful guides for initial selection of characters. Numerous other useful characters exist which should be included when individual families are studied intensively. Each of those finally selected was found to be diagnostic or systematically stable even though the evolutionary trends of specialization are as yet unknown for most of them.

Lamina structure: Dorsiventral or isobilateral.

Midrib: Shape or profile for the adaxial and abaxial surfaces. Also noted is the degree of abruptness or discreteness of the lamina as it joins the midrib. In all illustrations, adaxial is uppermost and all descriptive data are taken from that orientation.

Midvein and secondary veins: Shape or course in transsection. Presence and configuration of internal or intraxylary phloem. This is often described in relation to extraxylary fibers.

Extraxylary or periphloic fibers: These often affect the shape of the vein, especially secondary veins which may be transcurrent or round, etc., on the basis of the shape of fiber patches or sheaths.

Epidermis: Features include relative thicknesses of the adaxial and abaxial layers whether the surfaces are level or the cells papillose or other unusual shape, whether the cells are enlarged and/or rounded internally causing the palisade layer to undulate, and whether the cells have gummy, crystalline, or other contents.

Cuticle: Relative thickness, degree of ornamentation and whether the cuticle is flanged between the epidermal anticlinal walls. Normally, the adaxial epidermal cuticle is rated for thickness; the abaxial cuticle is usually thinner except on isobilateral leaves.

Stomata: These are noted as to the surface on which they occur and whether they are level, sunken, or otherwise modified.

Margin: There are a number of marginal shapes and modifications such as the type of marginal vasculature, thickenings, or gland types if present. Insufficient comparable data is at hand for this feature and it is therefore largely not taken into consideration in this report.

Hypodermis: Position and number of layers.

Mesophyll: Chlorenchyma is noted as to number of cell layers of the palisade zone and its percent of the total mesophyll thickness. The length/width ratio of palisade cells is also noted as is the approximate number of spongy layers. These features often appear surprisingly constant for certain families.

Sclereids: Type, position, and wall thickness are recorded.

Secretory cells, ducts: Type and position and presence of epithelium are recorded.

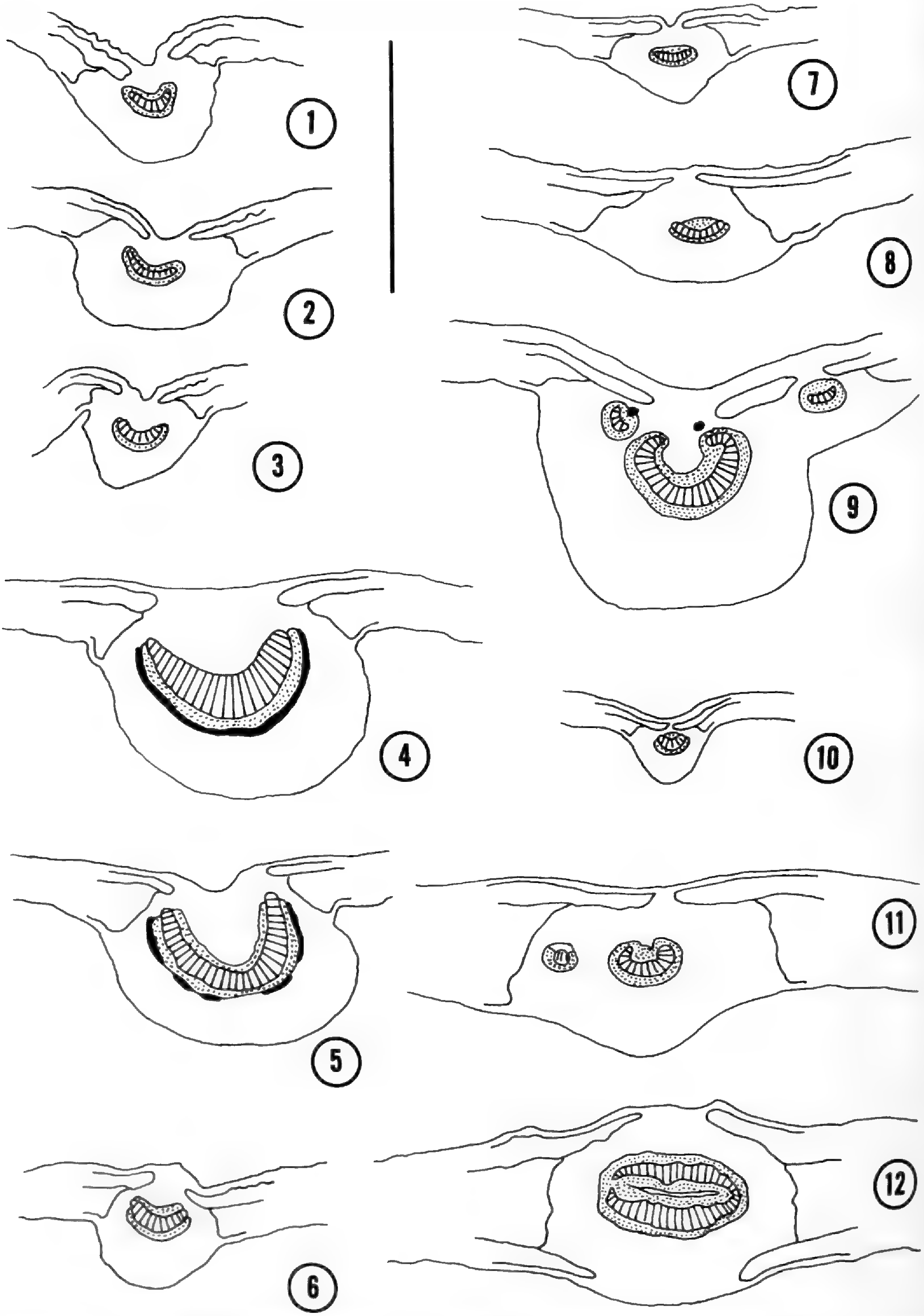
Cellular inclusions: Tannin cells are not usually noted since I have insufficient information as to the age of the specimens and its effect on tannin deposition. Crystal type, size, texture, and position are noted. Crystals are birefringent unless otherwise noted and probably made of calcium oxalate based on shape diagnosis (Franceschi & Horner, 1980; Frey-Wyssling, 1981).

Arrangement of the observations follows the systematic listing of Dahlgren and Thorne (1984). Individual genera are often noted separately if they have been noted in the past as being controversial or anomalous.

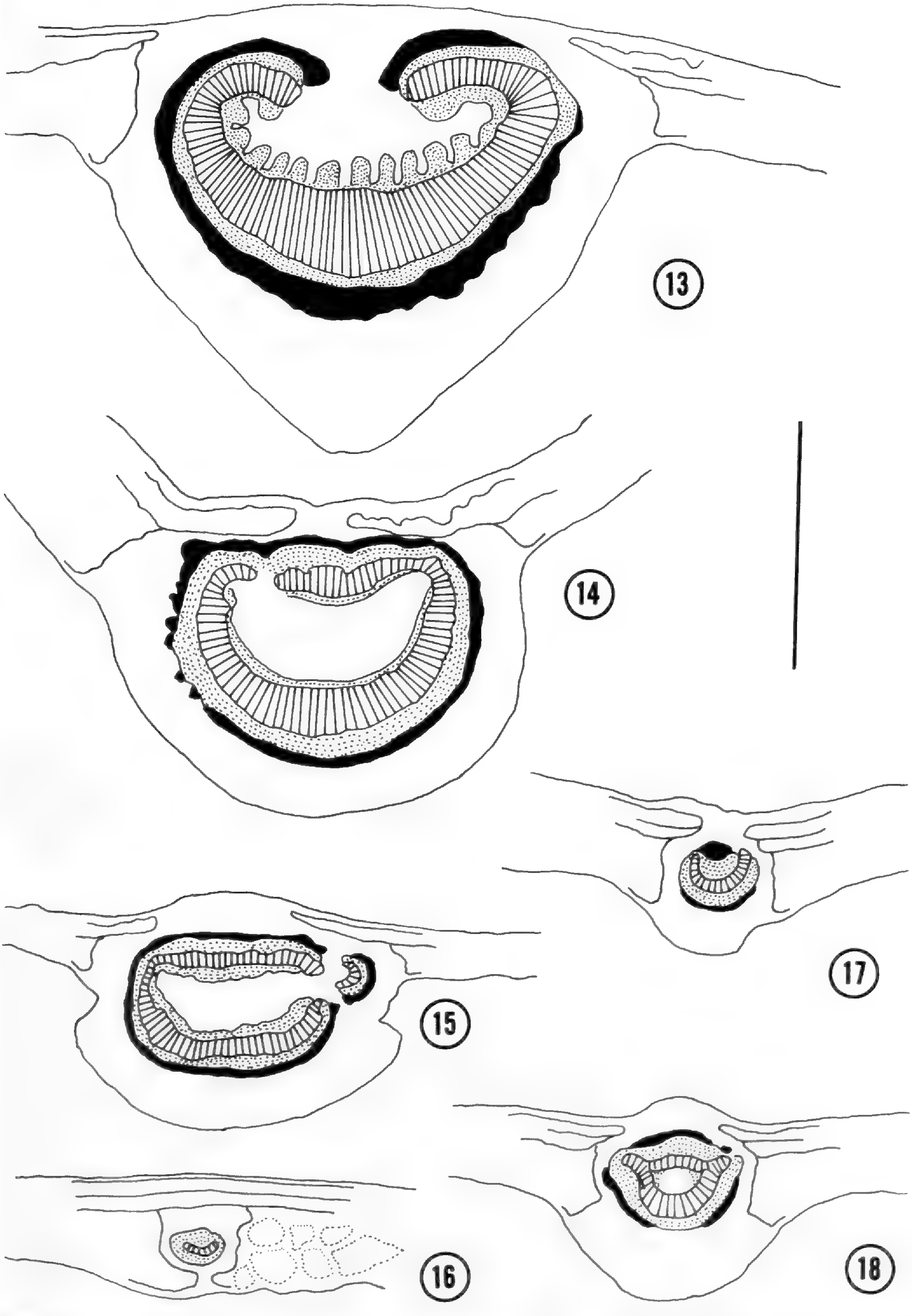
OBSERVATIONS

Lythraceae (Figs. 1–8, 10–15)

The genera *Duabanga, Sonneratia,* and *Punica,* often not included in the Lythraceae, are described separately below. In many species, one or both epidermal layers tend to be formed of large, rounded cells. Certain of them are con-



FIGURES 1–12. Midrib transverse sections of Lythraceae, Sonneratiaceae, and Punicaceae.—1. *Ammannia coccinia.*—2. *Cuphea spectabilis.*—3. *Heimia salicifolia.*—4. *Lagerstroemia speciosa.*—5. *Lafoënsia speciosa.*—6. *Lawsonia inermis.*—7. *Lythrum alatum* var. *lanceolatum.*—8. *Nesaea longipes.*—9. *Rhynchocalyx lawsonioides.*—10. *Punica granatum.*—11. *Sonneratia* sp.—12. *Sonneratia apetala.* Scale line = 1 mm. Legend for all figures: Hatching = xylem, stippling = phloem, solid black = extraxylary fibers.



FIGURES 13–18. Midrib transverse sections of Sonneratiaceae, Trapaceae, Oliniaceae, and Combretaceae.—13. *Duabanga grandiflora*.—14. *Duabanga moluccana*.—15. *Duabanga moluccana*.—16. *Trapa* sp.—17. *Olinia emarginata*.—18. *Terminalia* sp. Scale line = 1 mm.

spicuously larger than the others and may often have mucilaginous contents. The midrib may be grooved, level, or slightly ridged adaxially and often prominently rounded-convex abaxially. The midrib is nearly immersed in *Nesaea longipes* (Fig. 8). The midveins vary from a complete cylinder to deeply semicircular to a fairly shallow arc. Most midveins are bicollateral, but others are apparently collateral. Secondary veins are generally collateral. In most genera, secondary veins are rounded except in *Lagerstroemia speciosa* (Fig. 4) which has an adaxial transcurrent extension formed of parenchyma. Extraxylary fibers are generally absent. When present, they form an abaxial periphloic band on both the midvein and secondary veins [*Lafoënsia speciosa* (Fig. 5) and *Lagerstroemia speciosa*]. Sclereids are absent. Druses are common in the mesophyll and midrib ground tissue. Occasional prismatics are found in *Lafoënsia*. *Lythrum alatum* (Fig. 7) has a few epidermal cells containing radiating clusters of birefringent needle-like crystals.

Punica granatum (Fig. 10). The midrib is slightly and broadly grooved adaxially and is rounded abaxially. The midvein is a bicollateral short arc. Secondary veins are short arcs which are collateral and round in outline. Mesophyll tissue is developed in the midrib quite close to the lateral and adaxial sides of the midvein leaving most of the midrib ground tissue abaxial to the midvein. Extraxylary fibers and sclereids are absent. Very large prismatic crystals and some smaller ones occur in the palisade and spongy mesophyll. A few of the large crystals have central druse-like clusters around their equator.

Duabanga (Figs. 13–15). Adaxial epidermal cells are flattened on the surface but are deeply rounded internally. Some of the larger ones contain mucilage. Abaxial epidermal cells on two of the three species are all deeply papillose with baculum-shaped knobbed extensions, each of which has an ornamented cuticle on its distal surface. The midrib is level or slightly convex adaxially and prominently convex-rounded or V-shaped abaxially. The midvein is a somewhat flattened cylinder with one or two adaxial gaps or a broad crescent shape with deeply incurved adaxial ends. Midveins and secondary veins are bicollateral. Secondary veins are flattened arcs or are circular in different species. Periphloic fibers surround midveins and secondary veins. Some mesophyll cells appear to be lignified but markedly idioblastic sclereids were not found. Druses vary by species from absent to large, coarse and complex to medium-sized. They occur in mid-mesophyll and around veins.

Sonneratia (Figs. 11, 12). Stomata are surrounded by guard cells which are partially enclosed by larger epidermal cells. The stomata are thus somewhat sunken. The midrib is slightly convex abaxially or on both surfaces. Both samples are or tend toward isobilateral structure. The midvein is a dorsiventrally flattened cylinder or an open flattened "U" shape. The vasculature is bicollateral on the midvein and secondary veins. Secondary veins are round and are nearly encircled by phloem. Fibers are not present. Macro- and astro-sclereids are present in the mesophyll. Many large mucilage cells are present subepidermally which may be of epidermal origin. Small, coarse druses are present in the mesophyll and around veins.

Specimens examined: *Ammannia coccinia* Rottb., *Graham 489* (MICH), Texas; *Cuphea spectabilis* S. Graham, *Reveal et al. 4339* (MARY), Mexico; *Heimia salicifolia* (H.B.K.) Link., *Graham 141* (MICH), Mexico; *Lagerstroemia speciosa* (L.) Pers., cult. MO 74248, Brazil; *Lafoensis speciosa* (H.B.K.) DC., cult. FTG X-5-20, s. loc.; *Lawsonia inermis* L., *Raven 26570*, cult. MO, Hong Kong; *Lythrum alatum* var. *lanceolatum* (Ell.) Rothrock, *Graham 460* (MICH), Mississippi; *Nesaea longipes* A. Gray, *Turner 6163* (TEX), Mexico; *Punica granatum* L., *Raven 26569*, cult. MO, s. loc.; *P. protopunica* Balf. f., *Rudall s.n.* (K), Socotra; *Duabanga grandiflora* (Roxb. ex DC.) Walpers, *Sahni s.n.*, India; *Stone 12837*, Malaya; *D. moluccana* Bl., *Chai s.n.*, Borneo; *Madani s.n.*, 3/5/77, Sadah; *Sonneratia* sp., *Stone & Anderson 13165* (SAN), Sabah; *S. apetala* Buch.-Ham., *Thanikaimoni s.n.*, 3/15/77, India.

Rhynchocalycaceae (Fig. 9)

Rhynchocalyx lawsonioïdes. The midrib is slightly concave or level adaxially and prominently rounded-protruding abaxially. The midvein is semicircular, somewhat V-shaped abaxially with a tendency toward incurved ends with reduced xylem development. Phloem is bicollateral. Secondary veins are similar in configuration only smaller than the midvein. Minor veins are collateral with a circular patch of xylem and an abaxial rounded patch of phloem. Fibers are scanty. One or two small patches are found on the adaxial side of the midvein and secondary veins. Minor veins have a transcurrent adaxial fiber patch which nearly doubles the vein height. Sclereids are absent. Coarse-textured, medium-sized druses are common in midmesophyll and in midrib ground tissue. The large adaxial epidermal cells are flat on the surface and rounded on the palisade side making the palisade zone appear to undulate.

Specimen examined: *Rhynchocalyx lawsonioïdes* Oliv., *Raven s.n.*, cult. MO 7442, South Africa.

Trapaceae (Fig. 16)

Trapa. The midrib is immersed and centered within the zone of aerenchyma of this floating leaf. The small midvein has a rounded patch of xylem with an arc of phloem abaxial to it. A narrow zone of ground tissue (a bundle sheath) surrounds the vein and is in direct proximity to the palisade zone. The vein may be slightly bicollateral. Secondary and minor veins are uncommon. They appear to be bicollateral and are surrounded by a parenchymatous sheath. No fibers or sclereids are present. Druses are present around veins, in palisade, and in aerenchyma zones.

Specimen examined: *Trapa* sp., *Hellquist s.n.* 6/77, Massachusetts.

Oliniaceae (Fig. 17)

Olinia. The midrib is level adaxially and slightly rounded abaxially. The midvein is semicircular and bicollateral. Secondary veins are collateral or bicollateral. Periphloic fibers form a well-developed abaxial band as well as a deep adaxial patch over the midvein. Secondary veins may be surrounded by a circular sheath of fibers or by an interrupted sheath consisting of abaxial and adaxial portions. The adaxial portion may form a transcurrent ridge. Diffuse sclereids were not noted. Large or medium-sized, coarse-textured druses are found mostly near veins with some in mid-mesophyll. A large, dense mass of druses was found abaxial to the midvein fibers. The leaf margin is slightly recurved and consists of a multiple-layered hypoderm-like tissue.

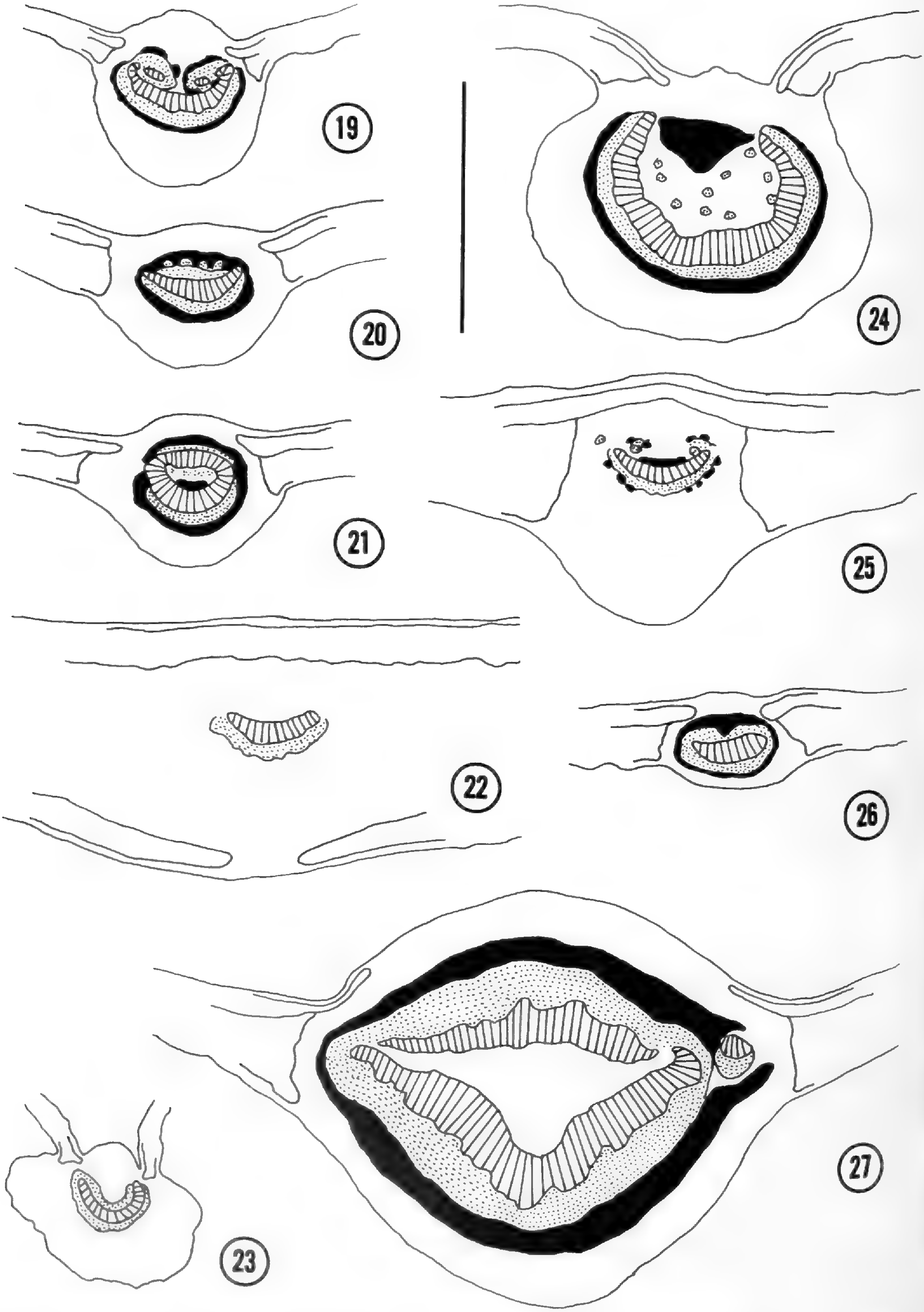
Specimen examined: *Olinia emarginata* Burtt-Davy, *Goldblatt 1466* (MO) cult. Kirstenbosch, South Africa.

Combretaceae (including *Strephonema*) (Figs. 18–27)

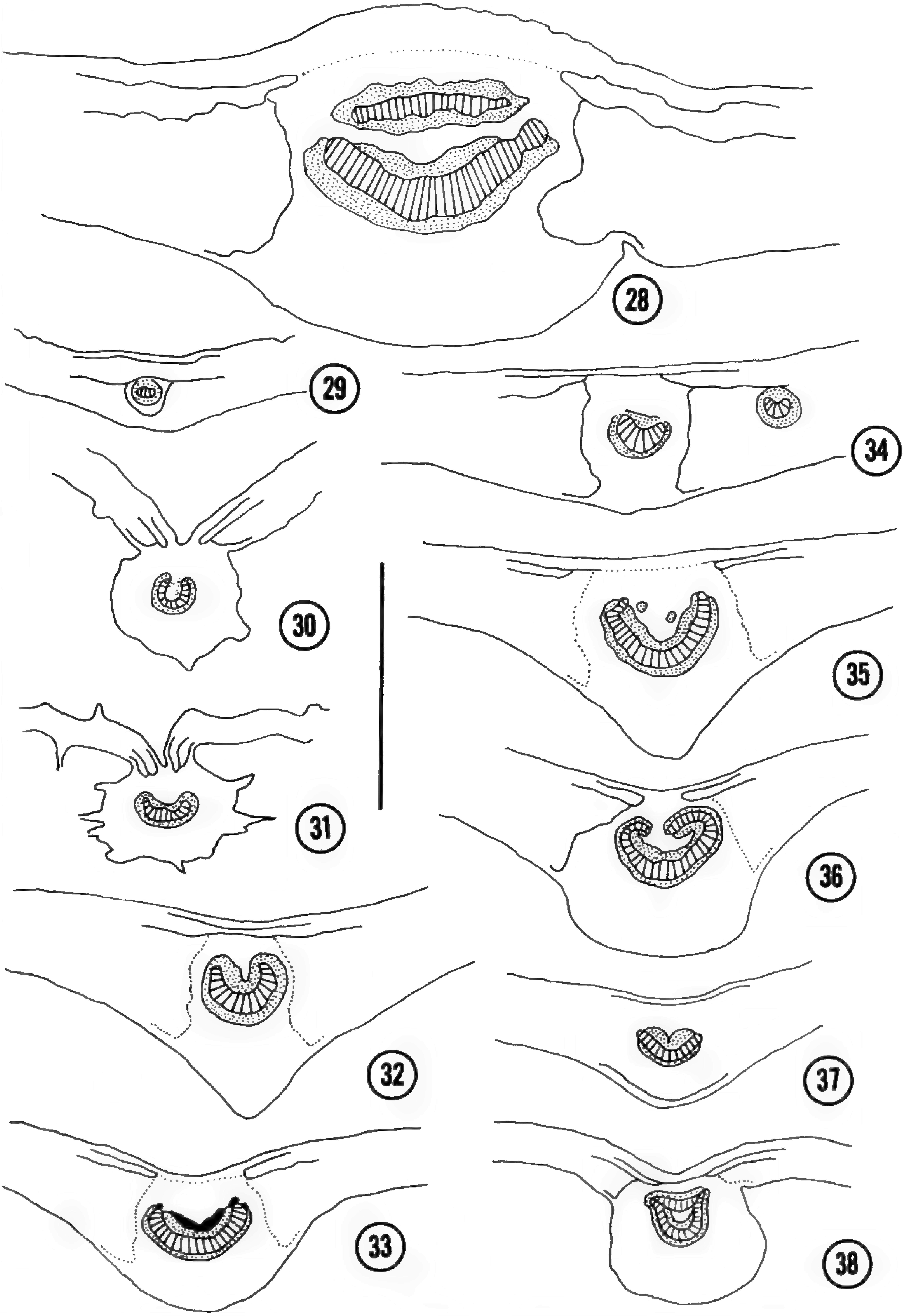
The midrib is often conspicuously circular in outline. Lamina sectors commonly insert laterally leaving a well-formed adaxial ridge. *Combretum* (Fig. 24) and *Quisqualis* (Fig. 23) have a midrib protruding prominently on the abaxial side. The midvein is commonly cylindrical or a flattened cylinder. A pair of gaps are often present opposite the lamina insertion. *Combretum* has a three-quarter cylinder open adaxially. *Quisqualis* and *Conocarpus* (Fig. 25) have semicircular or broad arc midveins. The midveins appear collateral with weak development of bicollateral phloem in some specimens. Secondary and tertiary veins are quite variable and possibly diagnostic. While some are circular, most tend to be transcurrent with parenchymatous sheath extensions. *Buchenavia* (Fig. 20) and *Terminalia* (Fig. 18) have fiber sheaths with extensions forming transcurrent veins. Other genera have fibers in sheaths, adaxial-abaxial patches, or in scanty patterns. Fibers also surround midveins. In *Buchenavia,* adaxial fibers form sheaths around prominent discrete patches of adaxial phloem. Sclereids are not common. In *Bucida* (Fig. 21), fibrous sclereids are well developed under the adaxial epidermis and attach to veins at transcurrent extensions. Some occur isolated in the palisade region. *Buchenavia* also has vein extensions where fibers occasionally develop away from the extensions. *Strephonema* (Fig. 27) has macrosclereids and trichosclereids common in the lamina in any orientation. Very large druses are common in enlarged cells of the mesophyll in all genera examined and some have styloid projections. A few prismatics are found in *Strephonema.*

Lumnitzera racemosa (Fig. 22). The cuticle is thick, smooth, and flanged over thickened outer periclinal walls on both adaxial and abaxial epidermal layers. Outer palisade layers beneath both surfaces have dense, red-staining contents. The midrib is nearly immersed but the abaxial side shows a slight convex curvature. The midvein is a broad arc with collateral phloem. Fibers and sclereids are absent. Medium-sized, coarse druses are common and randomly placed in the mesophyll.

Specimens examined: *Anogeissus leiocarpus* (DC.) Guill. & Perr., *Pilz 2088,* Nigeria; *Buchenavia capitata* (Vahl.) Eichler, *Raven 26623,* cult. MO, s. loc.; *Bucida buceras* L., *Raven 26618,* cult. MO, Puerto Rico; *Combretum grandiflorum* G. Don, cult. FTG X-2-328, s. loc.; *Conocarpus erectus* L., *Raven 26619,* cult. MO, Puerto Rico; *Guiera senegalensis* Lam., *Sreemadhavan 5800,* Nigeria; *Lumnitzera racemosa* Willd., cult. FTG 64-4585, s. loc.; *Quisqualis indica* L., *Raven 26572,* cult. MO, s. loc.; *Strephonema pseudocola* A. Chev., *Hall & Nabooh 46647,* Ghana; *Terminalia* sp., cult. FTG X-2-2700, s. loc.



FIGURES 19–27. Midrib transverse sections of Combretaceae.—19. *Anogeissus leiocarpus.*—20. *Buchenavia capitata.*—21. *Bucida buceras.*—22. *Lumnitzera racemosa.*—23. *Quisqualis indica.*—24. *Combretum grandiflorum.*—25. *Conocarpus erectus.*—26. *Guiera senegalensis.*—27. *Strephonema pseudocola.* Scale line = 1 mm.



FIGURES 28–38. Midrib transverse sections of Alzateaceae, Penaeaceae, and Melastomataceae.—28. *Alzatea verticillata.*—29. *Penaea mucronata.*—30. *Heterocentron subtriplinervum.*—31. *Tibouchina semidecandra.*—32. *Memecylon afzelii.*—33. *Memecylon aylmeri.*—34. *Memecylon parviflorum.*—35. *Memecylon lateriflorum.*—36. *Memecylon guineense.*—37. *Memecylon oligoneurum.*—38. *Memecylon blakeoïdes.* Scale line = 1 mm.

Alzateaceae (Fig. 28)

Alzatea. The midrib is moderately convex on both surfaces and not prominent. The midvein is a flattened cylinder with lacunae separating the bicollateral adaxial and abaxial portions. Secondary and minor veins are collateral and circular in outline. Extraxylary fibers are absent, but large, thin-walled sclereids are abundant throughout the mesophyll. They have been called branched foliar sclereids by Dahlgren and Thorne (1984). The cells are actually the same shape as the armed spongy or palisade chlorenchyma in which they appear and they occur as lignified single cells or groups of cells. A 1–2 layered adaxial hypoderm is present over the lamina which may become up to 7 layers deep over the midrib. Baas (1979) reported that the hypoderm is present only over the midrib in *A. verticillata* from Peru. Small druses are uncommon in the lower mesophyll and near the midvein and secondary veins.

Specimen examined: *Alzatea verticillata* Ruiz & Pavón, *Poveda s.n.*, Costa Rica.

Penaeaceae (Fig. 29)

The midrib is small, convex abaxially in *Endonema*, or totally immersed in *Penaea*. The partially bicollateral midvein is small, round to elliptical, and with a short arc of xylem. Adaxially, phloem development is restricted to the lateral portions of the xylem. Sclereids are fibrous in *Penaea*, beneath the epidermis and at random in the mesophyll. In *Endonema*, the abundant branched astrosclereids with elongated arms are found throughout the mesophyll but are concentrated in mid-mesophyll. Druses are large, coarse, and complex and are found beneath the epidermis on the adaxial and abaxial sides of the mesophyll.

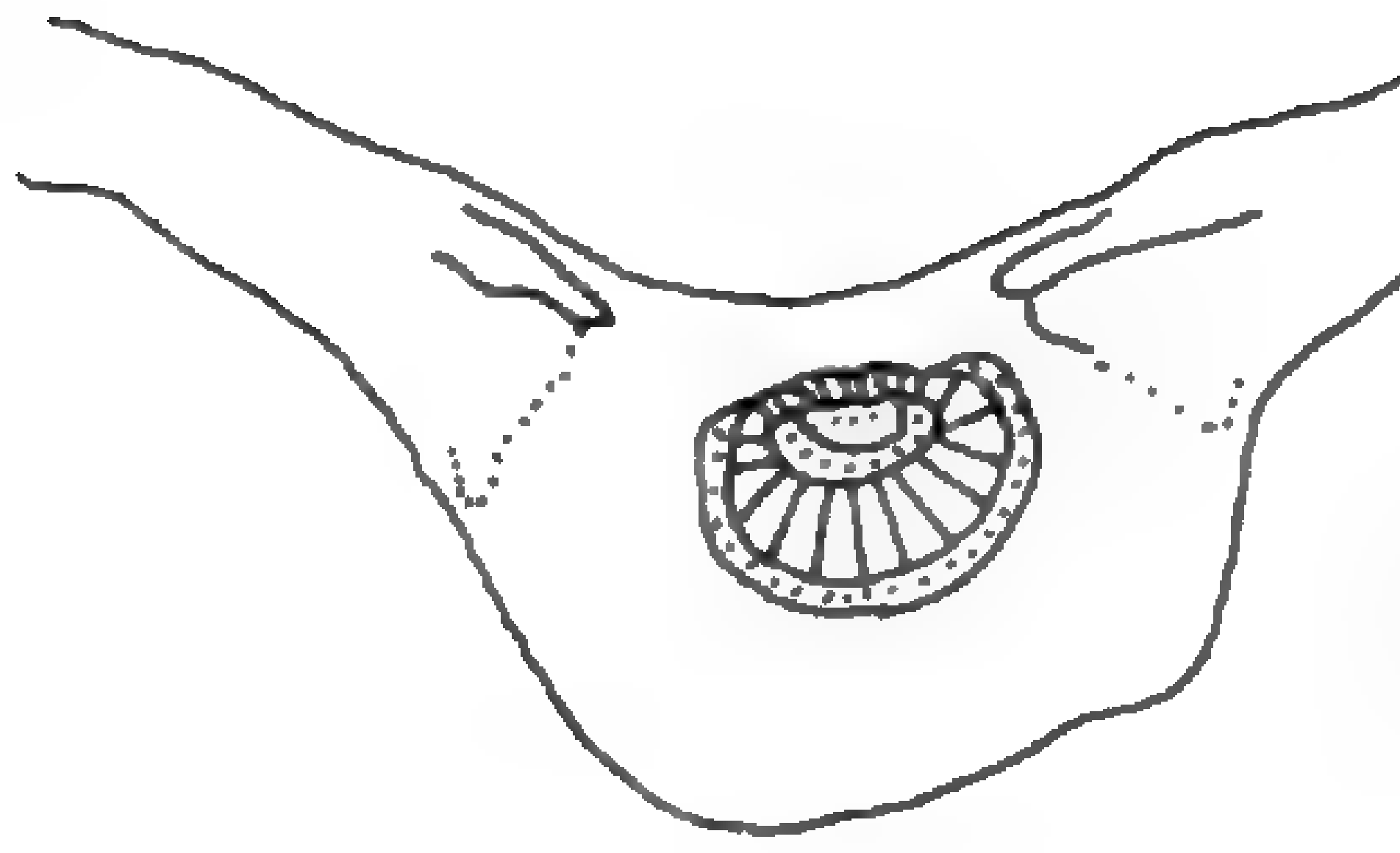
Specimens examined: *Endonema lateriflora* (L. f.) Gilg, *Rourke 1706*, South Africa; *Penaea mucronata* L., *Barker 332*, cult. Kirstenbosch, South Africa.

Melastomataceae (Figs. 30–41)

Adaxial epidermal cells are exceptional in *Heterocentron* (Fig. 30) in being large, flat on the surface and irregular and rounded on the palisade side. The midrib is large and rounded with lamina sectors inserted near the top of the adaxial side. Large, pyramidal, multicellular hairs may be present on the midrib surface. The midvein is a semi-circle or three-quarter circle and may be small or large. The bicollateral phloem is evenly dispersed on both sides of the xylem of the midvein and secondary veins. Minor veins are collateral with partially encircling abaxial phloem. Fibers and sclereids are absent. Large coarse druses are found in the mesophyll and midrib often in large round cells. Small druses may also be present in the midvein area of *Heterocentron*.

Memecyloideae, Memecylon. This genus forms midribs which are level or slightly grooved adaxially. Abaxially the midribs may be slightly convex, somewhat V-shaped or prominently rounded. The midveins vary from nearly cylindrical, flattened or rounded adaxially, semicircular or form only a broad arc in those species with the least prominent midribs. Midveins are cylindrical with an adaxial groove in *M. blakeoïdes* (Fig. 38), an incomplete cylinder with incurved ends in *M. guineense* (Fig. 36), or semicircular or broad arcs in other species. The veins are bicollateral with the adaxial phloem often better developed than the abaxial in both midveins and secondary veins. Extraxylary fibers are not common. *Memecylon aylmeri* (Fig. 33) has well-developed fiber patches on the adaxial side of the midvein phloem and similar development on the secondary veins. The *Memecylon* sp. (Fig. 41) has a fiber cylinder bounding both outer and inner phloem of its nearly cylindrical midvein. The secondary veins are also encircled. Phloem is often best developed closest to the protoxylem. Fiber-like sclereids are common subepidermally and throughout the mesophyll. They are commonly dispersed without relation to veins but in some species they attach to vein sheath fibers. They are variously seen to be without a visible lumen, with a large lumen and thin walls, rounded in outline, or irregular depending on the species. Druses also vary by species. Prismatics and coarse druses are found in *Memecylon* sp. Smaller druses, more finely textured, occur as do some with a hollow-appearing non-birefringent center. They occur in the midrib ground tissue, subepidermally in the lamina or in the mid-mesophyll.

Memecyloideae, Mouriri (Figs. 39, 40). The midrib is grooved adaxially and is protruding and somewhat flattened abaxially. Midvein xylem is a flattened cylinder surrounded by phloem externally and internally. Large midveins have periphloic fibers forming a thin sheath both ex-



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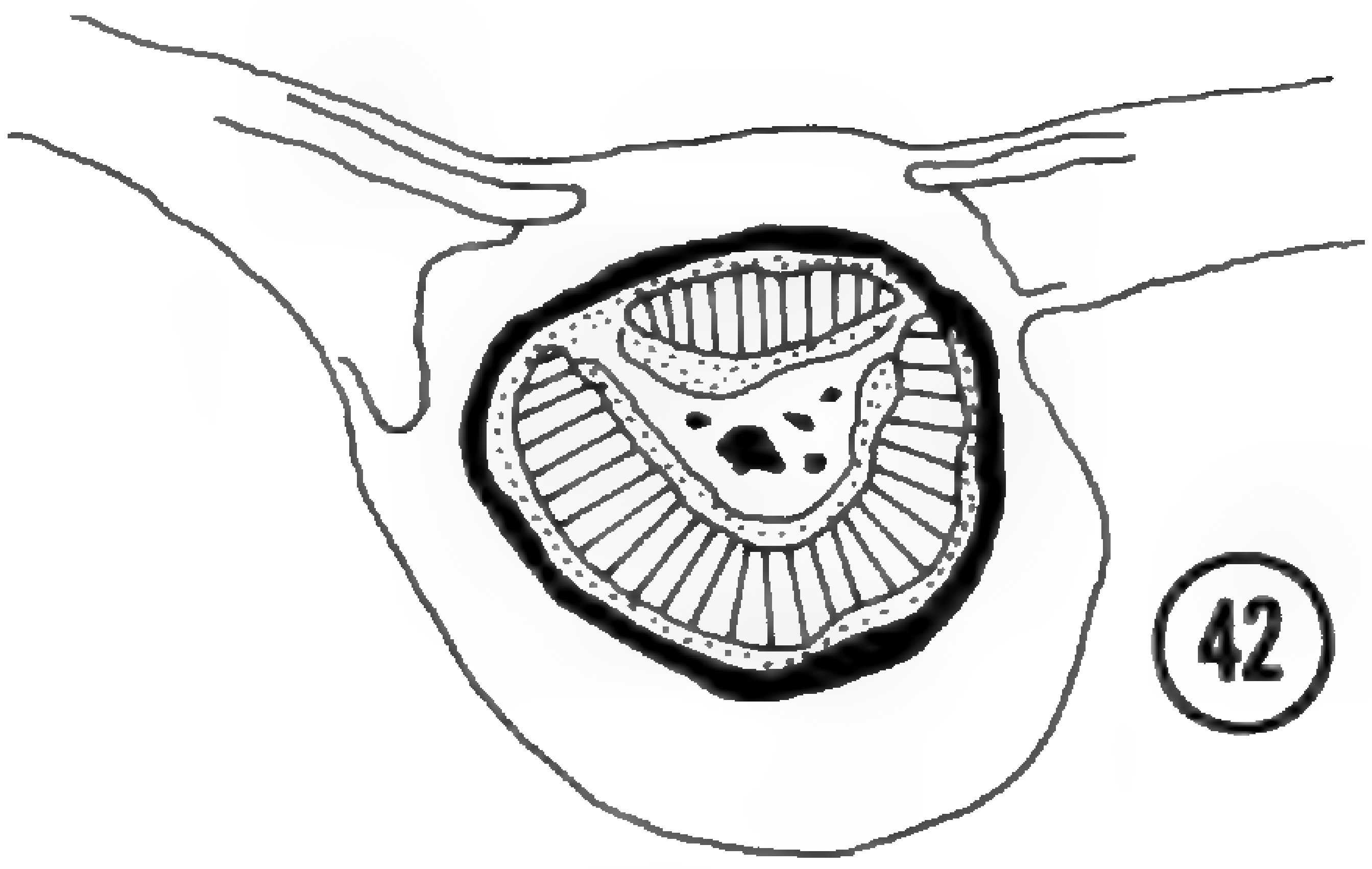

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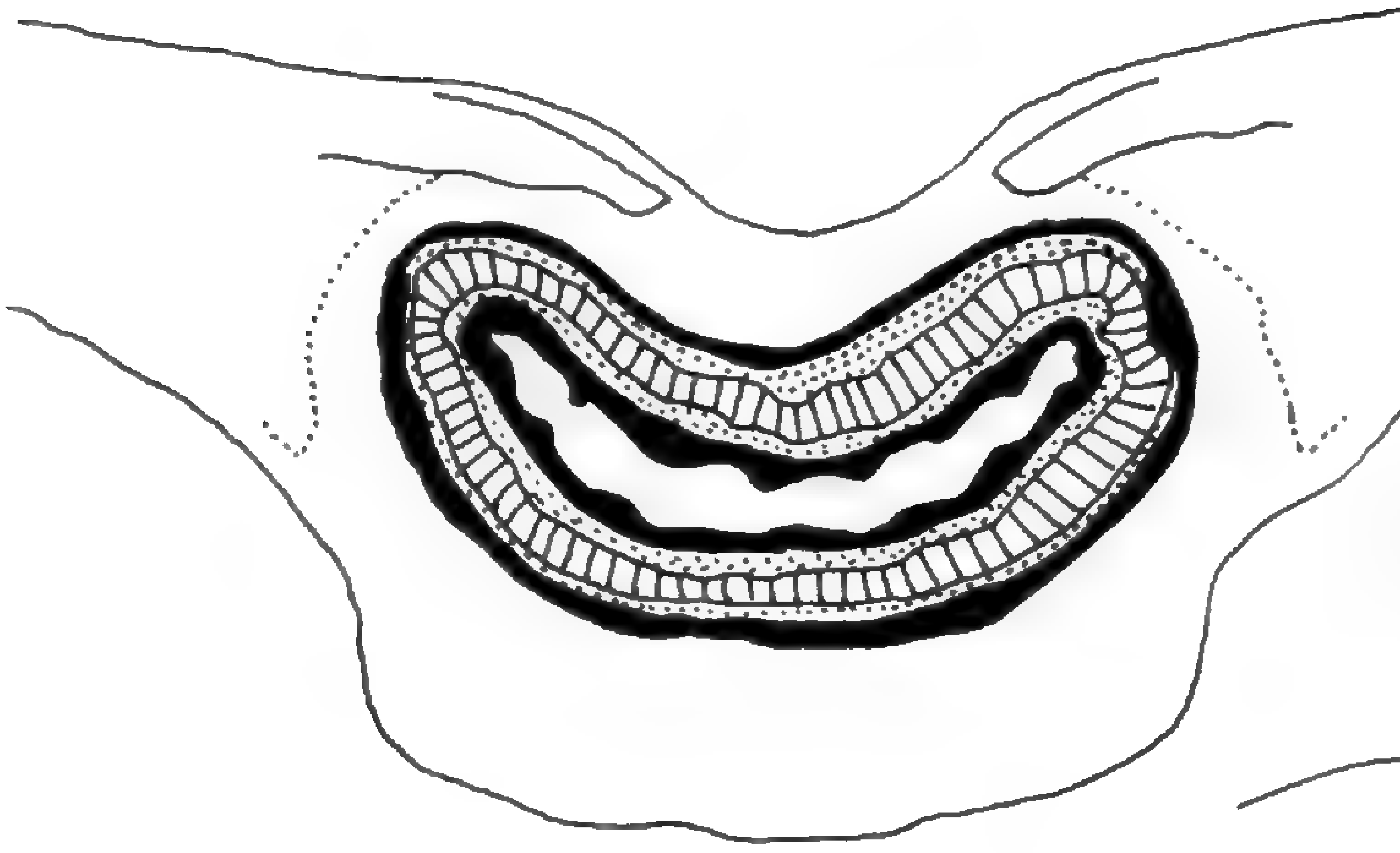

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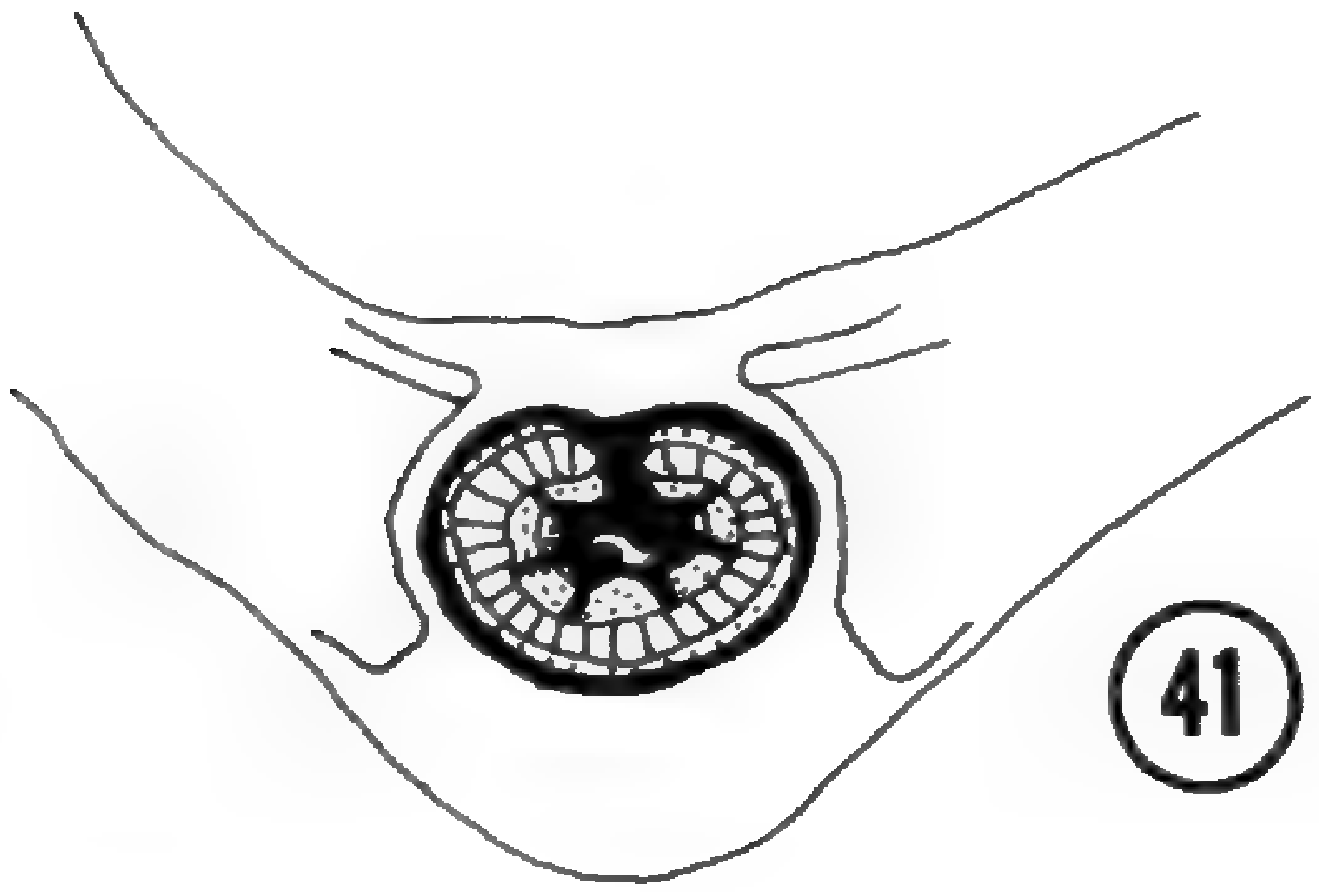

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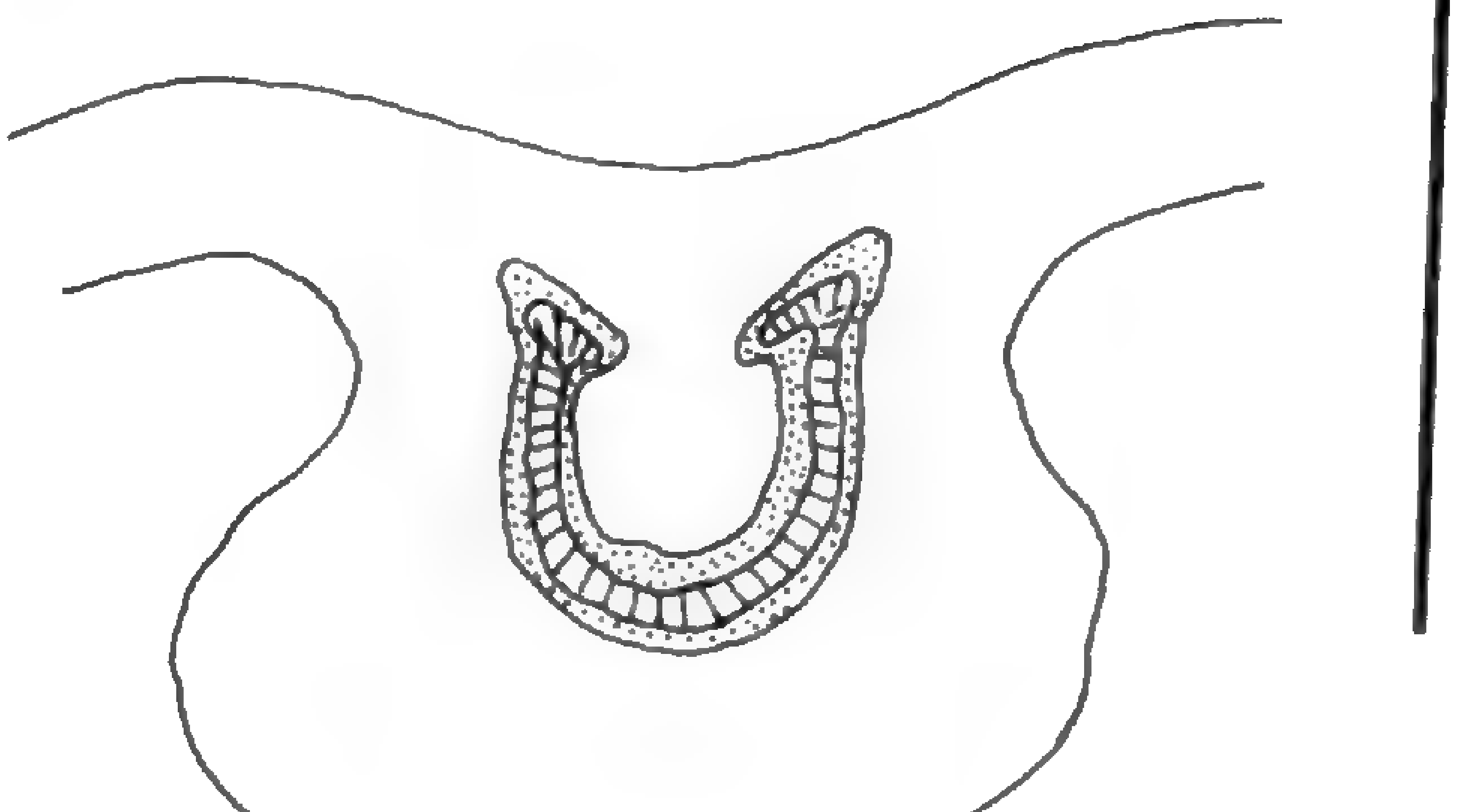

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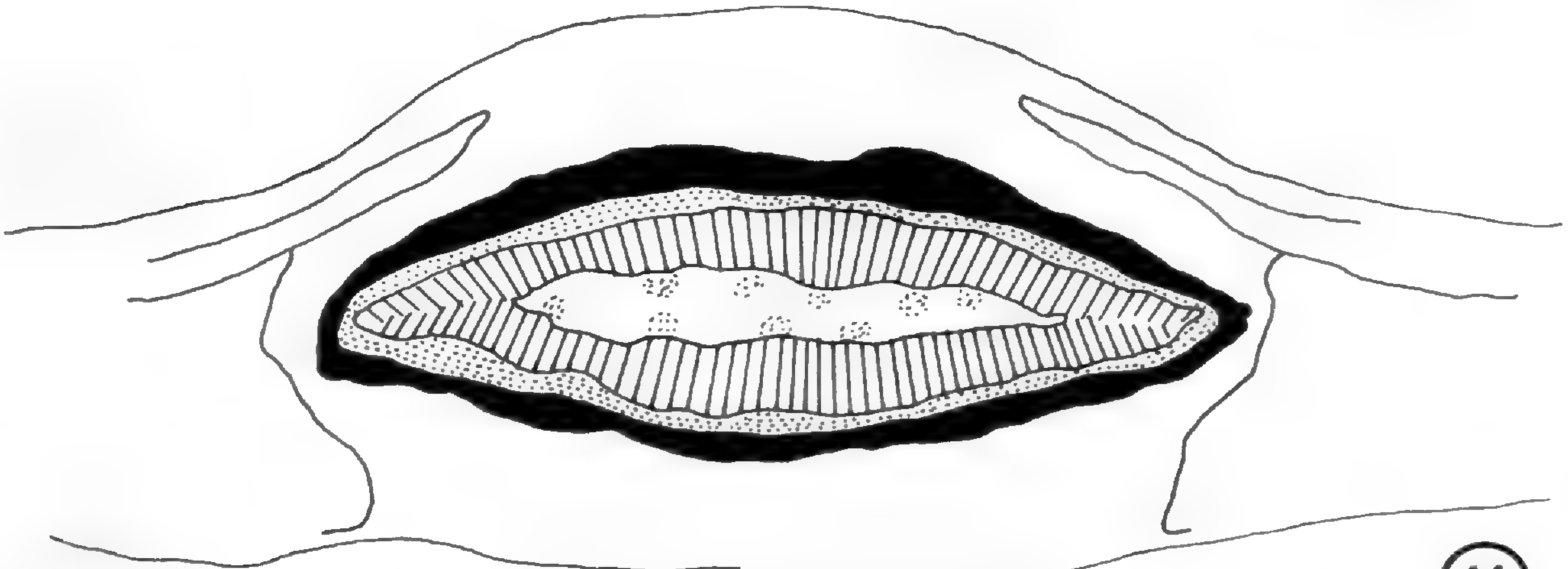

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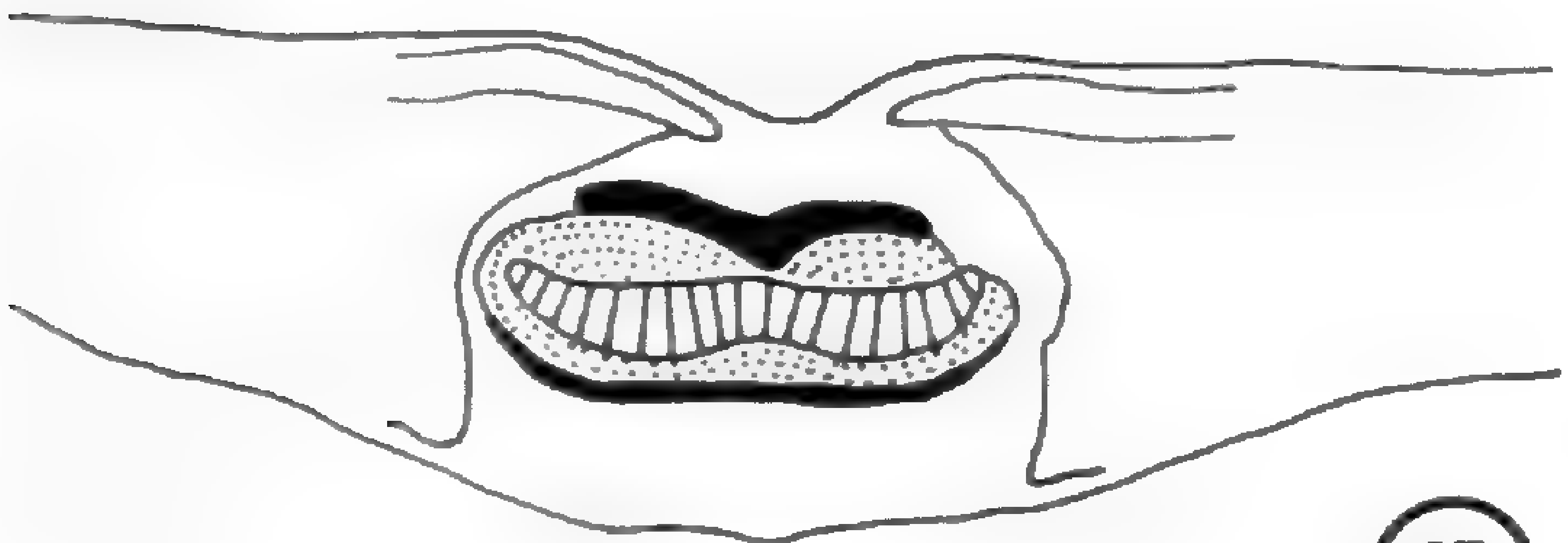

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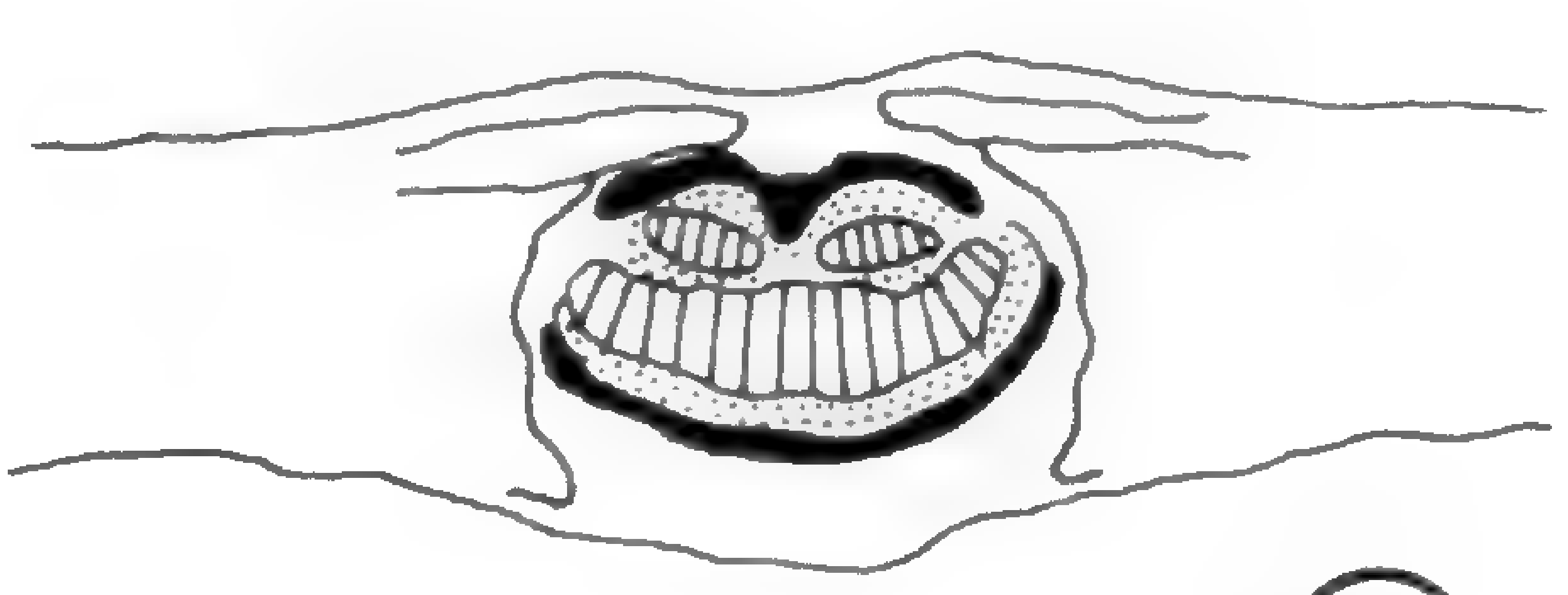

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FIGURES 39–46. Midrib transverse sections of Melastomataceae, Crypteroniaceae, Psiloxylaceae, and Myrtaceae.—39. *Mouriri myrtilloïdes.*—40. *Mouriri* sp.—41. *Memecylon* sp.—42. *Crypteronia paniculata.*—43. *Axinandra zeylanica.*—44. *Psiloxylon mauritianum.*—45. *Acmena smithii.*—46. *Eucalyptus micrantha.* Scale line = 1 mm.

ternally and internally. Secondary and minor veins are sheathed by fibers and the veins are bicollateral. Smaller leaves have no fibers. Diffuse sclereids are common in mid-mesophyll. They may be branched or armed and may have a large lumen. Druses are common in mid-mesophyll and are medium-sized and coarse-textured. Phloem of secondary veins is best developed on the adaxial side. Abaxial phloem is poorly formed or absent.

Specimens examined: *Heterocentron subtriplinervum* (Link & Otto) A. Braun & Bouche, cult. LA, s. loc.; *Memecylon afzelii* G. Don, *Hall & Nabooh 46601,* Ghana; *M. aylmeri* Hutch. & Dalz., *Hall & Nabooh 46632,* Ghana; *M. blakeoïdes* G. Don, *Hall & Nabooh 46628,* Ghana; *M. guineense* Keay, *Hall & Nabooh 46629,* Ghana; *M. lateriflorum* (G. Don) Bremek., *Hall & Nabooh 46630,* Ghana; *M. oligoneurum* Bl., *Chai s.n.,* Borneo; *M. parviflorum* Thw., *Leiden 2978,* cult. Bogor, s. loc.; *Mouriri myrtilloïdes* (Sw.) Poiret, *Wurdack & Wurdack 2624,* Jamaica; *Mouriri* sp., *Madani s.n.* 5/3/77 (SAN 81060), Sabah; *Mouriri* sp., *Gentry 18524,* Peru; *Tibouchina semidecandra* (Schr. & Mart.) Cogn., *Raven 26571,* cult. MO, s. loc.

Crypteroniaceae (Figs. 42, 43)

Crypteronia paniculata (Fig. 42). The midrib is nearly level adaxially and prominently rounded-protruding abaxially. The overall shape is circular with lamina inserted near the summit of the adaxial side. The midvein is circular with the xylem divided into abaxial and adaxial portions which are separated by lacunae opposite the position of lamina insertion. The vasculature is bicollateral. Extraxylary fibers form a well-developed cylinder around the outer phloem as well as scattered patches in the center of the midvein. Sclereids are absent. Medium-sized druses, of medium texture, are common around veins and in mid-mesophyll.

Axinandra zeylanica (Fig. 43). The midrib is slightly grooved adaxially and deeply rounded-convex abaxially. The midvein is deeply semicircular with small incurved ends. The vein is uniformly bicollateral. Secondary veins are short collateral arcs. No sclereids or fibers were seen. Prismatic crystals appear in midrib ground tissue and many small druses occur in the mesophyll.

Specimens examined: *Axinandra zeylanica* Thw., *Faden 76/466,* Sri Lanka; *Crypteronia paniculata* Bl., *Stone 13280,* Thailand.

Psiloxylaceae (Fig. 44)

Psiloxylon mauritianum. The thick adaxial epidermis has paradermal thickenings beneath the surface and is covered by a thick non-flanged cuticle. The midrib is broad with the lamina gradually increasing in thickness to a rounded adaxial convex ridge. The midrib is only slightly convex or level abaxially. Midvein vasculature is a flattened cylinder with deep xylem development and bicollateral phloem. A prominent band of periphloic fibers surrounds the midvein and secondary veins. Minor veins have adaxial-abaxial phloem caps. The palisade mesophyll extends prominently into the adaxial midrib ridge. Sclereids are absent. Secretory cavities lined with an epithelium are present subepidermally beneath both surfaces. A few medium-sized druses are found near veins.

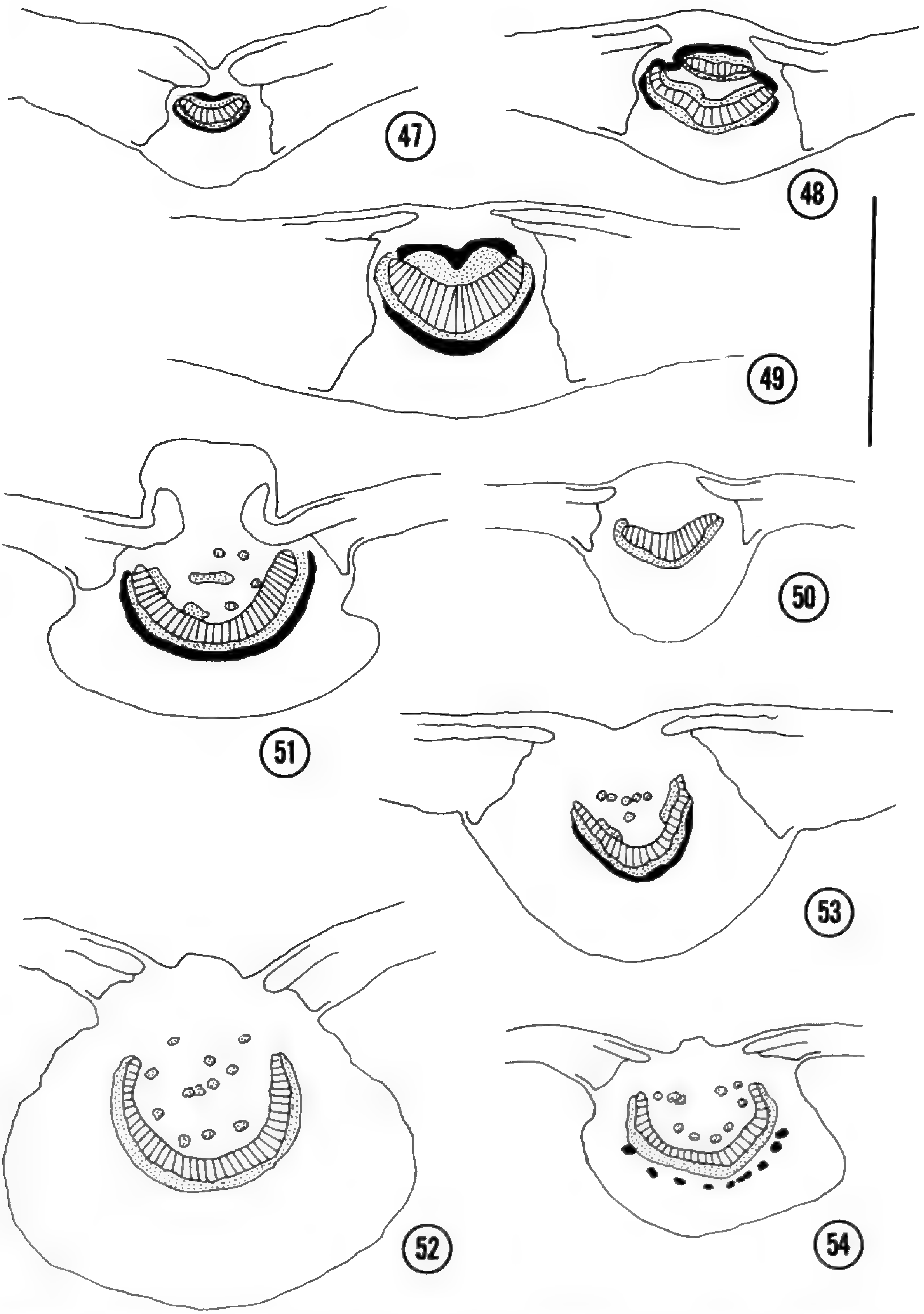
Specimen examined: *Psiloxylon mauritianum* Baill., *Gueho s.n.* 12/1976, Mauritius.

Myrtaceae (Figs. 45–50)

The midrib is adaxially grooved or ridged and abaxially rounded and the midrib is generally not prominent. The midvein is a broad arc or semicircle in most species but approaches a flattened cylinder with one or more gaps in *Eucalyptus* (Fig. 46) and *Tristania* (Figs. 48, 49). The midvein is collateral or bicollateral. Midveins may be bounded adaxially and abaxially by fiber layers. Secondary veins are circular or tending toward transcurrent. They may be surrounded by a ring of fibers or have prominent adaxial-abaxial bundle caps. No sclereids were seen. Secretory cavities are prominent beneath either epidermal layer. They are surrounded by a single distinct epithelial layer. Irregularly shaped prismatic crystals and druses of varying sizes and texture may be found in mesophyll and midrib ground tissue.

Heteropyxis (Fig. 50). Midrib vasculature is a broad arc with well-developed xylem somewhat similar to *Tristania* and *Syzygium* (Fig. 47). In the midrib, the palisade impinges adaxially somewhat more than the spongy layer. The sharp differentiation of midrib ground tissue from the mesophyll is also similar to the Myrtaceae. Large secretory cavities are also present. The secondary veins have parenchymatous sheath extensions which extend to both epidermal layers. All veins in my specimen appear to be collateral although they are reported to be bicollateral by Schmid (1980). Sclereids and periphloic fibers are absent.

Specimens examined: *Acmena smithii* (Poir.) Merrill & Perry, *Schmid 1968-A2,* cult. LAM, Australia; *Eucalyptus micrantha* DC., *Schmid 1969-A3,* cult LAM.



FIGURES 47–54. Midrib transverse sections of Myrtaceae and Onagraceae.—47. *Syzygium paniculatum*.—48. *Tristania conferta*.—49. *Tristania laurina*.—50. *Heteropyxis* sp.—51. *Ludwigia peruviana*.—52. *Fuchsia boliviana*.—53. *Hauya heydeana*.—54. *Hauya elegans*. Scale line = 1 mm.

Australia; *Heteropyxis* sp., cult. LAM, South Africa; *Syzigium paniculatum* Gaertn., *Schmid 1969-A1*, cult. LAM, Australia; *Syzigium* sp., *Faden 76/438B*, Sri Lanka; *Tristania conferta* R. Brown, *Ching s.n.*, 2/77, cult. LAM, s. loc.; *T. laurina* R. Brown, *Hagen s.n.*, cult. Lam, s. loc.

Onagraceae (Figs. 51–54)

The midrib is grooved or ridged adaxially and prominently convex-rounded abaxially in the largest dorsiventral leaves. Isobilateral leaves often have a midrib which protrudes equally above both surfaces. Midribs may be sharply demarcated from the lamina or may show a gradual decrease in thickness away from the midrib. Midveins vary from deeply semicircular to small arcs. Phloem may be bicollateral at the midvein but often the adaxial phloem is not closely and symmetrically disposed adjacent to the protoxylem but instead occurs as patches separated from the xylem. The smallest midveins are collateral. Secondary veins are generally circular, collateral, and always without fibers. Periphloic fibers are noted in the midribs in a few species of *Fuchsia* (Fig. 52), *Hauya* (Figs. 53, 54), and *Ludwigia* (Fig. 51). Sclereids are not present. Raphides are present in all genera with druses and prismatics restricted to a few genera.

Specimens examined: 125 species in 17 genera as listed in Keating (1982).

DISCUSSION

Lythraceae. Leaf anatomy is made quite heterogeneous with the addition of *Duabanga* and *Sonneratia* and the family is held to be a basal one in the Myrtales (Thorne, 1976; Cronquist, 1981). One specimen of *Lagerstoemia* has the largest midvein, a complete cylinder with substantial periphloic fiber development. Epidermal cells are characteristically irregular in thickness with frequent large, rounded, mucilage-filled cells. Baas and Zweypfenning (1979) stated that *Lagerstroemia* is unambiguously advanced in wood characters while Graham and Graham (1971) held that it was primitive for the family. On the hypothesis that more complex leaf histology is primitive in leaves of Myrtales, *Lagerstroemia* has to be judged primitive. Bailey (1951), however, stated clearly that different organs of the plant may evolve structurally at different rates.

Ross and Suessenguth (1926) reported nine out of ten American *Lafoënsia* spp. have leaves with a hydathodal tip. The tip is very similar in structure to the apical leaf hydathode in *Punica* (see below). The vascular supply is formed of a median vein and two lateral veins which converge on the epithem tissue.

Leaf histology of *Punica* as recorded here and in Metcalfe and Chalk (1950) fits well within the range of features recorded for Lythraceae. Baas and Zweypfenning (1979) noted similarities with *Punica* and the Lythraceae as well as the Myrtaceae. Leaf anatomy offers no objection to merging *Punica* with one of these families but this might be expected of any genus which has leaves as reduced as *Punica*'s seem to be. Turner and Lersten (1983) have reported on the structure and function of the leaf tip in *Punica granatum*. The acute, mucronate tip is hydathodal with the foramen connected to the external environment by a number of stomata. The foramen is subtended by epithem tissue which, in turn, is distal to three converging veins. The median vein is the largest as is true of all rosoid teeth (Hickey & Wolfe, 1975). Leaf tips in *Lafoënsia* (Ross & Suessenguth, 1926) differ in having a large schizenous or schizolysigenous cavity develop, lined with epithem and leading directly to the outside. Also, *Lafoënsia* may have heavily lignified tracheid development proximal to the epithem. Aside from these differences, Turner and Lersten (1983) note the obvious structural similarity between the families Lythraceae and Punicaceae on this complex feature. Bridgewater and Baas (1978) noted that wood anatomy of *Punica* is also specialized and that it shares derived status with several Lythraceae.

The genera *Duabanga* and *Sonneratia* have among the most strikingly complex leaf anatomy in the Myrtales and the two genera also differ from each other in several ways. Baas and Zweypfenning (1979) noted the distinctness of the genera from each other and Dahlgren and Thorne (1984) stated that the homogeneity of the Sonneratiaceae needs to be reconsidered. *Sonneratia*, the mangrove genus, has leaves which show tendencies toward isobilateral development. Adaxial and abaxial epidermal layers are nearly identical and the guard cells are markedly overarched by strongly cuticularized subsidiary cells. Rao and Chakraborti (1982) have reported on the structure of the apical knob of the emarginate leaf of *Sonneratia caseolaris* (L.) Engl. This leaf has a highly dentritic, flared, vascularized "pad" with veins ending in club-like aggregations of brachytracheoids. An epithem seems to be present, but the authors report finding no outlet to the surface. This apical knob is not rosoid nor does it seem to have any structural homologies with other teeth reported for the family. *Duabanga* of the lowland forests of Indomalaya has dorsiventral leaves with either a thicker adaxial epidermis or with an abaxial epidermis which is strongly papillate. Sclereids are found in both genera which also serve to separate them from Lythraceae (Bannerjee & Rao, 1975; Rao & Das, 1979). The question of whether the two genera are sufficiently closely related to be placed in the same subfamily is not easily answered. While the two are distinctive in my sample, there is considerable anatomical variation within each genus which must be assessed before venturing an opinion. Leaf venation architecture would be especially instructive here. Muller (1981) noted that the pollen of *Florschuetzia trilobata* of the Oligocene and Miocene of Borneo seems to combine characteristics of Lythraceae and Sonneratiaceae, supporting the hypothesis of a common evolutionary history. Venkateswarlu and Rao (1964) concluded on the basis of wood anatomy that *Duabanga* and *Sonneratia* should be included in the Lythraceae although Baas and Zweypfenning (1979) noted that this would certainly extend the range of features in that family. If we follow Thorne (1976) and add the two genera to the Lythraceae, they would certainly need their own subfamily or subfamilies.

Rhynchocalycaceae. Rhynchocalyx lawsonioïdes with its enlarged adaxial epidermis, midrib and midvein configuration, semi-transcurrent secondary veins, type and position of druses fits well within the Lythraceae. Most characteristic is the extension of palisade tissue from the lamina into the midrib, adaxial to the midvein, a pattern shown by nearly all leaves of Lythraceae. In short, the anatomy of *Rhynchocalyx* in no way extends the anatomical variation in leaf anatomy found in the Lythraceae.

Trapaceae. Leaf anatomy of *Trapa* reflects the specialized floating habit of the genus. The dorsiventral leaves have well-developed aerenchyma in the abaxial two-thirds of the lamina and stomata are on the adaxial surface only. Metcalfe and Chalk (1950) included *Trapa* in the Onagraceae and Airy-Shaw (1973) considered it a close relative of the Onagraceae. Takhtajan (1980) states that Trapaceae is related to the Onagraceae, especially to the genus *Ludwigia*. The leaves of the more generalized species of *Ludwigia* (Keating, 1982) show no resemblance to *Trapa* leaf anatomy. Even those *Ludwigia* species with floating leaves have not converged on the structure of *Trapa* leaves. The absence of raphides and its unusual histology distinguishes *Trapa* from Onagraceae and Lythraceae but leaves open the question of whether it might be closely related to them in spite of its ecological specializations. The thin, monarch root anatomy of *Trapa* (Fahn, 1974) is probably unique in the Myrtales. Evidence linking *Trapa* with any other family will not likely come from vegetative histological features.

Oliniaceae. Mújica and Cutler (1974) found that leaf anatomy is very useful in *Olinia* for defining intra-generic subgroupings. Rao and Das (1976) and Mújica and Cutler (1974) have noted the presence of terminal sclereids in *Olinia* although these were not observed in my preparations. As figured by Mújica and Cutler, the histological patterns of the leaf midrib and lamina are quite compatible with leaves of Lythraceae and Myrtaceae. Diffuse sclereids are not found. The adaxial patch of fibers at the midvein of *Olinia emarginata* is somewhat similar to the pattern found in *Memecylon aylmeri.* Mújica and Cutler (1974) noted that terminal sclereids similar to those of Oliniaceae occur in species of *Memecylon* and in *Mouriri.* They also noted the similarity of petiole structure in species of *Memecylon* and *Olinia.* Rao and Dahlgren (1968) noted similarities to leaf and wood anatomical features of the Rubiaceae although that family entirely lacks intraxylary phloem.

Combretaceae. In contrast to the work on the leaf epidermis by Stace (1980, and references cited therein), anatomy of the leaf does not produce a clear alignment according to the taxonomic tribes and subtribes of Exell and Stace (1966). The family has generally complex midrib vasculature except in *Conocarpus* which has reduced leaves. *Lumnitzera* and *Laguncularia,* the mangrove genera, also show reduced and specialized anatomy including hydathodes. Striking features of the family are the very large druses and styloid-druse combinations which are formed in large cells often occupying the entire height of the lamina in *Anogeissus,* and to a lesser extent in *Bucida, Terminalia,* and *Guiera.* In contrast to the finding of a number of unusual embryological features in *Guiera* by Venkateswarlu and Rao (1972), I found no particularly distinctive vegetative features in that genus. Tobe and Raven's (1983) conclusion, that *Guiera*'s unusual embryological features are of secondary origin, is supported by vegetative anatomy. Overall, the

Combretaceae appear to have a coherent set of leaf anatomical features and one can agree with Dahlgren and Thorne (1984) that no particularly close connection with other families of the order is obvious.

Strephonema seems clearly related to the Combretaceae with its midvein cylinder, and secondary veins with fiber caps. The large, coarse druses and prismatic crystals, fiber-like and macrosclereids, and the characteristic length/width ratio of the palisade cells are all clearly combretaceous. On the other hand, the midvein and secondary vasculature of *Strephonema* seem to be free of intraxylary phloem. This serves to isolate the genus somewhat but all of the Combretaceae I have observed have relatively weak intraxylary phloem development. Anomocytic stomata in *Strephonema* differ from the mostly parasitic members of the Combretaceae and the cyclocytic mangrove genera. Outer and Fundter (1976) felt that phloem, bark and wood characteristics plead for a less specialized and distinct subfamily of Combretaceae. However, the lack of intraxylary phloem would appear to be a secondary loss if that character is regarded as basic for the Myrtales.

Alzateaceae. Few specimens of the genus are known and we probably do not have a good circumscription of its variation. As with the specimen studied here, Baas (1979) noted that his Costa Rican specimen has a hypoderm over all of the mesophyll whereas the Peruvian specimens have a hypoderm extending over the veins only. The isolation from other myrtalean families pointed out by Dahlgren and Thorne (1984) can be confirmed on the basis of leaf histology although the genus does seem clearly to belong to the order. Features which serve to isolate *Alzatea* include the sclereids, which are simply lignified idioblastic cells of the same shape as spongy cells, the cyclocytic combined with anomocytic stomata, the three-trace, trilacunar node, the broken cylinder of midvein vasculature, and the particular form of small square epidermal cells as seen in transection.

The structure of the mesophyll and of the veins is generally similar to several myrtalean families (Crypteroniaceae, Myrtaceae, and Lythraceae) but not a clear fit into any of them. Midrib and lamina structure is quite different from *Rhynchocalyx* and does not support the contention of van Beusekom-Osinga and van Beusekom (1975) that they belong together in a subfamily of Crypteroniaceae. Maintenance of the monogeneric Alzateaceae is best supported on the basis of vegetative anatomy.

Penaeaceae. The seven, closely related genera have small coriaceous leaves, often with an ericoid habit (Airy-Shaw, 1973). Midveins and midribs are small and reduced in complexity which precludes useful systematic comparisons with those features. Dahlgren (1968) stated that leaf anatomy does not contribute much to differences between genera of the family. Dahlgren (1968) also noted that the families Geissolomataceae, Oliniaceae, Thymelaeaceae, Melastomataceae, Combretaceae, and Lythraceae have all been considered closely allied on the basis of a variety of features. The array of diffuse and terminal sclereids reported by Rao and Das (1976) as well as the leaf axil bristles serve to isolate the family from all other Myrtales except possibly the Melastomataceae-Memecyloideae. Sclereids of the Memecyloideae recall those of Penaeaceae as does the specialized leaf margin consisting of a parenchymatous ridge as found in both *Memecylon* and *Penaea*. Large, coarse and complex druses are also found in both groups.

Melastomataceae. The family is distinctive morphologically and anatomically. A comprehensive anatomical study of the young vegetative anatomy of the family would doubtless provide a number of diagnostic features and morphoclines (cf. Metcalfe & Chalk, 1950). By far the greatest number of leaf anatomical studies have been done of *Mouriri* and *Memecylon* of the Memecyloideae. These works have demonstrated that sclereids of all types occur in these genera and that they are biogeographically and systematically correlated (Foster, 1947; Subramanyam & Rao, 1949; Morley, 1953; Rao, 1957; Rao & Dakshni, 1963; Rao & Bhupal, 1974; Rao & Jacques-Felix, 1978; Bremmer, 1979; and Rao et al., 1980). Baas (1981) has called attention to the systematically useful stomatal and crystal types in the family. Midrib vasculature in the Melastomatoideae is much more diverse than implied by the sample included here and it should be thoroughly studied. Reduction and simplification of midrib structure in both subfamilies suggest parallel trends of specialization.

An interesting feature noted only in the Memecyloideae involves the configuration of the phloem. In both *Memecylon* and *Mouriri*, the intraxylary phloem of midveins and secondary veins is usually better developed than the abaxial or collateral phloem. In secondary veins, the abaxial phloem is often missing being replaced with robust development of the adaxial phloem. This tendency is especially pronounced in *Memecylon.* Relationships of the Melastomataceae to other myrtalean families are not readily suggested on the basis of leaf features.

Crypteroniaceae. The delimitation of this family by van Beusekom-Osinga and van Beusekom (1975) included five genera and resulted in a diverse group from the standpoint of leaf histology. In spite of that diversity, van Vliet et al. (1981) included the genera as a subfamily within the Melastomataceae. Removal of *Alzatea* and *Rhynchocalyx* improves the family (or subfamily) circumscription, although *Rhynchocalyx* does retain certain resemblances to *Axinandra.* These include the midrib shape, the midvein shape with the incurved ends of the semicircle. The *Axinandra* specimen examined here is probably somewhat immature and probably will not bear extensive comparison. *Crypteronia paniculata* examined here has more prominent vasculature than most Lythraceae but it has several features similar to that family. The simple trichomes, palisade cell measurement ratios, palisade percentage of the mesophyll, number of spongy layers, and the shape of secondary veins with a convex xylem adjacent to normal collateral phloem are all similar. Among myrtalean families, Lythraceae show the greatest similarities to the Crypteroniaceae even though van Vliet and Baas (1975) found no resemblance on wood features.

Psiloxylaceae. Psiloxylon mauritianum shows sufficiently distinct leaf histology to support the concept of its belonging to a separate family as Dahlgren and Thorne (1984) conclude in their review. The epithelium-lined secretory cavities found in *Psiloxylon* leaves are otherwise rare in the Myrtales except in the Myrtaceae. Midrib and midvein configuration in the genus are unique among reports known to me. On the basis of data from reproductive organs, Briggs and Johnson (1979) state that "a conceivable common ancestor of *Psiloxylon* and the Myrtaceae would be decidedly un-Myrtaceous, in contrast to such an ancestor for the genera included in the family . . . ." The array of leaf features compared in the present study at least confirm that *Psiloxylon* is properly placed in the Myrtales sensu stricto. If broad family concepts are used, *Psiloxylon* would be best assigned to the Myrtaceae as a subfamily as proposed by Schmid (1980). There is insufficient information on the leaf anatomy of many genera of Myrtaceae to make a judgment on that basis either to include or exclude *Psiloxylon* from the Myrtaceae.

Myrtaceae. Briggs and Johnson (1979; Johnson & Briggs, 1984) have provided a list of characters, including a few leaf histological and architectural features, which may be reasonably inferred to be present in primitive Myrtaceae. The specimens which I examined were mesomorphic, dorsiventral, and lacking a hypoderm, all generalized features by the criteria listed by Briggs and Johnson. As noted by Metcalfe and Chalk (1950), Johnson (1980), and Erdtman and Metcalfe (1963), isobilateral leaves with a hypoderm are common in the family. In leaf midvein vasculature patterns, one might hypothesize a trend of specialization which will have to be tested with much more data. A semicircular-shaped trace may have evolved in two directions: 1) the trace has become reduced to a broad then narrow arc of tissue by simple reduction, and 2) the trace has become incurved adaxially and then flattened as noted in *Eucalyptus obliqua* L'Herit. (Metcalfe & Chalk, 1950) and *Eucalyptus micrantha* (Fig. 46) as illustrated in this study. *Acmena smithii* may represent an extreme form of an arc where adaxial xylem portions have been lost and only the adaxial periphloic fibers remain. The trends noted by Briggs and Johnson (1979) toward microphylly, serial modification, more organized leaf architecture, isobilateral and centric growth, and anomalous secondary venation, suggest that discovery of many trends of vascular and other histological specialization will repay a comprehensive study of the family.

Histological features of *Heteropyxis* leaves, including the midrib vasculature, mesophyll structure, and the presence of the characteristic secretory cavities, are generally compatible with other myrtacean genera. These features plus those in the exhaustive list in Schmid's (1980) review, support the inclusion of the genus within the Myrtaceae.

The family as presently circumscribed does not show obvious affinities with any other families of the order except Psiloxylaceae. The inclusion of Lecythidaceae in the family by Bentham and Hooker (1862) was shown to be unreasonable by Metcalfe and Chalk (1950) and it seems clear that Lecythidaceae should be excluded from the order entirely.

Onagraceae. This family, without doubt the best studied family of its size among the flowering plants, was recently thoroughly examined for its leaf architectural and anatomical features

(Hickey, 1980; Keating, 1982). For leaf histology, 125 species representing all 17 genera were studied and only a brief summary of the conclusions will be repeated here. The family is a natural coherent group and all of the genera share a number of features which also serve to isolate the family within the Myrtales. These include the presence of raphide crystals (Keating, 1982), the four-nucleate (*Oenothera*-type) embryo sac (Tobe & Raven, 1983), and viscin threads on the pollen (Skvarla et al., 1977). The genera of Onagraceae which show the best developed midrib vasculature (*Ludwigia, Fuchsia,* and *Hauya,* as figured here) show a unique arrangement of intraxylary phloem compared to all other myrtalean specimens that I have examined. The traces are not strictly bicollateral but instead the phloem on the adaxial side consists of individual strands in the midvein ground tissue often at some distance from the midvein protoxylem. The adaxial phloem strands are not collectively oriented with respect to the shape of the midvein xylem.

As the evolution of the family is presently understood (cf. Raven, 1979) the leaf anatomy trends of the family represent a reduction series in complexity of structure and developmental sequences. In their general conformation of leaf histology, the Onagraceae show their greatest similarity to the Lythraceae. Punicaceae leaves are also compatible but are too reduced for reliable comparison. Many onagraceous genera have druses and prismatic crystals as well as styloids (especially *Ludwigia* and *Hauya*) which serve to link the family to other myrtalean families. Leaf teeth are highly distinctive having a hydathodal apparatus including an apical foramen, epithem tissue, and three converging veins. Named the "rosoid" tooth by Hickey and Wolfe (1975), it is only known from several saxifragalean genera (Stern, 1974, 1978; Stern et al., 1970; Styer & Stern, 1979a, 1979b), the Onagraceae (Hickey, 1980; Keating, 1982, 1984), the Lythraceae (Hickey, 1981; Ross & Suessenguth, 1926), and the Punicaceae (Turner & Lersten, 1983).

SUMMARY OF CROSS SECTIONAL LEAF HISTOLOGY FEATURES FOR THE ORDER MYRTALES

The following ordinal description is based mostly on the species described above, which have more generalized anatomy. The inclusion of a large sample of more specialized species would have lengthened this treatment several fold, decreasing its utility.

Leaf structure is mostly dorsiventral with isobilateral leaves occurring in several families. Adaxial and abaxial epidermal cells are of equal thickness or the adaxial cells may be up to 2–3 times as thick as the abaxial. Epidermal cells may be convex or level on the surface or facing the mesophyll, and regular or irregular in shape. Mucilage cells may occur in epidermal cells in the Lythraceae. The cuticle is thick to thin or not visible. A hypoderm layer is rarely present in most families although it is fairly common in the Myrtaceae in genera with isobilateral leaves. The midrib in dorsiventral leaves may be grooved, level, or ridged on the adaxial side. It may be very large and rounded on the abaxial side, ranging to immersed or level. In isobilateral leaves, the midrib may be biconvex or circular, to level or immersed. The lamina may be abruptly differentiated from the midrib or it may taper gradually from a poorly defined midrib. Midveins normally consist of a single trace varying from a deep semicircle to a broad or short arc and are either collateral or bicollateral. Secondary veins are collateral or bicollateral with the phloem on the adaxial side occasionally the best developed. Extraxylary fibers are absent to scarce or well developed when they form abaxial phloem caps or full sheaths. Fibers may form transcurrent extensions over the smaller veins. Sclereids, as astrosclereids, macrosclereids, or trichosclereids, may be absent or rarely present to abundant. The mesophyll may be weakly or sharply differentiated into palisade and spongy layers. The 1–2 palisade layers have cells which vary from 2:1 to 12:1 length/width ratios. Spongy mesophyll cells may form a well organized aerenchyma in genera with floating leaves. Stomata are mostly abaxial in dorsiventral leaves but are found on both surfaces on some dorsiventral leaves and on all isobilateral leaves. Calcium oxalate crystals are always present in one or more forms as styloids, prismatics, raphides, druses, or crystal sand. They may be randomly dispersed in the mesophyll, restricted to upper or lower layers of the mesophyll, or occur only around veins. Margins are usually without unusual modifications but occasionally hypoderm or other lignified or collenchymatous, non-mesophyll cells may form a thickened edge. Marginal teeth, when present, are probably always rosoid and have a hydathodal structure. Secretory cavities are rare but are present and epithelium-lined in some Myrtaceae.

Comments on Families often Included in the Myrtales

Thymelaeaceae. Leaf anatomical features of the family, minus *Gonystylus* are generally within the range as recorded for the core myrtalean families. Diverse anatomical features include a papillose adaxial epidermis, a characteristic form of fibrous sclereid (Metcalfe & Chalk, 1950), a hypoderm, mucilaginous epidermal cells, and several crystal types including styloids, prismatics, druses, and crystal sand. Margins may be supported by "veins" which are actually sclerenchymatous elements (Metcalfe & Chalk, 1950). About half of the genera are recorded as having bicollateral vascular bundles. In most of my specimens, the midrib is small with an arc of vasculature with two exceptions. A small cylinder is noted in *Lethedon* and *Daphnopsis.*

The remaining genus, *Gonystylus,* is quite exceptional for the family and it is certainly not myrtalean. Its midrib is very large, prominently protruding, and rounded abaxially. The vasculature consists of a broken cylinder in one species, and in the other, a broad cylinder of collateral bundles. The cylinder surrounds an inner U-shaped vein which in turn contains several smaller bundles. Each cycle of traces is capped by well-developed periphloic fibers. *Gonystylus* also contains epithelium-lined mucilage cavities which occur in the palisade region. Cronquist (1981) includes *Gonystylus* in the family while Dahlgren and Thorne (1984) state that evidence suggests that not only is *Gonystylus* questionably included in the family, it may not even be closely allied to it. A thorough study of the anatomy of the family would need to consider the specialized xeromorphic nature of many of the species.

Haloragaceae. Leaves of this family have reduced venation and generally simplified structure. With this data, it is impossible to affirm or deny affinities with practically any order.

Rhizophoraceae. This family fits poorly into the Myrtales on a number of grounds. The cylindrical or incurved arc of midvein vasculature shows a marked tendency to be dissected in many species. The phloem commonly remains a continuous collateral band. A prominent hypoderm is common which may be multilayered. The innermost layer is often comprised of large cells which extend separately down into the palisade zone in *Rhizophora* and *Gynotroches.* Some of these large cells may extend out to the adaxial epidermal surface. Laticifers, often articulated, are common in some species throughout the spongy and midrib zones. Complex midvein vasculature is present in *Carallia brachiata.* The family needs more anatomical study both for better circumscription and for a better understanding of its characters in light of its mangrove habit. The family is quite variable anatomically.

Lecythidaceae (including Barringtoniaceae). The family is distinctive in midrib shape and vasculature. Most specimens are convex adaxially and abaxially in various combinations of rounded and V-shaped profiles. The lamina sectors are horizontally or laterally inserted. The collateral midrib venation is highly complex. *Lecythis, Gustavia,* and *Couroupita* have one large flattened cylinder toward the adaxial side of the midrib which is encircled abaxially by a series of smaller cortical bundles which often have centrically arranged xylem, i.e., have radial symmetry with encircling phloem. A row of small bundles may also partially surround the main cylinder on the adaxial side. Each genus has a particular diagnostic arrangement of the bundles which in some cases are numerous. The genera *Barringtonia, Careya,* and *Combretodendron,* sometimes recognized as the Barringtoniaceae (Airy-Shaw, 1973) are distinguished as a group although they are comparable in complexity and clearly related to the Lecythidaceae sensu stricto. Those genera have an abaxially placed, deep U-shaped trace or flattened cylinder with an array of wing bundles pointing toward the laterally inserted lamina sectors. Adaxial or abaxial rows of accessory veins may be present. The palisade mesophyll extends into the midrib zone beneath nearly the entire adaxial surface but is not continuous across the midrib. Trichomes, when present, have a multicellular buttressed base of complex and characteristic form.

The closest pattern of midrib vasculature to this highly distinctive family appears to be among the Theales near the Guttiferae, Ochnaceae, Quiinaceae, and Theaceae as figured by Schofield (1968). The overall configuration of Lecythidaceae leaf histology is strikingly similar to those families.

Chrysobalanaceae. Species examined here all have cylindrical midvein vasculature with prominent midribs. *Parinari nonda* shows the most complex midrib venation described with xylem and phloem bands enclosed within the main vascular cylinder. Venation is collateral. What appears to be internal phloem in some species may be due to loss of part of the included vasculature. The genera examined could fit into Myrtales in terms of the configuration of characters present.

Elaeagnaceae. The peltate and multicellular stalked hairs are not matched by any other myrtalean families. Midveins and midrib configuration are compatible with the order but bicollateral phloem is absent. The raphides recorded throughout the leaf of *Elaeagnus philippinensis* are rare in the Myrtales. The Onagraceae, the only other family with raphides, otherwise shares few characters with the Elaeagnaceae.

Elatinaceae. Young vegatative features seem to exclude this family from the Myrtales, even when discounting obvious specializations for aquatic habitats. Nodal anatomy with split lateral traces, the presence of leaf lamina traces which were never fused with the midvein, leaf primordia fused to sheathing stipules at the nodal level, stalked glandular trichomes on the young stem, and strictly collateral vascular bundles form a combination of characters not found within the order.

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ULTRASTRUCTURE OF SIEVE-ELEMENT PLASTIDS OF MYRTALES AND ALLIED GROUPS[1]

H.-DIETMAR BEHNKE[2]

ABSTRACT

The core families of Myrtales (69 species investigated) contain S-type sieve-element plastids. In these, the presence of several medium-sized spherular starch grains is probably a common trend in the order. Among those families usually closely associated or more or less distantly related, the great majority also have S-type plastids, some with the same characteristics. However, Rhizophoraceae, in contrast to the close allies and Connaraceae, Gunneraceae, and Rhabdodendraceae of the distantly related families, have developed P-type plastids. That subtype PV-plastids, which exclude all starch, are found in all tribes of Rhizophoraceae except Anisophylleae supports family recognition of the latter.

Sieve-element characters investigated with the transmission electron microscope have repeatedly contributed to the circumscription and classification of higher taxa, e.g., Leguminosae (Behnke & Pop, 1981), Monocotyledoneae (Behnke, 1981b). Of these, the most intensively studied feature is the ultrastructure of sieve-element plastids. The great number of investigated angiosperms (some 2,000 species from nearly 400 families—as of 1983-12-31) allow a subdivision of the plastids into P- and S-type, a number of subtypes, and a great many of characteristic forms by using both chemical and morphological composition at the ultrastructural level (see Behnke, 1981a, for more detail). The successful delimitation of the order Caryophyllales to the PIII plastid families (Behnke, 1976; Mabry, 1977) and the use of sieve-element plastid data in separating Vitidales from Rhamnales (Behnke, 1974; Dahlgren, 1980) and Buxaceae from Simmondsiaceae and Euphorbiaceae (Behnke, 1982a) stimulated, among others, the screening of all the core families of Myrtales and of those closely or more distantly related to the order, with the results to be included in this symposium report.

MATERIALS AND METHODS

Preferentially young stem pieces of the plant species listed in Table 1 were cut into longitudinal sections fixed in a formaldehyde-glutaraldehyde mixture followed by 1% buffered OsO_4 and dehydrated in acetone. Small pieces containing phloem tissue were embedded and polymerized in epoxy resins, cut with an ultramicrotome, and the final ultrathin sections viewed and photographed with a transmission electron microscope (for exact procedures see Behnke, 1982a).

RESULTS AND DISCUSSION

Sieve-elements of many of the myrtalean families are extremely difficult to fixate in a close-to-natural condition. There is less plasmatic content which is more labile and, during preparation, sieve-element plastids burst more often than in the average dicotyledon family. Nevertheless, all of the 69 investigated species of the core families of Myrtales (cf. Dahlgren & Thorne, 1984) could be shown to contain S-type plastids (cf. Table 1). Number, size, and shape of the starch grains in these plastids certainly vary (Figs. 1–14), but some common trends may be recognized. There are always several starch grains in one plastid—often six or more (Figs. 1–4, 6, 8–11), their size being variable (sometimes all of the same size) but never very large and their shape almost exclusively is a spherule. Considerably smaller starch grains are present in ad-

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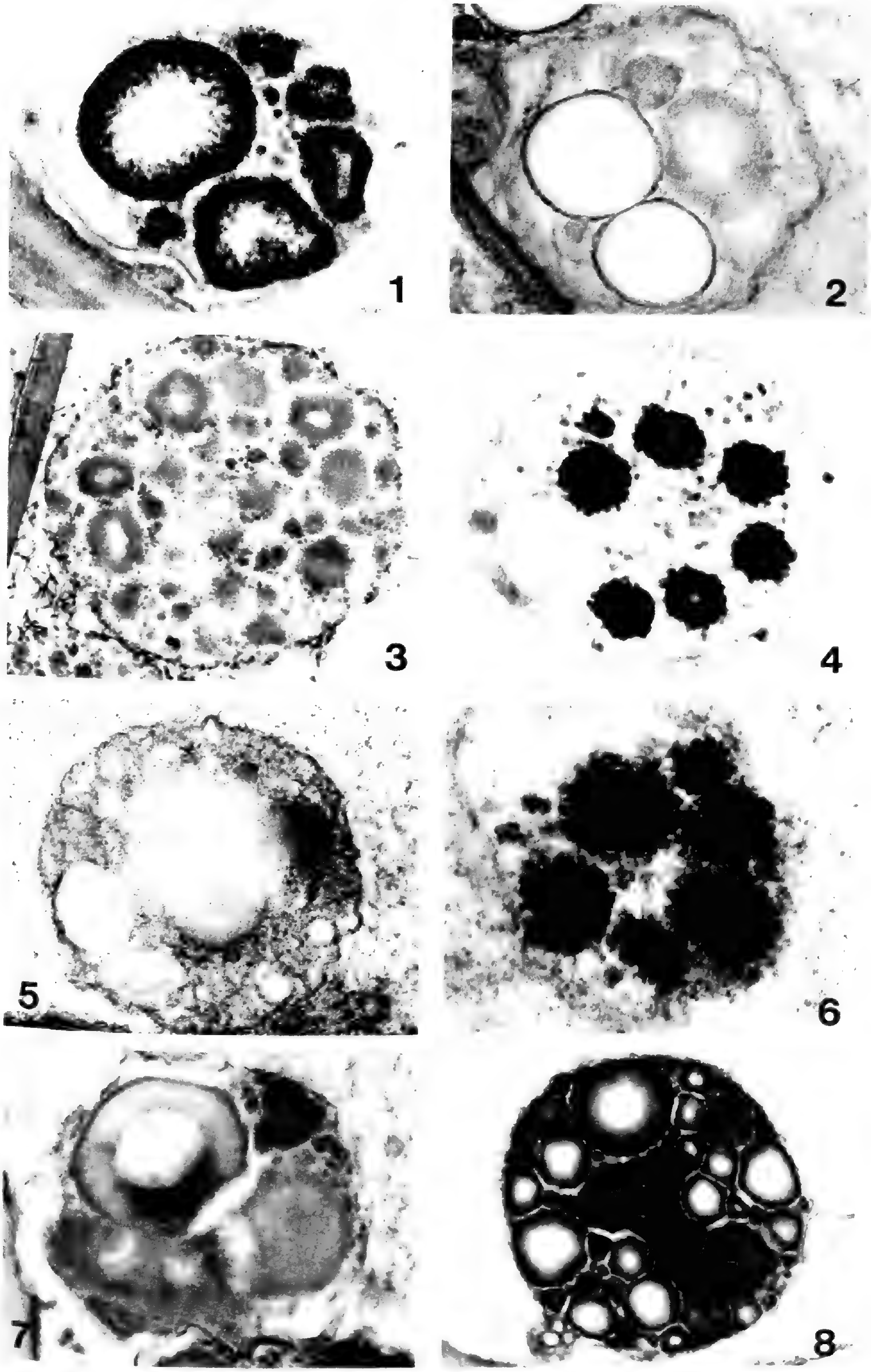
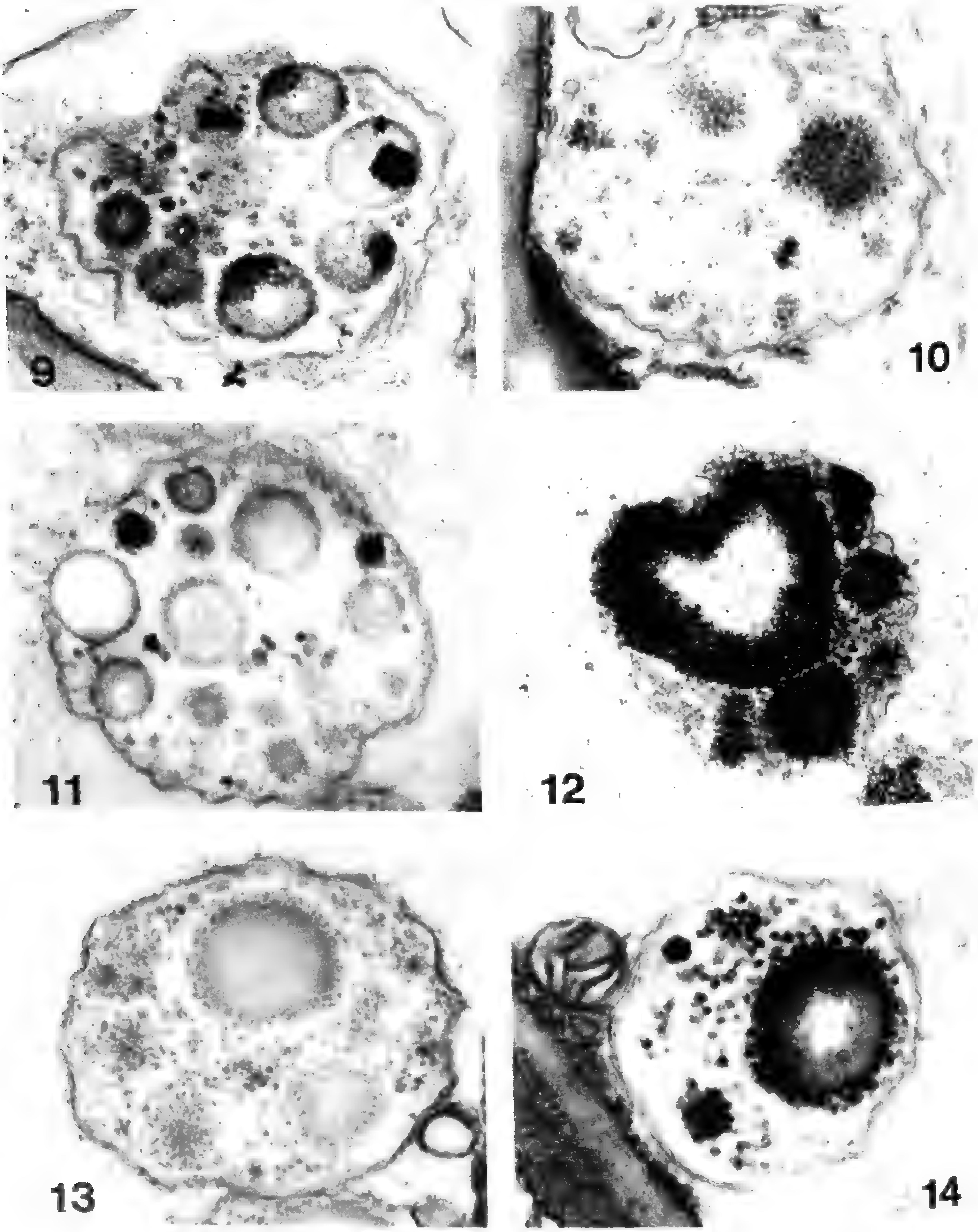
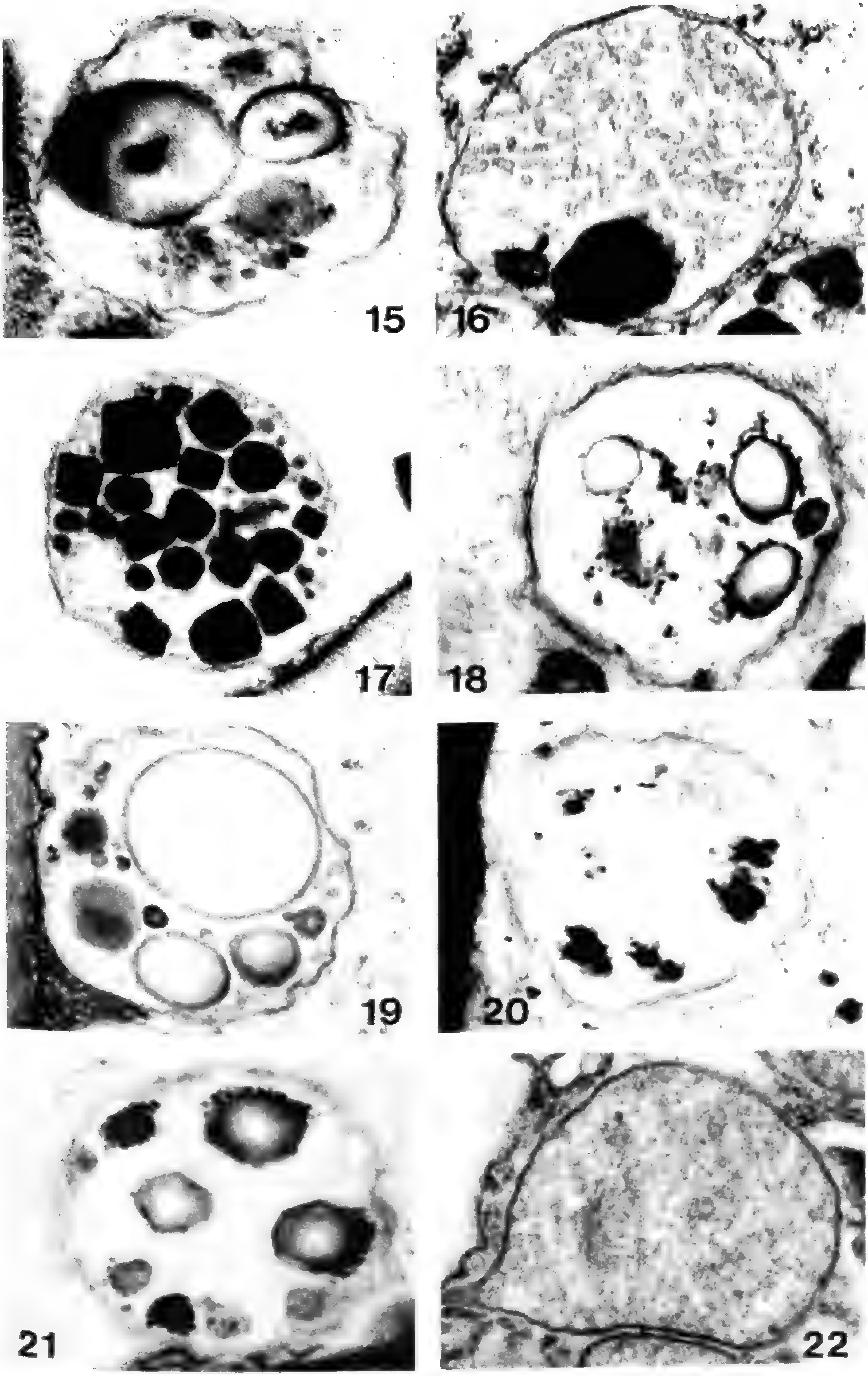


FIGURES 1–8. Sieve-element plastids of the core families of Myrtales I. All plastids are S-type, with examples from Melastomataceae.—1. *Schizocentron elegans.*—2. *Bertolonia maculata.*—3. *Medinilla magnifica,* Penaeaceae.—4. *Saltera sarcocolla,* Combretaceae.—5. *Combretum racemosa,* Rhynchocalycaceae.—6. *Rhynchocalyx lawsonioides,* Lythraceae.—7. *Lagerstroemia indica.*—8. *Duabanga sonneratioides.* Plastids reproduced to cover the same area, actual magnifications diverge around 20,000×.



FIGURES 9–14. Sieve-element plastids of the core families of Myrtales II. S-type plastids from Myrtaceae.—9. *Metrosideros excelsa.*—10. *Callistemon phoeniceus.*—11. *Psidium littorale,* Trapaceae.—12. *Trapa natans,* Onagraceae.—13. *Epilobium fleischerei.*—14. *Circaea cordata.*—Plastids reproduced to cover the same area, actual magnifications diverge around 20,000×.

FIGURES 15–22. Sieve-element plastids of families often allied to Myrtales. S-type plastids in Haloragaceae.—15. *Haloragis erecta.*—16. *Myriophyllum brasiliense,* P-type plastids in Rhizophoraceae.—17. *Rhizophora* cf. *conjugata,* S-type plastids in Thymelaeaceae.—18. *Daphne mezereum,* Lecythidaceae.—19. *Couroupita gui*



anensis. Coridaceae.—20. *Coris monspeliensis* and Chrysobalananceae.—21. *Chrysobalanus icaco,* S_0-plastids in Elaeagnaceae.—22. *Elaeagnus angustifolius,* young sieve element. Plastids reproduced to cover the same area, actual magnifications diverge around 20,000×.

TABLE 1. Sieve-element plastids in Myrtales and allied groups.

Family	Species	Source	Type of Plastids
Melastomataceae	*Amphiblemma cymosum* (Schrad.) Naud.	Utrecht	S
	Bertolonia maculata (Mart.) DC.	Edinburgh	S
	B. marmorata Naud.	Heidelberg	S
	Bredia tuberculata (Guillamin) Diels	Edinburgh	S
	Calvoa orientalis Taub.	Copenhagen	S
	Centradenia floribunda Planch.	Edinburgh	S
	Clidemia hirta (L.) D. Don	Bonn	S
	Dissotis rotundifolia (Sm.) Triana	Copenhagen	S
	Gravesia guttata (Hook.) Triana	Edinburgh	S
	Heterocentron subtriplinervium (Link & Otto) R. Br.	Edinburgh	S
	Medinilla magnifica Lindl.	Heidelberg	S
	Melastoma sanguineum D. Don	Edinburgh	S
	Memecylon sp.	Utrecht	S
	Monochaetum humboldtianum Walp.	Edinburgh	S
	Monolena primuliflora Hook. f.	Copenhagen	S
	Pachycentria constricta Bl.	Bogor	S
	Sakersia africana Hook.	Parc Nat. Comoé, Côte d'Ivoire (Leg. Merz, Têhé & Assi)	S
	Schizocentron elegans (Schl.) Meissn.	Edinburgh	S
	Tibouchina semidecandra (Schrank & Mart.) Cogn.	Heidelberg	S
	Tococa guianensis Aubl.	Heidelberg	S
	Triolena pustulata Triana	Heidelberg	S
	T. scirpioïdes Naud.	Copenhagen	S
Crypteroniaceae	*Crypteronia paniculata* Bl.	Bogor	S
Penaeaceae	*Penaea mucronata* L.	Kirstenbosch (J. P. Rourke)	S
	Saltera sarcocolla (L.) Bullock	Cape Point Nature Reserve (leg. D. Clark)	S
Oliniaceae	*Olinia emarginata* Burtt-Davy	B. I. Pretoria (D. M. C. Fourie)	S
Combretaceae	*Combretum racemosa*	Kew	S
	C. quadrangulare Kurz.	Bogor	S
	C. sundaicum Miq.	Bogor	S
	Quisqualis indica L.	Heidelberg	S
	Terminalia catappa L.	Heidelberg	S
Lythraceae			
subfam. Lythroideae	*Cuphea micropetala* H.B.K.	Berlin	S
	Lafoensia punicaefolia DC.	Bogor	S
	Lagerstroemia indica L.	Copenhagen	S
	Lawsonia inermis L.	Copenhagen	S
	Lythrum salicaria L. cv Robert	Heidelberg	S
	Rotala rotundifolia Buch.-Ham.	Mainz	S
subfam. Duabangoideae	*Duabanga sonneratioïdes* Buch.-Ham.	Rio de Janeiro (leg. K. Kutitzki)	S
subfam. Sonneratioideae	*Sonneratia caseolaris* (L.) Engl.	Bogor	S
subfam. Punicoideae	*Punica granatum* L.	Heidelberg	S
Rhynchocalycaceae	*Rhynchocalyx lawsonioïdes* Oliv.	Natal (leg. H. B. Nicholson)	S

TABLE 1. Continued.

Family	Species	Source	Type of Plastids
Myrtaceae	*Acca sellowiana* Burret	Heidelberg	S
	Agonis flexuosa (Willd.) Lindl.	Kew	S
	Angophora cordifolia Cav.	Kew	S
	Callistemon phoeniceus Lindl.	Heidelberg	S
	Calothamnus rupestris Schau	Mainz	S
	Eucalyptus diversifolius Bonpl.	Heidelberg	S
	Eugenia myrcianthes Niedenzu	Copenhagen	S
	Hexaclamys edulis Kausel ex D.	Mainz	S
	Kunzea ambigna (Sm.) Hochr.	Kew	S
	Leptospermum laevigatum F. Muell.	Heidelberg	S
	Lophomyrtus obcordata (Raoul) Burret	Utrecht	S
	Melaleuca acuminata F. Muell.	Heidelberg	S
	Metrosideros excelsa Soland ex Gaertn.	Heidelberg	S
	Myrceugenia luma Berg.	Mainz	S
	Myrtus communis L.	Heidelberg	S
	Pimenta racemosa (Mill.) J. W. Morre	Bonn	S
	Psidium littorate Raddi	Berlin	S
	Rhodamnia cinerea Jack.	Leila Forest, Sandakan, Sabah (leg. Behnke & Lee 83-07-22)	S
	Tristania conferta R. Br.	Leiden	S
Trapaceae	*Trapa natans* L.	Bonn	S
Onagraceae	*Circaea cordata* Royle	Heidelberg	S
	C. × *intermedia* Ehrh.	Zastler, Germany (leg. Behnke & Cole 80-08-26/1)	S
	Epilobium fleischeri Hochst.	Heidelberg	S
	Fuchsia arborescens Sims.	Heidelberg	S
	Godetia amoena G. Don.	Kew	S
	Oenothera biennis L.	Heidelberg	S
	O. missouriensis Sims.	Heidelberg	S
	Zauschneria californica Presl.	Heidelberg	S
Families allegedly allied (after Dahlgren & Thorne, 1984)			
Haloragaceae	*Haloragis erecta* (Banks & Murr) Eichl.	Copenhagen	S
	Myriophyllum brasiliense Cambess	Bonn	S
Rhizophoraceae	*Bruguiera gymnorrhiza* Lam.	Berlin	PVc
	Carallia brachyata	Brisbane, Australia (leg. R. Tracey)	PVc
	Cassipourea elliptica (Sw.) Poir.	Finca La Selva Costa Rica (Juncosa 26 VIII 74)	PVc
	C. cf. *killipii* Cuatrecasas	Chocó, Colombia (Juncosa 2540)	PVc
	Ceriops tagal var. *australis* C. T. White	Cape Ferguson, Queensland (leg. G. J. Muller)	PVc
	Crossostylis biflora Forst.	Edinburgh	PVc
	C. grandiflora Brongn. & Gris.	Mt. Panié, New Caledonia (Juncosa 20 IX 81A)	PVc
	Kandelia rheedii Wight & Arn.	Brisbane, Australia (Leg. R. Tracey)	PVc
	Rhizophora cf. *conjugata*	Bonn	PVc

TABLE 1. Continued.

Family	Species	Source	Type of Plastids
	R. mangle L.	Heidelberg	PVc
	R. sexangula	Copenhagen	PVc
	R. stylosa	Australia (leg. R. Tracey)	PVc
	Sterigmapetalum heterodoxum Steyem. & Liesner	Sierra de San Luis (Berry & Wingfielá 4304)	PVc
Anisophylleaceae	***Anisophyllea trapezoidales*** Baill.	Sepilol Forest Res., Sandakan, Sabah (leg. Behnke & Lee 83-7-21)	PVc
	Combretocarpus cf. ***motleyi*** Hook. f.	Sri Aman, Sarawak (Leg. Othman Ismawi)	S
Thymelaeaceae	***Dais cotonifolia*** L.	Mainz	S
	Daphne mezereum L.	Heidelberg	S
	Passerina filiformis L.	Bonn	S
	Phaleria disperma Baill.	Kew	S
	Pimelea ferruginea Labill.	Bonn	S
	Wikstroemia sp.	Kew	S
Lecythidaceae	*Barringtonia acutangula* (L.) Gaertn.	Bogor	S
	B. speciosa Forst.	Copenhagen	S
	Chydenanthus excelsus (Bl.) Miers	Bogor	S
	Couroupita guianensis Aubl.	Berlin	S
	Gustavia angusta L. f.	Berlin	S
	G. gracillinea Miers	Rio de Janeiro (K. Kubitzki)	S
	Napoleonaea imperialis Beauv.	Kew	S
	Planchonia vallida Bl.	Bogor	S
Elatinaceae	*Elatine hydropiper* L.	Berlin	(S_o)
Coridaceae	*Coris monspeliensis* L.	Berlin	S
Chrysobalanaceae	*Chrysobalanus icaco* L.	Berlin	S
	Couepia grandiflora (Mart. & Zucc.) Benth. ex Hook f.	Botucatu, Brazil (leg. I. S. Gottsberger)	S
	Moquilea tomentosa	Kew	
Elaeagnaceae	*Elaeagnus angustifolius* L.	Heidelberg	S_o
	E. umbellata Thunb.	Heidelberg	S_o
	Hippophae rhamnoïdes L.	Heidelberg	S_o
Families distantly related (all families mentioned under this heading by Dahlgren & Thorne (1984) contain S-type plastids except for:)			
Gunneraceae	*Gunnera magellanica* Lam.	Copenhagen	P
	G. manicata Lindl. ex André	Copenhagen	P
	G. tinctoria Mirbel	Bonn	P
Connaraceae	*Agelaea macrophylla* (Zoll.) Leenh.	Bogor	P
	Connarus conchocarpus	Atherton, Qld, Australia (leg. A. Irvine)	P
	C. oblongus Schellenb.	Bogor	P
	C. suberosus Planch.	Botucatu, Brazil (leg. I. S. Gottsberger)	P
	Rourea mimosoïdes (Val.) Planch.	Bogor	P
	Roureopsis emarginata (Jack.) Merr.	Bogor	P
Rhabdodendraceae	*Rhabdodendron amazonicum* (Spruce ex Benth.) Hub.	Manaus, Brazil (leg. G. T. Prance)	P
	R. macrophyllum (Spruce ex Benth.) Hub.	Manaus, Brazil (Prance 20187)	P

dition (see e.g., Figs. 3, 8), and all grains may show a tendency to disintegrate at their periphery into tiny particles—most prominent, e.g., in *Callistemon* (Fig. 10), *Epilobium* (Fig. 13), and *Circaea* (Fig. 16). These features make the sieve-element plastics of the core families in Myrtales not very distinctive, but exclude at least some starch forms, like the one-large-grain, the club-shaped, and the completely particulated starches.

Most of the suggested closer allies and the more or less distantly related families of Myrtales also contain S-type plastids (see Table 1), very few of which, however, fit the starch features described for the core families (e.g., Figs. 15, 18, 21; probably also Fig. 19 but note very large grains). More informative is the absence of S-type plastids in some of the families. While its quantity is much decreased in *Myriophyllum* (Fig. 16), starch is completely lost in Elaeagnaceae (Fig. 22) and probably also in Elatinaceae. Four families contain P-type sieve-element plastids—Rhizophoraceae (Fig. 17) of the closer allies and Connaraceae (Behnke, 1982c), Gunneraceae (see Behnke, 1981a), and Rhabodendraceae (Behnke, 1976) among the groups sometimes related. All of the latter families containing either subtype S_0 or P-type plastids should be excluded from the Myrtales.

Elaeagnaceae (S_0-plastids) contain crystalline P(hloem)-protein bodies, another sieve-element character which among the myrtalean core families is only found in Myrtaceae. However, the ultrastructural composition of the crystalline P-protein is unlike that of Myrtaceae, but comes very close to crystalline P-protein in Proteaceae, which is also among the distantly related group. However, sieve-element plastids in Proteaceae are of S-type.

The family Rhizophoraceae needs special mention, since according to traditional treatments it incorporates both S-type and P-type genera. While the 12 species examined from the tribes Gynotrocheae, Macarisieae, and Rhizophoreae (see Table 1) contain very specific sieve-element plastids (Fig. 17) that include numerous protein crystals but no starch at all (subtype-PV; the only other families recorded to have this subtype are Cyrillaceae and Erythroxylaceae, Behnke, 1982b), *Anisophyllea* and *Combretocarpus* were found to have S-type plastids. If further investigations on other genera and other characters (e.g. from vegetative and generative morphology, chromosome cytology) would corroborate the plastid diversity, a separation of the Anisophylleae as a distinct family, Anisophyllaceae, could be substantiated.

Certainly sieve-element plastids cannot be used as a critical character to positively shape the order Myrtales, but are helpful in negating close relationships of some of the peripheral families.

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REPRODUCTIVE ANATOMY AND MORPHOLOGY OF MYRTALES IN RELATION TO SYSTEMATICS[1]

RUDOLF SCHMID[2]

Evidence from reproductive morphology and anatomy (excluding palynology) favors an inclusive Myrtales of 11 core families (see below) over either a much broader Myrtales, as advocated, for example, by the Englerian school (most recently Melchior, 1964) or a narrower Myrtales and accompanying Lythrales, as advocated by Novák (1961, 1972) and more recently and in a rather different manner by Briggs and Johnson (1979), who, however, withdrew their concept in this symposium (Johnson & Briggs, 1984; see also argumentation in the appendix in Schmid, 1980). Embryology provides the best evidence for a concept of core Myrtales consisting of Combretaceae, Crypteroniaceae, Lythraceae, Melastomataceae sensu lato, Myrtaceae (including Psiloxylaceae[3] and Heteropyxidaceae; Schmid, 1980), Oliniaceae, Onagraceae, Penaeaceae, Punicaceae, Sonneratiaceae, and Trapaceae (familial arrangement strictly alphabetical; see also Tobe & Raven, 1983a).

The following embryological traits unite core Myrtales: anthers tetrasporangiate*, with conspicuous endothecium*, glandular tapetum, simultaneous cytokinesis; ovules anatropous*, bitegmic*, crassinucellate; antipodals ephemeral or absent*; endosperm nuclear*; seeds exalbuminous*. The asterisks indicate that exceptions are known. Table 1 (pp. 834–835) lists such exceptions, which in some cases are known for only one family or even only one species, for example, the trisporangiate anther of *Corynanthera flava* of Myrtaceae (Green, 1979). Other embryological features such as nuclear condition of pollen at time of shedding, persistence of anther epidermis, and types of anther wall development, embryo sac, and embryogeny vary appreciably (see Table 1). Significantly, Dahlgren and Thorne (1984) and Tobe and Raven (1983a) independently arrived at a very similar complex of embryological characters unifying core Myrtales.

Reproductive anatomy, that is, histology and vasculature, gives no special aid in resolving the makeup of Myrtales. Features such as bicollateral bundles (internal or intraxylary phloem) occur in peduncles, inflorescence axes, pedicels, flowers, and fruits of most myrtalean taxa (Schmid, 1972b, 1980, for Myrtaceae and Lythraceae; Schmid, unpubl. data and literature survey for other families). However, bicollateral bundles are really histological markers first described for vegetative parts of Myrtales and other orders (Cronquist, 1981; Dahlgren & Thorn, 1984; Metcalfe & Chalk, 1983; van Vliet & Baas, 1984) and then applied to their reproductive parts. The same pertains to vestured pits, which are unreported for myrtalean reproductive structures, but which occur in Lythraceae, Melastomataceae, Myrtaceae, *Alzatea* (Schmid, unpubl. data). In Myrtales, amphicribral bundles are common, especially in androecia and placentae (Schmid, 1972b, 1980, for Myrtaceae and Lythraceae; Schmid, unpubl. data and literature survey for other families). However, amphicribral bundles seem related to functional, nutritional factors for reasons elaborated elsewhere (Schmid, 1976, 1978).

There are no unifying features of floral vasculature for Myrtales (nor for other orders), let alone Myrtaceae. An axile ovular supply (Schmid, 1972a) is most common and clearly basic; the derived transeptal ovular supply (Schmid, 1972a) occurs variously in Myrtaceae, Oliniaceae, Onagraceae, Punicaceae, and *Rhynchocalyx* of core Myrtales (Eyde, 1981; Schmid, 1972a, 1972b, 1980, unpubl. data and literature survey), as well as in Lecythidaceae sensu lato, Rhizophoraceae

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[1] Text expanded somewhat from my symposium abstract (Schmid, 1981), with added references and table. A detailed account will be published in a future issue of this journal. In the interim Dahlgren and Thorne (1984) should be consulted, especially for discussion of embryological features. A detailed review of embryology of Myrtales has also been published by Tobe and Raven (1983a—see also comment in note a to Table 1). Supported in part by NSF grants BMS75-03811 and DEB78-04289.

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[3] Pollen morphology, sunken styles, and the occurrence of secretory cavities in all aerial organs are the strongest arguments for including *Psiloxylon* in Myrtaceae, albeit as a separate subfamily, Psiloxyloideae (see Schmid, 1980).

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sensu lato, and Thymelaeaceae, which were previously attributed to Myrtales (see Dahlgren & Thorne, 1984).

Various families can be fairly safely excluded from the aforecircumscribed core Myrtales on the basis of a combination of characters from both embryology and vegetative anatomy. For example, Rhizophoraceae sensu lato, Lecythidaceae sensu lato, Theligonaceae, Cynomoriaceae, Hippuridaceae, among others, lack bicollateral bundles and vestured pits and in some cases (Rhizophoraceae, Lecythidaceae) also have scalariform perforation plates (Cronquist, 1981; Dahlgren & Thorne, 1984; Metcalfe & Chalk, 1983; van Vliet & Baas, 1984), all of which are non-myrtalean attributes. And especially tenuinucellate and/or unitegmic ovules, which occur variously in Lecythidaceae sensu lato, Hippuridaceae, and Theligonaceae are significant in excluding these families from core Myrtales. Thymelaeaceae, however, have vestured pits and bicollateral bundles (Cronquist, 1981; Dahlgren & Thorne, 1984; Metcalfe & Chalk, 1983; van Vliet & Baas, 1984) and on the basis of wood anatomy (van Vliet & Baas, 1984), embryology (Table 1), and other aspects of reproductive anatomy and morphology (Cronquist, 1981; Dahlgren & Thorne, 1984; Schmid, unpubl. data) cannot be easily excluded from core Myrtales. Pollen and chemical evidence, nevertheless, do favor such an exclusion (Dahlgren & Thorne, 1984). There are, of course, additional arguments relevant to the aforenoted and other familial exclusions (see Dahlgren & Thorne, 1984; Orchard, 1975; Tobe & Raven, 1983a).

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TABLE 1. ⟶

TABLE 1. Some embryological features of core Myrtales and Thymelaeaceae.[a]

	Combreta	Cryptero	Lythrace	Melastom[b]	Myrtacea[b]
Number genera/species	20/400	3/10	29/590	200/4,000+	149/3,675
Number sporangia/anther	4	4	4	4	4(3)[c]
Anther with conspicuous endothecium at maturity	yes	no	yes	no (yes)[d]	yes
Anther with glandular tapetum	yes	yes	yes	yes	yes
Anther with simultaneous cytokinesis	yes	yes	yes	yes	yes[e]
Ovules anatropous	yes	yes	yes, very rare other[f]	yes, very occ. other[f]	yes, occ. other[f]
Ovules bitegmic	yes	yes	yes	yes	yes, very occ. uni[g]
Ovules crassinucellate	yes	yes	yes[h]	yes	yes
Antipodals	ephemeral, persistent[i]	ephemeral	ephemeral	ephemeral	ephemeral
Endosperm (initial)	nuclear	nuclear	nuclear	nuclear	nuclear
Seeds exalbuminous	yes	yes	yes	yes	yes, occ. no[j]
Anther epidermis persistent	yes	yes	no	yes	occ.
Type of anther wall development	Basic[l]	Dicot	Dicot	irregular[m]	Basic[n]
Pollen at shedding	bi-, occ. trinuc	binuc	binuc	trinuc	binuc
Type of embryo sac	Polygonum, Penaea[p]	Polygonum	Polygonum	Polygonum	Polygonum
Type of embryogeny	Asterad	??	Onagrad	Onagrad (Solanad)[q]	Onagrad (irreg)[r]

[a] Embryological features considered as unifying the 11 families of core Myrtales (arrangement of families strictly alphabetical; see also note b) are above the line; more variable embryological features are below the line. On embryology alone Thymelaeaceae could be included in Myrtales, but other evidence excludes this family (Dahlgren & Thorne, 1984). Some conspicuous exceptions are elaborated below. Descriptors such as "rarely," "occasionally," etc. are used as defined in Schmid (1982). Number of genera/species per family from Dahlgren and Thorne (1984) and Schmid (1980). Source of other data: Corner (1976), Cronquist (1981), Dahlgren and Thorne (1984), Davis (1966), Orchard (1975), Schmid (1972b, 1980), Tobe and Raven (1983b); references therein and below, other recent taxonomic and anatomical literature, and unpubl. data on various families.

This table was compiled independently of Tobe and Raven (1983a), which appeared while the present article was in press. These authors noted (pp. 87–88): "Thymelaeaceae differ from [core] Myrtales in possessing (1) a thick, 3- to 4-layered inner integument; (2) micropyle formed by the inner integument alone; (3) persistent antipodal cells that often multiply; and (4) albuminous seeds. Embryologically, these differences are decisive in ruling out any direct relationship between Thymelaeaceae and core Myrtales." Feature (1) is apparently unique to the family, but its overall systematic significance in angiosperms is unclear. Features (2) and (3) occur in core Myrtales, but are exceptional there (see Tobe & Raven and note i below). The old literature Tobe and Raven cite for feature (4) is not in agreement with the newer conclusion of Corner (1976) given in note k. Tobe and Raven did not cite Corner and also were unaware of the exception indicated in note j. I thus am less impressed than Tobe and Raven by the embryological distinctiveness of Thymelaeaceae from core Myrtales, in part because various families of the latter have peculiar embryological features. In other respects, Tobe and Raven and I are in substantial agreement regarding the embryological features unifying core Myrtales.

Key: binuc = binucleate; occ. = occasionally; trinuc = trinucleate; ? = information should be verified by critical examination; ?? = situation not known on basis of literature consulted and/or material examined.

[b] Melastomataceae including Memecylaceae fide Dahlgren and Thorne (1984). Myrtaceae including Psiloxylaceae and Heteropyxidaceae fide Schmid (1980, see text note 2). Embryological features of Psiloxylaceae and Heteropyxidaceae as far as is known correspond precisely with those of core Myrtaceae (Schmid, 1980).

[c] Trisporangiate only in *Corynanthera flava* (Green, 1979).

[d] Endothecium poorly developed and lacking fibrous thickenings in Melastomatoideae, but conspicuous, even with fibrous thickenings, in Memecyloideae (see Davis, 1966).

TABLE 1. Continued.

Oliniace	Onagrace	Penaeace	Punicace	Sonnerat	Trapacea	Thymelae
1/10	17/670	5/25	1/2	2/7	1/3	50/500
4	4	4	4	4	4	4
yes	yes	??	yes	yes	yes	yes
?yes	yes	??	?yes	yes	yes	yes
??	yes	??	??	yes	yes	yes
no[f]	yes	yes	yes	yes	yes	yes, to other[f]
yes	yes	yes	yes	yes	yes	yes
yes	yes	yes	yes	yes	yes	yes
ephemeral	absent	??	ephemeral	ephemeral	ephemeral or absent	persistent[i]
nuclear	nuclear	nuclear	nuclear	nuclear	ephemeral (nuclear) or absent	nuclear
yes	yes	yes	yes	yes	yes	yes, occ. no[k]
??	yes	??	?yes	yes	yes	yes
?Dicot	??	??	??	Dicot	Dicot	Basic, Monocot[o]
??	binuc	??	binuc	binuc	binuc	trinuc
Polygonum	Oenothera	Penaea	Polygonum	Polygonum	Polygonum	Polygonum
??	Onagrad	Asterad	??	Onagrad	Solanad	Asterad

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[e] No information in Davis (1966), but more recently simultaneous cytokinesis reported (Davis, 1968, 1969; Prakash 1969b, 1969c, 1969d, 1969e—citations in Schmid, 1972b).

[f] Ovules of Oliniaceae hemitropous to campylotropous (Dahlgren & Thorne, 1984). Ovules of Lythraceae also very rarely amphitropous (Schmid, 1980), of Melastomataceae also very occasionally campylotropous (Cronquist, 1981; other taxonomic literature), of Myrtaceae also occasionally campylotropous or other—hemitropous, amphitropous (Schmid, 1980), of Thymelaeaceae anatropous to hemitropous (Cronquist, 1981; Davis, 1966).

[g] Unitegmic ovules reported for five species of *Syzygium* sensu Schmid (1972a, 1972b), including some species formerly included under *Eugenia* (Davis, 1966).

[h] Nucellus of *Ammannia coccinea* is two-layered and regarded as tenuinucellate by Smith and Herr (1971). However, by conventional definitions this is crassinucellate or, at best, subcrassinucellate.

[i] *Guiera senegalensis* (monotypic) of Combretaceae has persistent, multiplicative antipodals (Davis, 1966; Venkateswarlu & Prakasa Rao, 1972), the only known member of core Myrtales with this feature, and thus similar to Thymelaeaceae with persistent, usually multiplicative antipodals.

[j] Endosperm occasionally scantily present according to Corner (1976), Petit (1908—citation in Schmid, 1980), Schmid (1980), and taxonomic literature.

[k] Endosperm "commonly absent from the seed or reduced to a trace, but copious in *Lachnaea* and *Pimelea*" (Corner, 1976: 270; see also Cronquist, 1981). See also note a.

[l] Anther development irregular, with only one middle layer, in *Guiera senegalensis* (Davis, 1966; Venkateswarlu & Prakasa Rao, 1972).

[m] Anther development irregular and not characterized according to type by Davis (1966) or other workers.

[n] No information in Davis (1966), but more recently anther development reported to be of Basic type (Davis, 1968, 1969; Prakash, 1969b, 1969c, 1969d, 1969e—citations in Schmid, 1972b).

[o] Basic type in *Wikstroemia canescens*, Monocotyledonous type in *Lasiosiphon eriocephalus* (Davis, 1966).

[p] The report of the tetrasporic *Penaea* type embryo sac for two species of *Combretum* needs confirmation (see Dahlgren & Thorne, 1984; Tobe & Raven 1983a; Venkateswarlu & Prakasa Rao, 1972).

[q] Solanad embryogeny type in *Melastoma malabathricum* and *Sonerila wallichii* (Davis, 1966).

[r] Irregular embryogeny in *Darwinia fascicularis*, *D. micropetala*, and *Angophora floribunda* (Prakash, 1969d, 1969e—citations in Schmid, 1972b).

THE EMBRYOLOGY AND RELATIONSHIPS OF *RHYNCHOCALYX* OLIV. (RHYNCHOCALYCACEAE)[1]

Hiroshi Tobe[2] and Peter H. Raven[3]

Abstract

This paper presents the first embryological study of *Rhynchocalyx,* a unique and problematical monotypic South African genus. The genus agrees well with other Myrtales in its basic embryological and other characteristics, including an ephemeral anther endothecium, a micropyle formed by the inner integument alone, and by other subsidiary features of the anther, nucellus, endosperm, and seed, as well as its megasporogenesis. *Rhynchocalyx* differs absolutely from *Axinandra* in many embryological characteristics, a fact that is not in agreement with a broad definition of Crypteroniaceae to include both genera. Also, *Rhynchocalyx,* despite its shared distinctive multicelled archesporium, differs from Lythraceae in many attributes. Thus, evidence from embryology, combined with that from other sources, supports the conclusion that *Rhynchocalyx* is not directly related to Lythraceae, and is, therefore, best assigned to a family of its own, Rhynchocalycaceae.

This paper reports the embryology of the rare monotypic South African genus *Rhynchocalyx,* and is the second concerning the unique genera of the order Myrtales. The first concerned *Axinandra* (Tobe & Raven, 1983b). The proper taxonomic assignment and relationships of *Rhynchocalyx,* like those of *Axinandra,* have often been disputed. Oliver (1895), who first described *Rhynchocalyx lawsonioides,* classified the genus under Lythraceae. Later, Engler (1900) treated *Rhynchocalyx* as one of the "Gattungen der Lythraceen von unsicherer Stellung," and Koehne (1903) excluded it from Lythraceae. Sprague and Metcalfe (1937), however, returned it to Lythraceae, stating that Koehne's grounds for its exclusion from that family were not tenable. Recently, van Beusekom-Osinga and van Beusekom (1975) proposed a broad definition of Crypteroniaceae that included *Rhynchocalyx,* together with *Crypteronia, Dactylocladus, Axinandra,* and *Alzatea.* Pollen morphology might or might not be taken to support a relationship of *Rhynchocalyx* with the other genera of Crypteroniaceae sensu lato (Muller, 1975): thus, *Rhynchocalyx* agrees with *Dactylocladus* and *Axinandra* in having heterocolpate pollen grains but differs from both *Crypteronia* (with bisyncolporate pollen grains) and *Alzatea* (with tricolporate pollen grains). *Rhynchocalyx* and *Alzatea* differ from the other three genera of Crypteroniaceae sensu lato in their wood anatomy, and share many characteristics with Lythraceae and Melastomataceae (van Vliet, 1975).

On the other hand, leaf, twig, and nodal anatomy suggests that *Rhynchocalyx* is closer to some Lythraceae, Oliniaceae, and Melastomataceae than to the other members of Crypteroniaceae sensu lato (van Vliet & Baas, 1975). Nevertheless, differences in floral structure and the presence of foliar sclereids in the petioles of *Rhynchocalyx* (Rao & Das, 1979) indicate that it is not directly related to Lythraceae. In addition, *Rhynchocalyx* may be distinguishable from Lythraceae in not having nectaries in its flowers, although this feature needs to be reviewed in Lythraceae.

Dahlgren and Thorne (1984) pointed out that *Rhynchocalyx* stood apart from Lythraceae in having petals and stamens on the hypanthial rim and sclereids in its leaf petioles. Taking all of these facts into account in their cladistic analysis, Johnson and Briggs (1984) concluded that *Rhynchocalyx* is not directly related to Lythraceae. This conclusion led them to describe the new family Rhynchocalycaceae for the genus, a family that is accepted both by Dahlgren and Thorne (1984) and by Graham (1984), who described a second new family, Alzateaceae, to accommo-

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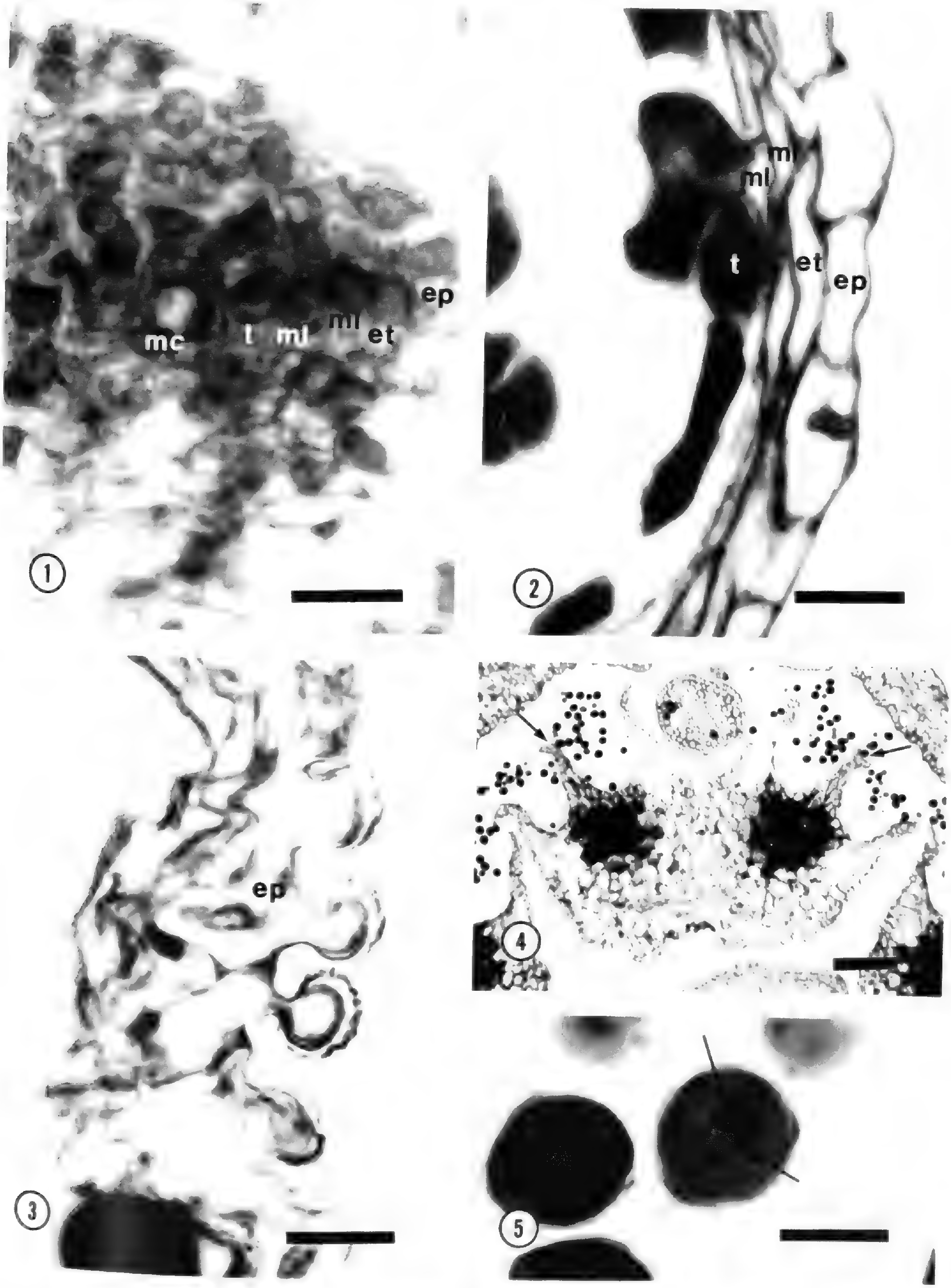
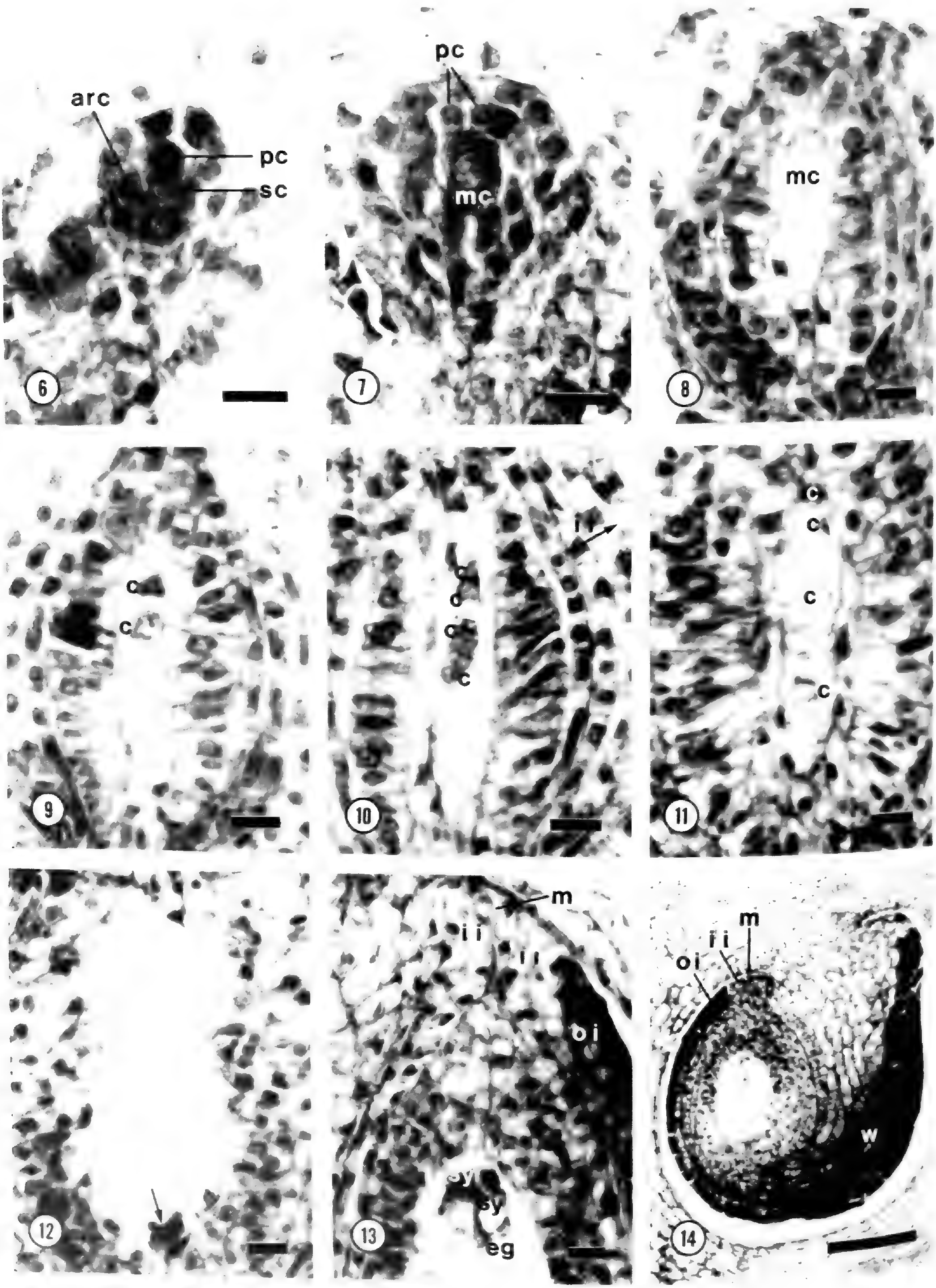


FIGURES 1–5. —1. Cross section of a young anther. Its wall is formed by an epidermis (*ep*), an endothecium (*et*), middle layers (*ml*), and a tapetum (*t*). *mc*: microspore mother cell. Bar = 10 μm.—2. Cross section of an older anther. Only the epidermis (*ep*) remains uncrushed while the endothecium (*et*), middle layers (*ml*) and the tapetum (*t*) are degenerating. Bar = 10 μm.—3. Cross section of a mature anther. Note persistent papillate epidermal cells (*ep*). Bar = 10 μm.—4. Cross section of a dehisced anther. Note the persistent septa (arrows) between two microsporangia on each side of the anther. Bar = 100 μm.—5. Two-celled pollen grain at the time of shedding. Arrows point out a nucleus of a generative cell and that of a vegetative cell. Bar = 10 μm.



FIGURES 6–14. —6. Longitudinal section of an ovule primordium with a multicelled archesporium. The only functional archesporial cell is already divided into a primary parietal cell (*pc*) and a sporogenous cell (*sc*). The rest of the archesporial cell (*arc*) remains undivided. Bar = 10 μm.—7. Longitudinal section of a young ovule with a young megaspore mother cell (*mc*) below parietal cells (*pc*). Bar = 10 μm.—8. Longitudinal section of a young ovule with an enlarged megaspore mother cell (*mc*). Note the position of a nucleus. Bar = 10 μm.—9. Longitudinal section of a young ovule with a dyad composed of a smaller micropylar megaspore (*c*) and a larger

date the equally unusual but not directly related *Alzatea.*

Until we recently reported on the embryology of *Axinandra* (Tobe & Raven, 1983b), no embryological information was available on the genera that were relegated to Crypteroniaceae sensu lato by van Beusekom-Osinga and van Beusekom (1975). On the basis of available embryological information, however, we cannot evaluate the proposed inclusion of *Axinandra* in Crypteroniaceae together with *Crypteronia* and *Dactylocladus,* since the latter two genera are unknown in this respect. The purpose of the present paper is to evaluate the relationship of *Rhynchocalyx* to *Axinandra,* Lythraceae, and other Myrtales, and in the light of this information to comment upon its phylogenetic relationships and proper taxonomic placement.

MATERIAL AND METHODS

Flower buds and fruits of *Rhynchocalyx lawsonioides* Oliv. were collected and fixed in FAA (five parts stock formalin: five parts glacial acetic acid: 90 parts 70% ethanol) at Uvongo River, Natal, Republic of South Africa, by Mr. H. B. Nicholson. The voucher specimen is *Nicholson s.n.,* in 1982 (MO). Preparations of microtome sections for the observation were made following the techniques discussed in a previous paper (Tobe & Raven, 1983b).

OBSERVATIONS

ANTHER AND MICROSPORES

The anther is tetrasporangiate. The wall structure prior to maturation comprises five layers, i.e., an epidermis, an endothecium, two middle layers, and a tapetum (Fig. 1). Since the outer and the inner middle layers share their developmental origins with the endothecium and the tapetum, wall formation conforms to the Basic type (Davis, 1966: 10). During the process of maturation, the epidermis remains uncrushed whereas the endothecium and the two middle layers degenerate (Fig. 2). The tapetum is glandular and its cells become two-nucleate before degeneration. Thus a mature anther wall at the time of dehiscence is composed only of the persistent epidermis (Figs. 3, 4). The outer half of each epidermal cell forms a conspicuous papilla (Fig. 3). A septum between two microsporangia on each side of the anther remains intact even at the time of anther dehiscence (arrows, Fig. 4), a condition that is unusual in angiosperms.

Meiosis in a microspore mother cell is accompanied by simultaneous cytokinesis. Shape of the resultant microspore tetrads is, on the basis of the examination of 20 selected tetrads, "usually" (65%) tetrahedral and "often" (35%) decussate (expressions of the frequency follow Schmid, 1982). Pollen grains are two-celled when they are shed (Fig. 5).

MEGAGAMETOPHYTE AND NUCELLUS

The ovule is anatropous and crassinucellate. The archesporium is hypodermal and is composed of three to five cells, only one of which further divides periclinally into two: i.e., the upper primary parietal cell and the lower sporogenous cell (Fig. 6). The primary parietal cell divides once anticlinally (Fig. 7) and both cells repeat periclinal divisions to form a massive parietal tissue. The sporogenous cell develops into a megaspore mother cell (Fig. 7) and becomes enlarged by the time of meiosis (Fig. 8). In the enlarged megaspore mother cell a nucleus occupies a position on the micropylar side (Fig. 8). Meiosis in the megaspore mother cell is accompanied by successive cytokinesis. By the first meiotic division, the megaspore mother cell is partitioned into a dyad of megaspores in which the micropylar cell is much smaller than the chalazal cell (Fig. 9). The second meiotic division occurs earlier in the micropylar cell of the dyad than in the chalazal cell. The two daughter cells thus formed on the micropylar side are always

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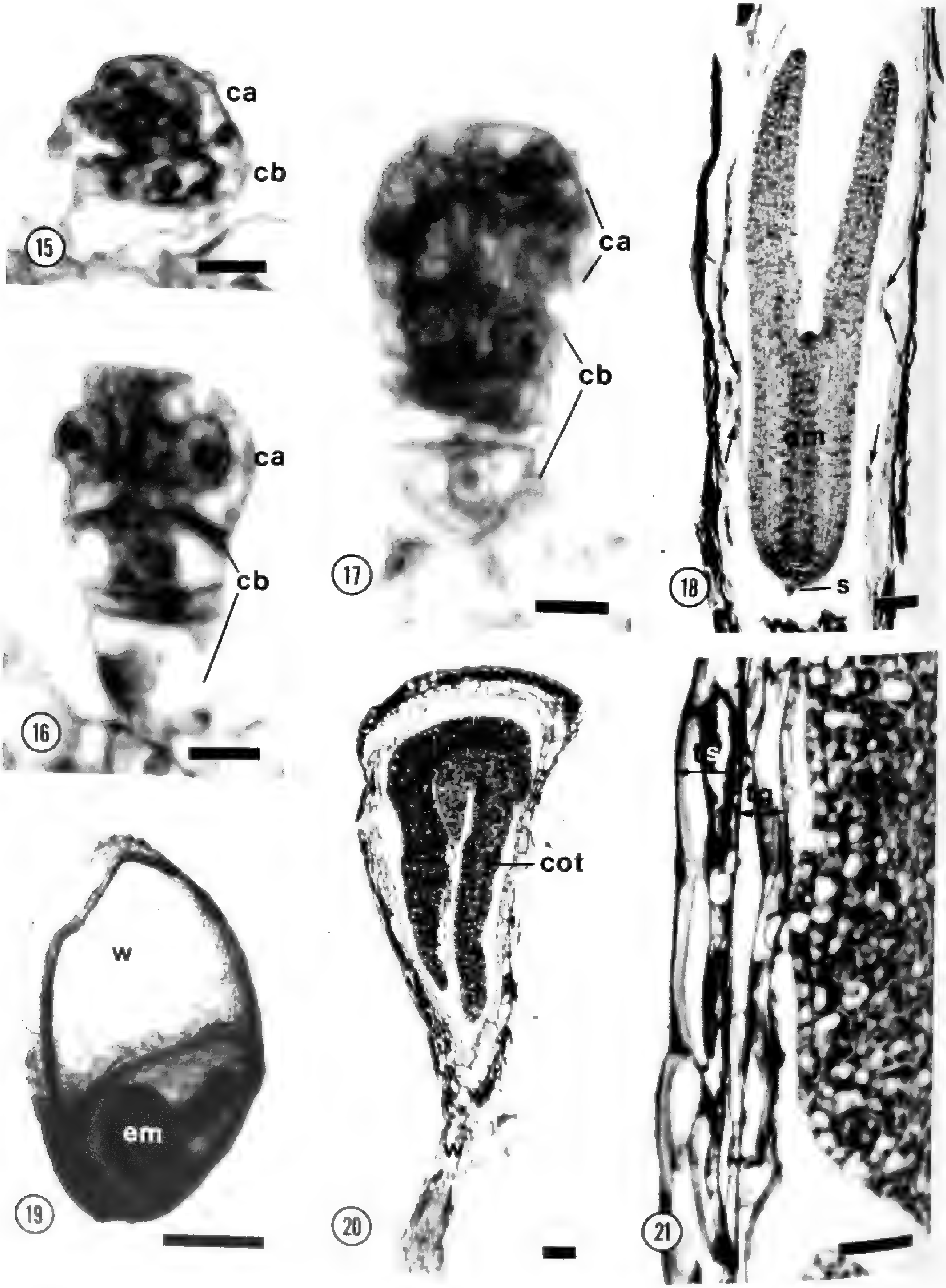
chalazal megaspore (*c*). Bar = 10 μm.—10. Longitudinal section of a young ovule with a linear tetrad of megaspores (*c*). Note that the two micropylar megaspores are already crushed while the two chalazal megaspores are being formed. Bar = 10 μm.—11. Longitudinal section of a young ovule with a functional chalazal megaspore enlarging (second *c* from bottom). Note that subdermal cells of the nucellus are radially elongated. Bar = 10 μm.—12. Longitudinal section of a mature embryo sac with degenerating antipodals (arrow). Bar = 10 μm.—13. Longitudinal section of a micropylar part of a mature ovule. Note the two-layered structure of the inner (*ii*) and the outer (*oi*) integument. A micropyle (*m*) is formed by the inner integument alone. *eg*: egg cell; *sy*: synergid. Bar = 10 μm.—14. Longitudinal section of a mature ovule to show the whole structure. Note the position wing (*w*) formed by the funicular tissue. *ii*: inner integument; *oi*: outer integument; *m*: micropyle. Bar = 100 μm.



FIGURES 15–21. —15. Longitudinal section of a two-celled proembryo composed of an apical cell (*ca*) and a basal cell (*cb*). The apical cell is dividing vertically. Bar = 10 μm.—16. Longitudinal section of an eight-celled proembryo. *ca*: cells derived from the apical cell at the two-celled stage; *cb*: cells derived from the basal cell. Bar = 10 μm.—17. Longitudinal section of an older proembryo. Note that cells derived from the apical cell (*ca*) form a global part of the proembryo whereas those derived from the basal cell (*cb*) form the lower rod. Bar = 10 μm.—18. Longitudinal section of a young seed including a young dicotyledonous embryo (*em*). Arrows indicate free endosperm nuclei. *s*: suspensor. Bar = 100 μm.—19. Nearly mature seed with a membranous wing

degenerating when the chalazal cell of the dyad is dividing (Fig. 10). A cell plate in the division of the chalazal cell of the dyad is also formed on the more or less micropylar side (Figs. 10, 11). Megaspore tetrads are always linear (Fig. 11) although the upper (i.e., micropylar) two are often arranged somewhat obliquely, and the lowest (chalazal) cell functions and thus develops into an eight-nucleate *Polygonum*-type embryo sac. Synergids are pyriform, and three antipodals are ephemeral; they degenerate without any sign of wall formation (arrow, Fig. 12). Consequently, an organized mature embryo sac just before fertilization comprises only five nuclei or cells—i.e., an egg, two synergids, and two polar nuclei.

During megasporogenesis, subdermal cells of the nucellus elongate radially and form a jacket around the enlarged megaspore mother cell or the megaspores (Figs. 8–11). This tissue, however, gradually degenerates or is absorbed as the embryo sac enlarges in the later stages.

INTEGUMENTS

The ovule is bitegmic (Figs. 13, 14). Both the inner and the outer integument are initiated by periclinal divisions of dermal cells of the nucellus and grow only by divisions of the cells derived from the dermal initial cells, resulting in a two-layered structure. Neither of the integuments show any secondary multiplication in thickness (Figs. 13, 14). Cells of the outer epidermis of the outer integument become tanniferous as early as the megaspore mother cell stage.

The inner integument exceeds the outer integument in its degree of elongation (Figs. 13, 14); thus the micropyle is always formed by the inner integument alone (Figs. 13, 14).

FERTILIZATION, ENDOSPERM, AND EMBRYO

Fertilization is porogamous. Endosperm formation is of the Nuclear type. The endosperm is very scanty even at the free nuclear stage and throughout the process of seed development (arrows, Fig. 18); it does not show any particular accumulations of free nuclei on the micropylar or on the chalazal side. Wall formation does not occur in free nuclei. We could not find cellular endosperm at any stage of seed development. The mature seeds completely lack endosperm (Figs. 20, 21).

Embryogenesis conforms to the Onagrad type. The apical cell of a two-celled proembryo divides vertically, and the basal cell transversely (Fig. 15). Cells derived from the apical cell contribute to the formation of a major part of the embryo, those derived from the basal cell only to a minor portion. The latter include the parts that are destined to form the root cap and cortex, as well as the suspensor (Figs. 16, 17). A young embryo has two equally developed cotyledons and a short and small suspensor (Fig. 18). The embryo in the mature seed is more or less flattened, its cotyledons folded inside (Fig. 20).

MATURE SEED AND SEED COAT

The mature seed is depressed-ovoid in shape with a flat membranous wing on the micropylar side (Fig. 19). The wing is formed by divisions and elongation of cells of the funiculus (Figs. 14, 19). No hypostase is formed throughout the development of ovule and seed.

The mature seed coat is derived from the two-layered testa as well as from the two-layered tegmen. All of the constituent cells are highly elongated, particularly longitudinally. The outer surface of the outer epidermis of the testa is conspicuously lignified.

DISCUSSION

The embryological characteristics of *Rhynchocalyx lawsonioides* may be summarized as follows:

Anther tetrasporangiate; anther wall five layers thick, its formation of the Basic type; anther epidermis persistent, the outer half part of each cell forming a conspicuous papilla; endothecium and two middle layers ephemeral; tapetum glandular, its cells two-nucleate; septum between the two microsporangia on each side of the anther persistent. Cytokinesis in microspore mother cells simultaneous; microspore tetrads tetrahedral or decussate in shape; pollen grains two-celled when shed.

Ovule anatropous, bitegmic, and crassinucel-

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(*w*). *em*: embryo. Bar = 1 mm.—20. Cross section of a mature seed. Cotyledons (*cot*) of the embryo are folded inside. *w*: wing. Bar = 100 μm.—21. Longitudinal section of a mature seed. Both the two-layered testa (*ts*) and the two-layered tegmen (*tg*) constitute a mature seed coat. *em*: embryo. Bar = 100 μm.

late, both integuments two-layered; subdermal cells of the nucellus elongated radially, forming a jacket around the megaspore mother cell or megaspores; micropyle formed by the inner integument alone; chalaza without hypostase.

Archesporium of ovule multicelled, comprising three to five cells, only one of them functioning and cutting off a parietal cell; cytokinesis at meiosis I resulting in a dyad composed of a smaller micropylar cell and a larger chalazal cell; the subsequent division of meiosis II earlier in the micropylar cell of the dyad than in the chalazal cell; tetrads of megaspores linear; chalazal megaspore functional, developing into an eight-nucleate *Polygonum*-type embryo sac; antipodals ephemeral.

Fertilization porogamous; endosperm formation of the Nuclear type; wall formation not occurring in free endosperm nuclei; embryogenesis conforming to the Onagrad type; embryo dicotyledonous with a short and small suspensor; seed exalbuminous with a single flat membranous wing on the micropylar side. Seed coat thin and fibrous, consisting of elongate cells of the two-layered testa as well as of the two-layered tegmen.

Rhynchocalyx shares six of the seven basic embryological criteria that define the order Myrtales (Tobe & Raven, 1983a): (1) anther tapetum glandular, (2) ovule crassinucellate, (3) inner integument two-layered, (4) antipodals ephemeral, (5) endosperm formation the Nuclear type, and (6) mature seed exalbuminous (cf. Tobe & Raven, 1983a). The only disagreement is that *Rhynchocalyx* has a micropyle formed by the inner integument alone instead of by both integuments, and this seems to be a feature subject to evolutionary modification within the group, indicating that the situation in *Rhynchocalyx* is a derived one.

As regards the view of van Beusekom-Osinga and van Beusekom (1975) that *Rhynchocalyx* should be assigned to Crypteroniaceae sensu lato, we still have embryological information only concerning *Axinandra*, but lack it for the other constituent genera. *Rhynchocalyx* agrees with *Axinandra* in having an ephemeral endothecium (which is also characteristic of the Melastomataceae as a whole), but differs from *Axinandra* in many features. In *Rhynchocalyx*, the septum between two microsporangia on each side of the anther is persistent; the archesporium is multicelled; the micropyle is formed by the inner integument alone; the endothelium is not formed; the seed wing is formed on the micropylar side. In contrast, in *Axinandra* the septum in the anther is ephemeral; the archesporium is one-celled; the micropyle is formed by both integuments; the endothelium is formed; the seed wing is formed on the chalazal side. Evidence from the embryology, as well as from vegetative anatomy (van Vliet, 1975; van Vliet & Baas, 1975), indicates the heterogeneity of Crypteroniaceae sensu lato and virtually excludes the possibility that it would be desirable to retain both *Rhynchocalyx* and *Axinandra* in the same family.

As regards the alternative view that *Rhynchocalyx* should be (re-)placed in Lythraceae (van Vliet, 1975; van Vliet & Baas, 1975), the presence of the multicelled archesporium in an ovule supports the view because this characteristic has been found only in Lythraceae (including Sonneratiaceae). Contradicting the view that *Rhynchocalyx* might be directly related to Lythraceae, however, are the facts that *Rhynchocalyx* has an ephemeral endothecium and a micropyle formed by the inner integument alone, both features that have not been reported in Lythraceae. In fact, in its ephemeral endothecium, *Rhynchocalyx* agrees with *Axinandra* and Melastomataceae rather than with Lythraceae. The micropyle difference constitutes a distinct gap between *Rhynchocalyx* and Lythraceae. Some additional points of difference in embryology between *Rhynchocalyx* and Lythraceae include the following. In *Rhynchocalyx*, the septum between two microsporangia on each side of the anther is persistent; nucellar subdermal cells elongate radially, forming a jacket around the megaspores; the homotypic division of meiosis occurs earlier in the micropylar cell of the dyad than in the chalazal cell; starch grains are absent in the nucellus; and the endosperm is too scanty to show accumulations of free nuclei in the embryo sac. In Lythraceae, on the other hand, the septum in the anther probably collapses, as is the case in most angiosperms; radially elongated nucellar subdermal cells have not been observed; the homotypic division occurs later in the micropylar cell of the dyad than in the chalazal cell; starch grains are present in the nucellus (*Cuphea*, Hubert, 1896); and the endosperm commonly shows accumulations of free nuclei on the micropylar and/or the chalazal region of the embryo sac (Joshi & Venkateswarlu, 1936) and may become cellular (Mauritzon, 1934).

In view of all these points of difference, we conclude that embryology provides strong support for the conclusion of Johnson and Briggs

(1984) that *Rhynchocalyx* should be assigned to a monotypic family not directly related to Lythraceae. *Rhynchocalyx* does share its distinctive archesporial characteristics with Lythraceae, but significant gaps between these two taxa are evident in the characters of the anther wall, micropyle, nucellus, megasporogenesis, and endosperm. There is no strong evidence linking this remarkable South African relict genus directly with any other group, and it seems clear that it is best placed in a family of its own in order to emphasize its great distinctiveness.

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THE EMBRYOLOGY AND RELATIONSHIPS OF *ALZATEA* RUIZ & PAV. (ALZATEACEAE, MYRTALES)[1]

HIROSHI TOBE[2] AND PETER H. RAVEN[3]

ABSTRACT

In this paper we present the first embryological studies of *Alzatea*, one of the genera of the order Myrtales whose placement has been most controversial. Although *Alzatea* agrees rather completely with the other Myrtales in its basic embryological characteristics, it stands apart from all other members of the order that have been examined in having a bisporic *Allium*-type embryo sac. Comparisons with related groups, including *Axinandra, Rhynchocalyx*, Lythraceae, and Melastomataceae, indicate that *Alzatea* shares many more characteristics with *Rhynchocalyx* than with the others. Among the groups mentioned, only *Alzatea* and *Rhynchocalyx* coincide in their micropyle form, and both genera further agree with Lythraceae in the multi-celled ovule archesporium, which is not known elsewhere in the order except in one of the small subfamilies of Lythraceae, Sonneratioideae. A totality of similarities and dissimilarities with the other Myrtales favors the establishment of a monotypic family, Alzateaceae, and suggests that *Alzatea* and *Rhynchocalyx* may be parallel descendants from a common ancestor, with which the modern Lythraceae possibly has a link.

This paper deals with the embryology of the rare monotypic Central-South American genus, *Alzatea*, and is the third concerning the unique genera of the order Myrtales, following papers on *Axinandra* (Tobe & Raven, 1983b) and *Rhynchocalyx* (Tobe & Raven, 1984). As in the case of *Axinandra* and *Rhynchocalyx*, there has been a long history of arguments about the taxonomic position of *Alzatea*. According to Lourteig (1965), who gave a historical review up to that time, *Alzatea* has been placed in Celastraceae (De Candolle, 1825; Bentham & Hooker, 1862), Rhamnaceae (Miers, 1872; Loesener, 1942; MacBride, 1951), and Lythraceae (Planchon, 1845; Hallier, 1911; Pilger, 1915). Lourteig (1965) herself concluded that *Alzatea* belonged in Lythraceae, based on its floral and vegetative characters as well as on anatomical and palynological characters. She considered the genus to be a member of subtribe Diplusodontinae of tribe Lythreae.

At other times in its history, *Alzatea* has been considered to have a close affinity with another unique genus, *Crypteronia*, regardless of the family to which *Crypteronia* was assigned at that time (Miers, 1872; Loesener, 1942). Recently, van Beusekom-Osinga and van Beusekom (1975) proposed broadening the definition of Crypteroniaceae to include *Alzatea* together with *Crypteronia, Dactylocladus, Axinandra*, and *Rhynchocalyx*. Muller (1975) suggested a possible relationship among these five genera based on their pollen morphology. But van Vliet (1975), van Vliet and Baas (1975), and Baas (1979), on the basis of their studies of the wood, leaf, twig, and nodal anatomy, suggested not only that *Alzatea* and *Rhynchocalyx* differed widely from the three other genera of Crypteroniaceae sensu lato, but also that these two genera differed to a substantial degree from each other. Dahlgren and Thorne (1984) and Johnson and Briggs (1984), accepted the establishment by S. Graham (1984) of a monotypic family, Alzateaceae.

Results of our recent embryological studies have indicated that *Axinandra* and *Rhynchocalyx* are very different from each other, and that the former occupies a satellite position to Melastomataceae (Tobe & Raven, 1983b, 1984). *Rynchocalyx* is of less certain placement, but probably deserves the family status that it was accorded by Johnson and Briggs (1984). We carried out the present study of the embryology of *Alzatea*, which has hitherto been unknown, as a contribution to determining its most appropriate systematic position.

MATERIALS AND METHODS

The only species of what is probably a monotypic family, *Alzatea verticillata* Ruiz & Pav.,

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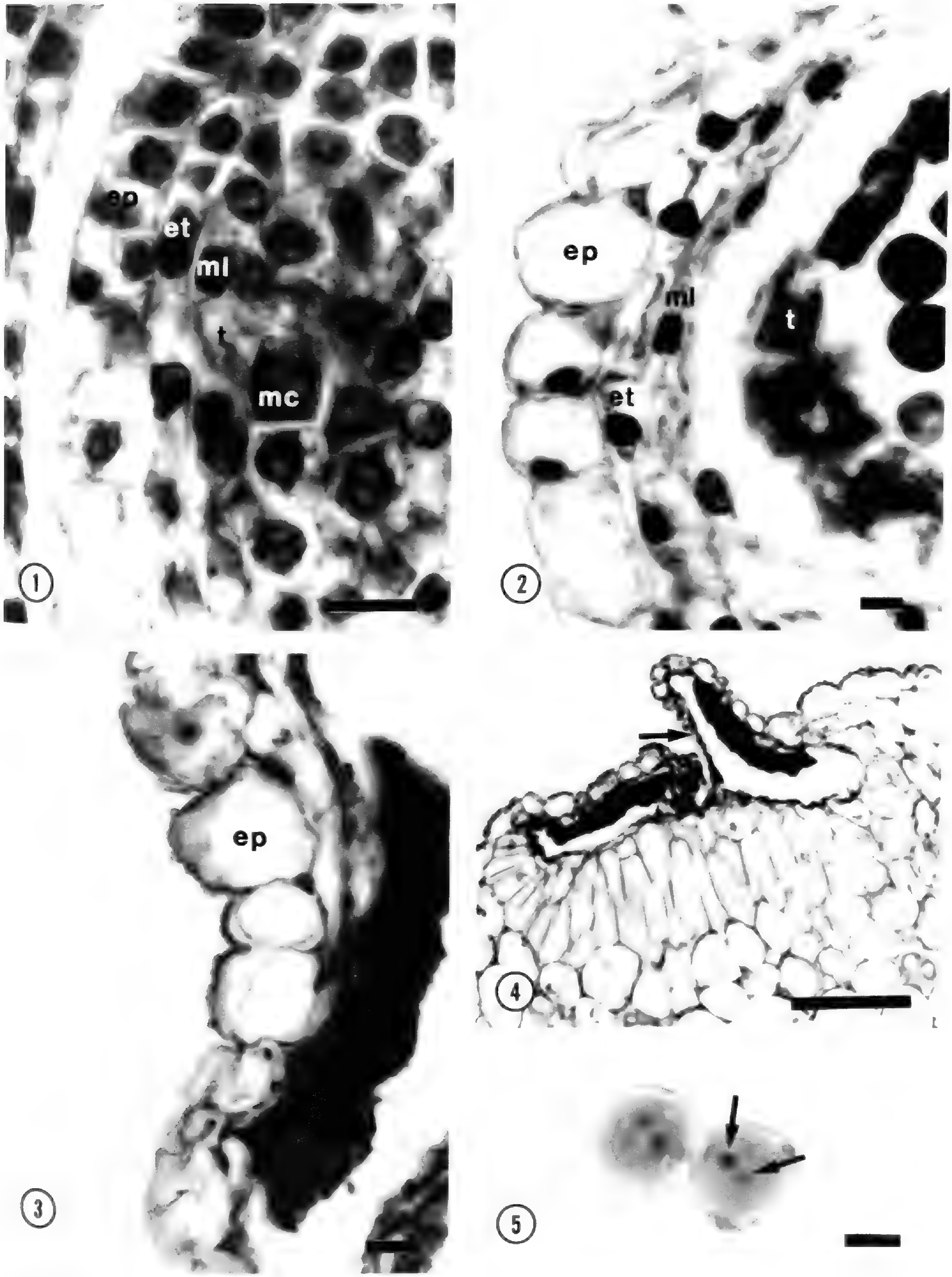
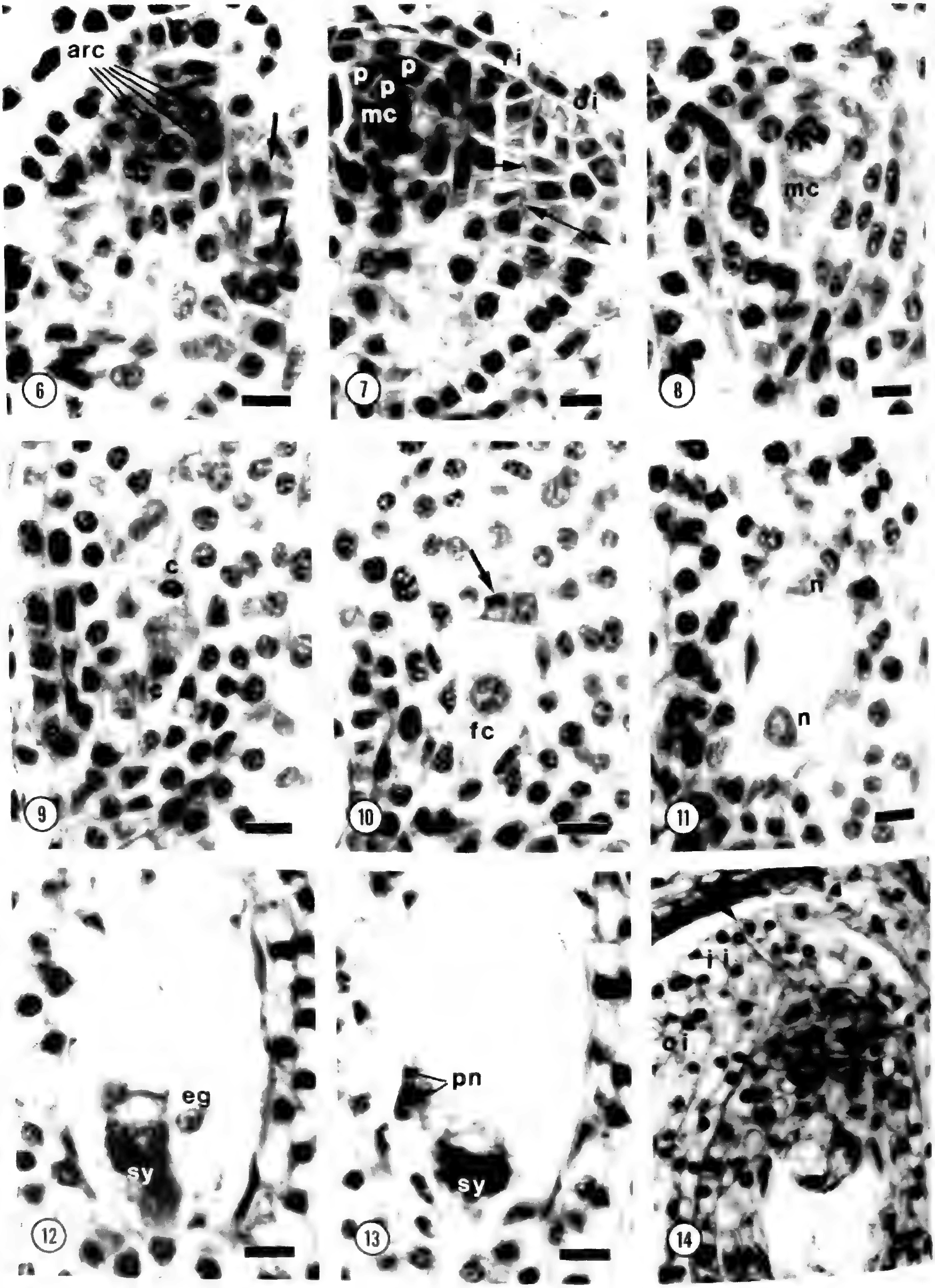


FIGURES 1–5. —1. Transverse section of a young anther. Its wall is formed by an epidermis (*ep*), an endothecium (*et*), a middle layer (*ml*) and a tapetum (*t*), inside the last of which microspore mother cells (*mc*) are produced. Bar = 10μm.—2. Cross-section of an older anther. The epidermal cells (*ep*) are enlarged while the endothecium (*et*), the middle layer (*ml*) and the tapetum (*t*) are degenerating. Bar = 10 μm.—3. Cross section of a mature anther, showing a persistent epidermis (*ep*). Bar = 10 μm.—4. Cross section of the mature anther. An arrow indicates the degenerating septum between two microsporangia. Bar = 100 μm.—5. Two-celled pollen grains at the time of shedding. Arrows point out nuclei of a generative and a vegetative cell. Bar = 10 μm.



FIGURES 6–14. —6. Longitudinal section of an ovule primordium with a multicelled archesporium. Arrows indicate periclinal divisions of the dermal initial cells of the inner and the outer integument. Archesporial cell (*arc*). Bar = 10 μm. —7. Longitudinal section of a young ovule with two growing integuments. Note that both the inner (*ii*) and the outer (*oi*) integument are two-layered in their original thickness. Only one of the archesporial cells functions to form parietal cells (*p*) and a single megaspore mother cell (*mc*). Bar = 10 μm. —8. Longitudinal

was examined in this study. Most of our observations were based on flower buds and fruits collected in Panama (voucher specimens: *Knapp 4336, 4087,* MO; *Knapp & Dressler 5392,* MO), supplemented, particularly with respect to mature seed morphology and anatomy, with material collected in Costa Rica (voucher specimen: *Poveda 3264,* MO). Both samples were fixed and preserved with FAA (five parts stock formalin : five parts glacial acetic acid : 90 parts 70% ethanol). Preparations of microtome sections were made following a technique described in a previous paper (Tobe & Raven, 1983b).

All of our flower samples from Panama (*Knapp 4336, 4087, Knapp & Dressler 5392*) have produced only sterile pollen sacs which have either crushed sporogenous tissues or, at most, aberrant pollen grains. Therefore, a different herbarium specimen from Peru (*Woytkowski 8331,* MO) was used for the observation of the shape of microspore tetrads and of the cell number of mature pollen grains. Pollen grains stained with 1% acetocarmine gave good results in counting the cell numbers in a few hours.

OBSERVATIONS

ANTHER AND MICROSPORES

The anther is tetrasporangiate. The wall structure prior to maturation comprises four layers, i.e., an epidermis, an endothecium, a middle layer, and a tapetum (Fig. 1). Since the endothecium and the middle layer have a common origin histogenetically, the wall formation is regarded as conforming to the Dicotyledonous type (Davis 1966: 10). During the process of maturation, the epidermal cells are enlarged while both the endothecium and the middle layer degenerate (Fig. 2). Consequently, the mature anther wall is composed only of the persistent epidermis, each of the epidermal cells being greatly enlarged (Fig. 3), and the cells of the connective tissue adjacent to pollen sacs are radially elongated (Fig. 4). The tapetum is glandular, and its cells become two-nucleate before they degenerate. A septum between two microsporangia on each side of the anther is broken down as is usual in angiosperms (arrow, Fig. 4).

The shape of microspore tetrads, on the basis of the examination of 20 selected tetrads, is "usually" (65%) tetrahedral and "often" (35%) decussate (expressions for the frequency follow Schmid, 1982). Pollen grains are two-celled at the time of shedding (arrows, Fig. 5).

Curiously, although pollen from Peru (*Woytkowski 8331,* MO) was 97% stainable, that of a collection from Costa Rica (*Dryer 941,* CR) was only about 31% stainable, and we have seen no fertile pollen in collections from Panama. These points clearly merit further investigation.

MEGAGAMETOPHYTE AND NUCELLUS

The ovule is anatropous and crassinucellate. An archesporium is hypodermal. Four to eight archesporial cells are differentiated from the other somatic cells (Fig. 6). Only one of them divides further, periclinally into two: the upper primary parietal cell and the lower sporogenous cell. The primary parietal cell divides once periclinally or anticlinally and both cells repeat periclinal and anticlinal divisions to form a massive parietal tissue (Fig. 7). The sporogenous cell develops into a megaspore mother cell (Fig. 8). After enlarging in volume, the megaspore mother cell undergoes meiosis to form a linear dyad of megaspores (Fig. 9). The upper micropylar megaspore of the dyad soon degenerates (arrow, Fig. 10), while the lower chalazal megaspore functions (Fig. 10). This functional megaspore involves three successive nuclear divisions, resulting in two- (Fig. 11), four-, and eight-nucleate embryo sacs. Thus the embryo sac formation conforms to the bisporic *Allium*-type. Synergids are pyriform (Figs. 12, 13), and antipodals are very ephemeral and disappear before fertilization. An organized mature embryo sac just before fertilization is composed of five nuclei or cells: an egg cell, two synergids, and two polar

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section of a young ovule with a single enlarged megaspore mother cell (*mc*). Bar = 10 μm.—9. Longitudinal section of a young ovule showing a dyad of megaspores (*c*). Bar = 10 μm.—10. Longitudinal section of a young ovule with a functional megaspore (*fc*) of the dyad enlarging. An arrow indicates a degenerated micropylar megaspore of the dyad. Bar = 10 μm.—11. Longitudinal section of a young ovule with a two-nucleate embryo sac. Nucleus in the embryo sac (*n*). Bar = 10 μm.—12, 13. Two successive longitudinal sections of a mature ovule with an organized mature embryo sac. Egg cell (*eg*); synergid (*sy*); polar nucleus (*pn*). Bar = 10 μm.—14. Longitudinal section of a mature ovule with an organized mature embryo. Note that the micropyle (at arrow) is formed by the inner integument (*ii*) alone. Outer integument (*oi*). Bar = 10 μm.

nuclei (Figs. 12, 13). Both the nucleus and the nucleolus of the egg cell are much smaller than those of synergids (Fig. 12).

During megasporogenesis and megagametogenesis, the nucellar tissue does not show any particular differentiation.

INTEGUMENTS

The ovule is bitegmic. Both the inner and the outer integument are initiated by periclinal divisions of dermal cells of the ovular primordium (arrows, Fig. 6); they grow only by divisions of the cells derived from the dermal initial cells. The growing inner integument is consistently two-layered and keeps its original thickness in the later stages as well. The outer integument also has a two-layered structure at the initiation stage but soon increases in thickness because of anticlinal divisions of the constituent cells, resulting in a two- to four-layered structure (Fig. 7). This multiplication is most conspicuous in those portions of the integument along the equatorial line of the ovules, which are horizontally placed in an ovarian locule, and represents the first sign of the formation of the seed wing.

The inner integument elongates more than the outer one. As a result, the micropyle is formed by the inner integument alone (Fig. 14).

EMBRYO AND ENDOSPERM

Since we could not locate the remnants of pollen tubes in microtome sections of fruit samples from Panama (*Knapp & Dressler 5392*), we are not certain whether the egg cell was actually fertilized in these samples or not. We did, however, encounter a fair number of proembryos in this collection. Based on our studies of these proembryos, embryogenesis apparently occurred normally until at least the globular proembryonal stage, and conforms to the Onagrad type. The apical cell of a two-celled proembryo divides vertically, and the basal cell transversely (Fig. 15). In an older proembryo, the upper globular portion is formed by cells derived from the apical cell at the two-celled proembryonal stage, while the lower part including the suspensor is formed by cells derived from the basal cell (Fig. 16). An embryo in a mature seed (from the sample collected in Costa Rica) has two equally developed cotyledons and a short and small suspensor. The cotyledons are not folded (Fig. 19).

Endosperm formation is of the Nuclear type (Fig. 16), although, as mentioned above, there is some doubt that fertilization actually occurred in these samples. The endosperm is very scanty throughout the seed development. Only about ten nuclei are observed even at the four-celled proembryonal stage. The endosperm does not show any accumulation of free nuclei in the chalazal region or in the micropylar region. Probably wall formation does not occur in free endosperm nuclei. The mature seed completely lacks endosperm (Fig. 17).

MATURE SEED AND SEED COAT

The mature seed has a membranous wing with the embryo centered (Figs. 18, 19). Its shape and size are diverse, depending on the degree of development of the wing. The wing is formed by tissues of both the funiculus and the outer integument along the horizontal line of the seed, and is composed mostly of undulating epidermal cells (Fig. 20). A hypostase is formed by the time the embryo sac is mature, but it does not become conspicuous even in the mature seed (Fig. 18).

The mature seed coat is thin except for a part of the wing, and it is made up mainly from the elongate outer epidermal cells of the testa. The inner epidermis and, if present, the mesophyll of the testa, as well as the inner and the outer epidermis of the tegmen, completely collapse, leaving only their cell walls when the seed is mature (Fig. 17).

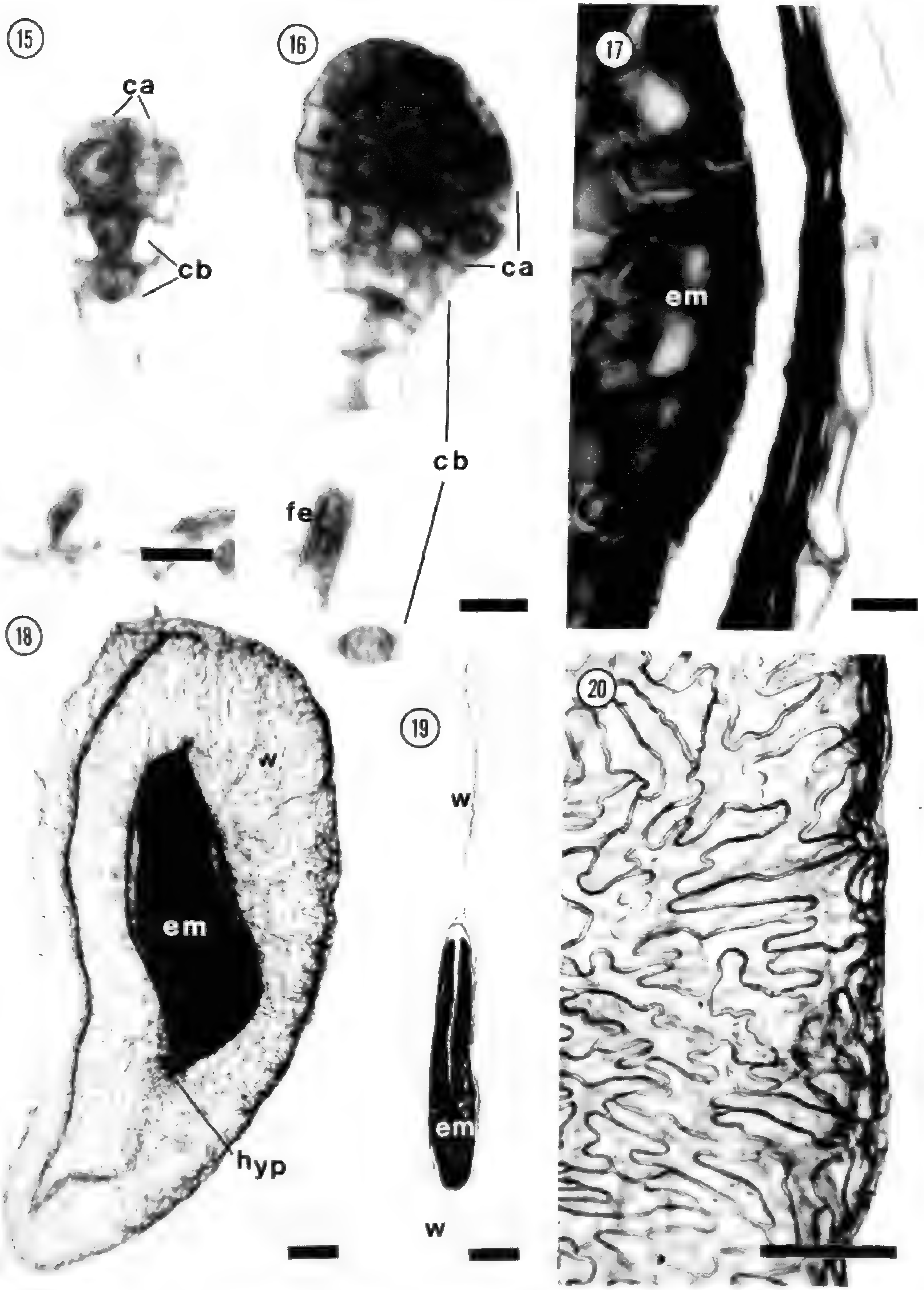
DISCUSSION

The embryological characteristics of *Alzatea verticillata* may be summarized as follows:

Anther tetrasporangiate; anther wall four layers thick, its formation of the Dicotyledonous type; anther epidermis persistent; both endothecium and middle layer ephemeral; tapetum glandular, its cells two-nucleate; septum between two microsporangia on each side of the anther collapsed; microspore tetrads tetrahedral or decussate; pollen grains two-celled when shed.

Ovule anatropous, bitegmic, and crassinucellate; both integuments initially two-layered, but later the outer integument two to four layers thick; micropyle formed by the inner integument alone; chalaza with hypostase.

Archesporium of ovule multicelled, comprising four to eight cells, only one of them functioning and cutting off a primary parietal cell; meiosis in the megaspore mother cell forming a linear dyad of megaspores; micropylar megaspore of the dyad degenerating; the chalazal



FIGURES 15–20. —15. Longitudinal section of a four-celled proembryo. Cells derived from an apical cell at the two-celled proembryonal stage (*ca*); cells derived from a basal cell (*cb*). Bar = 10 μm.—16. Longitudinal section of a globular proembryo. Cells derived from the apical cell at the two-celled proembryonal stage (*ca*); cells derived from the basal cell (*cb*); free endosperm nucleus (*fe*). Bar = 10 μm.—17. Cross section of a mature seed. Endosperm is absent. Note that a mature seed coat is composed of elongate outer epidermal cells of the testa as well as of walls of crushed cells of the other layers. Embryo (*em*). Bar = 10 μm.—18. Mature seed with a flat membranous wing (*w*). Embryo (*em*); hypostase (*hyp*). Bar = 200 μm.—19. Longitudinal section of a mature seed. Wing (*w*); embryo (*em*). Bar = 200 μm.—20. Part of the wing. Note the undulating epidermal cells constituting the wing. Bar = 100 μm.

megaspore developing into a bisporic eight-nucleate *Allium*-type embryo sac; antipodals ephemeral.

Endosperm formation Nuclear type; free endosperm scanty throughout seed development; mature seed exalbuminous; embryogenesis conforming to the Onagrad type; embryo dicotyledonous with a short and small suspensor; mature seed with a flat membranous wing along the horizontal line of the seed; wing formed by tissues of both the funiculus and the outer integument; mature seed coat thin except for a part of the wing, consisting only of elongate cells of the outer epidermis of the testa and of walls of the other collapsed cells of the testa and tegmen.

Alzatea has six of the seven ordinal characteristics which we gave for the Myrtales (cf. Tobe & Raven, 1983a): (1) anther tapetum glandular, (2) ovule crassinucellate, (3) inner integument two-layered, (4) antipodals ephemeral, (5) endosperm formation of the Nuclear type, and (6) mature seed exalbuminous. The only disagreement is that *Alzatea,* like *Rhynchocalyx* (Tobe & Raven, 1984), has a micropyle formed by the inner integument alone instead of by both integuments. *Alzatea* is an exceptional member of the Myrtales in this respect.

Alzatea is also characterized by having a bisporic *Allium*-type embryo sac, a feature that is unknown elsewhere in Myrtales. Among other Myrtales, Penaeaceae and Onagraceae are characterized by unique embryo sac types, namely *Penaea*-type and *Oenothera*-type (cf. Tobe & Raven, 1983a, for review). All other Myrtales including not only *Axinandra* and *Rhynchocalyx* (which have been relegated to Crypteroniaceae together with *Alzatea*) but also Lythraceae (which may be related to *Alzatea*), have a monosporic *Polygonum*-type embryo sac (Tobe & Raven, 1983a, 1983b, 1984). Possession of an embryo sac type unknown elsewhere in the order seems strongly to suggest an isolated position of *Alzatea* within Myrtales. Embryological comparisons between *Alzatea* and other possibly related Myrtales are presented below using other features.

As regards the possibility of a relationship with *Axinandra,* with which *Alzatea* has been included as a member of an enlarged Crypteroniaceae (van Beusekom-Osinga & van Beusekom, 1975), *Alzatea* agrees with *Axinandra* in having a persistent anther epidermis and an ephemeral endothecium but differs from it in many other characters. In *Alzatea,* the ovule archesporium is multicelled; an endothelium is not formed; and the micropyle is formed by the inner integument alone. In contrast, in *Axinandra* the ovule archesporium is one-celled; a distinctive endothelium is formed; and the micropyle is formed by both integuments (Tobe & Raven, 1983b). In addition, the following point of difference may be mentioned: the seed wing is formed by tissues of both the funiculus and the outer integument in *Alzatea,* but it is formed by tissues of the funiculus alone in *Axinandra* (Tobe & Raven, 1983b). This, especially taken together with the fact that the embryo is situated centrally in the wing in *Alzatea,* basally in *Axinandra,* strongly suggests that the wings on the seeds of *Alzatea* and *Axinandra* are not homologous, and that this feature should not be used to link the two genera. In summary, too many dissimilarities to accept a mutual close relationship lie between *Alzatea* and *Axinandra.*

As regards a relationship with *Rhynchocalyx, Alzatea* agrees much more closely in its embryological features with this genus than with any other genus studied thus far. Shared characteristics include: anther epidermis persistent; endothecium ephemeral; ovule archesporium multicelled; micropyle formed by the inner integument alone; free endosperm nuclei scanty; and, finally, embryogenesis of the Onagrad type (Tobe & Raven, 1984). *Alzatea* differs from *Rhynchocalyx,* however, in the following respects: the septum between two microsporangia degenerates in *Alzatea* but is persistent in *Rhynchocalyx*; the radial elongation of nucellar subdermal cells surrounding megaspores does not occur in *Alzatea* but is characteristic of *Rhynchocalyx*; a hypostase is present in *Alzatea* but absent in *Rhynchocalyx*; the seed wing is formed by tissues of both the funiculus and the outer integument in *Alzatea* but it is formed by tissues of the funiculus alone in *Rhynchocalyx* (Tobe & Raven, 1984). Once again this suggests that the seed wing in *Alzatea* may not be homologous with that in *Rhynchocalyx,* and should not be used as evidence of relationship between these genera. Moreover, as we have seen, the embryo is situated centrally in its wing in *Alzatea*; in *Rhynchocalyx,* it is situated apically in the wing. The totality of similarities and dissimilarities, however, suggests that *Alzatea* is more closely related to *Rhynchocalyx* than to *Axinandra,* although *Alzatea* is still very distinct from and almost certainly not directly related to *Rhynchocalyx.*

As regards a possible relationship to Lythraceae, *Alzatea* agrees with this family in having a multicelled ovule archesporium but differs from it in many respects. The anther epidermis is persistent in *Alzatea* but probably not in Lythraceae; the endothecium is ephemeral in *Alzatea* but seems to develop into fibrous thickenings in Lythraceae; starch grains are absent in the nucellus in *Alzatea* but present in Lythraceae (*Cuphea*, Hubert, 1896); the micropyle is formed by the inner integument alone in *Alzatea* but by both integuments in Lythraceae; the endosperm is scanty throughout seed development in *Alzatea*, much more abundant in Lythraceae (cf. Tobe & Raven, 1983a). Although we do not have complete enough information on the mature seed morphology and anatomy of Lythraceae to characterize the family fully, the points of difference just listed, in addition to the major difference in the embryo sac formation we have reported here, seem adequate to preclude the inclusion of *Alzatea* in Lythraceae on embryological grounds alone, thus supporting the conclusions of Graham (1984).

As regards the possibility of a relationship to Melastomataceae, which has recently been suggested on the basis of vegetative anatomy (van Vliet, 1975; van Vliet & Baas, 1975), *Alzatea* agrees with this family (only with the subfamily Melastomatoideae) in having a persistent anther epidermis and an ephemeral endothecium but differs from it in the following respects. Anther tapetal cells are two-nucleate in *Alzatea*, one-nucleate in Melastomataceae; the ovule archesporium is multicelled in *Alzatea*, one-celled in Melastomataceae; the micropyle is formed by the inner integument alone in *Alzatea*, by both integuments in Melastomataceae (cf. Tobe & Raven, 1983a). Thus embryological similarities between *Alzatea* and Melastomataceae are limited to anther wall characters alone whereas the dissimilarities include embryological features of many different kinds. *Alzatea* seems clearly to be much more distinct from Melastomataceae than from *Rhynchocalyx*.

In summary, evidence from the embryology of *Alzatea*, as well as from that of *Rhynchocalyx* (Tobe & Raven, 1984), clearly contradicts the broad definition of Crypteroniaceae to include both *Alzatea* and *Rhynchocalyx* proposed by van Beusekom-Osinga and van Beusekom (1975). *Alzatea* is distinct from all other Myrtales in having a bisporic *Allium*-type embryo sac. In addition, *Alzatea* differs from *Axinandra*, *Rhynchocalyx*, Lythraceae, and Melastomataceae in a considerable number of embryological characteristics in each case. These relationships strongly favor the establishment of a monotypic family Alzateaceae, standing apart from both Crypteroniaceae in a restricted sense and from Lythraceae, a treatment which is here proposed by Graham (1984), with support from Dahlgren and Thorne (1984) and from Johnson and Briggs (1984).

When compared embryologically with other Myrtales, *Alzatea* shares many more characteristics with *Rhynchocalyx* than with any other genus. Similarities with *Rhynchocalyx* are shown by the vegetative characters (such as stomatal type and overall wood anatomy), too, although a considerable number of points of difference with *Rhynchocalyx* in other vegetative features (such as cuticular texture, petiole anatomy, and vessel morphology) also remain (van Vliet, 1975; van Vliet & Baas, 1975). A relationship between *Alzatea* and *Rhynchocalyx* was likewise implied by their grouping as the only members of Crypteroniaceae subfamily Alzateoideae by van Beusekom-Osinga and van Beusekom (1975). *Rhynchocalyx* tends increasingly to be included in Lythraceae (van Vliet & Baas, 1975; Dahlgren & Thorne, 1984; Graham, 1984). Our recent study of the embryology of *Rhynchocalyx* suggests, however, that *Rhynchocalyx* is more distantly related to Lythraceae than might have been expected (Tobe & Raven, 1984). The fact that *Alzatea* has more similarities with *Rhynchocalyx* than with other Myrtales suggests that *Alzatea* and *Rhynchocalyx* are parallel descendants from a common ancestor, with which the modern Lythraceae possibly have a direct link. Our conclusion here agrees with that of Johnson and Briggs (1984), who, on the basis of their cladistic analysis, concluded that *Rhynchocalyx* was not directly related to Lythraceae but deserved to be assigned to a family of its own. We believe on the basis of the accumulating evidence that the similarities between *Alzatea*, *Rhynchocalyx*, Lythraceae (including Sonneratiaceae), and presumably Crypteroniaceae sensu stricto also are based on generalized ancestral features, not on derived ones indicative of direct relationship. The unambiguous conclusion seems to be that if any one of these groups deserves recognition at the family level, each of them does. The only distinctive embryological characteristic common to *Alzatea*, *Rhynchocalyx*, and Lythraceae is the possession of the multicelled ovule archesporium, which is unknown elsewhere in the order except in one of the subfamilies of Lythraceae, Sonneratioideae (Tobe & Raven, 1983a). This shared characteristic seems to be suggestive of a relationship between these groups, although we still cannot evaluate the systematic significance of such an embryological character.

From the viewpoint of vegetative anatomy, *Alzatea* is the only Myrtalean genus that has a trilacunar nodal type, which is considered an ancestral rather than a derived feature (Baas, pers. comm. in Dahlgren & Thorne, 1984). The tricolporate pollen grains of *Alzatea* clearly are also an unspecialized, ancestral feature, thus contrasting with the undoubtedly derived heterocolpate grains of *Axinandra, Dactylocladus, Rhynchocalyx,* and many other Myrtales and the specialized and very unusual bilaterally flattened bisyncolporate grains of *Crypteronia* (Muller, 1975). But the persistent anther epidermis, the ephemeral (or non-fibrous) endothecium, and the bisporic *Allium*-type embryo sac, all of which are characteristic of *Alzatea,* are undoubtedly derived features. They do not suggest a direct relationship of *Alzatea* with any other group, however, and thus do not contradict the notion that it may have had a long, independent evolutionary history of its own.

We believe that the studies we have reported here underscore the utility of embryological features in elucidating the pathways of evolution within Myrtales. In order to fix the exact position of unique genera such as *Alzatea* and *Rhynchocalyx* better, comprehensive embryological studies will be required not only of Lythraceae and Melastomataceae (both of which have been studied only to a limited degree), but also of other genera, especially *Crypteronia* and *Dactylocladus,* which are unknown embryologically. When these results are available, embryological studies should be able to make an especially strong contribution to our understanding of this very distinct austral order of angiosperms, and to help to illuminate the relationships between its ancient evolutionary lineages.

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FLAVONOIDS OF RHYNCHOCALYCACEAE (MYRTALES)

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ABSTRACT

Rhynchocalycaceae is a monotypic family represented by the rare *Rhynchocalyx lawsonioides* from South Africa. Although unquestionably myrtalean, it is isolated in the order with closest affinity to *Alzatea verticillata* in the monotypic Alzateaceae. Foliar flavonoids of *Rhynchocalyx* are reported for the first time. The flavonoid pattern comprises five quercetin 3-O-glycosides, present in approximately equal concentrations. These are quercetin 3-O-glucoside, 3-O-diglucoside, 3-O-rhamnoside, 3-O-xyloside, and 3-O-galactoside. Quercetin 3-O-glucoside and quercetin 3-O-diglucoside also occur in *Alzatea*. The pattern agrees with the typical profile of the Myrtales in which flavonols are common and flavones are rare. It differs in absence of myricetin, which is frequently found in the order. No more specific relationships are possible based on these flavonoid data due to the generalized nature and widespread occurrence of the compounds.

Rhynchocalycaceae is a newly recognized monotypic family based on the rare *Rhynchocalyx lawsonioides* Oliv. from Natal, South Africa. It has been regarded generally as a genus of the Lythraceae, related to *Lawsonia* in subtribe Lagerstromiinae (Oliver, 1895; Sprague & Metcalfe, 1937) although that position was rejected by the monographer of the family (Koehne, 1903). Recently, it was included in a remodeled Crypteroniaceae as sole member of the subfamily Alzateoideae, tribe Rhynchocalyceae (van Beusekom-Osinga & van Beusekom, 1975). Anatomical, embryological, and morphological data now support the relationship of *Rhynchocalyx* to the unigeneric Alzateaceae but reflect a degree of isolation that merits its recognition as a separate family (Johnson & Briggs, 1984; Graham, 1984).

Chemistry of *Rhynchocalyx* has not been previously reported. In this study, foliar flavonoids are isolated, identified, and compared to the general myrtalean flavonoid pattern.

MATERIALS AND METHODS

Dried leaf material of one population of *Rhynchocalyx lawsonioides* was examined (South Africa: Natal, *H. B. Nicholson s.n.* in 1982.) A voucher specimen is deposited at MO.

Techniques for chromatographic and spectral analyses of flavonoids follow those presented by Mabry et al. (1970). Briefly, the flavonoids were extracted overnight from the leaves with 85% methanol. The resulting extract was applied to Whatman 3MM chromatographic paper both directly and after concentration on a rotary evaporator. Solvent systems of t-butanol, glacial acetic acid, and water (3 : 1 : 1 v/v) and 15% glacial acetic acid in water were used to develop two-dimensional chromatograms. The chromatograms were observed over ultraviolet light and in the presence of ammonia vapor to detect color characteristics of the various compounds present. The procedure presented by Mabry et al. for the isolation and spectral analyses of the compounds was followed with the exception that fused sodium acetate was used for determining the spectral curve for that reagent.

Acid and enzyme hydrolyses were carried out routinely for glycosidic characterization and to obtain the aglycone for positive identification. Acid hydrolyses were carried out in 5% HCl at 70°C for about 1 hour. Normally this treatment is sufficient to remove O-glycosides from the flavonoid skeleton. Enzyme hydrolyses were accomplished at 27°C in water. These techniques as well as other pertinent data concerning the characterization of phenolic glycosides are discussed by Harborne (1965).

β-D-glucosidase was regularly employed because this enzyme is reliable for detecting the presence of glucose. The flavonoid glycosides on which enzyme hydrolysis was not effective were hydrolyzed in acid as outlined above. The resulting sugar was then taken up in water and spotted on cellulose thin-layer plates along with standard sugars for comparison. Circular thin-layer chromatograms were developed in ethyl acetate, pyridine, and water (6 : 3 : 2 v/v) as described by Exner et al. (1977). After drying, the

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TLC plates were sprayed with a 0.1 M solution of p-anisidine and pthalic acid in 96% ethanol and placed in an oven at 130°C for ten minutes. The sugars were then visible as dark brown, red, or green bands. The aglycones also were run, along with authentic reference compounds, by circular thin-layer chromatography.

RESULTS

Five flavonol glycosides, all based on quercetin, were present in the population of *Rhynchocalyx* examined: (1) quercetin 3-O-xyloside, (2) quercetin 3-O-galactoside, (3) quercetin 3-O-rhamnoside, (4) quercetin 3-O-diglucoside, and (5) quercetin 3-O-glucoside. Each of the compounds was present in approximately equal concentrations. Compounds (2) and (5) were inseparable by the methods utilized but both sugars were noted in the hydrolysates. Rf values were consistent with the respective monoglycosides and not with that of a diglycoside.

CONCLUSIONS

The flavonoid pattern in *Rhynchocalyx* consists of a range of flavonol monoglycosides. The emphasis on flavonols in the genus is consistent with its classification in the Myrtales where common flavonols are the most frequent constituents (Bate-Smith, 1962; Gornall et al., 1979). Both quercetin 3-O-glucoside and quercetin 3-O-diglucoside are also found in *Alzatea* (Graham & Averett, 1984). Their wide dispersal in the angiosperms, however, precludes any taxonomic implication. Myricetin, typical of the order, is absent in both *Rhynchocalyx* and *Alzatea*. Flavonoid data support placement of *Rhynchocalyx* in the Myrtales but offer no further indication of phylogenetic relationship.

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FLAVONOIDS OF ALZATEACEAE (MYRTALES)

SHIRLEY A. GRAHAM[1] AND JOHN E. AVERETT[2]

ABSTRACT

Three leaf flavonoids are reported from the Alzateaceae, a monotypic family of the New World tropics. Two are flavonol 3-O-glycosides: quercetin 3-O-glucoside and quercetin 3-O-diglucoside. The third is tentatively identified as 5,4'dihydroxy flavone. The presence of these flavonols is consistent with the position of *Alzatea* in the Myrtales. The profile differs from the common pattern of the order in absence of myricetin and is further distinguished by absence of C-glycoflavones and the presence of a flavone, supporting the segregation of *Alzatea* as a distinct family within the Myrtales. More specific relationships with taxa in the order cannot be suggested on this biochemical evidence because of the widespread occurrence of flavonols in the Myrtales.

Alzateaceae is a monotypic family of the New World tropics, long known from Peru and Bolivia, and more recently discovered in the low montane rain forests of Panama and Costa Rica. The single species, *Alzatea verticillata* Ruiz & Pavón was first described from Peru in 1798. Proposed affinities have since included nine families in five orders (Graham, 1984). In recent years the genus has been considered either a member of the Lythraceae (Lourteig, 1965) or the Crypteroniaceae in the order Myrtales (van Beusekom-Osinga & van Beusekom, 1975). It has been most closely associated with the African genus *Rhynchocalyx,* also of uncertain affinities. Classification and relationships of these infrequently collected genera have been restricted to comparison of macromorphological characters.

On the basis of newly accumulated evidence, much of it presented in this volume, the myrtalean position of *Alzatea* is confirmed. Anatomical studies demonstrate the presence of the internal phloem and vestured pitting definitive of Myrtales (van Vliet, 1975). Embryologically, six of seven ordinal characteristics are present (Tobe & Raven, 1984). Presence of ellagic acid in the leaves (Graham, 1984) is consistent with the Myrtales, an order especially characterized by ellagitannins (Bate-Smith, 1962). Within the order, *Alzatea* takes an isolated position. It retains some seemingly ancestral features, such as trilacunar nodes and generalized pollen features, but these are associated with a number of unique apomorphic attributes. Phylogenetically, *Alzatea* is separated from its nearest relative, *Rhynchocalyx,* by a substantial suite of specialized characters supporting recognition of the monotypic Alzateaceae.

Chemical characteristics, whose usefulness in suggesting phylogenies and taxonomic classification is widely accepted (Stuessy & Crawford, 1983), are not well known for *Alzatea.* Ellagic acid and flavonoid mono- and diglycosides, including 3-OH-flavonols, are reported but have not been specifically identified (Graham, 1984). In this study the foliar flavonoids are isolated and identified, and comparison made to the generalized myrtalean flavonoid profile.

MATERIALS AND METHODS

Dried leaf material of two populations of *Alzatea* was examined for flavonoids. Voucher specimens are deposited at MO (Costa Rica: Cartago, *Gómez 18725, 18728*; Panama: Chiriquí, *Knapp & Vodicka 5532*).

Techniques for chromatographic and spectral analyses of the flavonoids follow those presented by Mabry et al. (1970). Briefly, the flavonoids were extracted overnight from leaves with 85% methanol. The resulting extract was applied to Whatman 3MM chromatographic paper both directly and after concentration on a rotary evaporator. Solvent systems of t-butanol, glacial acetic acid, and water (3 : 1 : 1 v/v) and 15% glacial acetic acid in water were used to develop two-dimensional chromatograms. The chromatograms were observed over ultraviolet light and in the presence of ammonia vapor to detect color characteristics of the compounds present. The procedure presented by Mabry et al. (1970) for the isolation and spectral analyses of the compounds was followed with the exception that fused sodium acetate was used for determining the spectral curve for that reagent.

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TABLE 1. Absorption maxima for compound three (max$^{\text{n.m.}}$).

MEOH	NaOMe	$AlCl_3$	$AlCl_3/HCl$	NaOAc	H_3BO_3
277, 327	273, 388	280, 305, 346	282, 306, 345	275, 328	328

Acid and enzyme hydrolyses were carried out routinely for glycosidic characterization and to obtain the aglycone for positive identification. Acid hydrolyses were carried out in 5% HCl at 70°C for about one hour. Normally this treatment is sufficient to remove O-glycosides from the flavonoid skeleton. Enzyme hydrolyses were accomplished at 27°C in water. These techniques as well as other pertinent data concerning the characterization of phenolic glycosides are discussed by Harborne (1965).

β-D-Glucosidase was regularly employed because this enzyme is reliable for detecting the presence of glucose. The flavonoid glycosides on which enzyme hydrolysis was not effective were hydrolyzed in acid as outlined above. The resulting sugar was then taken up in water and spotted on cellulose thin-layer plates along with standard sugars for comparison. Circular thin-layer chromatograms were developed in ethyl acetate, pyridine, and water (6 : 3 : 2 v/v) as described by Exner et al. (1977). After drying, the TLC plates were sprayed with a 0.1 M solution of p-anisidine and pthalic acid in 96% ethanol and placed in an oven at 130°C for ten minutes. The sugars were visible as dark brown, red, or green bands. The aglycones also were run, along with authentic reference compounds, by circular thin-layer chromatography.

RESULTS

Three flavonoids were present in the two populations of *Alzatea* examined. Two of the compounds were flavonol 3-O-glycosides: quercetin 3-O-glucoside and quercetin 3-O-diglucoside. The third was tentatively identified as a 5,4′dihydroxy flavone. The latter compound is similar to apigenin in Rf values (0.86, TBA and 0.06, HOAc) and in color (purple in UV). Spectral data for the two compounds, however, differ significantly (Table 1). The data indicate fewer hydroxyls than apigenin and the absence of a 7 hydroxyl. Thus, while the identification of the third compound is less than certain, there are few other possibilities compatible with these data.

DISCUSSION

The emphasis on flavonols in *Alzatea* is consistent with its taxonomic placement in the Myrtales where the flavonoid profile of the order consists of common flavonols and their O-methyl derivatives (Bate-Smith, 1962). The same flavonol glycosides are also found in the related genus *Rhynchocalyx* (Averett & Graham, 1984) and are nearly ubiquitous in the woody angiosperms (Gottlieb, 1975). *Alzatea* is distinctive in the absence of myricetin, which is otherwise common in the order, and in the absence of C-glycoflavones reported from Lythraceae, Combretaceae, Onagraceae, and Myrtaceae (Gornall et al., 1979). The presence of a flavone is unusual for Myrtales, where flavones are very rare (Gornall et al., 1979). In lack of myricetin and presence of a flavone, *Alzatea* flavonoids are more similar to those of Rosales than Myrtales. The two orders are believed to share a common early ancestor (Dahlgren & Thorne, 1984) and the *Alzatea* pattern could reflect that putative relationship. Further evaluation of the presence of the flavone and the limited flavonoid profile exhibited are not feasible since Alzateaceae combines a mixture of primitive and advanced characters and the flavonoids may equally represent an early evolutionary or later reduced condition. The flavonoid data are consistent with other systematic information; viz. *Alzatea* has many common features of the Myrtales, but also sufficient differences to justify recognition as its own family in the order.

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POLLEN CHARACTERS IN RELATION TO THE DELIMITATION OF MYRTALES[1]

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ABSTRACT

Pollen grains representative of the Lythraceae (including subfamilies Punicoideae, Sonneratioideae, and Duabangoideae), Trapaceae, Oliniaceae, Combretaceae, Alzateaceae, Rhynchocalycaceae, Penaeaceae, Crypteroniaceae, Melastomataceae, Myrtaceae (including Psiloxylaceae and Heteropyxidaceae), and Onagraceae, the 11 families constituting the order Myrtales, were examined with scanning (SEM) and transmission (TEM) electron microscopy. With omission of the Trapaceae, Myrtaceae, and Onagraceae, the remaining families have enough similarities to be grouped together palynologically. Heterocolpate pollen characterizes the Lythraceae, Rhynchocalycaceae, Combretaceae, Oliniaceae, Penaeaceae, Crypteroniaceae, and Melastomataceae. In the latter five families, subsidiary colpi (pseudocolpi) were noted in all taxa examined except *Adelobotrys, Allomorphia, Astronia, Bredia, Oxyspora,* and *Tococa* of the Melastomataceae and *Buchenavia, Laguncularia,* and *Strephonema* of the Combretaceae. With the exceptions of the latter four genera these taxa possess intercolpar concavities. Subsidiary colpi and intercolpar concavities are considered to be functionally equivalent, their distinction being the larger size of the intercolpar concavities. Subsidiary colpi are equal to the number of apertures except in Lythraceae where *Ammannia, Nesaea,* and *Crenea* have twice the number; intercolpar concavities are also isomerous with apertures. In Oliniaceae, the subsidiary colpi are located on just one polar face and hence considered as half subsidiary colpi while Alzateaceae may have incipient subsidiary colpi. The pollen of Lythraceae subfamilies Sonneratioideae, Duabangoideae, and Punicoideae possess meridional ridges which alternate with the apertures; they are prominent in the former two subfamilies and weakly defined in the latter. Meridional ridges are also present in some Lythraceae lacking subsidiary colpi.

Exine sculpturing in the mesocolpia is variable throughout the order with Crypteroniaceae, Alzateaceae, Oliniaceae, and Penaeaceae basically psilate; Melastomataceae basically striate and rugulate; Combretaceae echinate, reticulate, rugulate, striate, and psilate; Lythraceae subfam. Lythroideae striate, psilate, verrucate, and granular; Lythraceae subfam. Punicoideae basically granular-microrugulate; and Lythraceae subfam. Sonneratioideae and Duabangoideae basically verrucate-rugulate. Commonly, the subsidiary colpi (and intercolpar concavities) and colpi have different sculpturing than the mesocolpial regions. Exine structure is essentially of the post and beam construction with the fundamental ektexine and endexine stratification layers. In all Combretaceae and some Melastomataceae the foot layer is strikingly delineated as domes, whereas in Alzateaceae the columellae layer follows a zig-zag course. The Oliniaceae and Penaeaceae are distinct throughout the order with remarkably thickened tectum and foot layer and negligible columellae; *Acanathella* of the Melastomataceae is somewhat similar, differing only in a better developed columellae layer.

In general, Lythraceae have the most diverse pollen at both sculptural and structural levels; Combretaceae also have considerable diversity, primarily exomorphically, and *Strephonema* is the only taxon noted in the order with a reticulate sculpture; Melastomataceae are diverse exomorphically, with the pollen of *Miconia melanotricha* shed as tetrads and that of *Tococa spadiciflora* as polyads, the only example of polyads in the order other than *Ludwigia* (Onagraceae); Oliniaceae, Penaeaceae, and Crypteroniaceae show rather uniform intrafamilial morphology. The monogeneric Trapaceae with protruding and domed apertures and meridional ridges resulting from exine folds is totally unique in Myrtales. One sample shows linked pollen grains suggestive of polyads while sections through the ridge area show an extremely thick endexine and loosely organized ektexine reminiscent of some Onagraceae. Myrtaceae, with pollen oblate-elliptic in lateral view and triangular in polar view, are also without a counterpart in Myrtales. Based on the nature of the colpi, three distinctive pollen groups are evident: (1) longicolpate, (2) syncolpate and parasyncolpate with and without intercolpar concavities, and (3) brevicolpate and brevissimicolpate. *Myrtus communis* and *Psidium littorale* shed pollen in tetrads as well as in monads and are the only tetrads recorded in Myrtales other than Onagraceae and *Miconia melanotricha* (Melastomataceae). The pollen morphology of *Psiloxylon* and *Heteropyxis,* genera of questionable taxonomic placement, suggests that they fit within the Myrtaceae. The final family, Onagraceae, is also very distinctive in Myrtales. The viscin threads, tetrads and polyads,

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exceptionally thick endexine, essentially spongy-paracrystalline ektexine with columellae absent or greatly reduced, absent foot layer, protruding apertures, and 2-aperturate grains (in *Fuchsia*) distinguish this family, which with a few superficial similarities to Trapaceae and Penaeaceae differs from all others in Myrtales.

Pollen morphology in the core families of the Myrtales as recognized by Dahlgren and Thorne (1984) has received surprisingly little study. The very extensive reference citations given in the four monumental pollen bibliographic indices of Thanikaimoni (1972, 1973, 1976, 1980) for these families include *all* studies in which pollen morphology is mentioned (e.g., atlases; regional and local floras; anatomical and embryological reports; horticultural, agricultural and geological records; chemical systematics, etc.), but relatively few of them are actually based on comprehensive pollen investigative research. Of those emphasizing pollen morphology, about 90% are confined to light microscopy (LM). Scanning electron microscopy (SEM) was utilized to a limited degree and, remarkably, structural data from transmission electron microscopy (TEM) (with the exception of Muller, 1973, 1975, 1978a, 1981; Lugardon & van Campo, 1978; Gadek & Martin, 1981, 1982; Skvarla et al., 1975, 1976; Skvarla et al., 1978) are virtually non-existent in the order. Furthermore, there are noticeably few modern studies in the three largest families, Melastomataceae, Combretaceae, and Myrtaceae, although the latter is currently under intensive examination by Gadek and Martin (1981, 1982, pers. comm.).

In this report we have attempted to provide a pollen morphologic overview of the major taxa in the core families (i.e., Lythraceae, including subfamilies Punicoideae, Sonneratioideae, and Duabangoideae; Trapaceae, Oliniaceae, Combretaceae, Alzateaceae, Rhynchocalycaceae, Penaeaceae, Crypteroniaceae, Melastomataceae, Myrtaceae including *Psiloxylon* and *Heteropyxis*, and Onagraceae). Our emphasis is on the exomorphic characters as revealed by SEM, however, this is supplemented in large part by structural information obtained by TEM.

MATERIALS AND METHODS

Most pollen was treated by the acetolysis method of Erdtman (1960). In some samples 5% KOH treatment followed acetolysis. For SEM, acetolyzed pollen was either critical point dried or air dried from 95% ethanol, sputter coated with gold, and examined with an ISI Super II SEM. For TEM, acetolyzed pollen was processed according to previously described methods (Skvarla, 1966) and examined with a Philips model 200 TEM. Some Onagraceae pollen was examined by TEM without acetolysis, that is, either freshly collected in 2.5% glutaraldehyde in 0.1 M cacodylate buffer at pH 7.2, or after rehydration from herbarium sheets. In both, subsequent processing basically followed earlier techniques (Skvarla, 1973). Pollen was examined with LM primarily to determine the nature of colpi and endoapertures.

Table 1 lists taxa examined, collecting information, ubiquity of subsidiary colpi, figure references, and select morphologic data.

The organization of this report is such that the core families are given individual discussion to include (1) general palynology, (2) specific morphology for taxa listed in Table 1, (3) a brief review of previous studies when relevant, and (4) significant morphological correlations with other core families. Following this treatment of the core families an attempt is made to summarize as well as synthesize the data for the entire order. Plate legends, in addition to being descriptive, frequently cite other reports in order to provide as complete a background as possible.

TERMINOLOGY

The terms used in this study to describe pollen grain morphology are essentially those of Erdtman (1971) for exomorphology and Faegri and Iversen (1975) for endomorphology. Although most are standard palynological jargon and therefore not in need of clarification, a few are particularly crucial to describing Myrtales pollen and are therefore discussed below.

1. *Subsidiary colpi* (*pseudocolpi*). According to Faegri and Iversen (1964: 225) a "Pseudocolpus (pseudopore): differs from a normal furrow (pore) in that it is not an exit for the pollen tube," while the definition of Erdtman (1971: 467) is "Colpoid streaks not functioning as apertures." Muller (1981) considers the term to be a misnomer because pseudocolpi function in volume changes of the pollen grain during expansion and contraction in response to moisture content (i.e., harmomegathy of Wodehouse, 1935),

TABLE 1. Pollen examined. (The parentheses ( ) in the column for subsidiary colpi mean that intercolpar concavities are recognized. Unless stated otherwise, all pollen grains are tricolporate.)

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
LYTHRACEAE							
subfam. Lythroideae							
Ammannia coccinea Rottb.	California, USA	*Twisselman 7983*	KE	6	TEM	5B	
A. robusta Keer & Regel	Oklahoma, USA	*Waterfall 3027*	OKL	6	SEM, TEM	2A, B, 5A	
Crenea surinamensis L.	Guyana	*de la Cruz 3301*	MO	6	SEM	1F	Meridional ridge
Cuphea carthagenensis (Jacq.) MacBr.	Guatemala	*Aguilar 104*	OKL	0	SEM	2C	Tectal ridges
C. nitidula HBK.	Mexico	*Graham 614*	KE	0	TEM	5D	Tectal ridges
C. petiolata (L.) Koehne	Arkansas, USA	*Demaree 40737*	OKL	0	SEM	2D–F	Variable striate sculpture
C. racemosa (L.f.) Spreng.	Veracruz, Mexico	*Graham 689*	KE	0	TEM	5C	
Diplusodon villosus Pohl	Brazil	*Irwin et al. 26402*	MO	0	SEM, TEM	3A, B, 6E	Tricolpoidorate, colpus very short
Heimia salicifolia (HBK.) Link	Mexico	*Graham 141*	KE	0	TEM	5G	
H. salicifolia (HBK.) Link	Mexico	*Ventura 2430*	MO		SEM	1C–E	Rarely dicolporate and syncolpate
Lafoënsia punicifolia DC.	Chiapas, Mexico	*Breedlove 40657*	MO	0	SEM, TEM	3D–F, 5E, F, 6A	Meridional ridges, apertural fields and polar caps
Lagerstroemia speciosa (L.) Pers.	Honduras, cultivated	*Lent 4*	OKL	0	SEM	3C	Meridional ridges
Nesaea schinzii Koehne	Bulawayo Distr., Rhodesia	*Best 395*	MO	6	SEM	1A, B	
subfam. Punicoideae							
Punica granatum L.	Iran	*Antonio s.n.*	OKL	0	—	—	
P. granatum L.	Iran	*Grant 15704*	MO	0	SEM, TEM	7A, B, 8A	Weak meridional ridges
P. protopunica	Yemen, Socotra	*Smith & Lavranos 730*	K	0	SEM, TEM	7C–G, 8B, C	Meridional ridges

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
subfam. Duabangoideae							
Duabanga moluccana Bl.	Los Banos, Philippines	*Elmer 18275*	MO	0	SEM	4F	Triporate, meridional ridges, apertural fields, polar caps
subfam. Sonneratioideae							
Sonneratia caseolaris Druce	Mahe Island, Seychelles	*Sauer 3808*	MO	0	SEM	4E	Triporate, meridional ridges, apertural fields, polar caps
TRAPACEAE							
Trapa japonica Flerov	Japan	*Boufford et al. 19962*	MO	0	SEM, TEM	10A–D, 11D	Meridional ridges over apertures
T. natans L.	unknown	Reverchon herbarium	MO 2532983	0	SEM	10E	Meridional ridges over apertures
T. natans L.	Germany	*Engelmann s.n.*	MO	0	SEM, TEM	9A, B, 10F, 11A	Meridional ridges over apertures
T. natans L.	New York, USA	*House 21708*	MO	0	SEM, TEM	9C–F, 11B, C	Meridional ridges over apertures; polyads
OLINIACEAE							
Olinia emarginata Burtt Davy	Natal, South Africa	*Hillard & Burtt 8691*	MO	3 (½)	SEM, TEM	13A–D, 14E	Asymmetric colpi, half subsidiary colpi
O. radiata Hofmeyr & Phill.	Zululand	*Wylie 8822*	K	3 (½)	SEM	12A–C	Asymmetric colpi, half subsidiary colpi
O. rochetiana A. Juss.	Malawi	*Chapman 996*	MO	3 (½)	SEM, TEM	12D–F, 14A	Asymmetric colpi, half subsidiary colpi
O. rochetiana A. Juss.	Mt. Meru, Tanzania	*Greenway & Fitzgerald 14970*	MO	3 (½)	TEM	14D	Asymmetric colpi, half subsidiary colpi
O. vanguerioides E. G. Baker	Rhodesia	*Chase 6774*	K	3 (½)	–		Asymmetric colpi, half subsidiary colpi
O. ventosa (L.) Cufod.	Cape Province, South Africa	*Fries et al. 660*	MO	3 (½)	SEM, TEM	13E, F, 14B, C	Asymmetric colpi, half subsidiary colpi

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
COMBRETACEAE							
Anogeissus acuminata Wall.	Burma	*Po Chin 6100*	MO	3	SEM	18D, F	Echinate surface
Buchenavia suaveolens Eichler	Amazonas, Brazil	*Gentry & Ramos 12906*	MO	0	SEM	18A–C	Echinate surface
Bucida macrostachya Standl.	Chiapas, Mexico	*Breedlove 25160*	MO	3	SEM, TEM	17A, 21B	
Calycopteris floribunda (Roxb.) Poir.	Mysore, India	*Saldanha 16363*	MO	3	SEM	15G	
Combretum cacoucia Exell	Stann Creek Distr., Belize	*Dwyer et al. 552*	MO	3	SEM	15A–C	
C. farinosum HBK.	Sinaloa, Mexico	*Boke & Florantos 1*	OKL	3	SEM, TEM	16D, 20B, C	
C. laxum Jacq.	Loma Tequerre, Brazil	*Duke 10994* (3)	MO	3	SEM, TEM	16E, G, 20A	
C. trifolium Vent.	Vietnam	*Squires 792*	MO	3	SEM	16F	
Conocarpus erecta L.	Sinaloa, Mexico	*Waterfall 16249*	OKL	3	SEM, TEM	17B, 20E	
Guiera senegalensis Lam.	Cameroun	*Leeuwenberg 7485*	MO	3	SEM	18E	
Laguncularia racemosa (L.) Gaertn.	Costa Rica	*Croat 593 A*	MO	0	SEM	19E, F	
Lumnitzera racemosa Willd.	Eastern Province, Sri Lanka	*Davidse 7545*	MO	3	SEM, TEM	19D, 21C	
Poivrea coccinea DC.	Tulear Prov., Madagascar	*Croat 31768*	MO	3	SEM	19C	
Pteleopsis myrtifolia (Laws.) Engl. & Diels	Wankie Distr., Zimbabwe	*Raymond 130*	MO	3	SEM	17C	
Quisqualis indica L.	Laguna, Philippines	*Quisumbing Q-2160*	OKL	3	SEM	15F	
Q. parviflora (Ridl.) Exell.	Malaya	*Stone 9082*	MO	3	SEM	16H, I	
Q. pellegriniana (Exell.) Exell.	Zaire	*Grant 4048*	MO	3	TEM	21D	
Ramatuella argentea Kunth	Venezuela	*Maguire et al. 41879*	MO	3	SEM	17E, G	
Strephonema pseudocola A. Chev.	Tchien Distr., Liberia	*Baldwin 8007*	MO	0	SEM, TEM	19A, B, 21A	Reticulate surface
Terminalia catappa L.	Tulear Prov., Madagascar	*Croat 30941*	MO	3	SEM	17F	

TABLE 1. *Continued.*

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
T. edulis Blanco	Luzon, Philippines	*Bernardo 23688*	MO	3	TEM	20D	
T. edulis Blanco	Laguna, Philippines	*Quisumbing 2156*	OKL	3	SEM	17D	
T. oblonga (R. & P.) Pois.	Colombia	*Renteria-Arriaga et al. 1889*	MO	3	SEM	16A–C	
Thiola inundata Ducke	Amazonas, Brazil	*Ducke 644*	MO	3	SEM	15D, E	Echinate surface
RHYNCHOCALYCACEAE							
Rhynchocalyx lawsonioides Oliv.	Natal, South Africa	*Nicholson s.n.*	MO	3	SEM, TEM	4A, C, 6D	
ALZATEACEAE							
Alzatea verticillata Ruiz & Pav.	Mendoza, Peru	*Woytkowski 8331*	MO	0	SEM, TEM	4B, D, 6B, C	
PENAEACEAE							
Brachysiphon acutus (Thunb.) A. Juss.	South Africa	*Dahlgren & Strid 3387*	LD	–	TEM	27B	
B. fucatus (L.) Gilg.	South Africa	*Dahlgren & Strid 2012*	LD	3	SEM	24A, B	Some tetracolporate
Endonema lateriflora (L. f.) Gilg.	South Africa	*Dahlgren & Strid 4979*	LD	3	SEM	25A–C	
Glischrocolla formosa (Thunb.) R. Dahlgren	South Africa	*Kerfoot 5723*	LD	5	SEM, TEM	23A, C, E, 27A	Some tetracolporate
Penaea cneorum Merrb. subsp. *cneorum*	South Africa	*Dahlgren & Strid 2982*	LD	4	SEM	23B, D, F	Tetracolporate
P. cneorum Meerb. subsp. *ruscifolia* R. Dahlgren	South Africa	*Dahlgren & Strid 2090*	LD	–	TEM	27F	
P. mucronata L.	South Africa	*Grant 2630*	MO	4	SEM, TEM	22A–C, 26A	Tetracolporate
Saltera sarcocolla (L.) Bullock	South Africa	*Dahlgren & Strid 3892*	LD	3	SEM, TEM	24C–E, 27C, D	Some 6-colporate
S. sarcocolla (L.) Bullock	South Africa	*Dahlgren & Strid 4988*	LD	–			
Sonderothamnus petraeus (Sond.) R. Dahlgren	South Africa	*Dahlgren & Strid 3654*	LD	3	SEM, TEM	25E, F, 26B, C	
S. speciosus (Sond.) R. Dahlgren	South Africa	*Dahlgren & Strid 3764*	LD	3	SEM, TEM	23G, 24F, 26D	Some tetracolporate

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
Stylapterus ericoides A. Juss. subsp. *pallidus* R. Dahlgren	South Africa	*Dahlgren & Strid 3365*	LD	4	SEM, TEM	22D–F, 27E	Tetracolporate
CRYPTERONIACEAE							
Axinandra zeylanica Thw.	Ratnapura Distr., Sri Lanka	*Waas 1210*	MO				
A. zeylanica Thw.	Sri Lanka	*Gunatilleke & Gunatilleke 582*	MO	3	SEM, TEM	28B, D, 30C	
Crypteronia leptostachys	Philippines	*Ramos 1478*	MO		TEM	30A	
C. paniculata Bl.	Thailand	*Niyomdham s.n.*	MO	2	SEM, TEM	30B, 31B, D	Dicolporate syncolpate
C. sp.	Burma	*Dickason 6680*	MO	2	SEM	31A	Dicolporate syncolpate
Dactylocladus stenostachys Oliv.	North Borneo	*Hassan 732 (A)*	A	3	SEM	28E	Some tetracolporate
D. stenostachys Oliv.	Sarawak	*Chai 39708*	MO		TEM	29B	
D. stenostachys Oliv.	Sarawak	*SPH 3975*	MO	3	SEM, TEM	28A, F, 29C	Some tetracolporate
D. stenostachys Oliv.	Sarawak	*Chai 1982*	MO	3	SEM, TEM	28C, G, 29A	
MELASTOMATACEAE							
Acanthella sprucei Hook. f.	Amazonas, Venezuela	*Davidse 2793*	MO	3	SEM, TEM	33E, 38D	
Adelobotrys tessmannii Marhgraf	Huanuco, Peru	*Woytkowski 7850*	MO	(3)	SEM, TEM	34A–C, 39A, B	Some grains were cube shaped with 4 colpi and 8 subsidiary colpi on its edges
Allomorphia caudata (Diels) Li	Yunnan, China	*Henry 10761*	MO	(3)	SEM	34D	
Astronia cumingiana Vidal	Sarawak	*James et al. S.34401*	MO	(3)	SEM, TEM	34E, 39C	
Bredia hirsuta Bl.	Tokunoshima, Japan	*Iwatsuki 523*	MO	(3)	SEM, TEM	34F, 39F	
Comolia stenodon (Naud.) Triana	Brazil	*King & Almeda 8370*	CAS	3	SEM	36H	
Dissochaeta celebica Bl.	Johore, Malaya	*Anderson 2667*	MO	3	SEM, TEM	33F, 38B	
Dissotis brazzae Cogn.	Yala, Zaire	*Agnew & Musumba 8572*	MO	3	SEM, TEM	33C, D, 38C	
Marumia nervosa Bl.	Selangor, Malaya	*Ahmad S.A. 1080*	MO	3	SEM, TEM	33A, B, 38A	

TABLE 1. *Continued.*

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
Memecylon normandii Jacques-Felix	Ghana	*Hall & Abbiw s.n.*	MO	3	SEM	31E	
Miconia alypifolia Naud.	Peru	*Ochoa 11675*	CAS	3	SEM	36A–C	Some 6-colporate with colpi and intercolpar concavities
M. caesia Cogn. & Gleason ex Gleason	Colombia	*Barclay et al. 3352*	US	3	SEM	36D	
M. hondurensis Donn. Sm.	Costa Rica	*Almeda & Nakar 4088*	CAS	3	SEM	35D, E	Some dicolporate, syncolpate with intercolpar concavities
M. melanotricha (Triana) Gl. var. *melanotricha*	Panama	*Wilbur & Luteyn 19393*	CAS	(3)	SEM	35A–C	
Mouriri cf. *glazioviana* Cogn.	Minas Gerais, Brazil	*Anderson 8895*	MO	3	SEM	31F	
Osbeckia polycephala Naud.	Matale Distr., Sri Lanka	*Lazarides 7219*	MO	3	SEM, TEM	32B, 37D, E	
Oxyspora paniculata DC.	Yunnan, China	*Henry 9010A*	MO	(3)	SEM	34G, H, 39D, E	
Tibouchina candolleana (DC.) Cogn.	Minas Gerais, Brazil	*Williams & Assis 8044*	OKL	3	TEM	37C	
T. urvilleana (DC.) Cogn.	Cult. UC-Berkeley; native, Brazil	*Schmid 1980-12*	MO	3	SEM	32C	
Tococa broadwayi Urban	Venezuela	*Steyermark 94999*	US	3	SEM	36F	
T. formicaria Mart.		*Ratter 3253*	CAS	0	SEM	36G	
T. spadiciflora Triana	Carretera, Colombia	*Forero et al. 5703*	MO	?	SEM, TEM	36E, 40A	Polyads
T. spadiciflora Triana	Colombia	*Archer 1976*	US	?	SEM	35F–I	
T. stephanotricha Naud.	Marischal Prov., Peru	*Schunke 8106*	MO	0	SEM, TEM	36E, 40B, C	Triporate
Trembleya phlogiformis DC.	Minas Gerais, Brazil	*Irwin et al. 19723*	MO	3	SEM, TEM	32A, 37B	
Tristemma littorale Benth.	Lagos State, Nigeria	*Brown 938a*	MO	3	SEM, TEM	32D, 37A	
Votomita monadelpha (Ducke) Morley	Brazil	*Ducke 18494*	K	4	SEM	32E, F	Tetracolporate
MYRTACEAE							
Acmena smithii (Poir.) Merrill & Perry	Victoria, Australia	*Beauglehole & Finck ACB 32281*	NSW	(3)	SEM	47B	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
Austromyrtus bidwillii (Benth.) Burret	New South Wales, Australia	*W. Bauerlen 584*	NSW	0	SEM	48F	
Baeckea virgata Andrews	Cult. UC-Berkeley; native, Australia, New Caledonia	*Schmid 1980-13*		0	SEM	44A	
Balaustion microphyllum C. A. Gardner	Western Australia	*A. M. Ashby 312*	NSW	0	SEM	44C	
Callistemon citrinus (Curtis) Stapf	Cult. UC-Berkeley; native, Australia	*Schmid 1980-11*	UC	(3)	SEM	43B, D	
C. teretifolius F. Muell.	Cult. UC-Berkeley; native, Australia	*Schmid 1978-198*	UC	(3)	SEM	43A, C	
Calothamnus validus S. L. Moore	Cult. UC-Berkeley; native, Australia	*Schmid 1980-14*	UC	(3)	SEM	43E	Some tetracolporate
Chamaelaucium uncinatum Schau.	Western Australia	*Webster 18570*	NSW	0	SEM	44F, H	Some dicolporate
Cleistocalyx operculata (Roxb.) Merrill & Perry	Darwin, Australia	*Byrnes 2786*	NSW	(3)?	SEM	47A	
Eremaea pauciflora Domin	Western Australia	*Coveny 8073*	NSW	0	SEM	43F	
Eucalyptus ficifolia F. Muell.	Cult. UC-Berkeley; native, Australia	*Schmid 1980-10*	UC	(3)	SEM	42C–E	
E. robusta Smith	Michoacan, Mexico	*Cutler 4044*	OKL	(3)	SEM	42F	
Eugenia capuli (Schl. & Cham.) Berg.	Cayo Distr., Belize	*Croat 23525*	OKL	0	SEM	47C	
E. elliptifolia Merrill	Leyte, Philippines	*Wenzel 1248*	MO	(3)	SEM	47D	
Heteropyxis natalensis Harv.	Natal, South Africa	*Davidson 2642*	MO	(3)	SEM	42A, B	
Homoranthus wilhelmii Cheel	Northern Eyre Peninsula, Australia	*Alcock 4038*	NSW	0	SEM	44B	
Hypocalymna angustifolium Schau.	Western Australia	*Coveny 8063*	NSW	0	SEM	44E, G	
Luma chequen (Molina) A. Gray	Cult. UC-Berkeley; native, Chile	*Schmid 1978-194A*	UC	0	SEM	47E	
Melaleuca decussata R. Brown	Cult. UC-Berkeley; native, Australia	*Schmid 1980-9*	UC	0	SEM	45C	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
M. hypericifolia Smith	Cult. UC-Berkeley; native, Australia	*Schmid 1978-195*	UC	(3)	SEM	45A, B	
M. preissiana Schau.	Cult. UC-Berkeley; native, Australia	*Schmid 1978-196*	UC	0	SEM	45D	
M. pulchella R. Brown	Cult. UC-Berkeley; native, Australia	*Schmid 1980-15*	UC	0	SEM	45G	Some tetracolporate
M. rhaphiophylla Schau.	Margaret River, West Australia	*Earle 70*	OKL	(3)	SEM	45E	
Metrosideros nervulosa C. Moore & F. Muell.	Lord Howe Is., Australia	s. col.	NSW 108602	(3)?	SEM	41B	
M. polymorpha Gaud.	Oahu, Hawaii, USA	*Chambers 3005*	OKL	(3)?	SEM	41A	
Myrceugenella apiculata DC.	Pucara Peninsula, Argentina	*Dawson & Schwabe 203A*	OKL	0	SEM	47F	
Myrtus communis L.	Cult. UC-Berkeley; native, Europe	*Schmid 1980-18*	UC	0	SEM, TEM	48B–D, 49A–D	Some tetrahedral tetrads
Osbornia octodonta F. Muell.	Idlers Bay, Papua New Guinea	*Womersley NGF 14065*	NSW	0	SEM	46G	
Pilidiostigma glabrum Burret	New South Wales, Australia	*Brown 1900*	NSW	0	SEM	46F	
Psidium littorale Raddi	Cult. UC-Berkeley; native, trop. America	*Schmid 1980-8*		0	SEM	46A–C	Some tetracolporate, some tetrahedral tetrads
Psiloxylon mauritianum Baill.	Mauritius	*Gueho s.n.*	MAU 14976	0	SEM	45F	Some tetracolporate
Rhodamnia argentea Benth.	New South Wales, Australia	*Maiden & Boorman s.n.*	NSW	0	SEM	48E	
Temu divaricatum Berg	Valdivia, Chile	*Buchtien s.n.*	NSW	0	SEM	48A	
Thryptomene calycina J. M. Black	Grampians, Victoria Australia	*Beauglehole ACB 28154*	NSW	0	SEM	44D	
Tristania conferta R. Brown	Cult. UC-Berkeley; native, Australia	*Schmid 1980-7*	UC	(3)	SEM	41C, D	
T. lactiflua F. Muell.	Western Distr., Papua New Guinea	*Henty & Foreman NGF 49383*	MO	(3)	SEM	41F	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
T. nereifolia R. Brown	New South Wales Australia	*Constable 5566*	K	0	SEM	41E	Triporate?
Ugni molinae Turcz	Cult. UC-Berkeley; native, Central and South America	*Schmid 1980-17*	UC	0	SEM	46D, E	Some di- or tetracolporate
ONAGRACEAE							
Boisduvalia densiflora (Lindl.) S. Wats.	Washington, USA	*Piper s.n.*	MO	0	SEM	58B, E	
B. densiflora (Lindl.) S. Wats.	Oregon, USA	*Thompson 5099*	MO	0	SEM	58C	
B. densiflora (Lindl.) S. Wats.	California, USA	*Abrams 6675*	DS	0	TEM	63C	
B. macrantha Heller	Oregon, USA	*Heller 12920*	MO	0	TEM	63A–C	
B. stricta (A. Gray) Greene	California, USA	*Jones s.n.*	MO	0	SEM	58A	
Calylophus berlandieri Spach subsp. *berlandieri*	Oklahoma, USA	*Towner 139*	DS	0	TEM	61E, F	
C. toumeyi (Small) Towner	Arizona, USA	*Towner 107*	DS	0	SEM	55A–D	
Camissonia arenaria (A. Nels.) Raven	California, USA	*Parish & Parish 254*	MO	0	SEM	57A, B	
C. arenaria (A. Nels.) Raven	Arizona, USA	*Nelson 10140a*	MO	0	SEM, TEM	57D, F, 61A	
C. cardiophylla (Torr.) Raven subsp. *cedrosensis* (Greene) Raven	Arroyo Malurino	*Moran & Reveal 19868*	MO?	0	SEM	57H	
C. robusta (Raven) Raven	California, USA	*Gould 978*	MO	0	SEM	57E, G	
C. tanacetifolia (Torr. & Gray) Raven subsp. *tanacetifolia*	Cult. UC-Berkeley; native, western NA	*UCB 69.1097*	UC	0	SEM	57C	
Circaea alpina L. subsp. *imaicola* (Ash. & Magn.) Kitamura	China, Xizang (Tibet)	*Monbeig s.n.*	MO	0	SEM	50D	
C. cordata Royle	Oslo, Norway	Cult. Missouri Bot. Gard.	MO	0	SEM	50C	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
C. mollis Sieb. & Zucc.	Kerita, Honshu, Japan	*Togasi 1797*	MO	0	TEM	60D, F	
Clarkia breweri Greene	California, USA	*Carter 1166*	LA	0	TEM	62D	
C. speciosa Lewis & Lewis subsp. *speciosa*	California, USA	*UCB 65.1421*	UC	0	SEM	52A, C	
C. unguiculata Lindl.	Cult. UC-Berkeley; native, western North America	*UCB 59.1244*	UC	0	SEM	52B, D, F	
Epilobium collinum C. C. Gmelin	Sortavala, Finland	*Lindberg s.n.*	MO	0	TEM	63G	
E. cylindricum D. Don.	Gulmarg, Kashmir	*Stewart 10353*	MO	0	TEM	63F	
E. glaberrimum Barbey	California, USA	*MacMillan 14618*	MO	0	SEM	59H	
E. hectorii Hausskn.	New Zealand	s. col.	CHR 202446	0	SEM	59I	
E. hirsutum L.	Pyrenees, France	*Gautier 489863*	DS	0	TEM	63D, E	
E. brachycarpum Presl	Oregon, USA	*Sheldon S11070*	MO	0	SEM	59A–D	
E. brachycarpum Presl	California, USA	*Greene, 1876*	MO	0	SEM	59E–G	
E. rigidum Hausskn.	Oregon, USA	*Kline M561*	MO	0	SEM	59I	
Fuchsia cylindracea Lindl.	Todos Santos, Mexico	*Linderman 2030*	MO	0	TEM	60A	
F. garleppiana Kuntze & Wittmark	Dept. Cochábamba, Boliva	*Melhus & Goodman 3618*	OKL	0	SEM	50B	
F. thymifolia HBK. subsp. *thymifolia*	Michoacan, Mexico	*Waterfall 16474*	OKL	0	SEM	50A	
Gaura calicola Raven & Greg.	Texas, USA	*Henrickson 11334*	US	0	SEM	53A	
G. coccinea Pursh	Texas, USA	*Reverchon 3844*		0	TEM	62A, B	
G. demareei Raven & Greg.	Arkansas, USA	*Demaree 62683*	US	0	SEM	53D	
G. lindheimeri Engelm. & Gray	Cult. UC-Los Angeles: native, central USA	*Raven*, 1971	LA	0	SEM	52E	
G. mutabilis Cav.	Chihuahua, Mexico	*Jones*, 1903	DS	0	SEM	52G, H	
G. neomexicana Wooton subsp. *neomexicana*	New Mexico, USA	*Towner 109*	US	0	SEM	53B, C	
Gayophytum micranthum Hook. & Arn.	Prov. Coquimbo, Chile	*Werdermann 200*	MO	0	SEM	53F, H	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Subsidiary Colpi	SEM-TEM	Figure No.	Remarks
G. micranthum Hook. & Arn.	Prov. Coquimbo, Chile	*Moore 216*	LA	0	TEM	61D	
G. ramosissimum Torr. & Gray	Wyoming, USA	*Gooding 510*	MO	0	SEM	53E, G, I	
Gongylocarpus fruitculosus (Benth.) T. S. Brandegee subsp. *glaber* (J. H. Thomas) Carlquist & Raven	Baja California, Mexico	*Moran 3529*	DS	0	SEM	56F	
G. rubricaulis Schlecht. & Cham.	Mexico	*Davidse 9790*	MO	0	TEM	61G, H	
G. rubricaulis Schlecht. & Cham.	Veracruz, Mexico	*Sharp 44846*	MO	0	SEM	56D	
Hauya elegans DC. subsp. *barcenae* (Hemsl.) Breedlove & Raven	Chiapas, Mexico	*Breedlove 10229*	MO	0	SEM	50G	
H. elegans DC. subsp. *elegans*	San Luis Potosi, Mexico	*Moran 13387*	MO	0	SEM	50E	
H. elegans DC. subsp. *elegans*	Queretaro, Mexico	*Rzedowski 9294*	DS	0	SEM	50F	
H. heydeana Donn. Sm.	Chiapas, Mexico	*Breedlove 15653*	DS	0	TEM	60C, E	
Heterogaura heterandra (Torr.) Cov.	California, USA	*Raven 20238*	MO	0	SEM	54A–C	
H. heterandra (Torr.) Cov.	California, USA	*Bacigalupi 2341*	DS	0	TEM	62C	
Lopezia grandiflora Zucc.	Jalisco, Mexico	*Breedlove 8066*	DS	0	TEM	61B	
L. longifolia (Decne.) Plitmann, Raven & Breedlove	Morelos, Mexico	*Breedlove 8044*	DS	0	SEM	51D–G	
L. racemosa Cav. subsp. *racemosa*	Jalisco, Mexico	*Breedlove 25800*	CAS	0	SEM	51A–C	
Ludwigia alternifolia L.	North Carolina, USA	*Peng 3738*	MO	0	SEM	58F	
L. brevipes (Long) Eames	South Carolina, USA	*Godfrey & Tryon 1237*	MO	0	TEM	60B	
L. goiasensis T. P. Ramamoorthy	Brasilia, Brazil	*Ramamoorthy 652*			SEM	58D, G	

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium	Sub-sidiary Colpi	SEM-TEM	Figure No.	Remarks
L. longifolia (DC.) Hara	Tucuman, Argentina	*Venturi 2873*	MO	0	SEM	58H, I	
Oenothera brachycarpa A. Gray	Durango, Mexico	*Anderson 5207* Cult. Stanford Univ.	MO	0	SEM	56A, B	
O. maysillesii Munz	Durango, Mexico	*Breedlove s.n.*	MO	0	TEM	62E	
O. texensis Raven & Parnell	Texas, USA	*Parnell s.n.*	MO	0	SEM	56C, E	
Stenosiphon linifolius (Nutt.) Heynh.	Kansas, USA	*Raven 26384*	MO	0	SEM	55E, F	
S. linifolius (Nutt.) Heynh.	Kansas, USA	*Raven 26554*		0	TEM	62F	
Xylonagra arborea Donn. Smith & Rose subsp. *wigginsii* Munz	Baja California, Mexico	*Verity et al. 032*	MO	0	SEM, TEM	54D–F, 61C	

therefore, he recommends the term "subsidiary colpi" and we are in complete accord (Patel et al., 1983b). Subsidiary colpi generally have a thinner ektexine than the surrounding mesocolpial areas but in contrast to the colpi, all exine layers are usually represented. Frequently, the thinning of the ektexine is gradual and thus the subsidiary colpi often are not as clearly delimited as the colpi, although the endexine is increased in thickness just as in the colpi. Further, the surface sculpture in the subsidiary colpi is often different from that of the colpi. In the present study subsidiary colpi have been observed in Lythraceae, Combretaceae, Melastomataceae, Rhynchocalycaceae, Oliniaceae, Penaeaceae, and Crypteroniaceae, characterizing all pollen examined in the latter four families. Other families in which they have been observed are the Acanthaceae, Boraginaceae, Hydrophyllaceae, Leguminosae, and Verbenaceae (Erdtman, 1971; Nowicke & Skvarla, 1974; Faegri & Iversen, 1975; Ferguson & Skvarla, 1981, 1983; Raj, 1983). Subsidiary colpi are either equal to the number of colpi (= isomerous) and alternating with them or there can be additional subsidiary colpi, as particularly noted in the Lythraceae.

2. *Intercolpar concavities.* As originally defined by Wodehouse (1928: 453) for pollen in the Compositae tribe Mutisieae "These two species . . . are unique in the possession of three distinct concavities appearing as the impressions one could make with the thumb in a ball of soft dough. Since these impressions are between the furrows, I shall call them intercolpar concavities, and their position on the equator suggests the further designation of equatorial concavities." We consider them to be structurally and functionally similar to subsidiary colpi, distinguished only in that they are markedly larger. In this study intercolpar concavities are found in some Melastomataceae, Penaeaceae, and Myrtaceae. They may also be present in Lythraceae as they appear to be in light photomicrographs of *Peplis portula* by Guers (1970). In *Crypteronia* large concavities in the mesocolpia have been considered by Muller (1975) as pseudocolpoid depressions. Intercolpar concavities have also been described in Calyceraceae (Skvarla et al., 1977) and, if our interpretations of Erdtman (1971) and Raj (1983) are correct, perhaps in Hoplestigmataceae, Verbenaceae, and Olacaceae. Like subsidiary colpi, it will be of considerable interest to learn of their occurrence in other angiosperm groups.

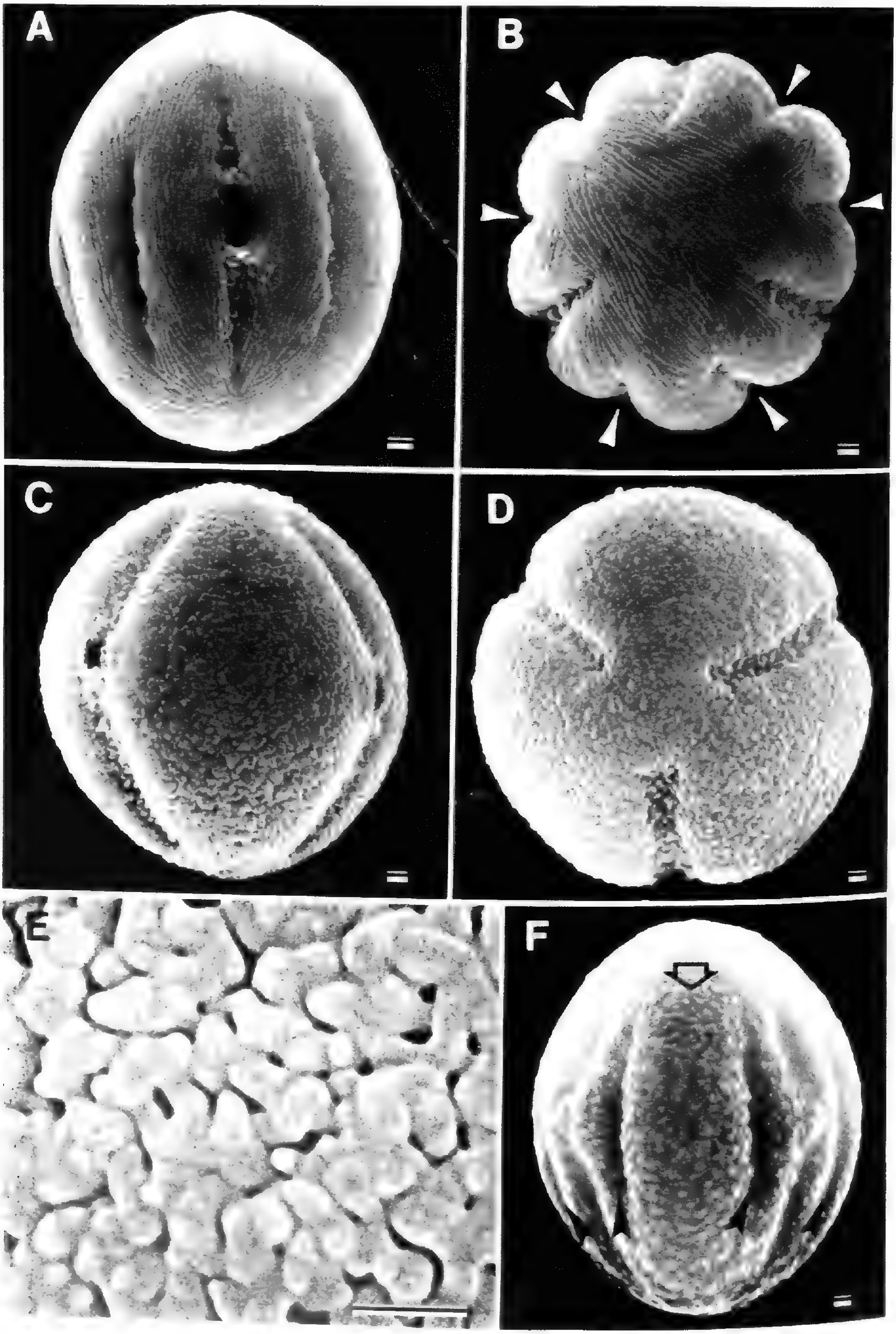

FIGURE 1. Scanning electron micrographs of Lythraceae subfam. Lythroideae pollen. A, B. *Nesaea schinzii* – A. Lateral view showing granular colpus with circular endoaperture (at center) and two subsidiary colpi. The exine surface is striate. — B. Polar view. Each of the three colpi alternates with two subsidiary colpi (arrowheads Note that *all* of the nine mesocolpia are equal in size. Comparison should be made with the scanning electron micrograph of *N. longipes* (Graham, 1977, figs. 4–6) in which the three mesocolpia that are flanked by subsidia colpi are prominent and larger than the remaining six mesocolpia. C–E. *Heimia salicifolia* (*Ventura* 2430) – Lateral view. — D. Polar view. — E. Surface detail. The three colpi have a granular surface. Subsidiary colpi a absent. The mesocolpium consists of elongated, branched, often overlapping elements. Comparison with t scanning electron micrograph of Graham (1977, figs. 1–3) indicates a somewhat different sculptured surface – F. *Crenea surinamensis*. Lateral view showing two shallow colpi and four subsidiary colpi (arrowheads) The

3. *Heterocolpate*. This term signifies the presence of subsidiary colpi or intercolpar concavities in addition to colpi and was originally defined by Faegri and Iversen (1950: 129) "Some furrows with, others without pores, free pores absent."

RESULTS AND DISCUSSION

LYTHRACEAE

Subfamily Lythroideae

Pollen is tricolporate (some heterocolpate with either three or six subsidiary colpi), radially symmetrical, and isopolar. Great variability exists in shape, surface sculpture, aperture system, and to a lesser extent, exine structure. Apart from *Nesaea* (Fig. 1A, B) and *Ammannia* (Fig. 2A, B) which are similar, each genus we examined has a distinct morphology and is described below.

Ammannia: A. robusta (Fig. 2A, B) is heterocolpate with six subsidiary colpi, subprolate in lateral view, circular in polar view. The surface is striate. Colpi are long with obtuse ends and with a smooth, slightly granular surface. The endoapertures are circular to slightly elliptic-lalongate. Subsidiary colpi are short with a slightly granular surface. *Ammannia coccinea,* which also has a striate surface and six subsidiary colpi, was examined along with *A. robusta* in TEM (Fig. 5A, B). The endexine is as thick or slightly thinner than the ektexine in the mesocolpial area. The foot layer is thick and often shows irregular channels near its lower margin, columellae are thick, short, and simple and the tectum is very thin and imperforate. In cross section, the striae composing the tectum appear deeply grooved and constricted at the base. In the colpal and subsidiary colpal regions, the endexine is as thick or slightly thicker than in mesocolpial regions and the foot layer appears to be continuous as a very thin film. Near the endoaperture, the endexine is granular and continues as a very thin layer over the pore.

Crenea: C. surinamensis (Fig. 1F) was examined only with SEM. The pollen is spheroidal to subprolate in lateral view, while in polar view the slightly collapsed grains are triangular with meridional ridges forming obtuse corners. Pollen is heterocolpate with six subsidiary colpi, the mesocolpia between each pair of subsidiary colpi are wide and thick, forming three meridional ridges. Colpi are long and indistinct; subsidiary colpi are shorter than the colpi and also indistinct. Endoapertures are circular and raised. The surface is verrucate-rugulate.

Cuphea: Both *C. carthagenensis* (Fig. 2C) and *C. petiolata* (Fig. 2D–F) are tricolporate-syncolpate, oblate-suboblate in lateral view, triangular (sub-triangular to circular in *C. petiolata*) in polar view, and goniotreme (i.e., angulaperturate). In *C. carthagenensis,* the surface is psilate with meridional folds or ridges on the mesocolpia toward the pores. Colpi are very narrow and united at the poles. The pores are aspidote, like a cylindrical extension, and open by a vertical splitting of the cylinder. In *C. petiolata,* the corners are obtuse, the surface is basically striate, but on the equator on each side of the colpus two elliptic areas are delineated in some grains. The size and the sculpture of these areas are highly variable and range from striate-spinulate to rugulate-striate in grains from the same collection. Colpi have a granular surface and the endoapertures are lalongate.

Cuphea nitidula (Fig. 5D) and *C. racemosa* (Fig. 5C) were examined with TEM. The former is oblate-triangular with protruding pores (SEM not included here). It has a uniform endexine which is thickened at the base of the pores. The foot layer is thin, columellae are simple and extremely short. The tectum is thin and tectal perforations are rare. Tectal ridges are solid. The protruding pore (not illustrated in plate figures) has a thin granular endexine, a fragmented and thin foot layer, short columellae, and a very thin but continuous tectum. *Cuphea racemosa* has suboblate, tricolporate grains (Cos Campos, 1964). In thin section (Fig. 5C), the endexine is thin and uneven, the foot layer is thick, columellae are short, and the tectum is thin with some perforations. However, the endexine is very thick below the colpi and granular near the endoapertures (not illustrated).

Diplusodon: D. villosus was examined with SEM and TEM (Figs. 3A, B, 6E). The tricolpoi-

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mesocolpium (open arrow) between the subsidiary colpi is wide and forms a meridional ridge. The exine surface is verrucate-rugulate. This pollen grain (see also scanning electron micrograph of Muller, 1981, Pl. 1, figs. 1, 2) is in marked contrast to other grains with six subsidiary colpi (viz. Figs. 1A, B, 2A) in that adjacent colpi and subsidiary colpi are not all equidistant. Scales equal 1 μm.

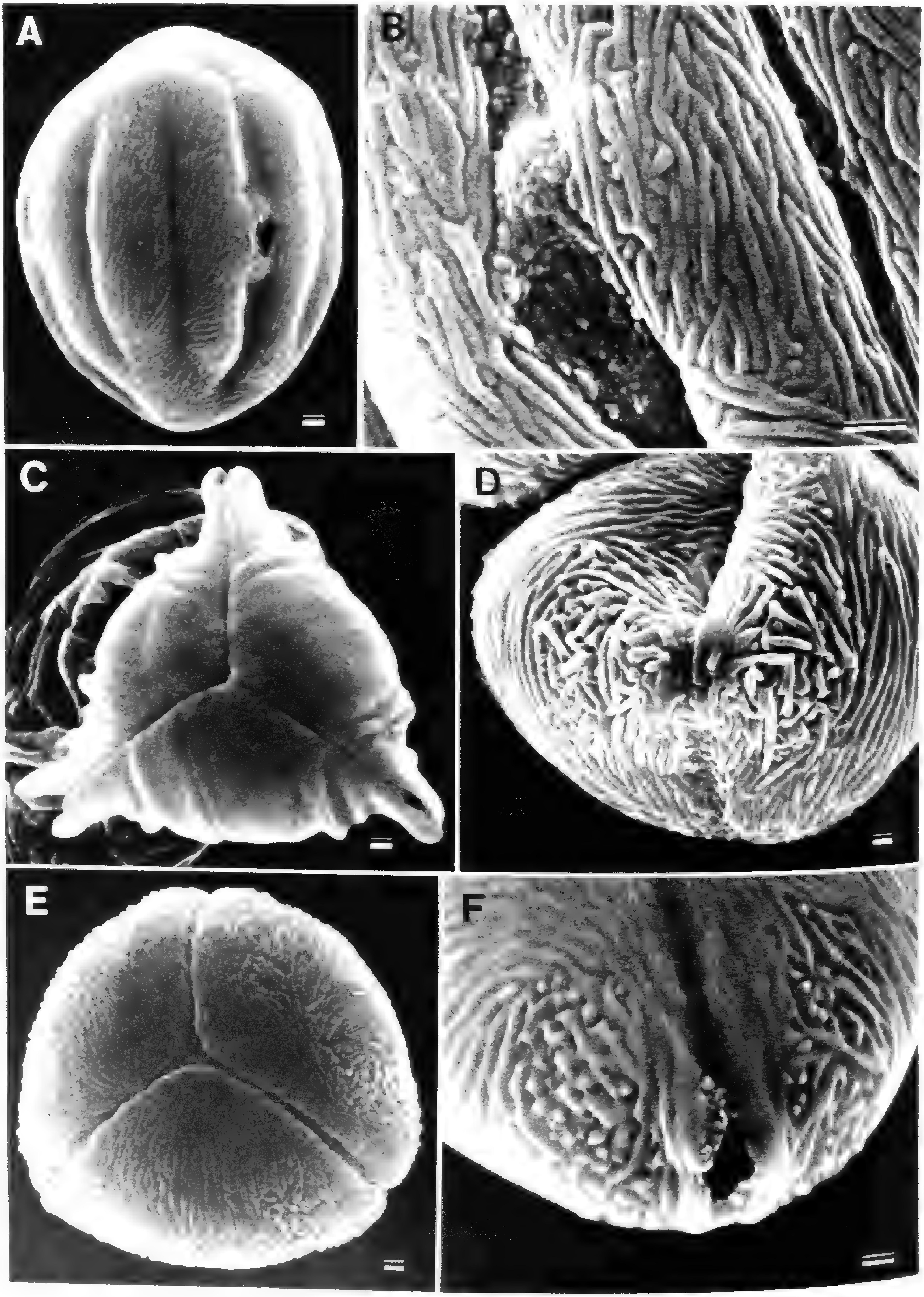

FIGURE 2. Scanning electron micrographs of Lythraceae subfam. Lythroideae pollen. A, B. *Amman robusta*.—A. Lateral view. Each colpus is separated by two subsidiary colpi. The exine surface is striate.— Surface detail near the endoaperture which is covered by a granular colpus membrane.—C. *Cuphea car genensis*. Polar view. Pores are located in the cylindrical extensions on the three corners; colpi are narr and united at the pole. The surface is psilate with large ridges (see transmission electron micrograph of *nitidula*. Fig. 5D) near the pores. D–F. *Cuphea petiolata*.—D. Lateral view with randomly oriented striae in aperture region.—E. Polar view showing syncolpate apertures.—F. View of open endoaperture and surround striate surface. See also transmission electron micrograph surface replicas of other species of *Cuphea* (Graha et al., 1968, figs. 4, 5, 8). Scales equal 1 μm.

dorate grains are subprolate in lateral view. Endoapertures are circular. The surface is verrucate-rugulate with tightly packed verrucae as well as with elongated, convoluted rugulate elements. Colpi are very short and have large spherical elements on the surface. In section, the verrucate-rugulate surface elements appear to be composed of a thick tectum which is supported by several thin columellae. A foot layer is absent. The endexine is thick and uniform, near the pore it increases in thickness and is granular.

Heimia: H. salicifolia was examined with both SEM and TEM. Tricolporate pollen grains are spheroidal in lateral view and circular in polar view (Fig. 1C–E). The surface has irregularly shaped elements with overlapping fingerlike branches and irregular gaps between them (Fig. 1E). Blunt spinules are also scattered on the surface. Colpi are long, with obtuse ends and a granular surface. Endoapertures are lalongate. Thin section (Fig. 5G) shows a thick endexine, a foot layer which is either as thick as or thinner than the endexine, and simple or branched columellae which are erect and tall but becoming shorter toward the colpi. The lower margin of the tectum is more or less straight while the upper margin is irregular. Tectal perforations are numerous and often large. The endexine is very thick below the colpi; near the endoaperture, its lower margin is granular. The membrane over the endoaperture consists of very thin granular endexine. The granules on the colpi surface (not illustrated in plate figures) appear to be solid and constricted at the base or rarely with fine columellae under them.

Lafoënsia: L. punicifolia was examined with both SEM (Fig. 3D–F) and TEM (Figs. 5E–F, 6A). The tricolpoidorate grains are subprolate in lateral view, and triangular-pleurotreme with obtuse corners and straight sides in polar view. The three protruding pores are situated midway between the sides of the triangular pollen grain. The three meridional ridges and the polar caps separate three elliptic, apertural fields (Muller, 1981). The surface of the apertural fields is granular-verrucate-rugulate; the surface of the ridges and the margins of the apertural fields near the apocolpia are rugulate but coarser than the rest of the apertural fields. The apocolpia have a psilate surface. The short colpus appears as a slightly depressed area with fewer and smaller granular elements than the surrounding area. The pores are circular, the membrane over them is similar to and continuous with the surrounding area. In TEM (Figs. 5E, F, 6A) the ektexine is thick in the ridge areas and thin in the apertural fields and at the poles. In the ridge areas, the foot layer is thick, with the upper margin often irregular or raised into domes, columellae are tall, erect and simple, and the tectum is thick, but discontinuous due to the rugulate surface. In the apertural fields (Fig. 6A), the columellae are shorter, the foot layer is thinner, and the tectum irregular in thickness and discontinuous but with tightly packed verrucate units. The endexine in the ridge and aperture fields is thick and uniform (Figs. 5E, 6A). At the poles (Figs. 5F, 6A) the entire exine is thinner. Here the endexine is very thin, and the foot layer and tectum are thicker than the endexine. The tectum is continuous and has a smooth upper margin and an irregular lower margin; the very short columellae are wider at their distal ends and appear to be finely branched (Fig. 5F).

Lagerstroemia: L. speciosa was examined only with SEM. Tricolporate grains are subprolate in lateral view and circular to hexagonal in polar view (Fig. 3C). The surface appears to be microrugulate with cylindrical, often branched and overlapping irregularly compacted elements. On the mesocolpia, a poorly developed meridional ridge with two slightly depressed parallel areas on each side is discernible. Colpi are long with obtuse ends and a granular surface. Endoapertures are circular with a slightly raised membrane over them.

Nesaea: N. schinzii was examined only with SEM (Fig. 1A, B). The tricolporate grains are heterocolpate with six subsidiary colpi. They are subprolate in lateral view and circular in polar view. The surface is striate. Colpi are long with acute ends and a granular surface. Subsidiary colpi are shorter than the colpi and have a granular surface.

Subfamily Punicoideae

Punica protopunica and *P. granatum,* the only two species in the subfamily, were examined with SEM and TEM (Figs. 7, 8). The pollen is tricolporate, radially symmetrical, isopolar, subprolate in lateral view, and circular in polar view with slightly angular mesocolpia. In *P. protopunica* the meridional ridges, polar caps, and ovoid apertural fields are weakly developed (Fig. 7D). The surface of the polar caps is smooth-punctate with fine channels, that of the meridional ridges is coarsely rugulate. In the apertural fields, two faint subsidiary colpi with a rugulate surface (Fig. 7E) are present on the sides of each meridional ridge. In *P. granatum* only three weakly developed meridional ridges with rugulate surfaces were clearly observed in the center of the mesocolpia (Fig. 7A). Exclusive of ridges, the surface is granular-rugulate (Fig. 7B). In both species, colpi are long, with acute ends and with a granular surface. Endoapertures appear to be circular to slightly oblong and lalongate.

Thin sections show that the foot layer is narrow and discontinuous (Fig. 8A, B), although in the polar caps of *P. protopunica* it is continuous (Fig. 8C). The columellae are very short, thick, and numerous. They are branched where the exine is most thickened. The tectum is thick. The prominent endexine increases in thickness in the colpal regions and decreases at the polar caps. Near the endoapertures the endexine is granular. Punicoideae pollen is comparable to some Lythroideae although apertural fields, meridional ridges and polar caps are not as well developed.

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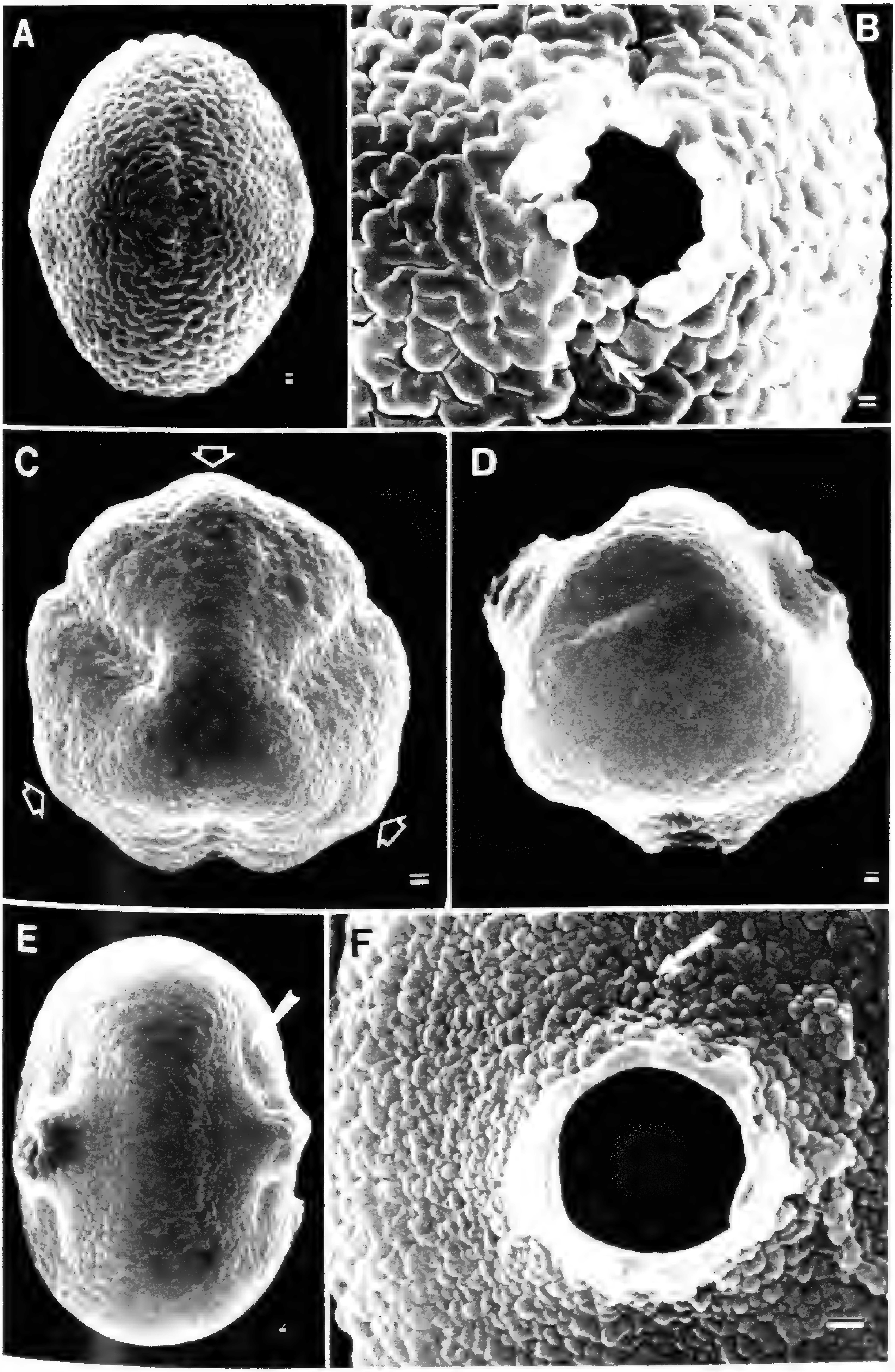
FIGURE 3. Scanning electron micrographs of Lythraceae subfam. Lythroideae pollen. A, B. *Diplusodon villosus.*—A. Lateral view. The aperture system consists of a short colpus and circular endoaperture.—B. A verrucate-rugulate surface encompasses the short colpus (arrow) and prominent circular endoaperture.—C. *Lagerstroemia speciosa.* Polar view showing weakly developed meridional ridges (arrows) between each colpus. This scanning electron micrograph complements the one of Muller (1981, Pl. 1, figs. 3, 4) for the same species. D–F. *Lafoënsia punicifolia.*—D. Polar view showing prominently psilate polar cap, three protruding apertures, and three meridional ridges.—E. Lateral view with meridional ridge separating two apertural fields. Arrow indicates colpus.—F. The surface of the aperture field surrounding the pore is verrucate-rugulate. A portion of the colpus is indicated by an arrow. These scanning electron micrographs should be compared with those of Muller (1981, Pl. 7, figs. 1, 2). Scales equal 1 μm.

FIGURE 4. Scanning electron micrographs of pollen from Rhynchocalycaceae (A, C), Alzateaceae (B, D), and Lythraceae subfams. Sonneratioideae (E) and Duabangoideae (F). A, C. *Rhynchocalyx lawsonioides.*—A. Lateral view.—C. Polar view. Subsidiary colpi appear to be united (i.e., they are "synpseudocolpate") (arrow) at the pole. See also scanning electron micrograph of Muller (1975, Pl. V, figs. 7–11). B, D. *Alzatea verticillata.*—B. Polar view.—D. Lateral view. For both figures, the surface is psilate but at the middle of the mesocolpia slightly depressed psilate-punctate areas are noted (open arrows). These have been interpreted as incipient pseudocolpi (see scanning electron micrograph of Muller, 1975, Pl. IV, figs. 6–9). A distinct margin (solid arrow) is present around the colpus.—E. *Sonneratia caseolaris.* Sublateral view. Polar cap has a psilate surface with a few punctae. The well-developed meridional ridge has a rugulate surface. Note the two elliptic apertural fields and the protruding pores which are enclosed by two small ridges (arrowheads). The surface of the apertural fields and the membranes over the pores is verrucate. (See also scanning electron micrograph of Muller, 1978a, several plates.)—F. *Duabanga moluccana.* Lateral view. The surface is smooth on the polar caps; elsewhere it is verrucate-rugulate. The meridional ridge has a coarser surface than the apertural fields. In contrast to *S. caseolaris* (E) polar caps and meridional ridges are less distinct and the protruding pores are without surrounding ridges. Scales equal 1 μm.

FIGURE 5. Transmission electron micrographs of Lythraceae subfam. Lythroideae pollen.—A. *Ammannia robusta.* Cross section of the area between two colpi (short arrows) which includes three mesocolpia and two subsidiary colpi (long arrows). Note the distinct "white line" between the foot layer and endexine. The latter is granular on the right indicating the presence of an endoaperture.—B. *Ammannia coccinea.* Section of a mesocolpium. The striae are cut perpendicularly, are deeply lobed, and are constricted at their bases. The tectum (arrow) is very thin, columellae are short and thick; the foot layer is highly irregular and has some lamellae. The endexine is as thick as the entire ektexine.—C. *Cuphea racemosa.* Portion of a mesocolpium. Note thin, irregular endexine.—D. *Cuphea nitidula.* Section of the mesocolpium near pore (to the right but not included). The ridges (r) (as described in scanning electron micrograph Fig. 2C) are solid, columellae (arrow) are short, and the foot layer is essentially uniform. The endexine increases in thickness toward the pore and is stained darker than the ektexine. E, F. *Lafoensia punicifolia.*—E. Section perpendicular to mesocolpium and including adjacent pores. The ektexine on the meridional ridge (within arrows) is more prominently developed than on the adjacent apertural fields. The endexine is well developed: under the meridional ridge it is nearly equal in thickness to the ektexine, toward the pores it becomes granular as well as increasing in thickness. This transverse section is in contrast to Figure 6A which represents a section parallel to the polar axis (i.e., a longitudinal section) and includes part of the polar cap and apertural field. These two different sectioning planes represented in E and Figure 6A explain the disparity in respective endexine thicknesses. See also Muller (1981, Pl. IV) for additional transmission electron micrographs.—F. Section of polar cap. In contrast to E and Figure 6A note particularly the smooth, solid tectum, and the thick and branched columellae. The uniform foot layer is thicker than the narrow endexine. This section is directly comparable to the transmission electron micrograph of Muller (1981, Pl. IX, fig. 3).—G. *Heimia salicifolia* (*Graham 141*). Section of a mesocolpium. Scales equal 1 μm.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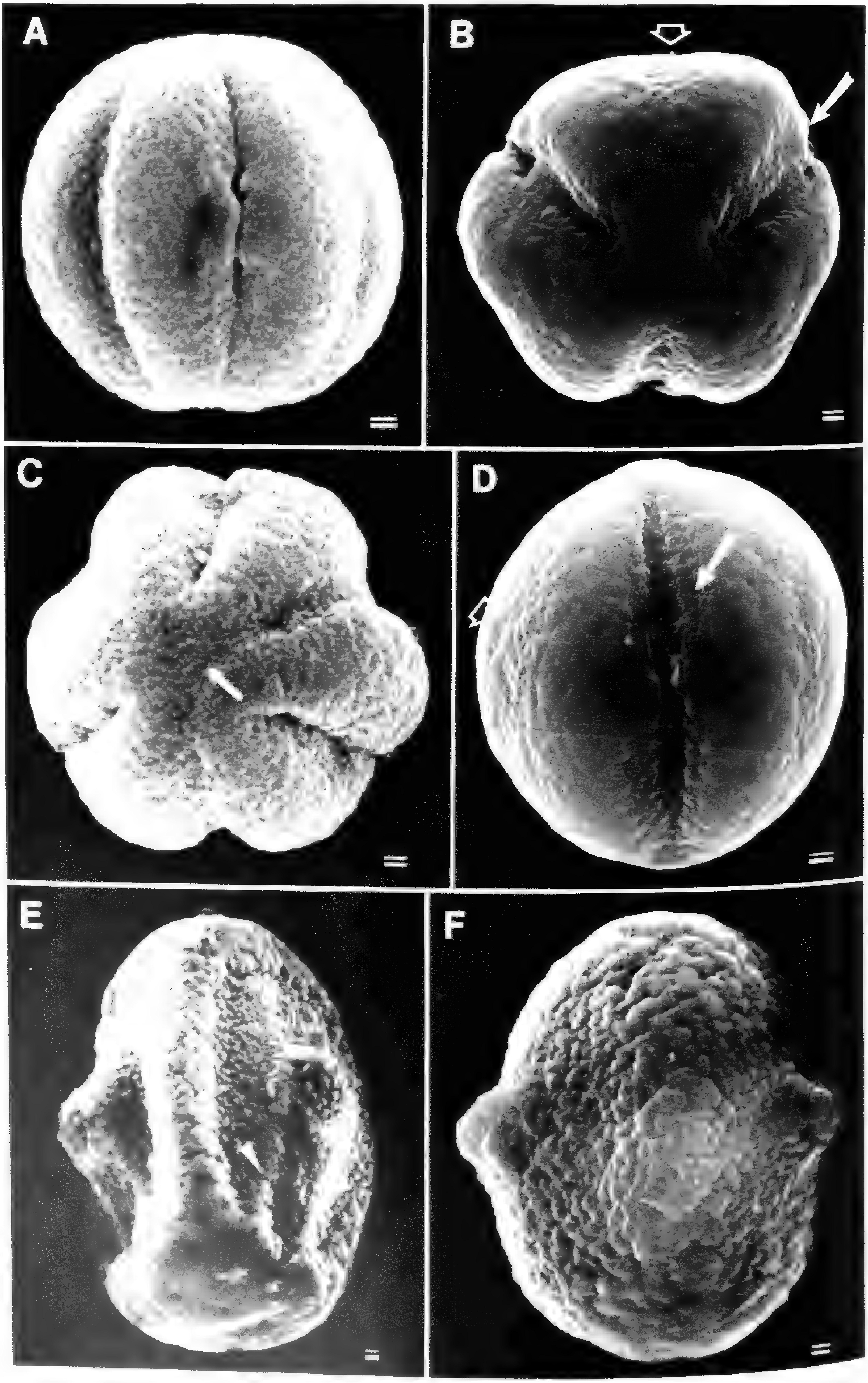
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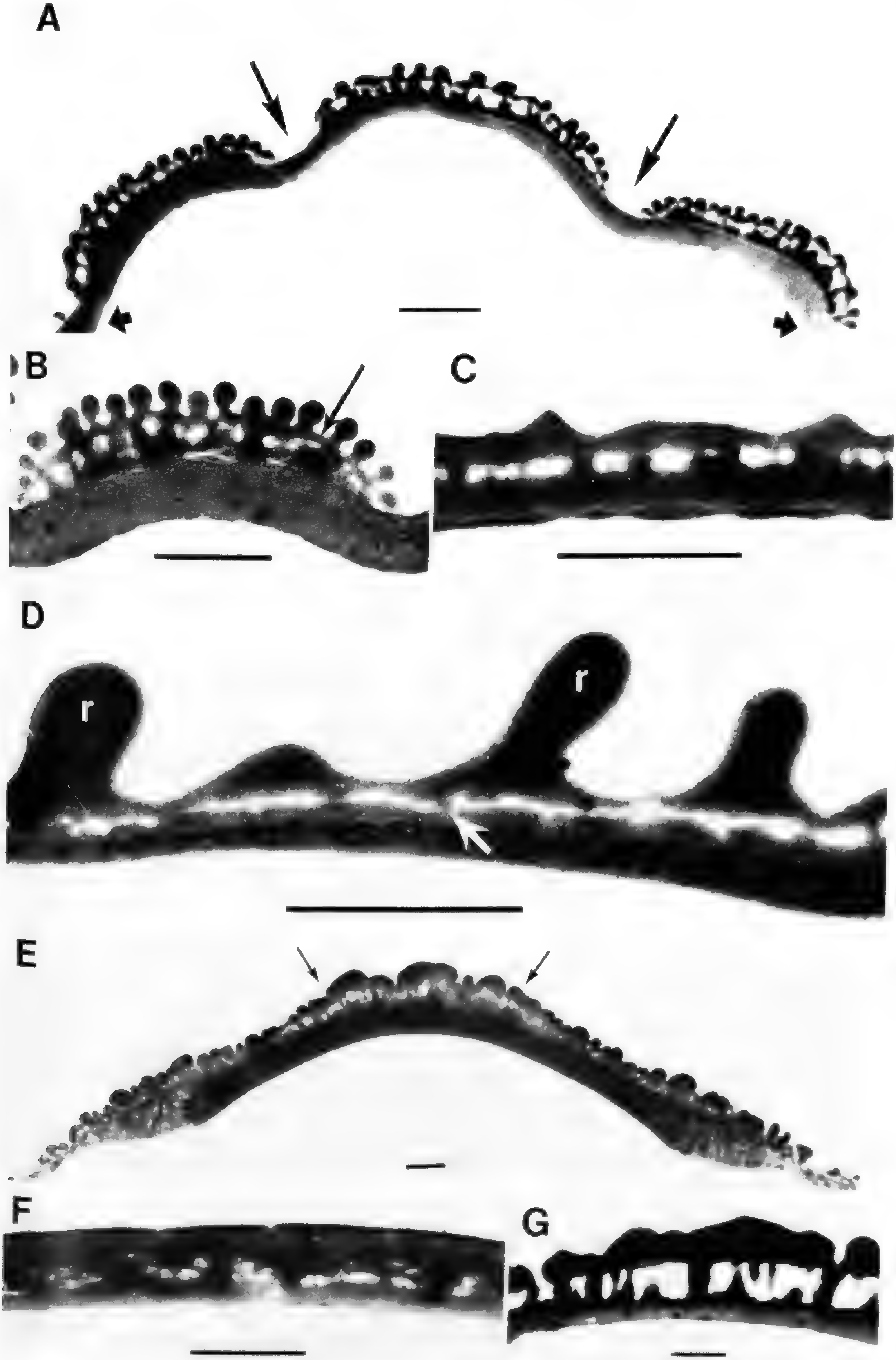
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Subfamily Sonneratioideae

Sonneratia caseolaris was examined with SEM (Fig. 4E, F). The pollen is triporate, radially symmetrical, and isopolar. *Sonneratia* grains are prolate, cylindrical in lateral view, and triangular-hexagonal in polar view, and three well-developed, meridional ridges alternating with three, oblong apertural (pore) fields are present. The surface is verrucate in the apertural fields and verrucate-rugulate on the ridges. Each apertural field has a protruding pore at its center. The surface of the pore membrane is similar to that of the surrounding field. In addition to the three large ridges, six smaller ridges are present, two in each apertural field. They are parallel to the larger ridges and have a rugulate surface. The pore is located between the two smaller ridges, and the large, triangular polar caps have a psilate surface with a few punctae scattered over them.

In a light microscope study, Muller (1969) described the pollen morphology for five species and two interspecific hybrids of *Sonneratia*. Major conclusions from his study were: (1) that *S. alba* and *S. caseolaris* pollen showed great intraspecific variability that is geographically related and considered as genotypic, and (2) the dominant pollen morphology of one parent of the two intraspecific hybrids suggested introgressive hybridization. Later, pollen of *S. alba* and *S. caseolaris* was examined by SEM and TEM (Muller, 1978a) in order to supplement the morphological data of earlier studies (Muller, 1969). Since our study did not include TEM observations, the pollen ultrastructure of *Sonneratia* is summarized from Muller's work as follows:

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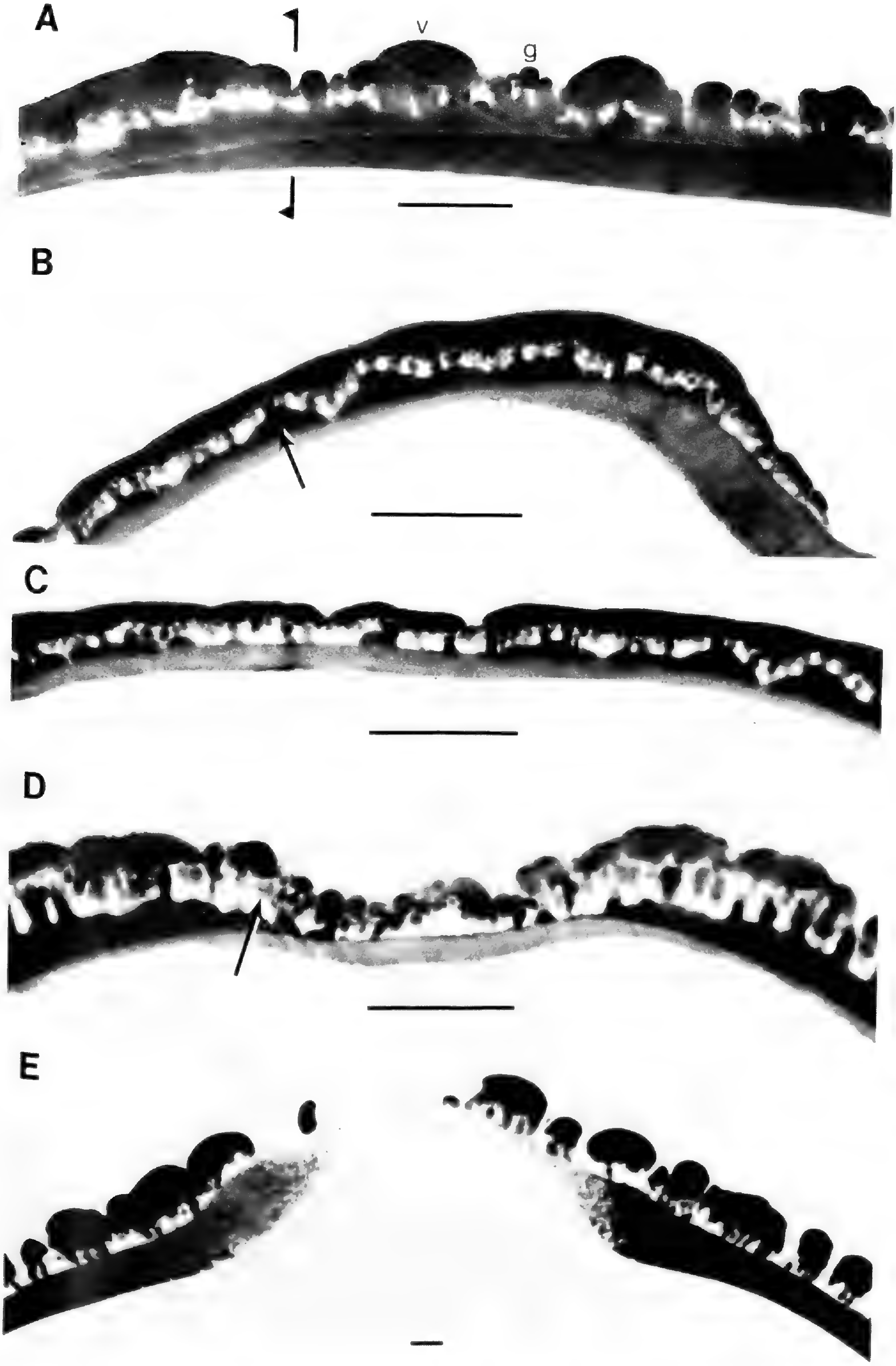
FIGURE 6. Transmission electron micrographs of pollen from Lythraceae subfam. Lythroideae (A, E), Alzateaceae (B, C), and Rhynchocalycaceae (D).—A. *Lafoënsia punicifolia.* Section through the polar cap (left of "bracket") and apertural field. In the apertural field, the verrucae (v) are composed of a thick tectum and short, perpendicular columellae. Between the verrucae the surface granules (g) of the scanning electron micrograph (Fig. 3D–F) are supported by columellae. The foot layer is well developed and has an irregular upper margin. The endexine is thick and more densely stained than the ektexine. Toward the polar cap the tectum is continuous and has a finely granular layer below it. The columellae are shorter and the foot layer is thicker than in the apertural field. The endexine decreases in thickness from right to left (i.e., toward the polar cap). (See additional comments to Fig. 5E, F and also Muller, 1981, Pl. IV.) B, C. *Alzatea verticillata.*—B. Section of a portion of the mesocolpium. At the extreme right is the colpus. The foot layer is highly irregular and forms "hills" (double arrow) and "valleys." The thickness and shape of the tectum is in direct correspondence with that of the foot layer, between them is a more or less uniform, columellae layer. Near the colpus, the tectum is thin, the columellae are short, and the foot layer is extremely thin. The endexine, which is relatively thin in the mesocolpium, is very thick in the colpus.—C. A continuation of the section in B to show the middle portion of the mesocolpium. Here, the entire exine decreases in thickness. The tectum is thinner than the surrounding areas and more perforate. The columellae either remain the same or slightly increase in length and are branched near the base of the tectum. The foot layer is either absent or present only as thickened bases of columellae. The endexine has increased in thickness, although considerably less so than in the colpus region.—D. *Rhynchocalyx lawsonioides.* The section is near the end of a colpus or subsidiary colpus and includes portions of two mesocolpia. The arrow indicates granules at the inner (lower) margin of the tectum (see also Muller, 1975, Pl. VII, figs. 1–3).—E. *Diplusodon villosus.* Section passing through a pore and including parts of the adjacent mesocolpia. The verrucae forming the surface sculpture are composed of a thick tectum supported by several thin columellae. A foot layer appears to be absent. The endexine is thick and uniform; in the pore area it is granular. Scales equal 1 μm.

FIGURE 7. Scanning electron micrographs of Lythraceae subfam. Punicoideae pollen. A, B. *Punica granatum* (*Grant 15704*).—A. Lateral view. A wide meridional ridge (between arrows) is discernible.—B. Granular-rugulate surface of mesocolpia near a part of a colpus. C–G. *Punica protopunica.*—C. Scanning electron micrograph of a fractured exine near the pole. Note the inner surface which is smooth toward the pole. The granules below the tectum (arrow) were not observed in sections.—D. Lateral view. A distinct meridional ridge is present, and is connected with the polar caps forming weakly developed apertural fields similar to those found in Lythraceae (Muller, 1981). Slightly coarser, elongated areas lateral to the ridge and suggesting subsidiary colpi are also distinct.—E. Lateral view showing the rugulate surface of the ridge (center) and the subsidiary colpi.—F. Polar view. Compare with Figure 3C.—G. Inner surface of the exine near the endoaperture. Scales equal 1 μm.

FIGURE 8. Transmission electron micrographs of Lythraceae subfam. Punicoideae pollen.—A. *Punica granatum* (*Grant 15704*). Transverse section of a mesocolpium. B, C. *Punica protopunica.*—B. Transverse section of a mesocolpium. Note the "white line" separating the discontinuous foot layer and the thick endexine.—C. A vertical section passing through an open pore. Note the thinning of the endexine at the poles (arrows). In contrast to other areas, the foot layer at the poles is thick and continuous. Scales equal 1 μm.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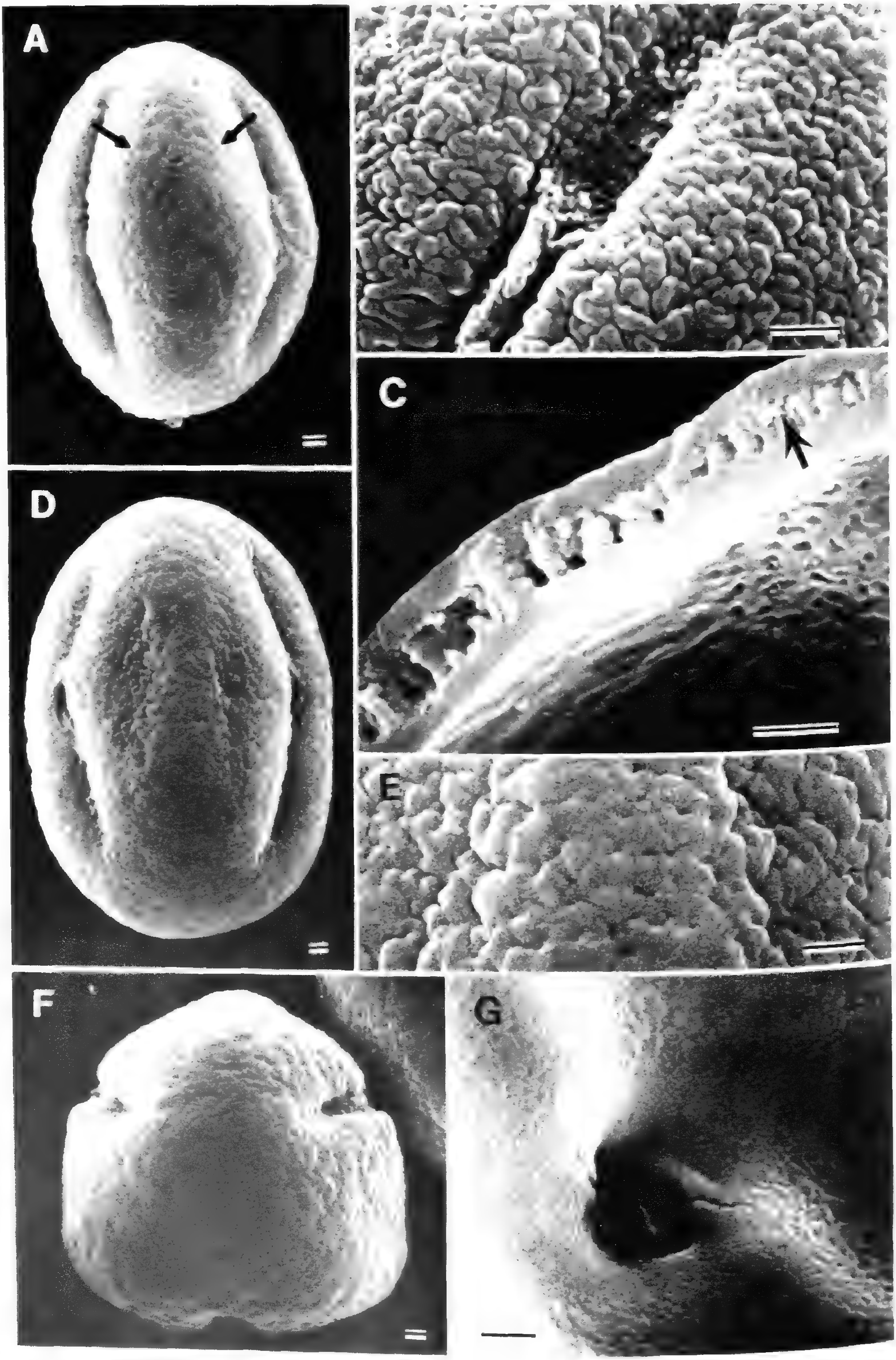
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the endexine is thin on the polar caps and thick in the equatorial zone. It is granular around the pores. The sole (= foot layer) on the other hand, is thick on the polar caps and thinner in the equatorial zone. In the porate fields of the equatorial zone, short columellae connect the verrucae to the sole. In the meridional ridge areas in *S. alba,* the columellae are longer and rather widely spaced, and support a tectum. At the polar caps, distinct columellae grade into areolate protrusions of the sole. The tectum is continuous on the polar caps, partially broken on the ridges (in *S. alba*) and occurs as separate verrucae over the porate fields. A granulate layer completely or partially fills the infractectal cavities. Muller emphasized that in *S. alba* well formed meridional ridges united with polar caps which markedly delineated apertural or porate fields, while in some grains of *S. caseolaris* the lack of meridional ridges did not confine the pores to fields, and in other grains, indistinct meridional ridges were found. The conclusion was that pollen of *S. alba* was more advanced in "... controlled harmomegathy than that of *S. caseolaris* and it is significant in this connection that the latter species has been proven to be phylogenetically older" (Muller, 1978a: 287–289).

Recognizing the taxonomic problems associated with distinguishing pollen of *S. caseolaris* from *S. alba* (Muller, 1969, 1978a), our SEM results show that at least superficially, *S. caseolaris* (Fig. 4E) appears more similar to Muller's SEM of *S. alba* (Muller, 1978a, Pl. II, fig. 1, 1981, Pl. VI, fig. 2) than to his SEM of *S. caseolaris* (Muller, 1978a, Pl. 1, figs. 1, 2, 1981, Pl. VII, fig. 3). The similarity is seen in the well-developed meridional ridges and apertural fields in our *S. caseolaris* and Muller's *S. alba.*

Subfamily Duabangoideae

Duabanga molucanna was examined with SEM (Fig. 4F). The pollen is triporate, radially symmetrical, and isopolar, and the shape is subprolate, elliptic in lateral view, and triangular-hexagonal in polar view. As in *Sonneratia,* three well-developed, meridional ridges alternating with three, oblong apertural (pore) fields are present, although the ridges are less pronounced in *Duabanga.* The surface is verrucate in the apertural fields and verrucate-rugulate on the ridges. Each apertural field has a protruding pore at its center. The surface of the pore membrane is similar to that of the surrounding field. The large, triangular polar caps have a psilate surface with a few punctae scattered over them.

Discussion

This report is in agreement with others which indicate that Lythraceae have the most diverse pollen morphology of the Myrtales. Much of this diversity centers on the apertural systems, for example, tricolporate grains are documented in *Physocalymma* (Cos Campos, 1964), *Pemphis, Rotala* (Guers, 1970), *Heimia* (Graham, 1977), *Adenaria, Pleurophora, Galpinia, Woodfordia* (Erdtman, 1971), and *Diplusodon* (Muller, 1981); heterocolpate grains with isomerous subsidiary colpi are present in *Lythrum* (Cos Campos, 1964; Guers, 1970; Heusser, 1971), *Rotala* (Guers, 1970), and *Peplis* (Heusser, 1971); grains with six subsidiary colpi occur in *Nesaea, Ammannia* (Erdtman, 1971; Cos Campos, 1964; Guers, 1970; Graham, 1977; Lobreau et al., 1969), *Crenea* (Erdtman, 1971; Muller, 1981), and *Lawsonia* (Muller, 1981), and grains with three meridional ridges that alternate with apertural fields are present in *Lafoënsia, Crenea,* and *Lagerstroemia* (Muller, 1981).

This pollen diversity is also common at the infrageneric level; for example, *Cuphea,* with over 250 species, shows a wide variation in morphology with pollen ranging from basic tricolporate-spheroidal to tricolporate-syncolpate-oblate triangular (Erdtman, 1971; Cos Campos, 1964; Graham et al., 1968; Graham & Graham, 1971; Guers, 1970. Graham et al. (1968) examined the pollen of 153 species of *Cuphea* in order to determine the extent of diversity among species as well as the potential use of pollen in the systematics of the genus. Starting with a basic oblate, tricolporate, striate, tectate grain, *Cuphea* was shown to be remarkably eurypalynous with great variation at sectional, subsectional, specific, and varietal levels. Twelve morphological categories representing eight sections and nine subsections were established. Of particular concern was the great number of pollen types present in bud clusters, buds, and individual anthers in pollen of *C. crassiflora, C. koehneana,* and *C. jorullensis.* These authors felt it was crucial to the interpretation of the pollen data to determine whether the pollen polymorphism suggested heterostyly or if a single basic pollen type with several variations was produced. As discussed by them (Graham et al., 1968: 1087–1088):

> The term "polymorphisme" has been used

to describe the multiple pollen types produced by individual plants or anthers in *Cuphea* (Cos Campos, 1964), but in our opinion use of the term has been preempted by a different situation existing in certain species of *Primula, Lythrum,* and other genera. As early as 1841, Vaucher noted three floral forms in *Lythrum,* and Darwin (1865) made a study of trimorphism in *L. salicaria* L. According to S. Graham (1964), 'In this species there are three style lengths and three sets of stamens of lengths corresponding to those of the styles. The forms are termed long-, mid-, or short-styled, depending on whether the style exceeds, lies between, or is shorter than the two whorls of stamens. Pollen differs in color, size and amount of stored starch in each of the three stamen lengths. The longest stamens have the largest grains, the anthers are green, and the pollen is filled with starch. The two shorter stamen lengths have yellow anthers and correspondingly smaller pollen containing less starch.' Thus *Lythrum salicaria* produces three morphologically distinct kinds of pollen and each is consistently associated with another feature of floral structure, viz., stamen length. In *Cuphea* the multiplicity of pollen types is greater (up to 12 in *C. strigulosa,* fide Cos Campos, 1964, p. 332), occurs within a single anther, and is not correlated with any other feature of the plant.

Therefore, in order to determine the nature of the multiple pollen types in *Cuphea,* size studies of single anther lactic acid preparations were conducted (Graham et al., 1968). The statistical data rather definitively gave support to the idea of normal pollen variations rather than to heterostyly.

A very comprehensive light microscope study by Lee (1979) included 26 genera and 62 species of Lythraceae pollen. Great emphasis was placed on the number of subsidiary colpi and three major pollen groups were established: (1) three-pseudocolpate (*Lythrum, Pemphis, Peplis, Physocalymma, Rhynchocalyx*); (2) six-pseudocolpate (*Ammannia, Capuronia, Crenea, Ginoria, Haitia, Lagerstroemia, Lawsonia, Nesaea, Pleurophora, Rotala*); and (3) non-pseudocolpate (*Adenaria, Alzatea, Cuphea, Decodon, Didiplis, Diplusodon, Galpinia, Grislea, Heimia, Lafoënsia, Rotala*). Based on number of subsidiary colpi this study did not support the tribal classification of Lythraceae (Koehne, 1903) into Lythreae and Nesaeae and their respective subdivisions. All had a mixture of the above three pollen groups. It was also concluded that, based on its non-subsidiary colpate pollen, *Alzatea,* which was originally placed near to *Physocalymma* and *Diplusodon* (Lourteig, 1965), is better assigned near to *Grislea* or *Adenaria.* Also, the placement of *Rhynchocalyx* near *Lawsonia* (Sprague & Metcalfe, 1937) was disputed on the basis of three subsidiary colpi and indistinct pores in the former and six subsidiary colpi and distinct pores in the latter. Both *Alzatea* (Graham, 1984) and *Rhynchocalyx* (Johnson & Briggs, 1984) are now regarded as separate monotypic families.

In the most recent study of Lythraceae, pollen of *Crenea, Diplusodon, Lafoënsia,* and *Lagerstroemia,* as well as *Sonneratia* (subfam. Sonneratioideae), were compared from a harmomegathic functional standpoint, and several structural pollen types were established (Muller, 1981). Starting with a tricolporate, longiax prototype, Muller (1981) postulated that the relationship between pollen form and function was indicative of adaptive radiation in the following directions or series: (1) in the first series there is a trend toward increasing the number of colpi (i.e., subsidiary colpi), (2) in the second series harmomegathic functions are transferred from individual colpi to flexible apertural fields alternating with meridional ridges, (3) in the third series harmomegathic functioning is transferred to prominent pores, and (4) in the last series harmomegathic functioning is lost in the ecto- and endoapertures.

The usefulness of pollen morphology in the taxonomy of Lythraceae is summarized by Muller (1981: 121–122) whereby he emphasizes the need:

> . . . for ecologic interpretations of function and for detailed ultrastructural studies to uncover those characters which reflect ancient phylogenetic links. This can perhaps best be illustrated by a discussion of possible affinities between the genera *Lafoënsia, Lagerstroemia,* and *Sonneratia,* assuming that it is decided to place the latter in the Lythraceae. If convergences in recent pollen morphology are stressed, *Lafoënsia* would be considered closely related, but the differences in ultrastructure and the heterocolpate nature in some pollen types of this genus would argue against affinity with *Sonneratia.* If fossil evidence is taken into account, the genus *Lagerstroemia* appears a much

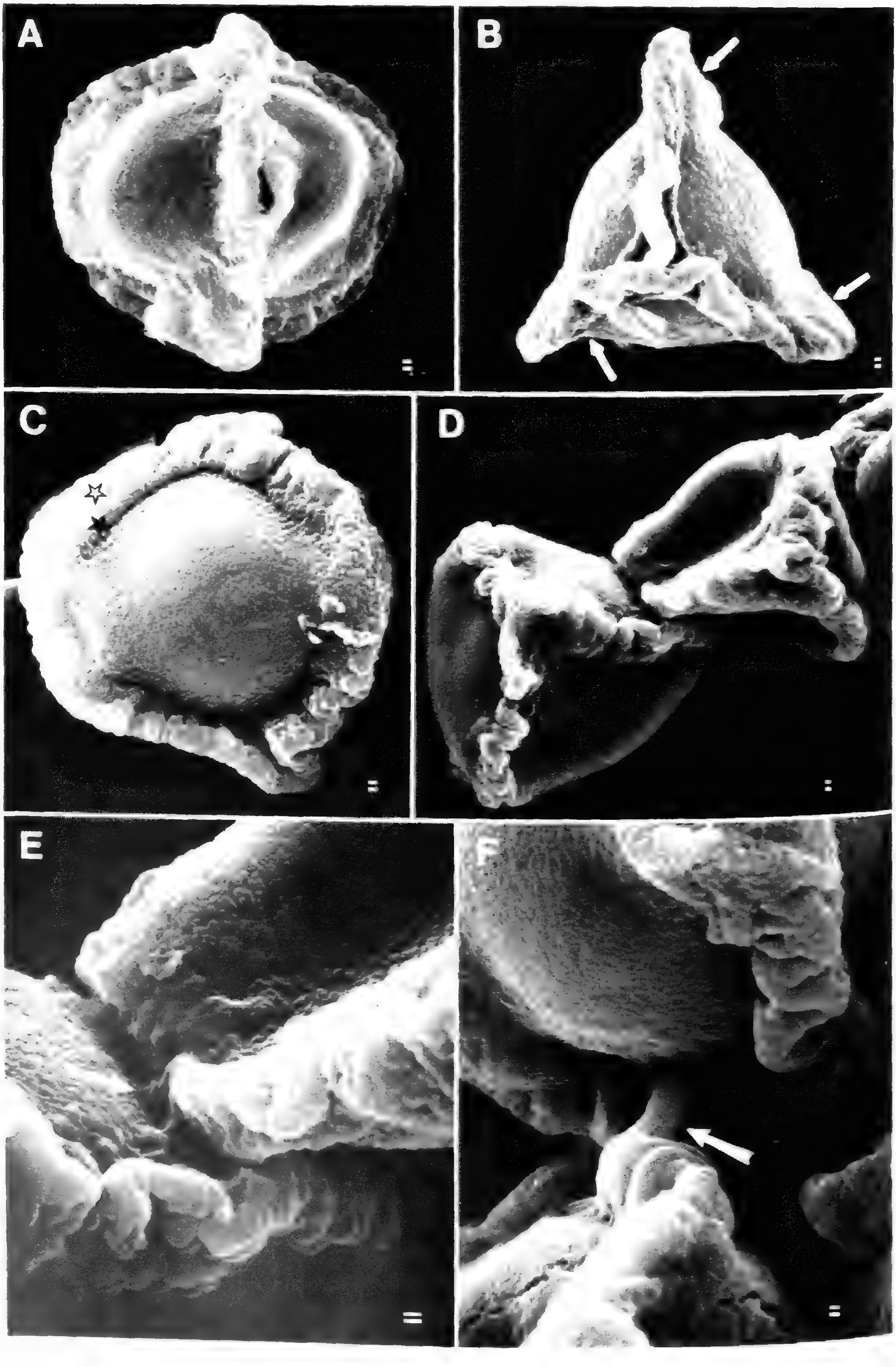

FIGURE 9. Scanning electron micrographs of Trapaceae pollen. A–F. *Trapa natans*.—A. (*Engelmann s.n*
Lateral view showing three meridional ridges. The vertically cracked area of the dome in the central ridge expose part of the colpus.—B. (*Engelmann s.n.*). Polar view. The three protruding domes (arrows) are covered b meridional ridges, which in turn, are united at the pole.—C. (*House 21708*). Lateral view of the area betwee two meridional ridges. Note that the ridges are continuous over the domed areas. The two-part nature of th

stronger candidate, although its present-day types show less similarity with living *Sonneratia* types, having diverged rather strongly from a postulated common ancestral matrix, although the peculiar granular deposits in the intercolumellar space appear to be present both in *Lagerstroemia* and *Sonneratia.*

In a more general sense and concerning the taxa examined in this study (Table 1), *Lafoënsia* is similar to *Sonneratia* of subfam. Sonneratioideae (Muller, 1969, 1978a, 1981, Fig. 4E); *Diplusodon* is similar to *Duabanga* of subfam. Duabangoideae (Muller, 1981; Fig. 4F); and *Lagerstroemia* bears resemblance to *Punica* (subfam. Punicoideae, Fig. 7D, F). These similarities strongly support the view of Dahlgren and Thorne (1984) that *Sonneratia, Duabanga,* and *Punica* should be regarded as separate subfamilies independently related to Lythraceae.

TRAPACEAE

Trapa japonica and *T. natans* were examined with SEM and TEM. Pollen from both species are basically similar. They are tricolpate, radially symmetrical, isopolar, spheroidal in lateral view; and triangular, goniotreme with obtuse corners, and straight to convex sides in the polar view (Figs. 9, 10). There are three meridional ridges on the grains. The surface is granular. The three apertures are protruding and swollen as elongated domes. In *T. japonica* these domes are better developed than in *T. natans*. Within them there is an elongated lens-shaped opening or colpus (Erdtman, 1943: 104–105, figs. 221–223) which is not visible in scanning electron micrographs as it is covered by the meridional ridge. The meridional ridges are formed by the folding of the ektexine and they are united at both poles where their fused triangular base is greatly enlarged (Figs. 9B, 10B). The ridges are taller at the poles; as they extend toward the equator in a folded, undulating manner their height decreases. The surface at the upper portion of the ridge near the poles is smooth with many channels. The lower portion shows a granular-verrucate surface (Fig. 9C). Toward the equator, the upper portion of the ridge is more rugulate-verrucate. Over the colpi, the upper portion of the ridge continues as a wide and not very tall, verrucate-granular band. The lower portion spreads over the swollen domes and is continuous with the surrounding interapertural areas (Fig. 10C–E). The surface of the domes is granular like that on the mesocolpia. It is not clear how the colpi open, but they appear to do so by an irregular splitting of the exine (Figs. 9A, 10D, F).

One sample of *Trapa natans* (*House 21708*) showed clumps of grains (polyads?) along with free monad grains. Exinous connections between the members of these "polyads" are present (Fig. 9D–F). However, there is no discernible specific arrangement of the polyad members, and the bridges connect different parts of the adjacent grains. This phenomenon is not yet clearly understood.

In *T. natans* the fine, granular surface of the grain is due to the tightly packed clavate and rod-shaped elements that form a very thin layer as seen in the thin sections (Fig. 11A–C). These clavae are either solid in their entire length, or show a fine, fuzzy granular layer below them. The exine structure of *T. japonica* (Fig. 11D) is similar to *T. natans* but the fuzzy layer is not evident. When cut obliquely, the clavate layer appears to be beaded and spongy. The thick, more or less solid layer below the fuzzy layer appears to be the endexine which becomes granular near the pores. The foot layer is difficult to recognize but it is perhaps present as a very thin layer between the fuzzy layer and the solid endexine. On the granular endexine near the pores, such a layer is clearly visible.

Sections passing through the ridge show that it encloses a cavity (star in Fig. 11A). The clavate layer (CL in Fig. 11A), along with the fuzzy granular layer (G in Fig. 11A), lifts to form the ridge wall. It continues as such for a short distance (i.e., the granular lower portion of the ridge as seen from the outside and designated by a solid

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ridge is indicated by the stars: the open star shows the upper part which is highly folded, the solid star shows the lower part which is granular.—D. One sample of *T. natans* (*House 21708*) contained numerous fused grains (polyads). A part of such a polyad is shown here.—E. (*House 21708*). Enlarged area of Figure 7D showing fusion of two adjacent exine surfaces.—F. (*House 21708*). Extexinous bridges appear to be another mechanism of pollen grain adhesion: the arrow shows a bridge connecting the meridional ridges of two pollen grains. Scales equal 1 μm.

star in Fig. 9C) and then becomes a more or less discontinuous, solid layer (the psilate upper portion of the ridge seen from the outside, the open star in Fig. 9C). The inner margin of this solid layer is highly irregular. Clavae at the base of the ridge cavity are large and often appear to be branched. Just above these clavae, the cavity is filled with circular or elongate ektexinous elements.

Discussion

Structurally, the meridional ridge of *Trapa* is different from that found elsewhere in the order. It is formed by the uplifting and folding of the ektexine and encloses a cavity. In contrast, the ridge found in Lythraceae (*Lagerstroemia*, see also van Campo, 1966; and *Punica*) and Onagraceae (*Ludwigia*) is formed by the increased thickness of the exine. Moreover, the ridge passes over the colpi in *Trapa*, whereas it alternates with the colpi in the other groups.

The distinctiveness of *Trapa* pollen was recognized by Erdtman (1971), who examined three species and felt that the genus merited family status. *Trapa* pollen shows a distant resemblance to Onagraceae pollen in surface sculpture and in the nature of the protruding apertures (see Figs. 50–53 of Onagraceae pollen below). Similarities to Onagraceae are further evident in the very thick endexine and indistinguishable, or at least, very thin, foot layer (compare Figs. 11 and 60–63).

OLINIACEAE

Olinia emarginata, O. radiata, O. rochetiana, O. vanguerioides, and *O. ventosa*, which comprise all species of the family, were examined with SEM and TEM. Pollen from all of the species is remarkably similar, both at the exomorphological and the endomorphological levels.

Pollen is tricolporate, radially symmetrical, ovoidal to subovoidal in lateral view (Muller, 1978b) and circular to triangular in polar view (Figs. 12, 13). It is heteropolar because the plane

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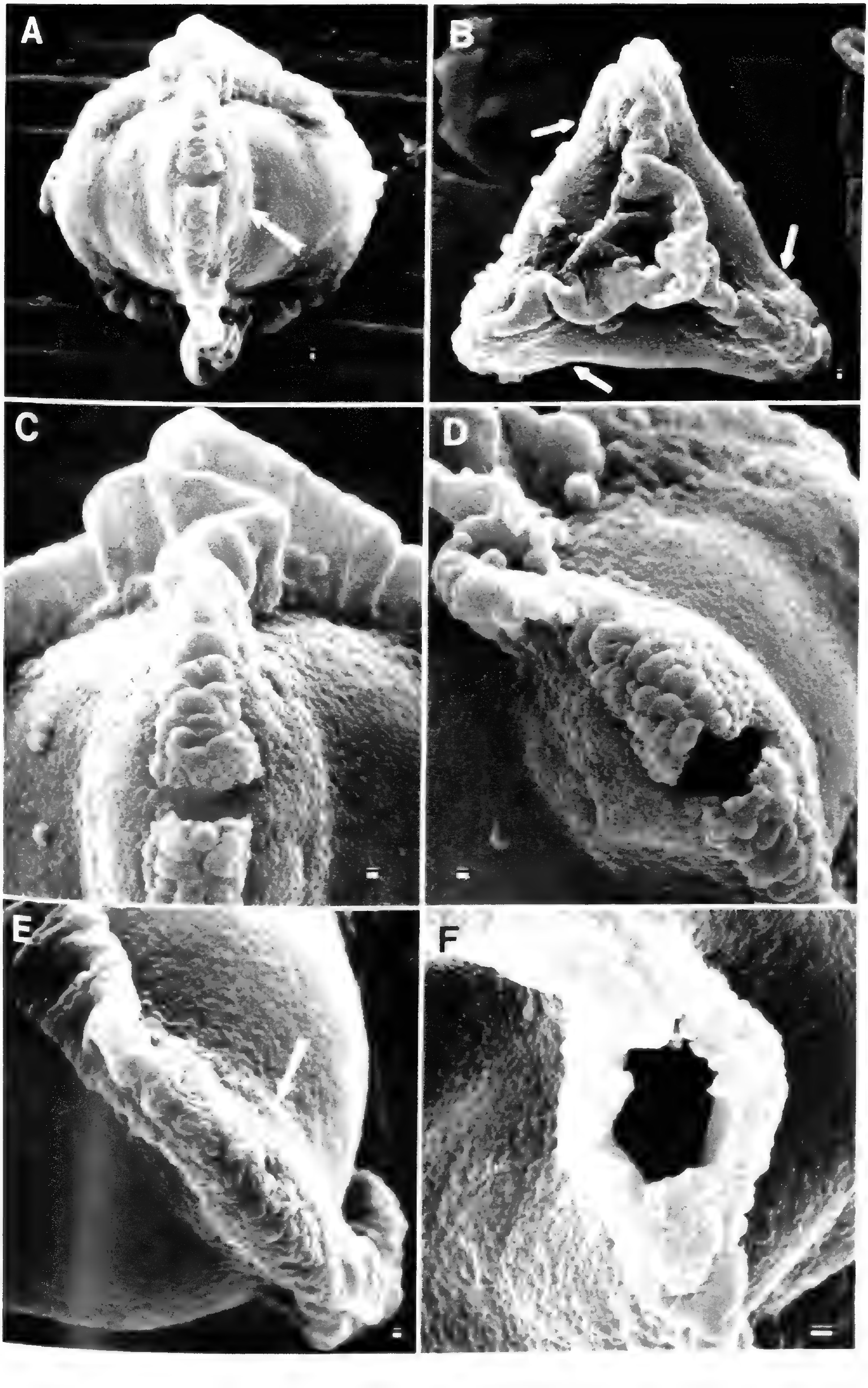
FIGURE 10. Scanning electron micrographs of Trapaceae pollen. A–D. *Trapa japonica*.—A. Lateral view with a domed area (arrow) and a meridional ridge that passes over it (in this grain the ridge is discontinuous at the equator). The maximum height of the ridge is at the poles. An elongated lens-shaped colpus is enclosed within this domed area which is only visible with light microscopy (Erdtman, 1943, Pl. XIII, figs. 221–223).—B. Polar view showing three protruding, domed areas (arrows) and the three ridges that unite at the poles.—C. Surface detail of A.—D. Close-up of domed area which has split horizontally. E, F. *Trapa natans*.—E. (MO 2532983). Close-up of domed area (arrow) which is less prominent than in *T. japonica* (see A, C, D). The ridge is composed of verrucate, granular elements.—F. (*Engelmann s.n.*). View showing irregular splitting of the ridge in the dome area. Scales equal 1 μm.

FIGURE 11. Transmission electron micrographs of Trapaceae pollen. A–C. *Trapa natans*.—A. (*Engelmann s.n.*). Section of the meridional ridge with cavity (star) and surrounding area. The upper portion of the ridge (within bracket) is essentially homogeneous; the lower portion has a clavate layer (CL) over an expanded granular layer (G). Large, solid, irregular elements (unlabeled arrow) are present at the base of the ridge cavity. The endexine (en) is extremely thick and uniform.—B. (*House 21708*). Section of colpus. The endexine is thick, granular (star), and finely lamellate. The absence of endexine (bracket) indicates a colpus which is a lens-shaped meridional area (not evident here, see Fig. 10A legend discussion). This area is covered by clavae and a coarsely granular layer (arrow).—C. (*House 21708*). Two sections of the mesocolpium. The ektexine is thin and composed of tightly packed clavae with a fuzzy basal layer (arrowhead). The foot layer cannot be readily distinguished and the endexine is thick (significantly thicker than the ektexine).—D. *Trapa japonica*. Section of a mesocolpium. In all transmission electron micrograph preparations of *Trapa* pollen, the endexine has shown little, if any, difference in electron density from the ektexine. Studies with fresh pollen should help to clarify this exine layer, as well as the presence or absence of the foot layer. Scales equal 1 μm.

FIGURE 12. Scanning electron micrographs of Oliniaceae pollen. A–C. *Olinia radiata*.—A. Polar view showing the polar face without subsidiary colpi.—B. Lateral view. The colpus is asymmetrical with the long segment extending into the polar face that lacks subsidiary colpi (lower half in this figure) and the short segment extending into the polar face that has the subsidiary colpi (a subsidiary colpus is indicated between arrows). An elliptic, lalongate endoaperture is discernible at the modal plane.—C. Polar view showing the polar face that has three subsidiary colpi alternating with the short segments of the colpi. D–F. *Olinia rochetiana* (*Chapman 996*).—D. Subpolar view. Arrow points to a partially visible subsidiary colpus.—E. Polar view. Subsidiary colpi with a rugulate-granular surface alternate with short segments of the colpi.—F. Polar view of the polar face that does not have subsidiary colpi. Scales equal 1 μm.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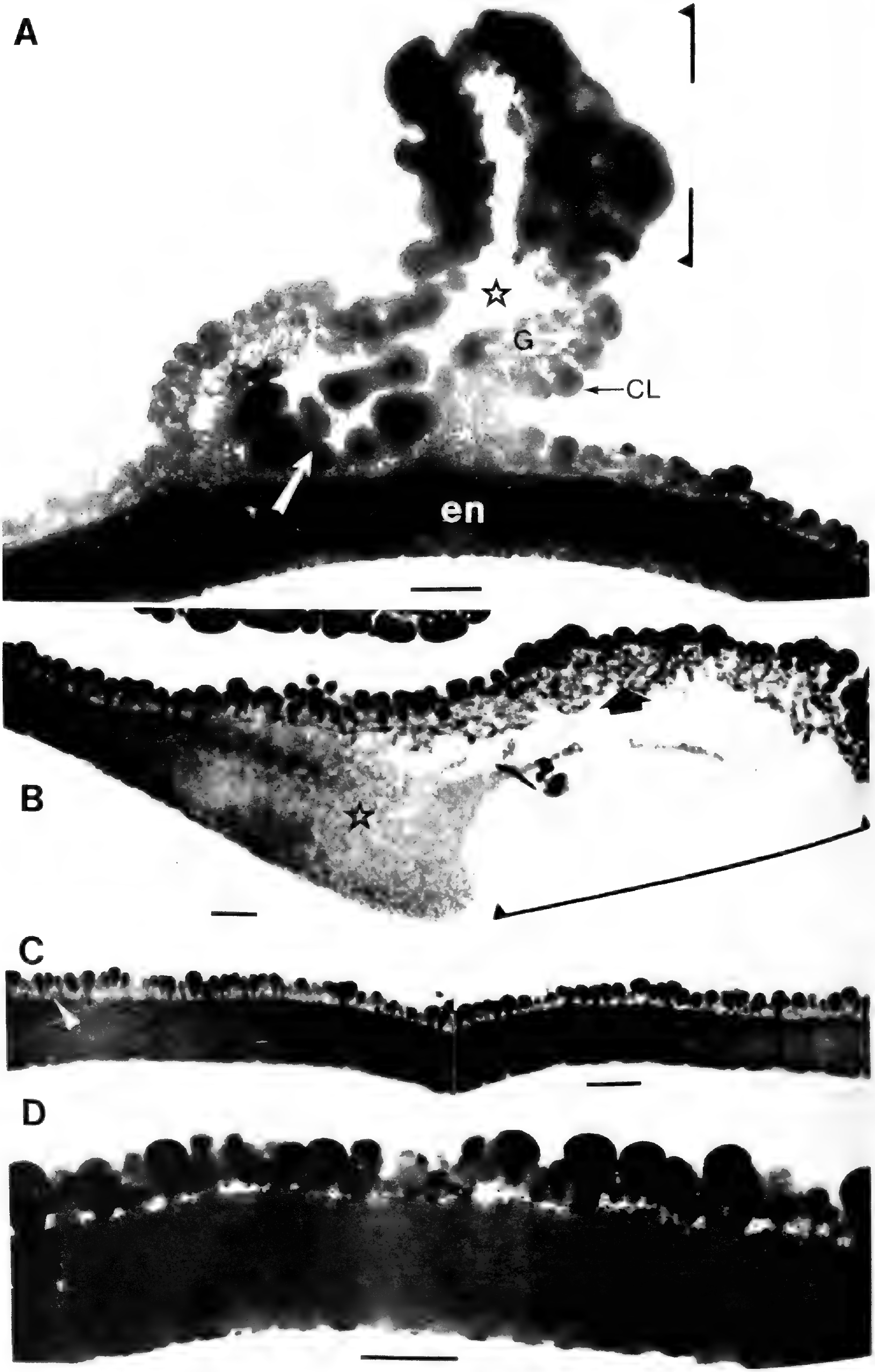
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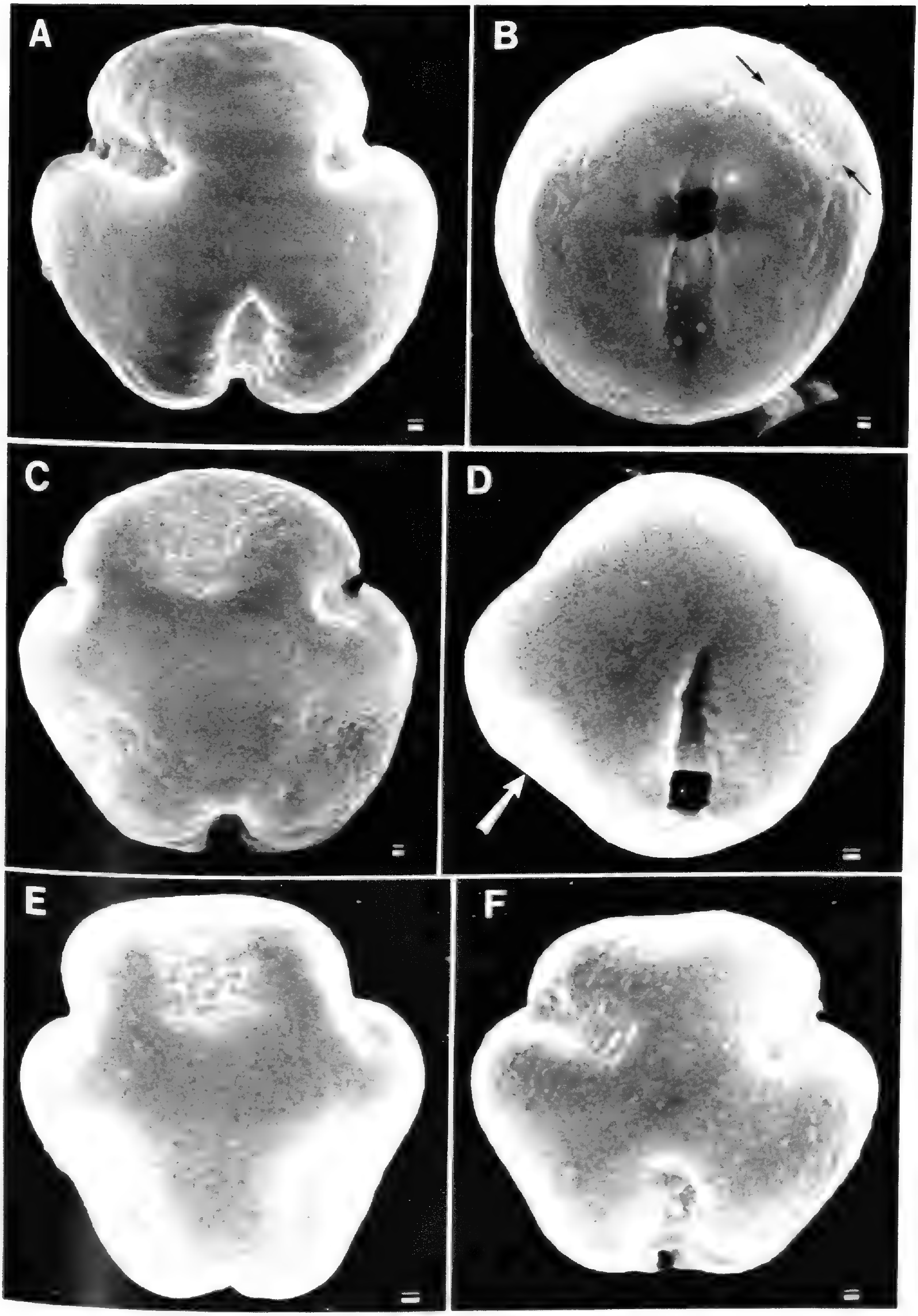
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that is perpendicular to the polar axis and situated at the greatest width of the grain divides it into two unequal polar faces. This is referred to as the modal plane (Muller, 1978b). The surface is usually psilate, or rarely psilate-punctate as in *O. radiata* (Fig. 12B, C).

The aperture system in *Olinia* is unusual in that the pollen grains have asymmetrical colpi and half subsidiary colpi (Patel et al., 1983b). Each colpus consists of a long segment and a short segment. The long segments are on the larger polar face of the grain (Fig. 12A, F) and they are slightly wider than the short segments (Fig. 13A, F). The surface of the colpi is smooth or granular and the ends are acute. An elliptic, lalongate endoaperture is present on the modal plane where the two segments of the colpus meet. The endoapertures are covered by extensions of the mesocolpia.

The second unusual character of *Olinia* pollen is the presence of three half subsidiary colpi which do not extend into both polar faces of the grain. They are present on the polar face that has the short segments of the colpi. Their surface is rugulate, with irregular, branched channels (Figs. 12C–E, 13A, D–F). They are often wide and therefore tend to resemble intercolpar concavities. This type of aperture system can also account for the grains being heteropolar. However, in some grains a size difference between the two polar faces is not evident and such grains are spheroidal in lateral view. Rarely, the subsidiary colpi extend slightly beyond the equator into the opposite polar face.

The ektexine in the mesocolpia consists of a very thick foot layer (Fig. 14) which becomes extremely thick toward the colpi (Fig. 14D, E). From the foot layer arise the thick and short, often prostrate or irregular-mound-like columellae which are usually narrower at their distal ends where they form an infratectal granular layer (Fig. 14C). The tectum is thick, uniform and

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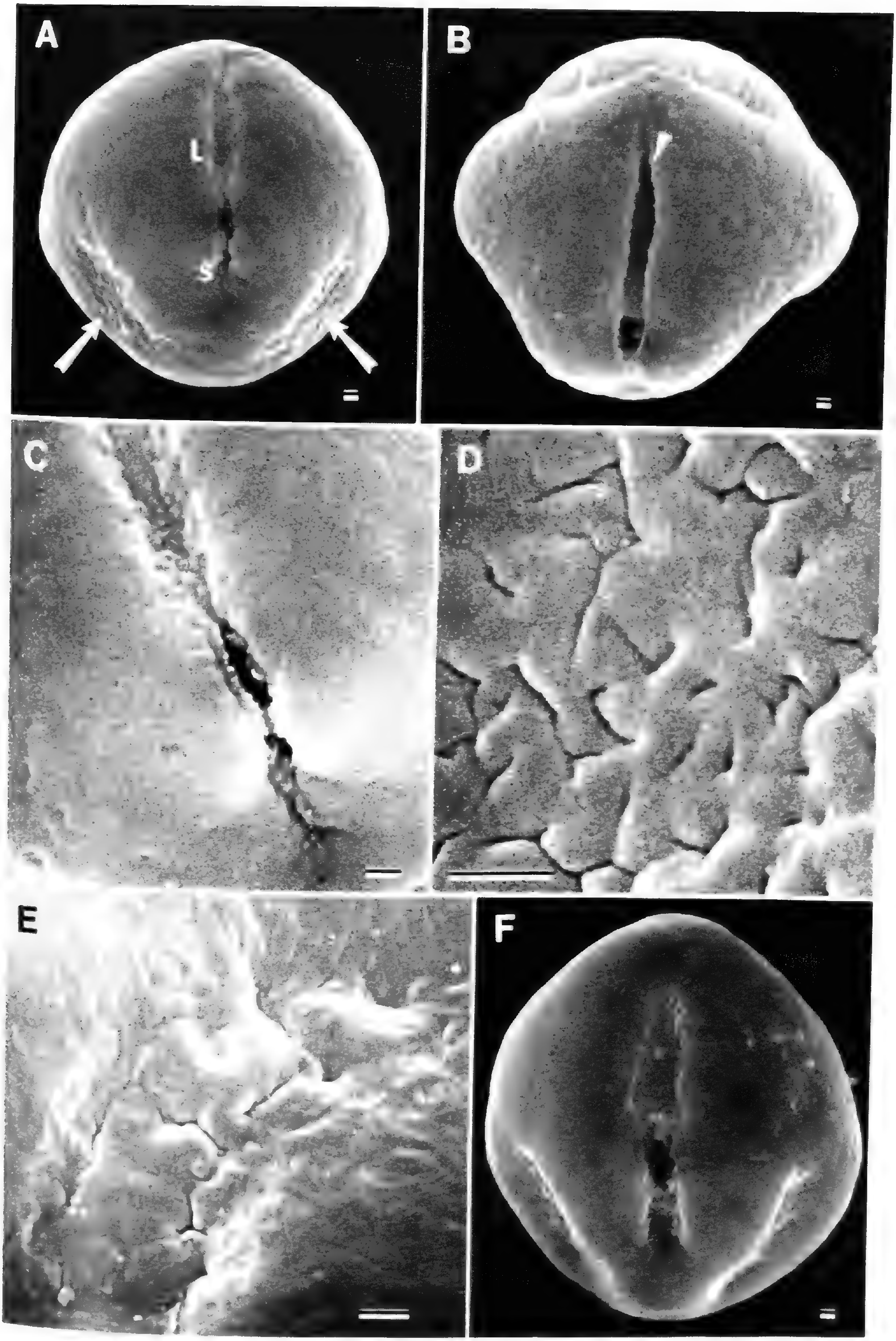
FIGURE 13. Scanning electron micrographs of Oliniaceae pollen. A–D. *Olinia emarginata.*—A. Lateral view clearly showing two subsidiary colpi (arrows) alternating with the short segment (S) of the colpus on the lower polar face. The upper polar face has the long segment (L) of the colpus and no subsidiary colpi.—B. Subpolar view showing the polar face that lacks subsidiary colpi. The long segments of the three colpi are visible (arrowheads).—C. Details of part of the colpus of A.—D. Details of a subsidiary colpus showing a rugulate smooth exine surface with irregularly branched channels. E, F. *Olinia ventosa.*—E. View of a subsidiary colpus with a rugulate surface.—F. Lateral view showing two subsidiary colpi, asymmetrical colpus, and psilate exine surface. Scales equal 1 μm.

FIGURE 14. Transmission electron micrographs of Oliniaceae pollen.—A. *Olinia rochetiana* (*Chapman 996*). Section of a subsidiary colpus. The rugulate surface elements described in scanning electron micrograph (Fig. 12E) appear in transmission electron micrograph as a dome-shaped tectum below which is an infratectal granular layer. Columellae are absent and the foot layer (arrowhead) is narrow but consistent over the subsidiary colpus. The endexine (en) is thick and uniform. B, C. *Olinia ventosa.*—B. Section of a mesocolpium. The tectum is uniform, thick, and imperforate. The arrow indicates an infratectal granular layer immediately beneath the tectum. Columellae are extremely short. The foot layer is nearly as thick as the tectum and the underlying endexine is uniform and approximately one-half the thickness of the foot layer.—C. Section includes a mesocolpium (right of bracket) and part of subsidiary colpus (left of bracket). Note the prominent thickening of the endexine under the subsidiary colpus.—D. *Olinia rochetiana* (*Greenway & Fitzgerald 14970*). Section through the aperture region including part of the endoaperture (at the left). The mesocolpial extension over the endoaperture is indicated by the bracket. The thick tectum is gently undulating and imperforate; the infratectal granular layer is prominent and is supported by short but stout columellae. The foot layer (fl) is thickened at the endoaperture margin; similarly, the endexine also is thickened as well as being markedly granular.—E. *Olinia emarginata.* Section passing through endoaperture. The arrow within the endoaperture indicates free "hanging columellae" and disrupted foot layer typical of this area. Note underlying granular endexine. The sections in Figure 14 resemble the sections of Penaeaceae pollen in Figures 26 and 27. Scales equal 1 μm.

FIGURE 15. Scanning electron micrographs of Combretaceae pollen. A–C. *Combretum cacoucia.*—A. Polar view showing three colpi with extensions of mesocolpia over the endoapertures and three subsidiary colpi.—B. Lateral view. The endoaperture appears as a wide elliptic shadow. The colpus membrane is granular. Two subsidiary colpi are also visible.—C. Finely regulate surface in polar view. D, E. *Thiola inundata.*—D. The exine surface consists of echinate plate-like areas that are delimited by channels and punctae. The colpus has echinae over the endoaperture (arrow).—E. Subpolar view showing three apertures and three subsidiary colpi.—F. *Quisqualis indica.* Polar view. The three subsidiary colpi are wide and appear to be more like intercolpar concavities.—G. *Calycopteris floribunda.* Sublateral view showing a subsidiary colpus (center) alternating with colpi. The exine surface is rugulate. Scales equal 1 μm.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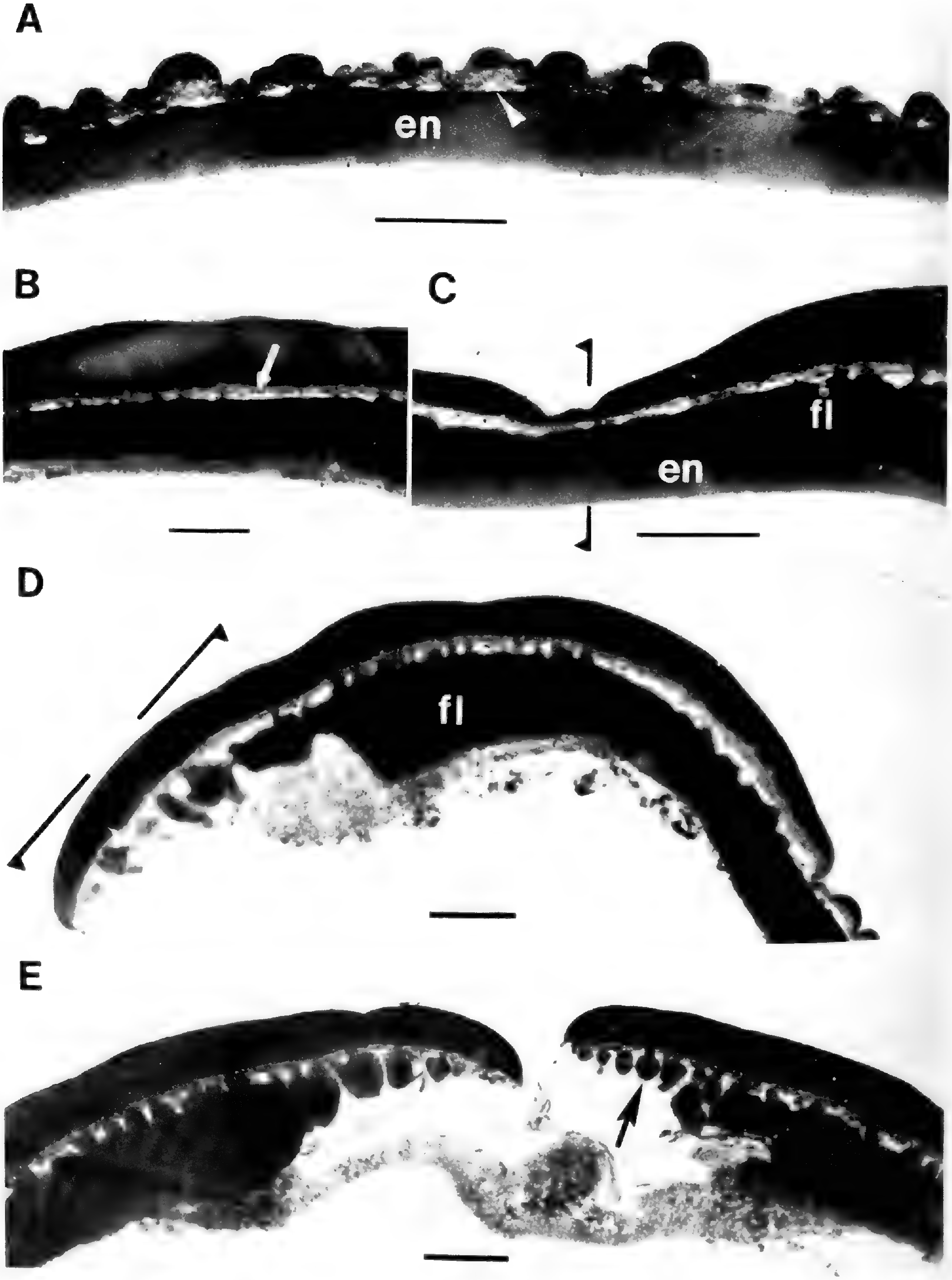
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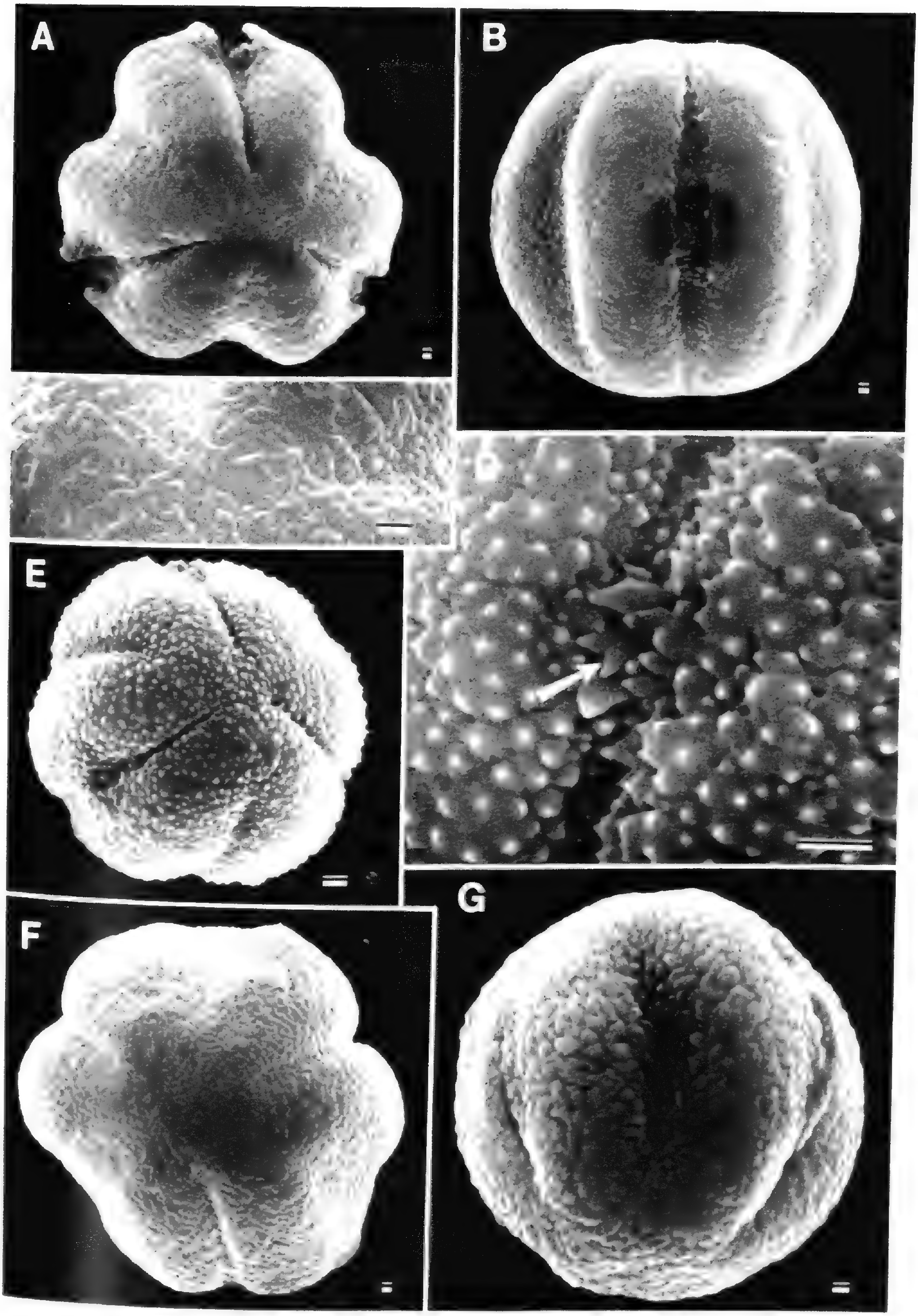
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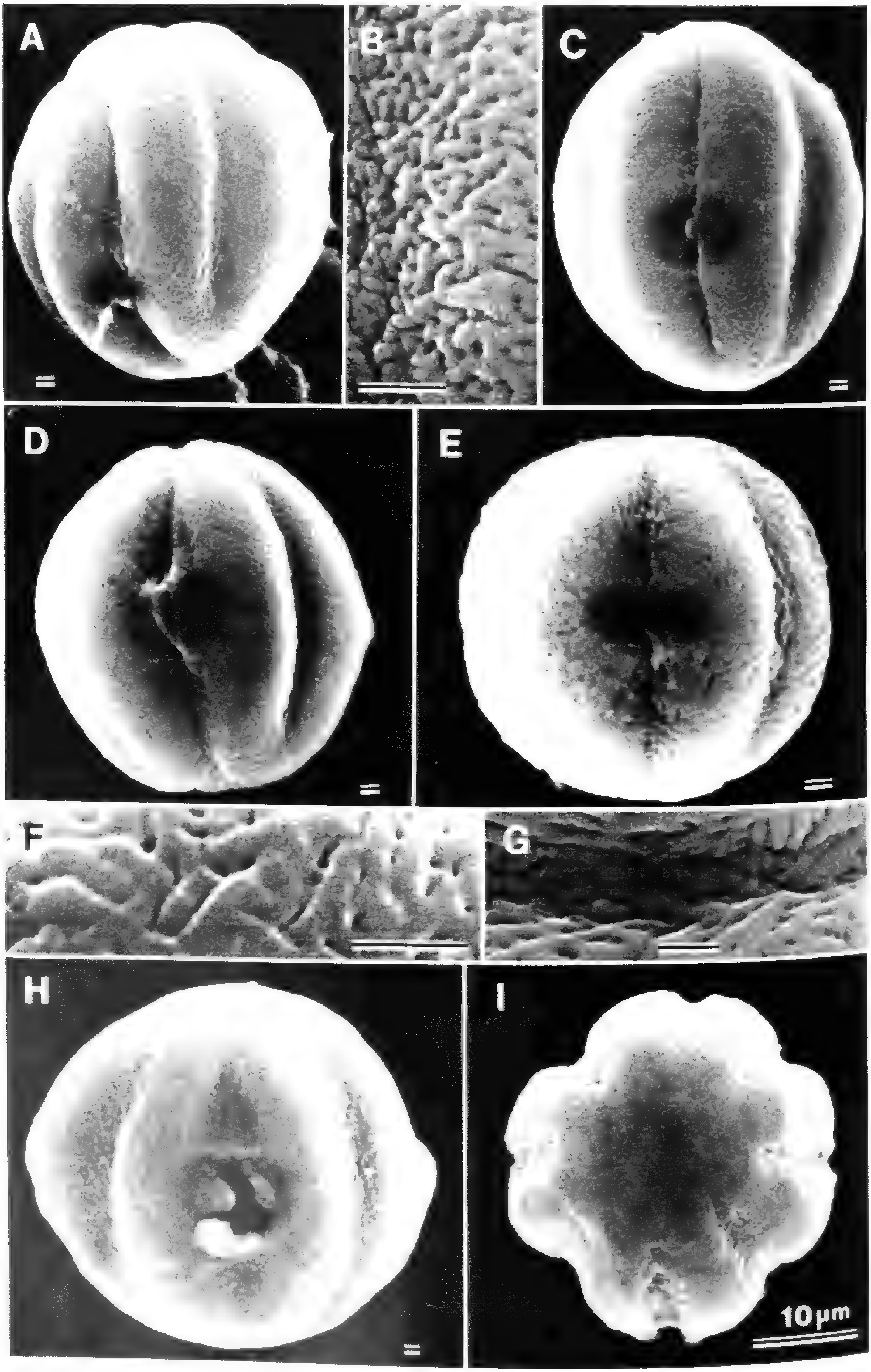
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without perforations (except in *O. radiata*). The upper margin of the tectum is smooth. The endexine is thin but becomes markedly thickened in the colpi and subsidiary colpi regions. The subsidiary colpi show a thinner, undulating, often dome-shaped tectum (Fig. 14A). The infratectal granular layer is continuous here. The columellae appear as short connections between it and the very thin, discontinuous foot layer.

In the area of the endoapertures (Fig. 14D, E), the endexine is granular. The extensions of the mesocolpia show a disrupted thin foot layer, and a thin infractectal granular layer below a slightly thinner tectum.

Discussion

Oliniaceae pollen grains differ from all other groups in their unusual aperture system, i.e., the asymmetrical colpi and the half subsidiary colpi (Patel et al., 1983b). All species examined are very similar in exo- and endomorphology and are difficult or impossible to distinguish. Erdtman (1971) reported three subsidiary colpi in *O. cymosa* (= *O. ventosa*) and that subsidiary colpi were absent in *O. volkensii* (= *O. rochetiana*). Samples of *O. rochetiana* examined in this study show half subsidiary colpi and asymmetric colpi, similar to the other species of *Olinia*. Since half subsidiary colpi occupy small areas on only one polar face and differ only slightly in surface sculpturing from the surrounding exine, it is not surprising that their true nature is difficult to reveal with the light microscope. However, in the light micrograph of *O. rochetiana* by Archangelsky (1971, fig. 1, Pl. 20), three half subsidiary colpi are clearly visible.

Apart from the unusual apertures, the colpi and the half subsidiary colpi, pollen of Oliniaceae resembles that of Penaeaceae. Pollen from both families compare very well in the psilate surface as well as in exine structure, that is, there is a very thick foot layer and tectum, and a thin columellae layer with an infratectal granular layer extending over the subsidiary colpi (compare Fig. 14 to Fig. 26).

COMBRETACEAE

Pollen is tricolporate (rarely tetracolporate in *Quisqualis parviflora* and *Terminalia oblonga*), mostly heterocolpate (except in *Buchenavia, Laguncularia,* and *Strephonema*), radially symmetrical, and isopolar. The shape of the grains is spheroidal to subprolate in lateral view and circular to hexagonal in polar view. In the heterocolpate species, the colpi are long, with acute ends, and with a granular surface. Syncolpate grains are present in *Combretum farinosum* (Fig. 16D) and in *T. oblonga* (Fig. 16A) where the syncolpus is undulating like the line on a tennis ball. Endoapertures are lalongate and elliptic in *Combretum cacoucia* (Fig. 15B), *C. laxum* (Fig. 16E), and *Lumnitzera racemosa* (Fig. 19D), circular in *Poivrea coccinea* (Fig. 19C) and *Anogeissus acuminata* (Fig. 18D), and circular to elliptic in *Bucida macrostachya* (Fig. 17A), *C. farinosum* (Fig. 16D), *Q. parviflora* (Fig. 16H), and *T. oblonga* (Fig. 16A, C). Subsidiary colpi are wide and often united at the poles in *Ramatuella argentea* (Fig. 17E), *Terminalia catappa, T. oblonga* (Fig. 16A), and *Guiera senegalensis* (Fig. 18E).

Diverse surface sculpture patterns are present in the family. The surface is striate in *Combretum laxum, Guiera,* and *Poivrea.* In *C. laxum* (Fig. 16E, G), thick striae are separated by short, punctate channels while the surface of the subsidiary colpi is striate-rugulate. In *Guiera* (Fig. 18E), small groups of short striae cross, and the subsidiary colpi appear to have a finer, granular, striate surface. *Poivrea* (Fig. 19C) shows bands of fine, long striae while the subsidiary colpi are striate-rugulate.

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FIGURE 16. Scanning electron micrographs of Combretaceae pollen. A–C. *Terminalia oblonga.*—A. Lateral view of a tetracolporate, syncolpate grain. The subsidiary colpi are also united. Note that the two visible endoapertures (arrows) are situated at two different horizontal planes of the grain.—B. Finely rugulate surface of a mesocolpium (right half) near a subsidiary colpus (left half). The rugulate-punctate surface becomes finer in the subsidiary colpus.—C. Lateral view of a tricolporate grain.—D. *Combretum farinosum.* Lateral view of a tricolporate, syncolpate grain. E, G. *Combretum laxum.*—E. Lateral view. Note the striate-rugulate surface.—G. Striate-rugulate surface of a subsidiary colpus and striate surface of the two surrounding mesocolpia.—F. *Combretum trifolium.* Surface of a mesocolpium showing interwoven muri and punctae. Compare with Figure 15C. H, I. *Quisqualis parviflora.*—H. Lateral view of a tricolporate grain.—I. Polar view of a tetracolporate grain. Compare with Figure 23B. Unless otherwise indicated, scales equal 1 μm.

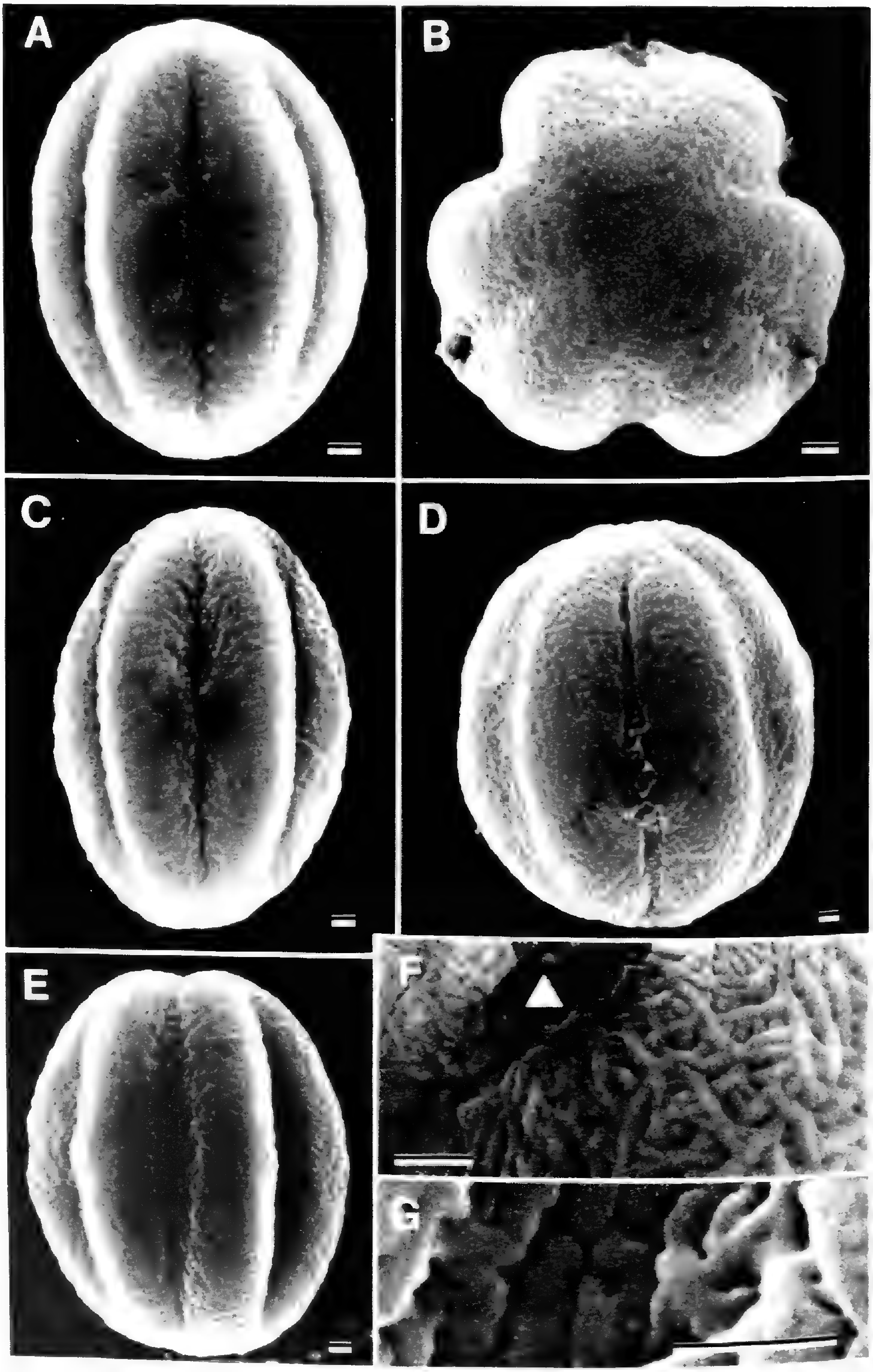


FIGURE 17. Scanning electron micrographs of Combretaceae pollen.—A. *Bucida macrostachya*. Lateral view showing a colpus (at center) and two subsidiary colpi.—B. *Conocarpus erecta*. Polar view with mesocolpial extensions over the apertures. Also note three subsidiary colpi.—C. *Pteleopsis myrtifolia*. Lateral view with a colpus (at center) and two subsidiary colpi.—D. *Terminalia edulis* (*Quisumbing Q-2156*). Lateral view with a colpus (at center) and two subsidiary colpi. E, G. *Ramatuella argentea*.—E. Lateral view with a subsidiary colpus (at center) and two colpi.—G. Surface detail of a rugulate subsidiary colpus.—F. *Terminalia catappa*. Surface of the mesocolpium near colpus and endoaperture (triangle). Elongate, branched, interwoven elements form the surface sculpture. Scales equal 1 μm.

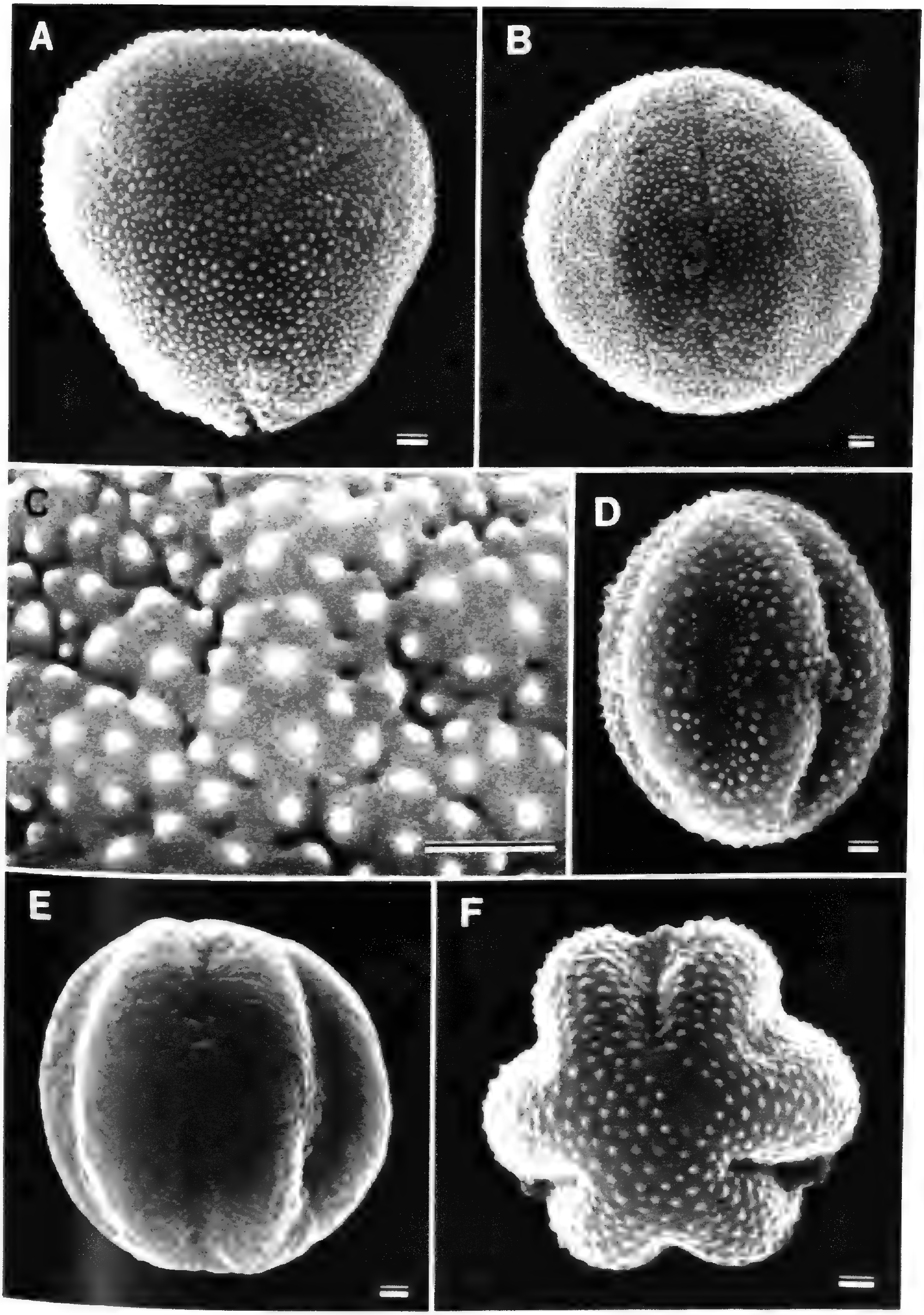


FIGURE 18. Scanning electron micrographs of Combretaceae pollen. A–C. *Buchenavia suaveolens.*—A. Polar view. Colpi are narrow (subsidiary colpi are absent) and the surface is echinate.—B. Lateral view.—C. Details of the echinate-punctate surface. Note similar surface in *T. inundata* (Fig. 15E). D, F. *Anogeissus acuminata.*—D. Lateral view with a wide and granular subsidiary colpus (at center). Two colpi are also evident. The exine surface is echinate.—F. Polar view showing colpi alternating with subsidiary colpi.—E. *Guiera senegalensis.* Lateral view with a colpus at center and two subsidiary colpi. The exine surface is striate. Scales equal 1 μm.

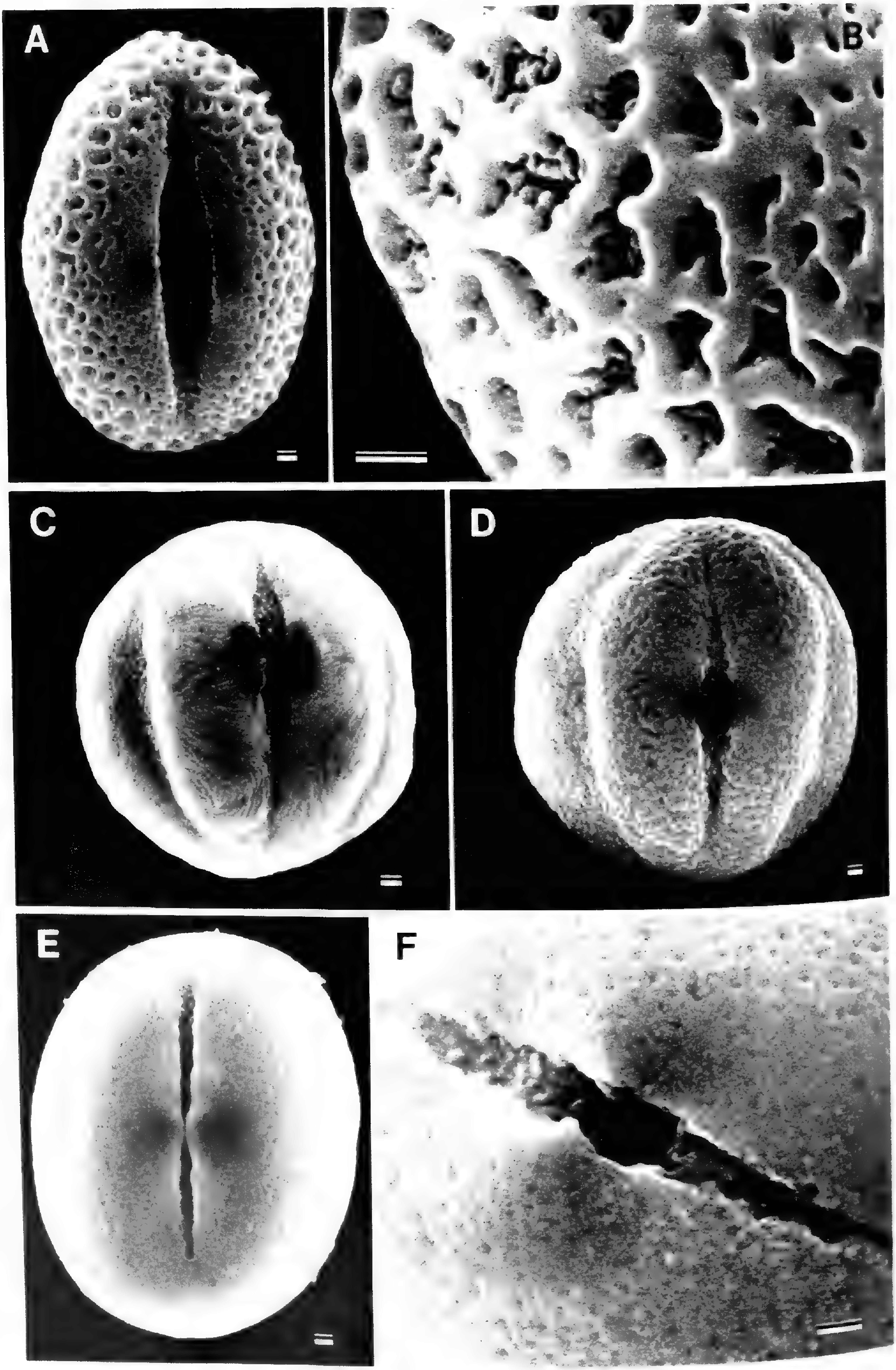


FIGURE 19. Scanning electron micrographs of Combretaceae pollen. A, B. *Strephonema pseudocola* —A. Lateral view. The exine surface is reticulate with lumina becoming smaller toward the colpus. The par opened endoaperture is lalongate-elliptic. —B. Detail of the surface showing rod-shaped elements in the la

In *Combretum trifolium* (Fig. 16F), *Quisqualis indica* (Fig. 15F), *Ramatuella* (Fig. 17E, G), *Terminalia edulis* (Fig. 17D), and *T. catappa* (Fig. 17F) narrow, elongated, and branched muri appear tightly interwoven. Punctae are present in the channels separating the muri. The pattern is finer at the margins of the mesocolpia and less so at the poles where it appears to be punctate in *Q. indica.* The surface of the subsidiary colpi is rugulate-granular in *Ramatuella* (Fig. 17G), and *C. trifolium.* In *Q. indica* (Fig. 15F), the subsidiary colpi are wider than in the other taxa examined and their surface appears to be similar to the surface on the meso- and apocolpia. In *Q. parviflora* the surface is psilate (Fig. 16H, I).

In *Combretum farinosum, Bucida* (Fig. 17A), *Pteleopsis myrtifolia* (Fig. 17C), and *Conocarpus erecta* (Fig. 17B), the surface is more or less smooth to finely rugulate with punctae and short channels that are more pronounced at the margins of mesocolpia. In *Combretum cacoucia* (Fig. 15A–C) and *Terminalia oblonga* (Fig. 16A–C) the surface is finely rugulate. The subsidiary colpi in *C. farinosum, C. cacoucia, Bucida, T. oblonga,* and *Conocarpus* show a coarse, granular-verrucate surface.

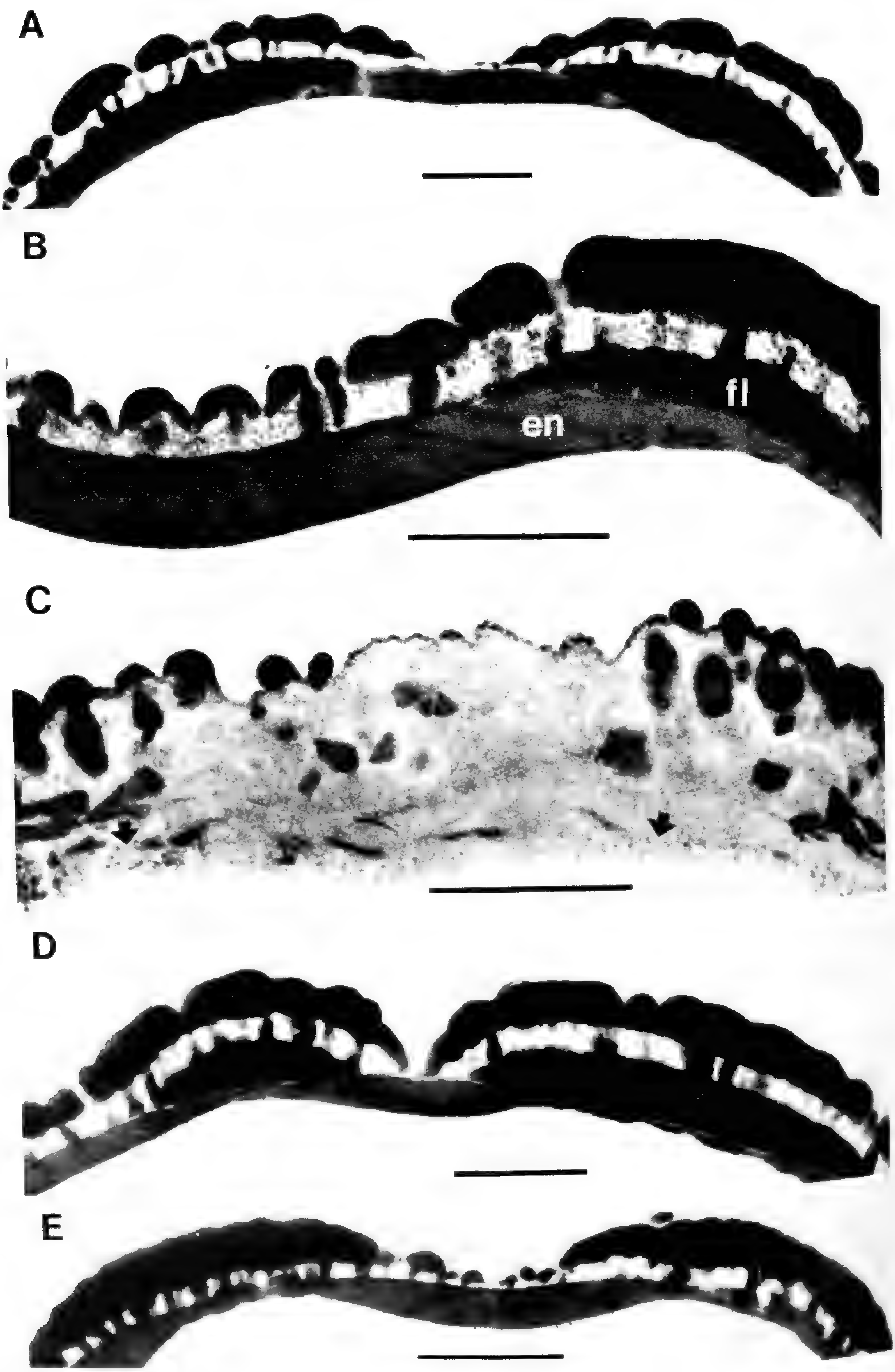
A rugulate surface is present in *Lumnitzera racemosa* (Fig. 19D) and *Calycopteris floribunda* (Fig. 15G). In *Lumnitzera* the surface of the subsidiary colpi appears to be granular, whereas in *Calycopteris* it is rugulate-verrucate with slightly smaller rugulate elements than on the mesocolpia.

Anogeissus acuminata (Fig. 18D, F) and *Thiola inundata* (Fig. 15D, E) have an echinate surface with spinules. In *Anogeissus,* scattered spinules are situated on a smooth surface. They become smaller and more numerous at the margins of the mesocolpia. They are also present on the subsidiary colpus and the colpus membrane over the endoaperture. In *Thiola,* in addition to the spinules, there are large punctae and deep channels that also have punctae. Due to the channels, the surface appears to consist of more or less fused "plates or islands" (Fig. 15D). The surface of the subsidiary colpi also has spinules and punctae. Longer spinules are present on the colpus membrane over the endoapertures.

Buchenavia suaveolens, Laguncularia racemosa, and *Strephonema pseudocola* are without subsidiary colpi. In *Buchenavia* (Fig. 18A–C), grains are spheroidal in lateral view and triangular in polar view. The surface is echinate, like that in *Thiola,* with spinules, punctae, and deep channels forming "plates." Colpi are long and narrow. Endoapertures are lalongate. In *Laguncularia* (Fig. 19E, F), grains are subprolate in lateral view and circular to triangular in polar view. The surface is smooth with minute punctae. Colpi are medium length and have a granular surface. Extensions of mesocolpia are present over the lalongate endoapertures. *Strephonema* (Fig. 19A, B) is subprolate in lateral view and circular to triangular in polar view. The surface is reticulate with large lumina which gradually decrease in size toward the margins of the mesocolpia. The large lumina are filled with rod-like, short elements, some of which are free standing while others extend diagonally and fuse with the muri. Colpi are long and wide with obtuse ends and a granular surface. Endoapertures are lalongate and elliptic.

Bucida (Fig. 21B), *Combretum laxum* (Fig. 20A), *C. farinosum* (Fig. 20B, C), *Conocarpus erecta* (Fig. 20E), *Lumnitzera* (Fig. 21C), *Quisqualis pellegriniana* (Fig. 21D), *Strephonema* (Fig. 21A), and *Terminalia edulis* (Fig. 20D) were examined with TEM. In general, the tectum is thick and the columellae are short, erect and simple. In *Q. pellegriniana,* some columellae appear to ramify into two or three straight, fine, very short segments just below the tectum. A well-developed infratectal granular layer is present in *Lumnitzera.* The foot layer is well developed in all taxa. It is either uniform in thickness (*C. farinosum, Strephonema, Lumnitzera*) or dome-shaped with the lower margin straight and the upper margin convex (*Bucida, T. edulis, C. laxum*). In *Conocarpus,* in some areas the foot layer is dome-shaped and in others it is thin and

lumina.—C. *Poivrea coccinea.* Sublateral view. The circular endoaperture (dark area) is clearly evident through the ektexine. The colpus and subsidiary colpus membrane are granular. The surface is striate (cf. with striate surface of *G. senegalensis,* Fig. 18E).—D. *Lumnitzera racemosa.* Lateral view showing colpus with open endoaperture and two subsidiary colpi. The surface is rugulate. E, F. *Laguncularia racemosa.*—E. Lateral view. Colpi are narrow with a granular surface (subsidiary colpi are absent).—F. Surface detail near an open endoaperture. The surface is punctate. Scales equal 1 μm.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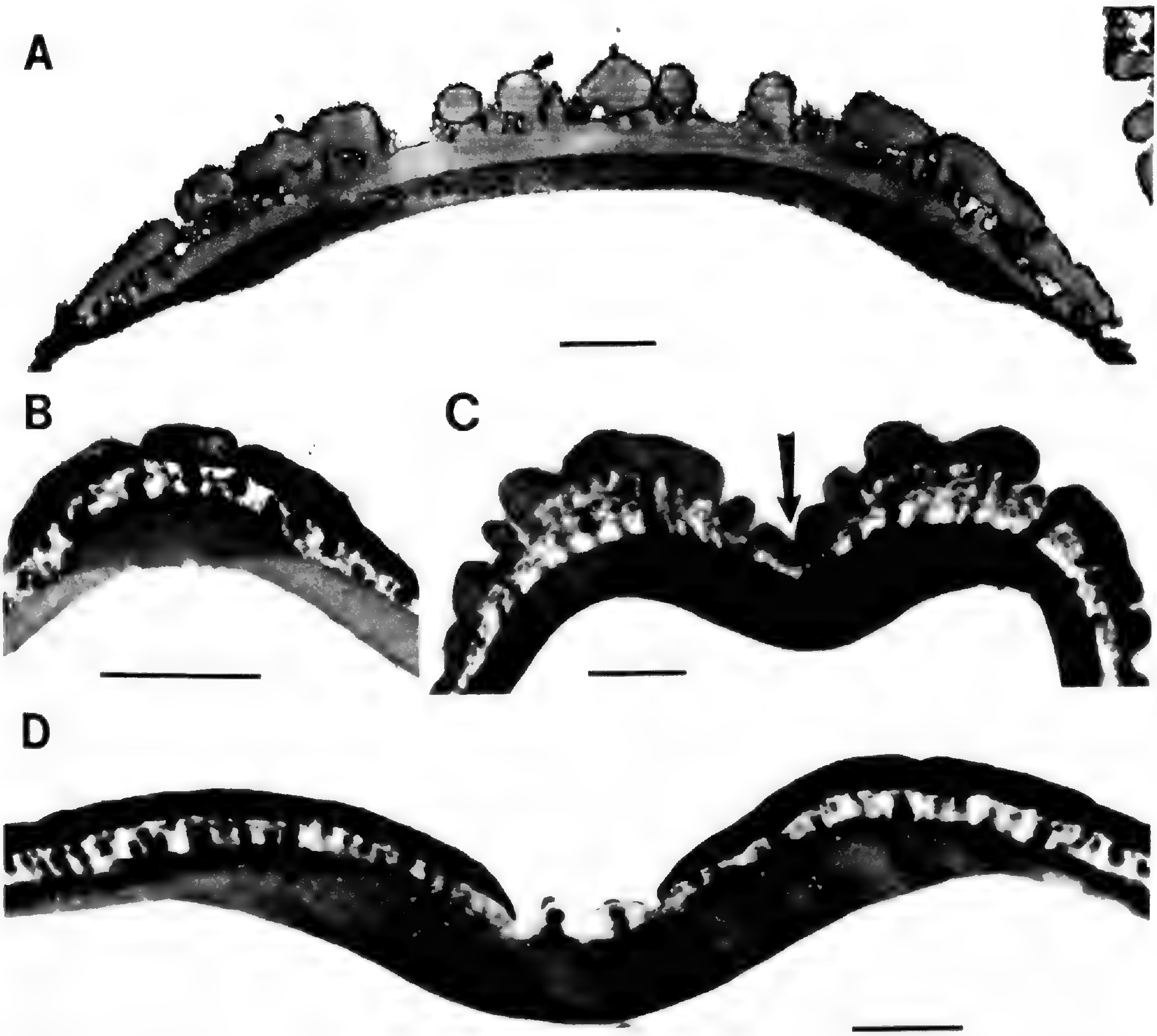

FIGURE 21. Transmission electron micrographs of Combretaceae pollen.—A. *Strephonema pseudocola.* Section of a mesocolpium. The thinning of endexine on both ends indicates the presence of endoapertures. The black outline of the ektexine is due to the precipitation of osmium.—B. *Bucida macrostachys.* Section of a mesocolpium between a colpus and a subsidiary colpus.—C. *Lumnitzera racemosa.* Section passing through two mesocolpia and an end of a subsidiary colpus (arrow). Note a thick infratectal granular layer.—D. *Quisqualis pellegriniana.* Section of a colpus and adjacent mesocolpia. Note the fine granular layer that covers the ektexinous processes on the colpus and extends into the intercolumellar spaces of the mesocolpia. Scales equal 1 μm.

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FIGURE 20. Transmission electron micrographs of Combretaceae pollen.—A. *Combretum laxum.* Section of two adjacent mesocolpia and a colpus or subsidiary colpus between them. Note the thick, dome-shaped foot layer. The endexine is thicker below the colpus (or subsidiary colpus) than below the mesocolpia. B, C. *Combretum farinosum.* Section through a portion of a mesocolpium (on the right) and a portion of a subsidiary colpus (on the left). Note the granular matrix between the columellae. In the subsidiary colpus the tectum is thin and discontinuous and the endexine (en) is greatly thickened. At the mesocolpial margin the thick foot layer (fl) tapers toward the subsidiary colpus.—C. Aperture region showing a thick, granular matrix covered by a fine membrane. Columellae are embedded in the matrix: the lower ends are free and the upper ends protrude as granules on the colpus surface. The foot layer appears to consist of fragmented lamellae. The endexine (arrows) is suggested by a slightly coarser, granular, narrow band at the lowermost margin.—D. *Terminalia edulis* (*Bernardo 23688*). Section includes two mesocolpia and the colpus or subsidiary colpus between them. Note the dome-shaped foot layer (identical to *C. laxum,* A). A "white line" separates the foot layer and endexine. The endexine is thick below the colpus or subsidiary colpus and thin elsewhere.—E. *Conocarpus erecta.* Section of two mesocolpia and the subsidiary colpus between them. Although the foot layer is thin and discontinuous in this section, other sections show it to be dome-shaped in the mesocolpia (similar to A and D). The striking dome-shaped foot layer in A and D is also present in Melastomataceae pollen (see Figs. 36–38). Scales equal 1 μm.

straight. The endexine is very thin in the mesocolpia, and thick at the colpi and subsidiary colpi. In *Strephonema,* it is either uniform or thin at the middle of the mesocolpia. At the margins of the mesocolpia near the subsidiary colpi, the foot layer usually terminates but sometimes appears to continue as a very fine layer over the endexine of the subsidiary colpi. In *T. edulis, C. laxum, Conocarpus,* and *Q. pellegriniana,* finer and shorter columellae and a thinner tectum are present in the subsidiary colpi region. In *C. laxum,* the endexine is granular near the endoaperture and granular-lamellate in *Conocarpus* and *T. edulis.*

Combretum farinosum (Fig. 20B, C) differs from the other three taxa examined with TEM in having a very fine granular matrix in the columellae layer. This matrix fills the spaces between the columellae and is also continuous in the subsidiary colpi region. Here, the columellae are shorter, the tectum is slightly thinner and often discontinuous as domes forming the granular and rugulate units on the exine surface. The granular matrix is also continuous in the colpi. The columellae are embedded in it with their protruding distal ends forming the granules of the colpus surface. The tectum appears as a thin film on the matrix (Fig. 20C). Irregular, broken lamellae of ektexinous material (foot layer?) are also present. The thick endexine also appears granular in the vicinity of the endoaperture and is difficult to distinguish from the granular matrix. In *Q. pellegriniana* (Fig. 21D) such a granular matrix is present over the thick endexine of the colpus. It extends into the intercolumellar spaces of the adjacent mesocolpia for a short distance, but is not as well developed as in *C. farinosum.*

Discussion

Apparently, there are no modern detailed studies of Combretaceae pollen (see Thanikaimoni, 1984). The following, therefore, is presented as a brief background of the basic morphology. Erdtman (1971) described *Quisqualis indica* as having colpi alternating with "pseudocolpoid thin walled areas" and made favorable comparisons with *Cacoucia, Combretum,* and *Terminalia.* He also described *Laguncularia racemosa* but did not mention the presence or absence of subsidiary colpi. *Quisqualis latialata* was described as having three pseudocolpi by Lobreau et al. (1969). Sowunmi (1973) described pollen of *Combretum glutinosum, Terminalia avicennioides, T. glaucescens, T. macroptera,* and *T. superba* in general as resembling each other and possessing a characteristic shape, aperture system, and exine. All grains were noted to have "colpoid streaks" (= subsidiary colpi) alternating with colpi. Lastly, Guers (1974) and Guers et al. (1971) also showed a fundamental similarity in the pollen of *Combretum aculeatum, C. grandiflorum, C. lokele, C. micranthum, C. platypterum, C. smeathnianni, Conocarpus erectus, Pteleopsis diptera, Terminalia glaucescens, T. laxiflora,* and *T. superba.* All had colpi alternating with subsidiary colpi. The one SEM illustrated, that of *Combretum aculeatum,* is similar to *C. cacoucia* (Fig. 15A–C).

From a comparative point of view, Erdtman (1971: 117) felt that "Pollen grains ± similar to those in Combretaceae occur in Melastomataceae (cf. also Lythraceae and Penaeaceae). The grains in Haloragaceae, Hernandiaceae, Myrtaceae, Punicaceae, Sonneratiaceae, etc. are ± different."

Our SEM observations indicate several rather distinctive groups. *Combretum* (Figs. 15A–C, 16D–G), *Quisqualis* (Figs. 15F, 16H, I), *Bucida* (Fig. 17A), *Conocarpus* (Fig. 17B), *Pteleopsis* (Fig. 17C), *Terminalia* (Figs. 16A–C, 17D, F), *Ramatuella* (Fig. 17E, G), *Guiera* (Fig. 18E), *Poivrea* (Fig. 19C), and *Lumnitzera* (Fig. 19D) comprise the first group and are similar in having colpi alternating with subsidiary colpi. Various surface patterns are repersented in this group. A second group, characterized by the presence of an echinate surface and subsidiary colpi is represented by *Thiola* (Fig. 15D, E) and *Anogeissus* (Fig. 18D, F). A third group, consisting only of *Buchenavia* (Fig. 18A–C) has an echinate surface but lacks subsidiary colpi. A fourth group, also consisting of just one taxon, *Laguncularia* (Fig. 19E, F), has a punctate surface and lacks subsidiary colpi. The fifth group, represented only by *Strephonema* (Fig. 19A, B), also lacking subsidiary colpi, is completely different from all other Combretaceae in having a reticulate surface. Interestingly, this reticulate surface has not been observed in any other member of the Myrtales core families. In contrast to the diverse surface morphology are the TEM data which indicate structural similarities. However, these data are limited at present. *Strephonema* is so distinct from all other members of Combretaceae that it might best be considered to constitute a separate subfamily Strephonematoideae, as suggested by Dahlgren and Thorne (1984) and others.

Generalized comparisons with pollen from the core families essentially agree with Erdtman's (1971) suggestions given above. The pollen included in our first group shows broad resemblances to some Penaeaceae, some Melastomataceae, and some Crypteroniaceae. Genera of Penaeaceae with these resemblances are: *Endonema* (Fig. 25A, C), *Brachysiphon* (Figs. 24A, B, 25D), and *Sonderothamnus* (Fig. 25E). Genera of Melastomataceae that show these resemblances are: *Memecylon* (Fig. 31E), *Mouriri* (Fig. 31F), *Trembleya* (Fig. 32A), *Osbeckia* (Fig. 32B), *Tibouchina* (Fig. 32C), *Tristemma* (Fig. 32D), *Votomita* (Fig. 32E), *Marumia* (Fig. 33A), *Dissotis* (Fig. 33C, D), *Acanthella* (Fig. 33E), and *Dissochaeta* (Fig. 33F). Genera of Crypteroniaceae that show these resemblances are *Axinandra* (Fig. 28B) and *Dactylocladus* (Fig. 28A, C, E). The other four groups do not, at least to this time, show resemblances to other Myrtales. In TEM, the very markedly domed foot layer of Combretaceae (Fig. 20A, B, D, F) was recognized also in Melastomataceae (*Tristemma,* Fig. 37A; *Trembleya,* Fig. 37B; *Osbeckia,* Fig. 37D, E; *Marumia,* Fig. 38A), and Penaeaceae (*Penaea,* Fig. 26A; *Sonderothamnus,* Fig. 26B; *Glischrocolla,* Fig. 27A; *Stylapterus,* Fig. 27E). Furthermore, the entire exine structure of *Lumnitzera* compares favorably with that in Penaeaceae (*Glischrocolla,* Fig. 27A).

ALZATEACEAE

In *Alzatea verticillata,* the only member of this monotypic family, pollen is tricolporate, radially symmetrical, isopolar, spheroidal to subprolate in lateral view, hexagonal to triangular (goniotreme with obtuse corners and straight sides) in polar view (Fig. 4B, D). The surface is psilate except in the elliptical areas at the middle of the mesocolpia where it is psilate-punctate; these areas are slightly depressed and possibly represent subsidiary colpi or intercolpar concavities. Colpi are long, with obtuse ends, and a smooth surface. A wide, coarse margin is present around the colpus. Endoapertures are lalongate. Extensions of the mesocolpia are present over the endoapertures.

On the sides of the mesocolpia (i.e., around the punctate, elliptic areas) the foot layer is well developed in the form of continous "hills" or "domes" (Fig. 6B). The thick tectum has a smooth, slightly undulating upper margin. Its lower margin corresponds in shape to that of the foot layer, resulting in an undulated or a zig-zag columellae layer between the tectum and the foot layer. The short, erect columellae are unbranched. The endexine is relatively thin. At the middle of the mesocolpia (Fig. 6C), where the surface is punctate, the exine becomes thinner: the foot layer at first becomes thinner and then is present only as wide bases of the columellae; the columellae slightly increase in height and become branched; and the thin tectum has large perforations and an infratectal granular layer. The endexine increases in thickness as it does in taxa with subsidiary colpi.

Near the colpi, the endexine is very thick and the foot layer tapers and is present either as a thin layer or is absent. At the margins of the mesocolpia, the very short columellae and the thin tectum with an infratectal granular layer are present on this thick endexine. The endexine is granular in the vicinity of the endoapertures.

Discussion

The punctate areas at the middle of the mesocolpia in *Alzatea* are suggested as being incipient subsidiary colpi by Muller (1975). The exine indeed is thinner in this area as is shown in the TEM (Fig. 6C). As mentioned by Muller, *Alzatea* pollen is comparable with that of those species of *Rotala* that show indistinct subsidiary colpi (Guers, 1970). Pollen of this genus has been characterized as (1) three colporate, (2) three colporate with indistinct subsidiary colpi, and (3) three colporate with distinct subsidiary colpi (Guers, 1970). Further, a spectrum of heterocolpateness also occurs within a single species (Cos Campos, 1964). *Alzatea* pollen may also be compared with *Physocalymma* (Cos Campos, 1964; van Campo in Lourteig, 1965). A detailed examination involving electron microscopy of these two lythraceous genera (i.e., *Rotala* and *Physocalymma*) should be instructive.

Alzatea has been treated in several taxonomic systems (see Dahlgren & Thorne, 1984). Muller (1975) treated it in Crypteroniaceae following the system of van Beusekom-Osinga and van Beusekom (1975), as an ancestral tricolporate type, deriving from it the bisyncolporate bilateral *Crypteronia* type and the heterocolporate triradiate *Dactylocladus* type. In a sense, he considered *Alzatea* to have the relatively unspecialized pollen common in some angiosperm families, particularly in Lecythidaceae, Rhizophoraceae, Combretaceae, and Lythraceae (including Pun-

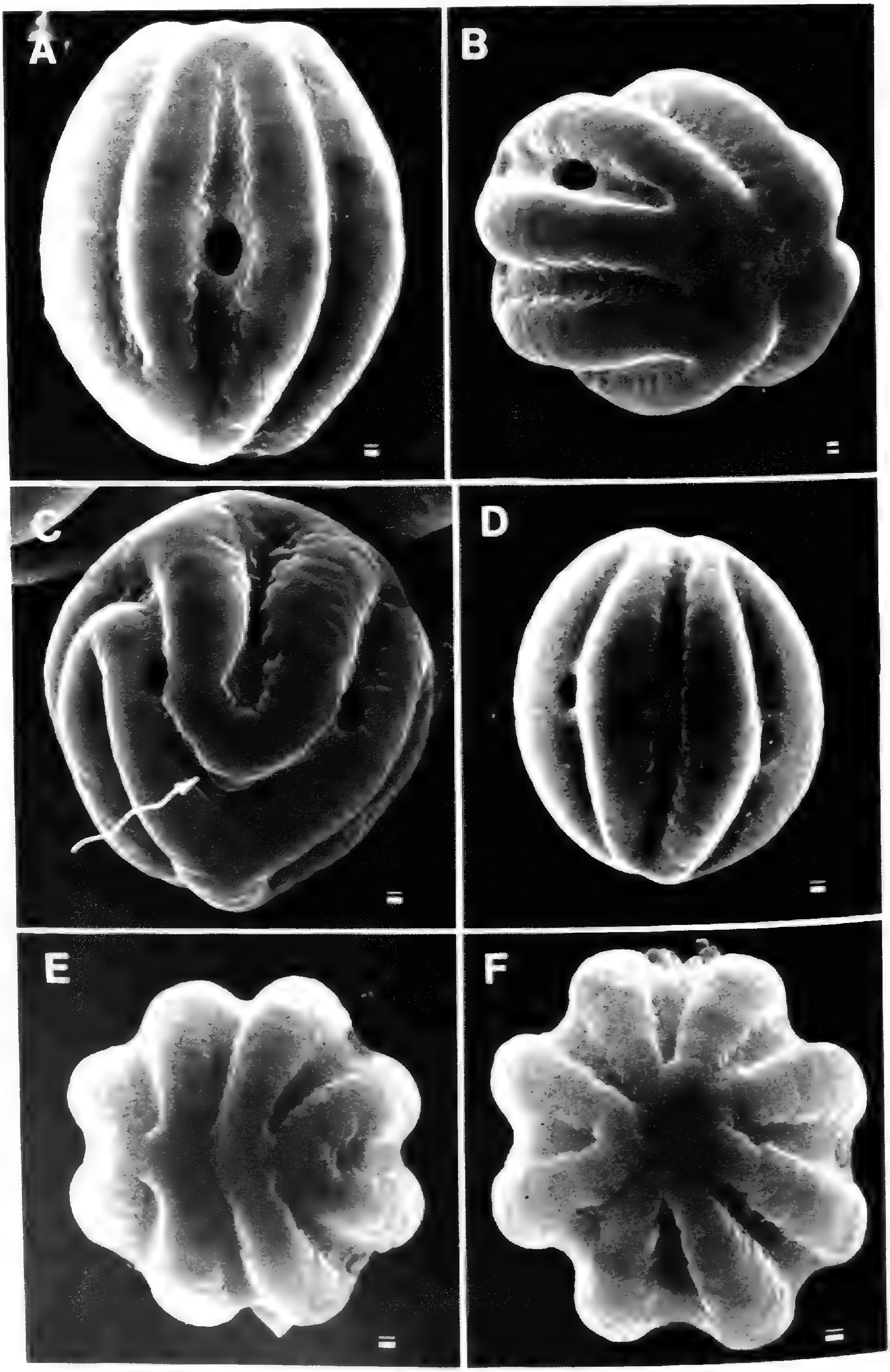

FIGURE 22. Scanning electron micrographs of Penaeaceae pollen. A–C. *Penaea mucronata.*—A. Lateral view with colpus at center. Note the irregular development of the subsidiary colpi. The subsidiary colpus at the left appears to unite with other subsidiary colpi at the top pole while at the bottom pole it is free. The subsidiary colpus at the right appears to unite with subsidiary colpi at both poles (see also Fig. 25E). The exine surface is psilate; in the colpus and subsidiary colpus it is granular.—B. Subpolar view showing portions of four colpi alternating with four subsidiary colpi. Note the patch of granular exine at the pole. See also scanning electron micrograph of Dahlgren (1971, fig. 2).—C. Sublateral view showing colpi united to form an undulating syncolpus (arrow). Note the two circular endoapertures as well as fused subsidiary colpi (i.e., "synsubsidiary colpi"). D–F. *Stylapterus ericoides.*—D. Lateral view with a subsidiary colpus at center. Grains similar to C of *P. mucronata*.

icoideae, and in Lythroideae particularly *Adenaria, Pemphis, Pehria, Pleurophora, Physocalymma, Woodfordia,* and some *Rotala*).

Although the pollen of *Alzatea* is generalized, we feel that it is very similar to that of Chrysobalanaceae (Patel et al., 1983a) in shape as well as in surface features. Endomorphically, it is similar to *Dactylocladus, Axinandra,* and Chrysobalanaceae (see also Corynocarpaceae, Nowicke & Skvarla, 1983) in having a zigzag columellae layer.

RHYNCHOCALYCACEAE

Rhynchocalyx lawsonioides was examined with both SEM (Fig. 4A, C) and TEM (Fig. 6D). Pollen is tricolporate, heterocolpate with three subsidiary colpi, radially symmetrical and isopolar, spheroidal in lateral view and triangular-hexagonal in polar view. The surface is coarse, with many punctae and irregular channels. Colpi are long, narrow with acute ends, and have a granular surface. Endoapertures are lalongate. Mesocolpial extensions are present over the endoapertures. Subsidiary colpi are wide and in some grains they appear to be united at the poles. Their surface is similar to that of the mesocolpia. Thin section (Fig. 6D) shows the foot layer to be well developed in the mesocolpial regions; columellae are numerous, erect, and branched distally, often forming an infratectal granular layer (see Muller, 1975). The tectum is thick, perforate, with an undulating upper margin that is locally discontinuous and separated into domes. The endexine is very thin and has an irregular lower margin. At the colpi and subsidiary colpi the endexine is thick, columellae are shorter, and the tectum and foot layer are thinner than in the mesocolpial areas. In the region of the endoaperture, the endexine is granular, the foot layer is tapered and the shorter columellae and thin tectum lie directly on the endexine. Additional comments regarding *Rhynchocalyx* pollen can be found in the discussion of Lythraceae and Crypteroniaceae.

PENAEACEAE

Pollen grains are tricolporate in *Brachysiphon rupestris* (Fig. 25D), *B. fucatus* (Fig. 24B), *Endonema laterifolia* (Fig. 25A, C), *Sonderothamnus petraeus* (Fig. 25E), *S. speciosus* (Fig. 24F), and *Saltera sarcocolla* (Fig. 24C, D). They are tetracolporate in *Penaea cneorum* (Fig. 23B, D), *P. mucronata* (Fig. 22A–C), and *Stylapterus ericoides* (Fig. 22D–F), and 5-colporate in *Glischrocolla formosa* (Fig. 23A, C). Some tetracolporate grains were also present in *Brachysiphon fucatus* (Fig. 24A), *Glischrocolla,* and *Sonderothamnus speciosus,* whereas 6-colporate grains were observed in *Saltera* (Fig. 24E). Pollen of these taxa are heterocolpate with isomerous subsidiary colpi or intercolpar concavities (in *Saltera* and *Glischrocolla*) alternating with colpi. They are radially symmetrical, isopolar (except some in *Penaea, Saltera,* and *Stylapterus,* see below), spheroidal to subprolate in lateral view, and circular to hexagonal (in tricolporate species) or circular to octagonal (in tetracolporate species) in polar view. The surface is psilate in *Penaea, Brachysiphon, Saltera, Glischrocolla, Sonderothamnus,* and *Stylapterus,* with few pits and punctae. In *Endonema* it is rugulate with punctae.

Colpi are long, with acute (*Brachysiphon rupestris, Penaea, Saltera,* and *Stylapterus*) or obtuse (*Endonema, B. fucatus, Glischrocolla, Sonderothamnus*) ends, the pollen surface is granular with the exception of *Brachysiphon rupestris, Sonderothamnus speciosus,* and *Saltera,* where it is smooth. Asymmetric colpi similar to those in *Olinia* were common in *Glischrocolla* (Fig. 23C), *Saltera* (Fig. 24D), and *Sonderothamnus* (Fig. 24F). Endoapertures in such grains are located either on the equator, or on one polar face. The shape of these grains is spherical except in *Saltera* which also has some ovoidal, heteropolar grains. Endoapertures are circular in *Penaea* and *Stylapterus,* and lalongate-elliptic with two lateral extensions in *Endonema* (Fig. 25B) and *Brachysiphon.* In *Endonema,* extensions of the mesocolpia are present over the endoapertures. They are either very small or absent in *Brachysiphon* and are absent in the remaining taxa. In *Sonderothamnus* and *Saltera,* the endoapertures are slightly elliptic-lalongate and in *Sonderothamnus petraeus* (Fig. 25F) the colpus membrane often persists as a horizontal bar over the

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also occur in *S. ericoides* but are not herein illustrated.—E,F. Polar views. Four colpi alternate with four subsidiary colpi. The subsidiary colpi are united at the poles in various combinations. For example, in E the two opposite subsidiary colpi are united while in F all four are united. The exine is smooth with few punctae and channels. Scales equal 1 μm.

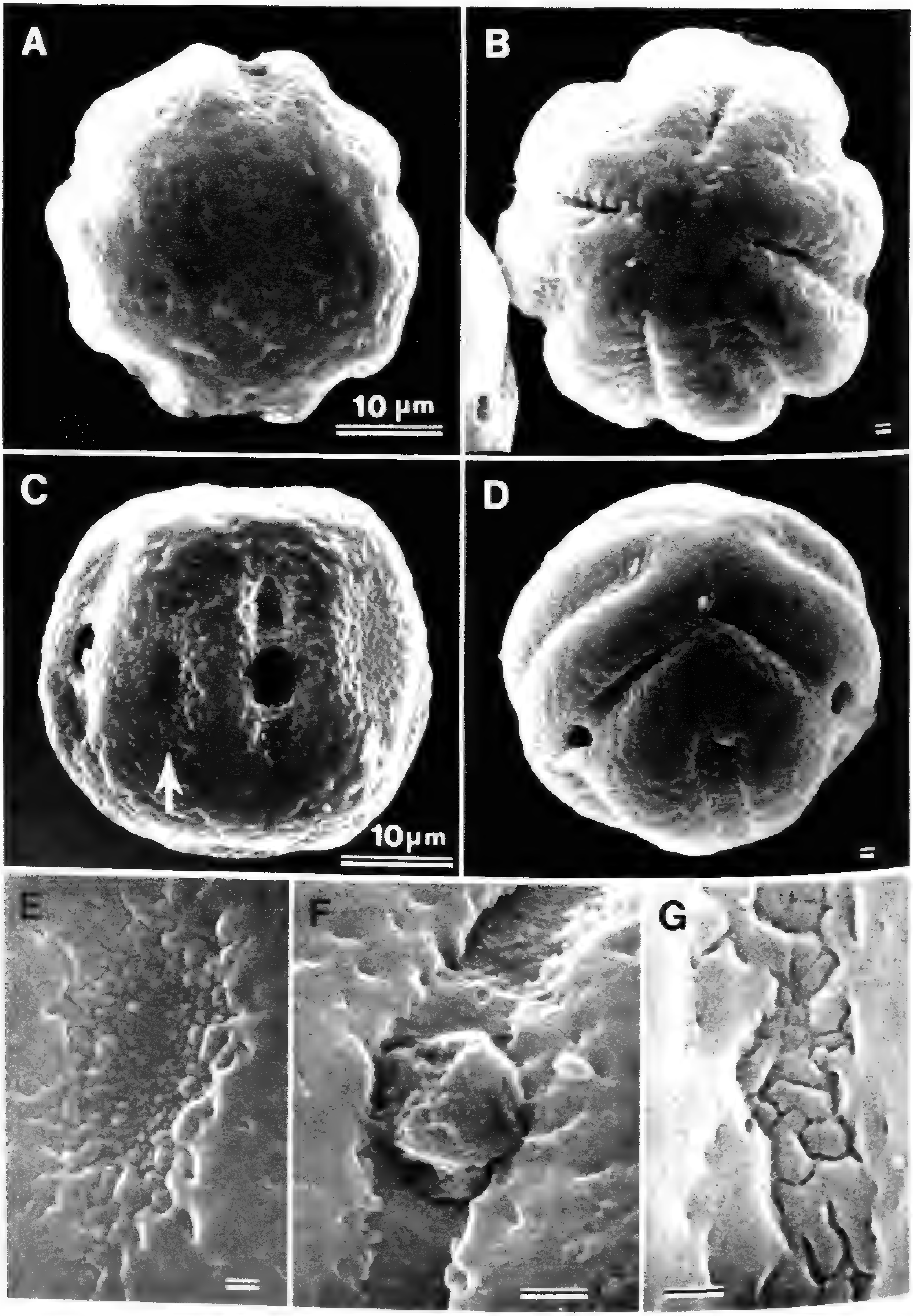


FIGURE 23. Scanning electron micrographs of Penaeaceae pollen. A, C, E. *Glischrocolla formosa.*—A. Polar view.—C. Lateral view. Note the difference in the size and position of the two visible intercolpar concavities (arrows). The central colpus is slightly asymmetric.—E. Details of an intercolpar concavity showing rugula margin and granular center. B, D, F. *Penaea cneorum.* subsp. *cneorum.*—B. Polar view. Compare with *Quisqu* (Fig. 16D).—D. Subpolar view of a grain with united colpi. Note the opercula near the endoapertures.—F. circular endoaperture which is covered by an operculum.—G. *Sonderothamnus speciosus.* Rugulate surface a subsidiary colpus. Compare with Oliniaceae (Fig. 13D). Unless otherwise indicated, scales equal 1 μm.

open endoapertures. Round opercula were observed in *Penaea cneorum* (Fig. 23F), *Brachysiphon fucatus* (Fig. 24A), *Saltera,* and *Stylapterus.*

The subsidiary colpi are long and have a smooth to granular surface except in *Endonema* (granular-verrucate) and *Sonderothamnus* (rugulate and similar to *Olinia*). The intercolpar concavities of *Saltera* and *Glischrocolla* have a rugulate surface on the margin and become granular toward the center. Subsidiary colpi are often united in *Brachysiphon* and *Sonderothamnus.* Heteropolar grains with colpi or subsidiary colpi or intercolpar concavities united in various configurations were observed in *Penaea* (Figs. 22C, 23D), *B. fucatus* (Fig. 24A), *Saltera,* and *Stylapterus* (Fig. 22E, F). In *Saltera,* 6-colporate grains with five intercolpar concavities and three very small, rudimentary or incipient (?) colpi were observed (Fig. 24E). In *Sonderothamnus speciosus* some grains appear to be fused in random configurations.

In TEM (Figs. 26, 27), the tectum along the mesocolpia is very thick and without perforations in all taxa except *Glischrocolla* (Fig. 27A). A thin infratectal granular layer is present in all taxa except *Penaea* (Figs. 26A, 27F). The foot layer is also prominent, usually thicker than the tectum and dome-shaped. The upper margin of the foot layer is irregular. Between it and the tectum, problematical columellae are usually distinguishable. They are thick, very short and irregular and often surrounded by the infratectal granular layer. This columellae layer is undulating or zig-zag in *Saltera* (Fig. 27C, D), and slightly so in *Brachysiphon acutus* and *Sonderothamnus* (Fig. 26B); in *Penaea* (Figs. 26A, 27F), it is represented by a very thin, undulating gap between the tectum and foot layer.

Toward the colpi and subsidiary colpi or intercolpar concavities, the endexine increases in thickness while the foot layer and tectum decrease. In the subsidiary colpus region in *Sonderothamnus* (Fig. 26C) and *Brachysiphon acutus* (Fig. 27B), a fragmented, thin foot layer supports an elaborate granular, spongy layer. This granular layer is a continuation of the infractectal layer of the mesocolpia but is much wider and better developed here. The intercolpar concavity of *Glischrocolla* and *Saltera* also has such a layer but it is not as thick as in the above two taxa. The spongy granular layer is covered by a thin tectum. In *Stylapterus* and *Penaea,* the tectum, granular layer, and foot layer are all very thin in the subsidiary colpi. The endexine is very thick and granular near the endoaperture.

Discussion

Pollen of the seven genera constituting Penaeaceae are best known through the light microscope studies of Dahlgren (1967a, 1967b, 1967c, 1968, 1971) as part of his comprehensive study of the family. While variations in pollen size and shape are common the pollen is fairly uniform and is characterized by colpi alternating with subsidiary colpi. The only major difference is in the number of apertures which seem to be the most variable in *Penaea* and *Saltera* (Dahlgren, 1968, 1971). These observations are also supported in other studies (i.e., Erdtman, 1971; Archangelsky, 1971).

Our results indicate that exomorphically, Penaeaceae pollen resembles that of Oliniaceae (see Oliniaceae discussion), Melastomataceae (compare *Endonema,* Fig. 25A, C, with *Tristemma,* Fig. 32D, and *Dissotis,* Fig. 33C, D) and Combretaceae (compare *Brachysiphon,* Fig. 25D, with *Combretum,* Fig. 15B, and *Quisqualis,* Fig. 16I, with *Penaea,* Fig. 23B). Endomorphically, the exine structure in the mesocolpium is similar to that of Oliniaceae (Fig. 14B–E) while the subsidiary colpal areas show a somewhat distant similarity to Onagraceae pollen (compare *Sonderothamnus,* Fig. 26C, with Figs. 60–63).

CRYPTERONIACEAE

Crypteronia paniculata (Figs. 30B, 31B–D), *Dactylocladus stenostachys* (Figs. 28A, C, E–G, 29), and *Axinandra zeylanica* (Figs. 28B, D, 30C) were examined with SEM and TEM. *Crypteronia* sp. (Fig. 31A) was examined only with SEM and *C. leptostachys* (Fig. 30A) only with TEM. *Crypteronia* (Fig. 31A–D) pollen is dicolporate, syncolpate, and bilaterally symmetrical. It is shaped like a football with the two endoapertures situated at the opposite pointed ends. It is elliptic in polar view and in lateral view (away from the endoapertures, or facing the mesocolpium); and circular to square in lateral view facing the endoaperture. The colpi have a smooth surface. They are united at both poles forming a circle around the grain. The endoapertures are lalongate, elliptic. The surface of the mesocolpia is rugulate. At the middle of each mesocolpium there is an equatorially elongated intercolpar concavity which has a verrucate-rugulate surface.

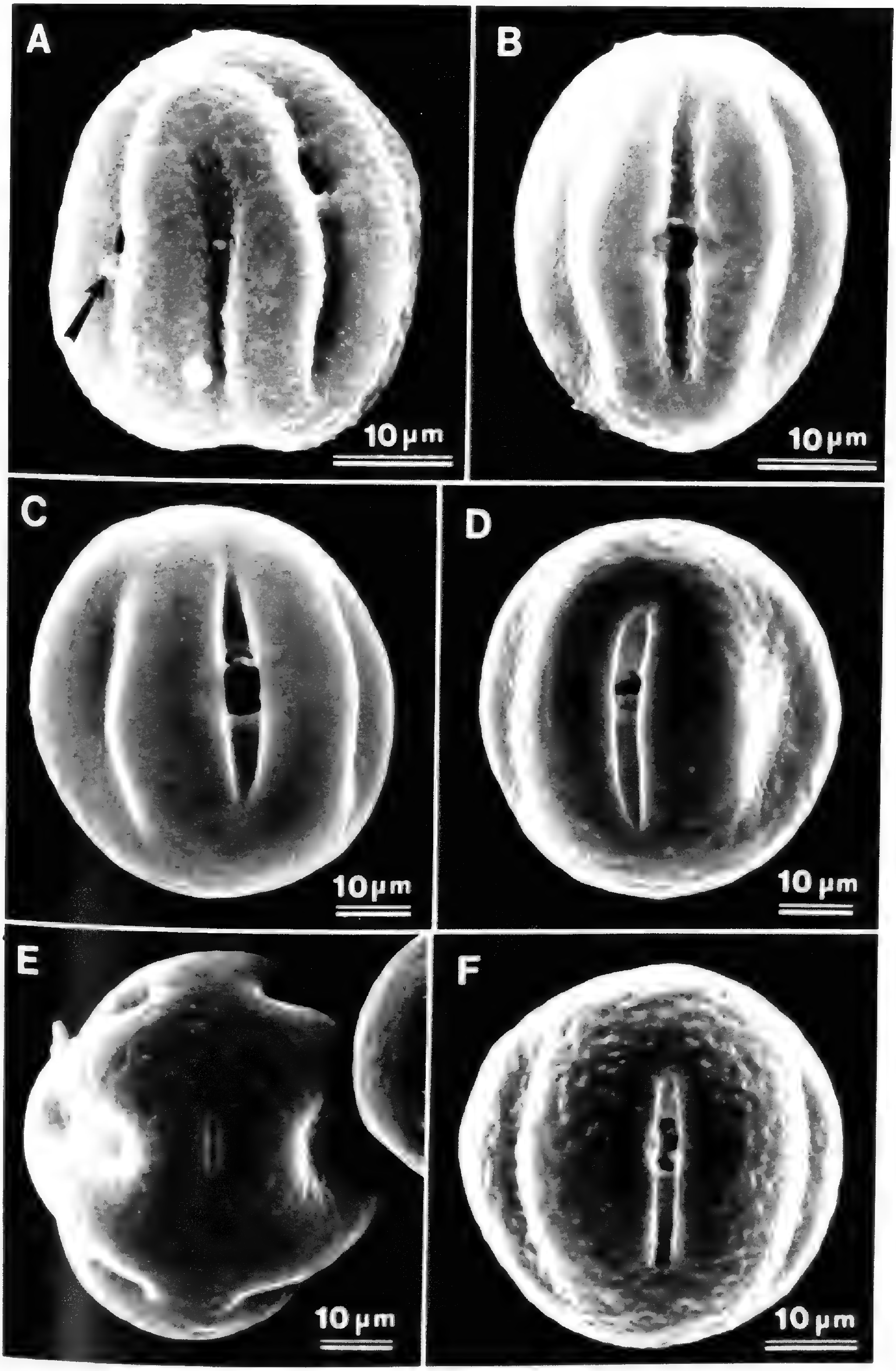
Dactylocladus and *Axinandra* both have tricolporate (rarely tetracolporate in *Dactylocladus*), heterocolpate, radially symmetrical, isopolar pollen (Fig. 28). Pollen is spheroidal in lateral view and triangular-hexagonal in polar view. In *Axinandra,* the surface of the mesocolpia is psilate, with a few scattered punctae. The colpi have acute ends, a smooth appearing surface, and are narrower than those in *Dactylocladus.* The obscure endoapertures are covered by exine extensions of the mesocolpia. The subsidiary colpi are long and sometimes united at the poles. Often, they are wide, appearing like intercolpar concavities. Their surface is punctate. The margin of the mesocolpia around the subsidiary colpi is often more punctate than other areas of the pollen grain. In *Dactylocladus,* the surface is psilate with some punctae and channels on the mesocolpia around the subsidiary colpi. The colpi are wide with a granular surface and obtuse ends which are sometimes united in tetracolporate grains. The obscure endoapertures are slightly protruding and have extensions of the mesocolpia over them. The subsidiary colpi are wide, with a granular surface, and irregular channels. At the poles the subsidiary colpi are united.

The exine of *Crypteronia* is thin (Fig. 30A, B). The narrow and more or less uniform tectum and foot layer are separated by short, thick, and simple (unbranched) columellae. The endexine is thick below the colpi and intercolpar concavities but thin elsewhere. It is granular-lamellate near the endoapertures. In contrast, the exine of *Dactylocladus* (Fig. 29A–C) is thick. It has a thick tectum and a broad foot layer which is often dome-shaped (Fig. 29B, mesocolpium to the left). A narrow columellae layer with thin, short columellae separates the tectum and foot layer. In some parts of the grain, the columellae layer follows a zig-zag pattern. The endexine is thick be-

FIGURE 24. Scanning electron micrographs of Penaeaceae pollen. A, B. *Brachysiphon fucatus.*—A. Lateral view of a tetracolporate syncolpate grain. Note that the two visible endoapertures are not on the same horizontal plane. Arrow indicates an operculum.—B. Lateral view of a tricolporate grain. C–E. *Saltera sarcocolla.*—C. Lateral view. The endoaperture is on the equatorial plane and the colpus is symmetrical.—D. Lateral view. Note the asymmetrical colpus with a short and a long segment. The endoaperture is above the equatorial plane. The surface of the intercolpar concavities is granular.—E. Many grains with abnormal number of colpi and intercolpar concavities were noted, such as this one with six colpi, five intercolpar concavities, and three rudimentary or incipient (?) colpi. Fusion of the exines of grains was also present.—F. *Sonderothamnus speciosus.* Lateral view. Note the asymmetric colpus and the endoaperture situated above the equator. Scales equal 10 μm.

FIGURE 25. Scanning electron micrographs of Penaeaceae pollen. A–C. *Endonema lateriflora.*—A. Lateral view. The surface is rugulate while the subsidiary colpus has a verrucate-granular surface.—B. Elliptic, lalongate endoaperture as viewed from the inside of the pollen grain. The arrows show two lateral extensions of the endoaperture.—C. Polar view showing three colpi and three subsidiary colpi. Extensions of the mesocolpia are evident over the endoapertures.—D. *Brachysiphon rupestris.* Lateral view with a colpus at the center and two subsidiary colpi. The exine surface is psilate while the subsidiary colpus is granular. E, F. *Sonderothamnus petraeus.*—E. Lateral view with colpus at center and adjacent subsidiary colpi. At the lower pole the two visible subsidiary colpi and presumably the subsidiary colpus at the back of the pollen grain appear to be united. At the upper pole the subsidiary colpus to the left is not united with other subsidiary colpi (see also Fig. 22A).—F. View of colpus. An ektexinous bar over the endoaperture gives the impression of two pores being present within each colpus. Ektexinous bars are also common in some Melastomataceae pollen (see Figs. 32B, C, 33A, C, D). The surface of the mesocolpia is psilate with few pits and channels while the colpus (and subsidiary colpus of E) is granular. Scales equal 1 μm.

FIGURE 26. Transmission electron micrographs of Penaeaceae pollen.—A. *Penaea mucronata.* Section of a mesocolpium with an endoaperture (arrow) on the left and a subsidiary colpus on the right. A very thin undulating electron translucent "line" separates the thick tectum from the thick foot layer. Near the endoaperture, both layers are thin and discontinuous; over the subsidiary colpus they are extremely thin. The endexine is relatively thin in the middle of the mesocolpium and thick near the subsidiary colpus and endoaperture. In the latter area it is also granular. B, C. *Sonderothamnus petraeus.*—B. Section of a mesocolpium. The thick tectum is imperforate. An infratectal granular layer is partially obscured by osmium precipitate. The foot layer is much thicker than the tectum. The endexine is thin and relatively uniform.—C. Section of a subsidiary colpus. The tectum is thin with a wavy or lobed outer margin. The infratectal layer is well developed. Immediately below, the foot layer (arrow) appears to be highly disrupted or fragmented. There are no distinguishable columellae. The endexine (en) is as thick or thicker than the ektexine. This section is reminiscent, in a sense, to sections of Onagraceae (see Figs. 60–63).—D. *Sonderothamnus speciosus.* Section of a mesocolpium near a subsidiary colpus (on the right). Compare with B and C. The exine sections represented in Figure 26 should be compared with Oliniaceae sections in Figure 14. Scales equal 1 μm.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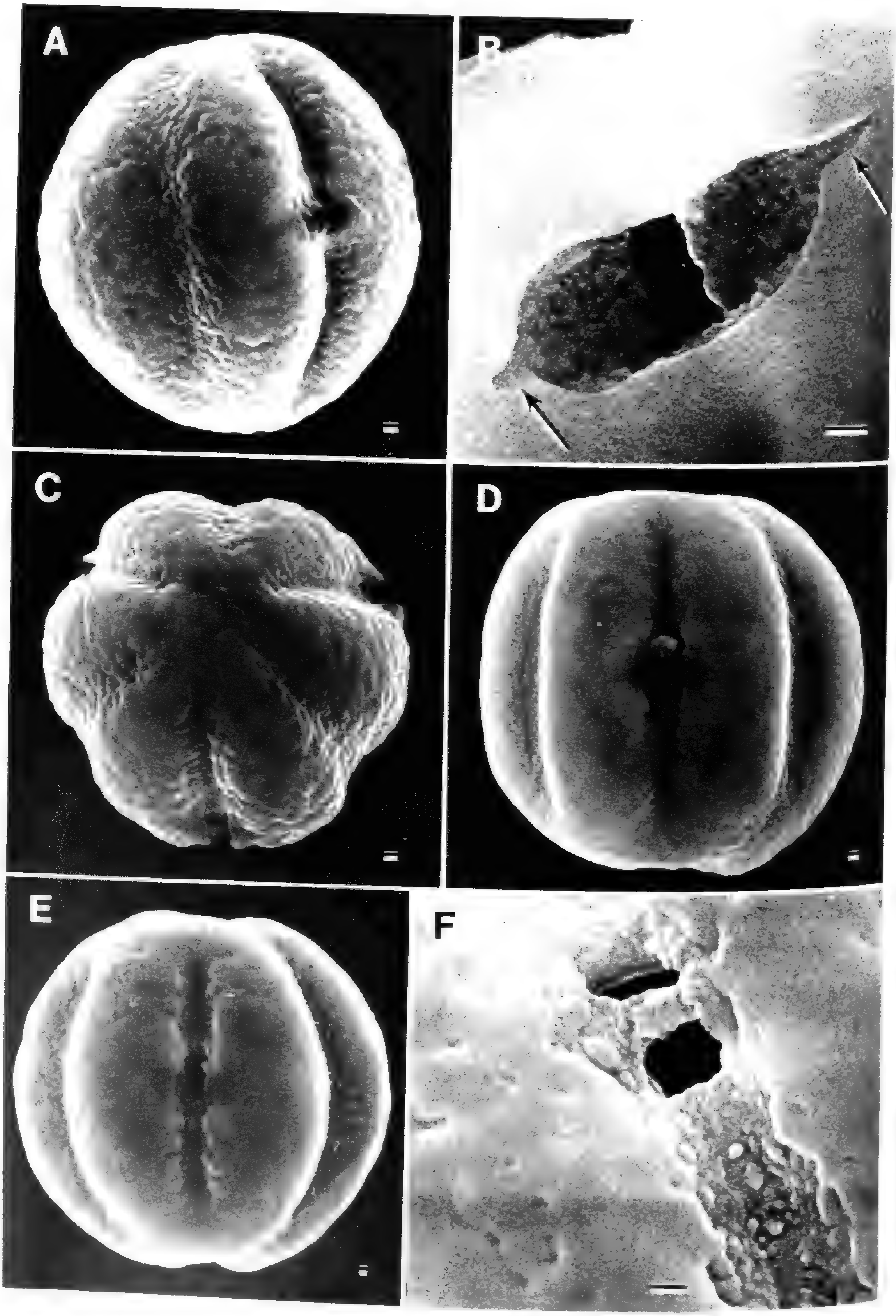
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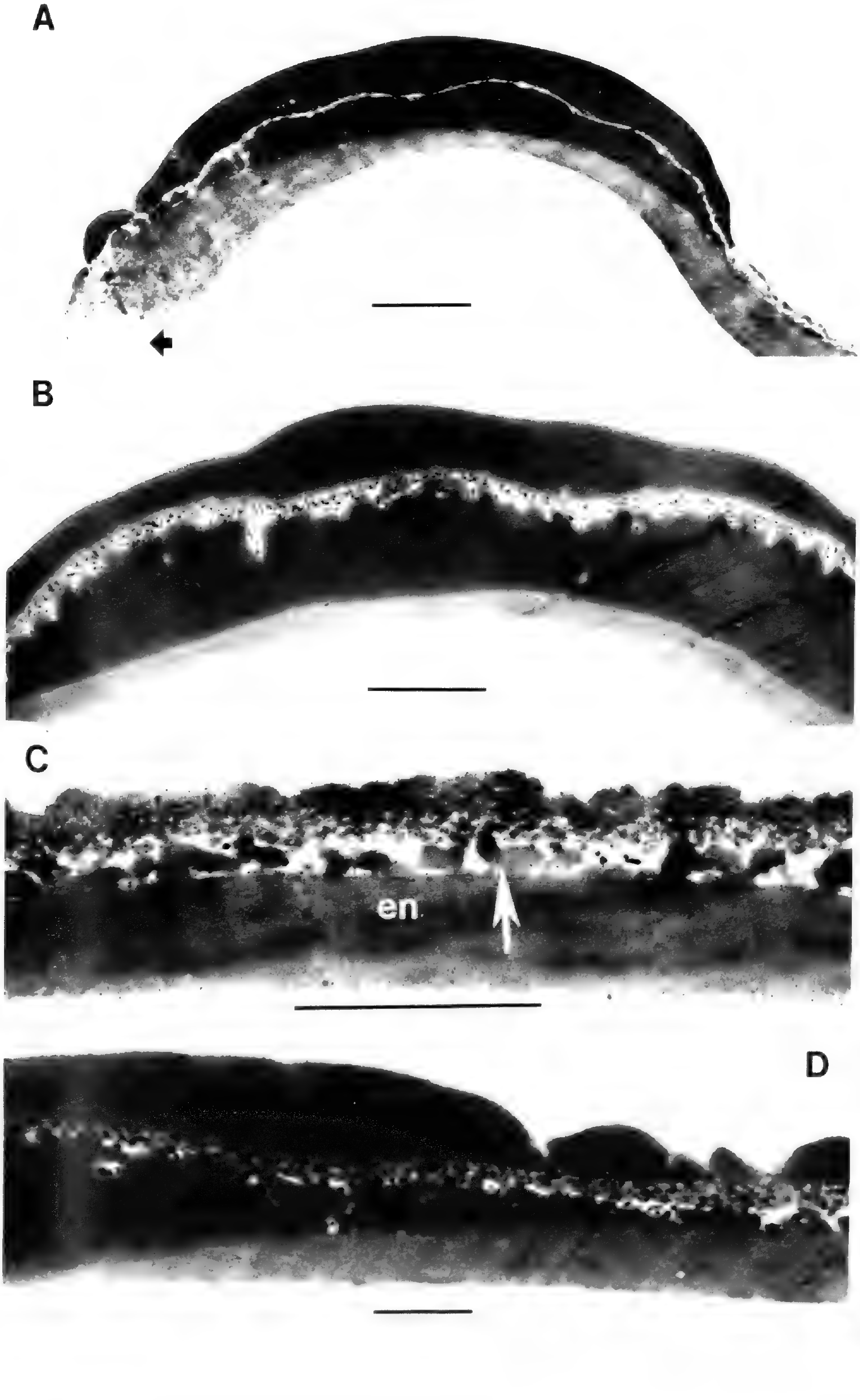
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low the colpi and subsidiary colpi and thin elsewhere. It is granular near the endoapertures. In the subsidiary colpi the tectum, foot layer, and columellae become very thin. In our TEM, we did not clearly recognize the small granules which Muller (1975) described as best developed on the lower tectum surface of *Dactylocladus* and weakly developed on *Crypteronia*.

Axinandra (Fig. 30C) has a thin exine with a narrow tectum and foot layer. The columellae are thick or thin and short. Occasionally, a zig-zag pattern of the columellae layer is seen. The endexine is thick below the colpi and subsidiary colpi, thin elsewhere, and granular near the endoapertures. In the subsidiary colpi the tectum and foot layer are narrow and the columellae are short.

Discussion

Muller (1975) described with light and electron microscopy (SEM and TEM) the pollen morphology of *Axinandra beccariana, Dactylocladus stenostachys, Crypteronia paniculata, C. cumingii, C. griffithii, Rhynchocalyx lawsonioides*, and *Alzatea verticillata*. The latter two species are treated now as separate monotypic families (i.e., *Rhynchocalyx* in Rhynchocalycaceae, and *Alzatea* in Alzateaceae). As discussed previously (see Alzateaceae), three pollen types were recognized in the Crypteroniaceae (Muller, 1975: 276) ". . . the tricolporate *Alzatea*-type, the heterocolpate *Dactylocladus*-type (*Dactylocladus, Axinandra*, and *Rhynchocalyx*) in which three colporate apertures alternate with three pseudocolpi, and the bisyncolporate *Crypteronia*-type." The less specified *Alzatea*-type was regarded as ancestral in the family.

In a general sense, we are in complete agreement with Muller (1975) that *Axinandra* and *Dactylocladus* pollen compare with pollen in Melastomataceae (see dicolporate grain of *Miconia*

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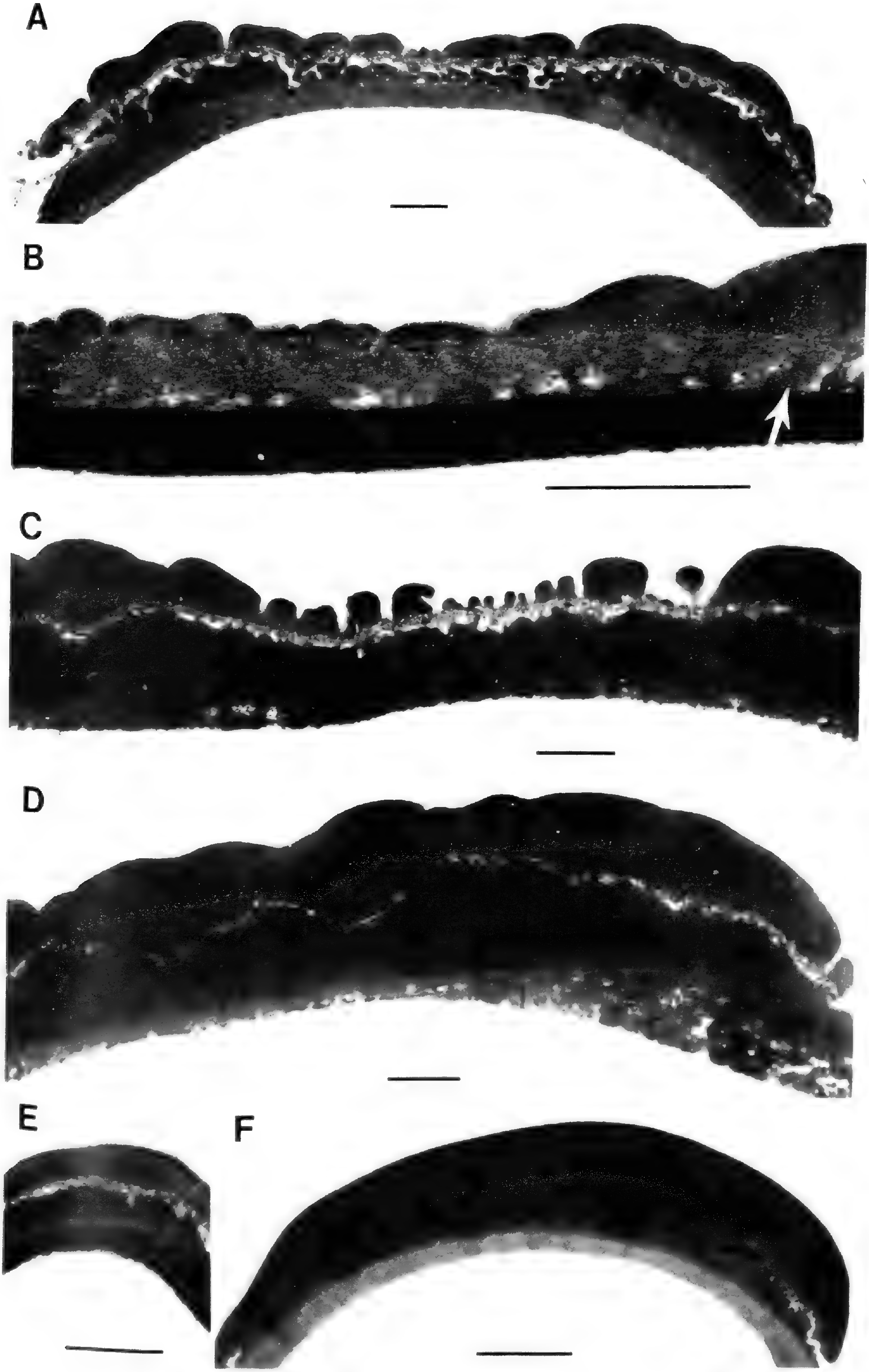
FIGURE 27. Transmission electron micrographs of Penaeaceae pollen.—A. *Glischrocolla formosa.* Section of two mesocolpia and an intercolpar concavity (center). The outer margin of tectum appears lobed due to the punctae of the surface. A thin and uniform infratectal granular layer is present in the mesocolpia and the intercolpar concavity. The foot layer is dome-shaped in the mesocolpia. Its upper margin is wavy and irregular. In the intercolpar concavity, it is thin and highly disrupted. It is difficult to distinguish columellae due to the irregular upper margin of the foot layer. The endexine is thick and uniform becoming thicker below the colpi (extreme left and right).—B. *Brachysiphon acutus.* Section of a subsidiary colpus and part of a mesocolpium (at right). Note a thin tectum which becomes thicker over the mesocolpium. A very thick infratectal granular layer is present in the subsidiary colpus which is reduced slightly in the mesocolpium. The well-developed endexine is stained darker than the ektexine layers. Between the endexine and the infratectal granular layer irregular, disrupted ektexinous elements (arrow) are present, which could be either columellae or fragments of the foot layer, or both. In the mesocolpium, however, distinct columellae and well-developed, dome-shaped foot layer (not included here) are present. C, D. *Saltera sarcocolla.*—C. Section of an intercolpar concavity and adjacent mesocolpia.—D. Section of a mesocolpium. Note the undulating columellae layer between the very thick tectum and foot layer. The colpus is to the right and the endexine increases in thickness toward the right.—E. *Stylapterus ericoïdes.* Section of a mesocolpium.—F. *Penaea cneorum* subsp. *ruscifolia.* Section of an entire mesocolpium. Note that the very thick tectum and foot layer are separated by an undulating gap (columellae layer), which appears dark due to osmium precipitate. Scales equal 1 μm.

FIGURE 28. Scanning electron micrographs of Crypteroniaceae pollen. A, C, E–G. *Dactylocladus stenostachys.*—A. (*SPH 3975*). Lateral view with a subsidiary colpus at the center. The subsidiary colpi are united at the poles. Compare also with scanning electron micrograph of Muller (1975, Pl. IV, figs. 1–3).—C. (*Chai*, 1982). Subpolar view.—E. (*732A*). Polar view of a tetracolporate grain.—F. (*SPH 3975*). Subpolar view of a tetracolporate, syncolpate grain.—G. (*Chai*, 1982). A subsidiary colpus with rugulate surface. B, D. *Axinandra zeylanica* (*Gunatilleke & Gunatilleke 582*).—B. Lateral view. Endoaperture is covered by colpus membrane.—D. Fused grains were occasionally noted in this collection. Rugulate surface of the subsidiary colpi of both grains is visible. Scales equal 1 μm.

FIGURE 29. Transmission electron micrographs of Crypteroniaceae pollen. A–C. *Dactylocladus stenostachys.*—A. (*Chai*, 1982). Section of an entire grain cut in plane that includes two colpi (arrows) and one subsidiary colpus. Note that the thin columellae layer has a distinct zig-zag configuration in some portions of the exine.—B. (*Chai 39708*). Section showing two mesocolpia and a subsidiary colpus between them. The mesocolpium on the right shows a zig-zag columellae layer which is straight in the mesocolpium on the left. Arrow indicates an endoaperture.—C. (*SPH 3975*). Same as above but a distinct zig-zag columellae layer is not visible. In the subsidiary colpus, thin tectum, fine columellae, and a very thin foot layer are present. Note the increase in the thickness of the endexine below colpi and subsidiary colpus. Arrow indicates an endoaperture where the endexine is lamellated. Scales equal 1 μm.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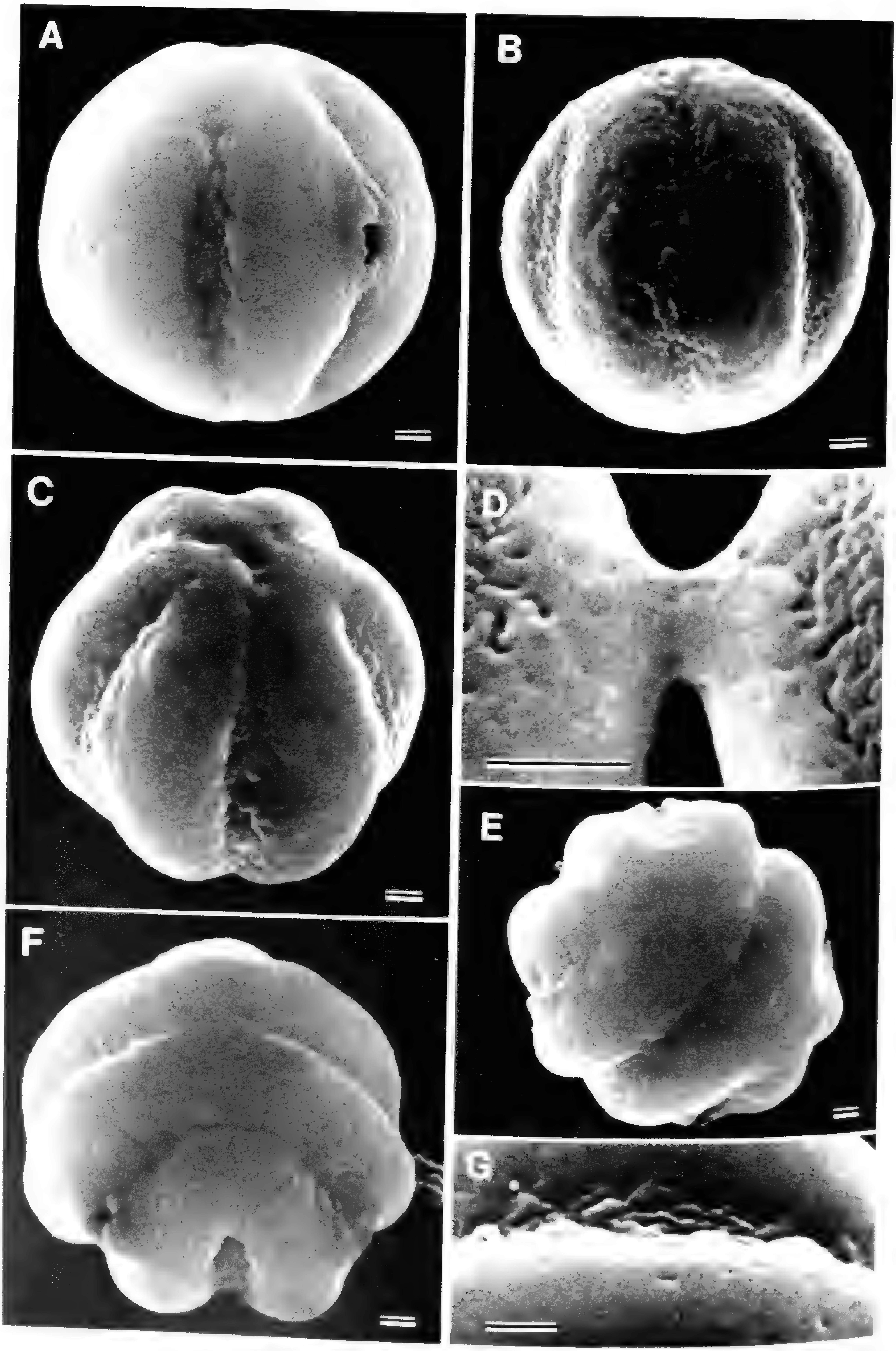
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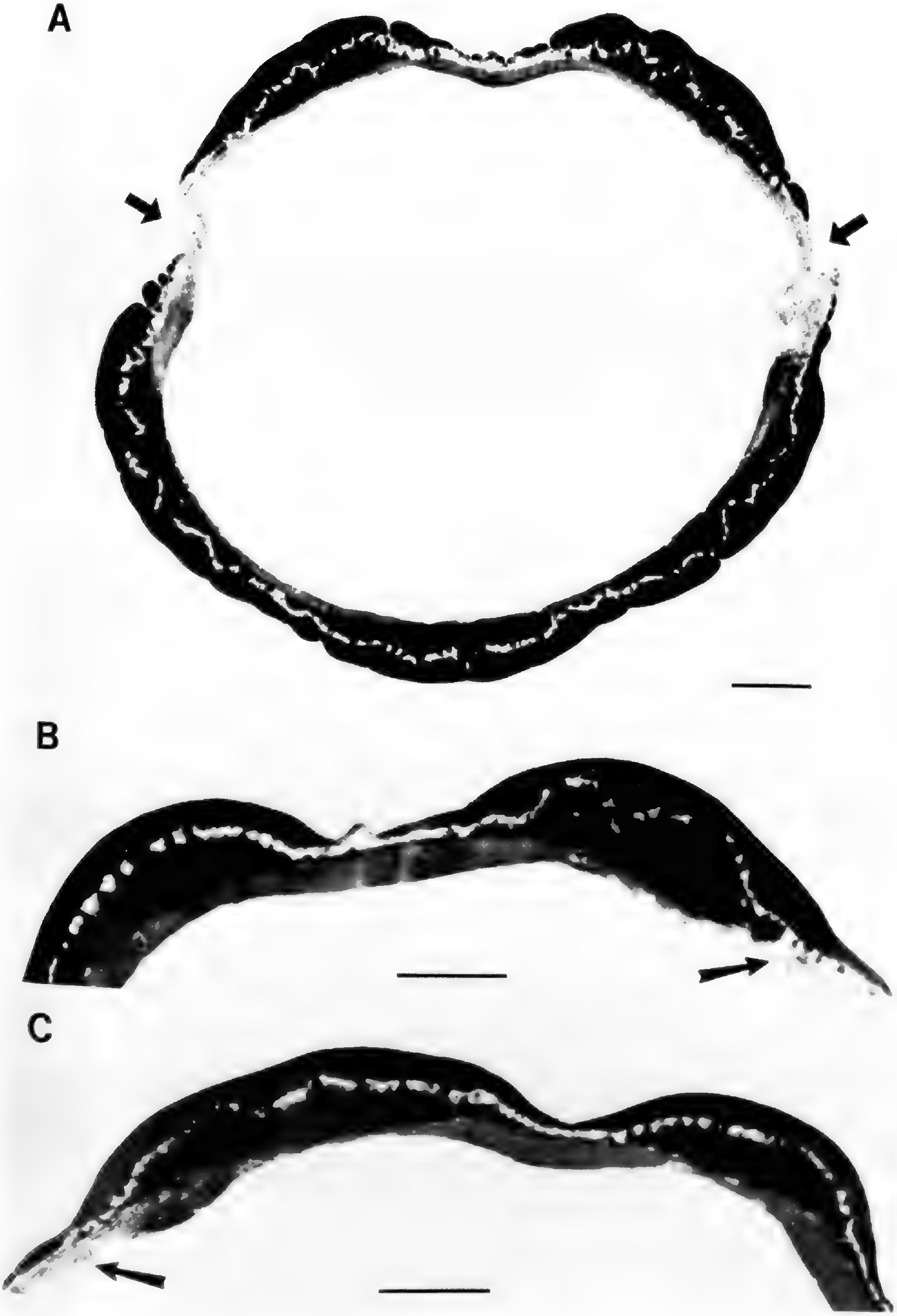
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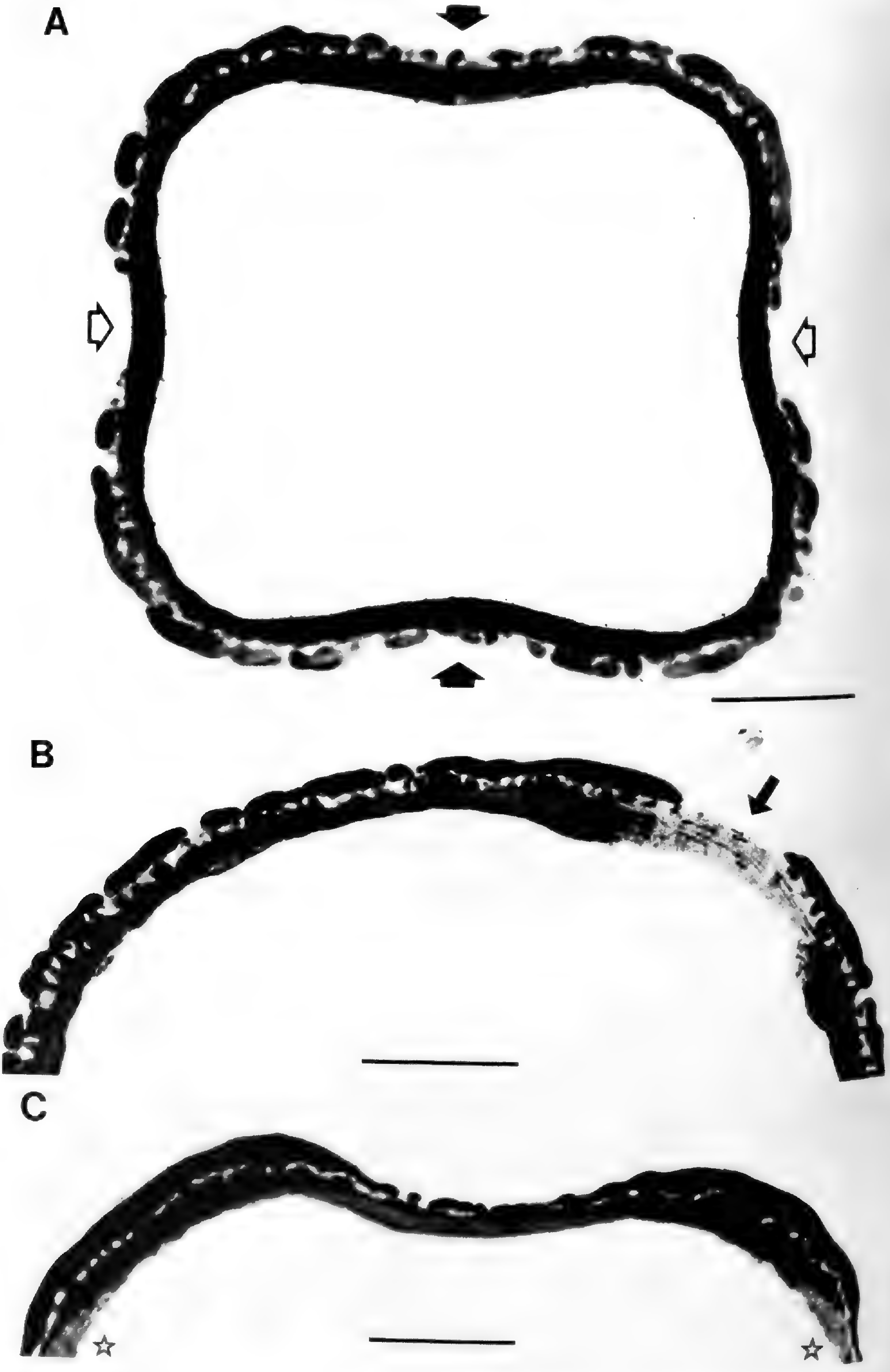


FIGURE 30. Transmission electron micrographs of Crypteroniaceae.—A. *Crypteronia leptostachys.* A vertical section of an entire grain passing through two colpi (open arrows) (which are syncolpi, and hence pass through the poles) and two subsidiary colpi (solid arrows).—B. *Crypteronia paniculata.* Section of a mesocolpium and an endoaperture (arrow).—C. *Axinandra zeylanica* (*Gunatilleke & Gunatilleke 582*). Section of two mesocolpia and the subsidiary colpus between them. The right mesocolpium shows a zig-zag columellae layer. Stars indicate endoapertures. Scales equal 1 μm.

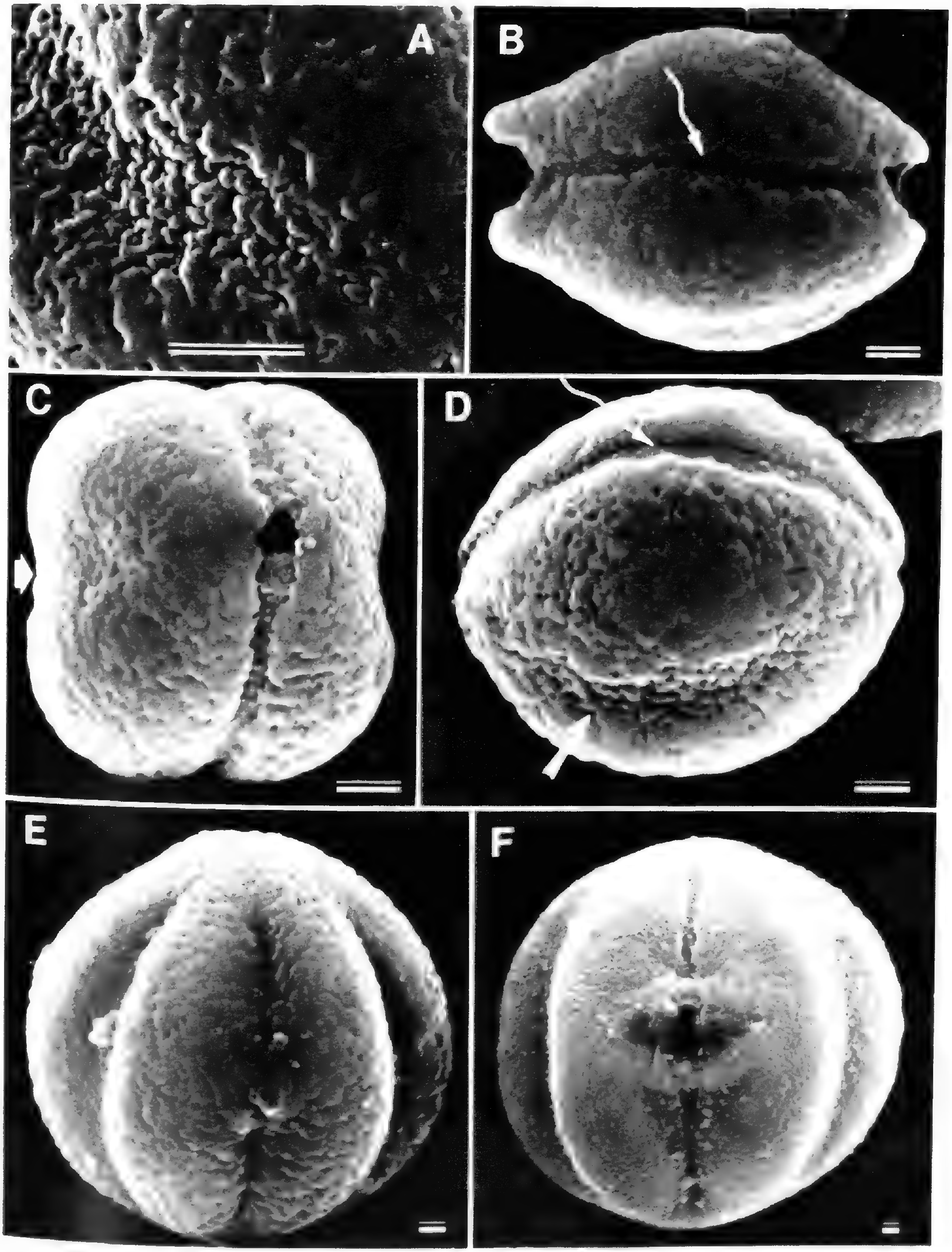
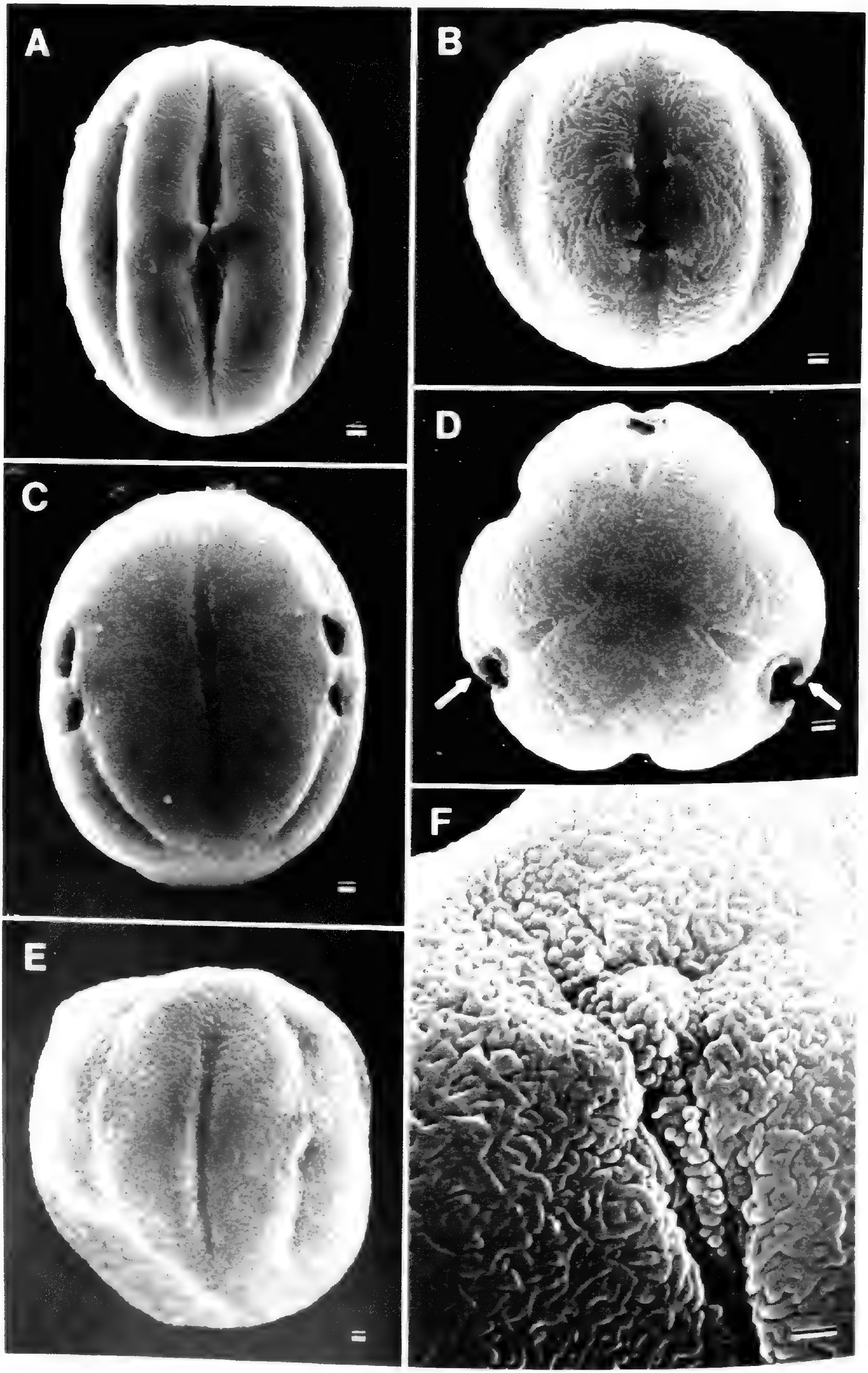


Figure 31. Scanning electron micrographs of pollen from Crypteroniaceae (A–D) and Melastomataceae (E, F). —A. *Crypteronia* sp. Enlarged portion of a subsidiary colpus and surrounding mesocolpia. The surface of the subsidiary colpus is granular-rugulate. B–D. *Crypteronia paniculata.*—B. Polar view. Arrow points to the pole over which passes the syncolpus. The two endoapertures (at the sides) are open.—C. Lateral view facing an endoaperture. Arrow indicates the laterally elongated intercolpar concavity.—D. Sublateral-subpolar view. The two colpi are united forming a circle passing through poles (wiggly arrow). Thick arrow indicates an intercolpar concavity.—E. *Memecylon normandii.* Sublateral view. The surface is rugulate.—F. *Mouriri glazioviana.* Lateral view. Note the elliptic, lalongate, thick-margined endoaperture. The surface consists of fine, elongate, branched muri. Scales equal 1 μm.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hondurensis, Fig. 35E), Combretaceae, Penaeaceae, Oliniaceae, and Lythraceae (*Lythrum, Peplis,* some species of *Ammannia, Nesaea,* and *Rotala*). Further, the *Crypteronia*-type pollen of Muller relates to Corynocarpaceae, Cunoniaceae, Eucryphiaceae, and Saxifragaceae (Muller, 1975; see also Erdtman, 1971). In endomorphology, *Dactylocladus* resembles *Alzatea,* Chrysobalanaceae (Patel et al., 1983a), and Corynocarpaceae (Nowicke & Skvarla, 1983) in having the zig-zag columellae layer.

MELASTOMATACEAE

Pollen of Melastomataceae is tricolporate, radially symmetrical, and isopolar. Grains are spheroidal to subprolate in lateral view with a circular, hexagonal, or triangular shape in the polar view. Monads are found in all taxa examined with the exception of *Tococa spadiciflora* which has polyads (Fig. 35F, H), and *Miconia melanotricha* (Fig. 35A, B) which has tetrads (Patel et al., unpubl. data). On the basis of exomorphology, three pollen groups can be established: heterocolpate with subsidiary colpi, "heterocolpate" with intercolpar concavities, and tricolporate.

In the heterocolpate group with subsidiary colpi, the three colpi (four in *Votomita*) alternate with three (four in *Votomita*) elongate, narrow subsidiary colpi. This type of pollen is present in *Trembleya phlogiformis* (Fig. 32A), *Tibouchina urvilleana* (Fig. 32C), *Tristemma littorale* (Fig. 32D), *Dissotis brazzae* (Fig. 33C, D), *Marumia nervosa* (Fig. 33A, B), *Dissochaeta celebica* (Fig. 33F), *Osbeckia polycephala* (Fig. 32B), *Acanthella sprucei* (Fig. 33E), *Memecylon normandii* (Fig. 31E), *Mouriri glazioviana* (Fig. 31F), *Votomita monadelpha* (Fig. 32E, F), *Miconia hondurensis* (Fig. 35D), *M. alypifolia* (Fig. 36A), *M. caesia* (Fig. 36D), *Comolia stenodon* (Fig. 36H), and *Tococa broadwayi* (Fig. 36F). The surface sculpture is variable. A more or less smooth surface with a few pits and punctae is present in *Acanthella* (Fig. 33E). In *Dissotis* (Fig. 33C, D) many channels, pits, and punctae are present on a smooth to rugulate surface. In *Marumia* (Fig. 33A, B), *Dissochaeta* (Fig. 33F), and *Memecylon* the surface is coarsely rugulate-punctate. It is striate-rugulate in *Tristemma* (Fig. 32D), *Comolia* (Fig. 36H), and *Osbeckia* (Fig. 32B), with elongate, more or less parallel muri, which in the latter become shorter and separated at the poles where the surface then becomes verrucate-rugulate. In *Trembleya* (Fig. 32A) and *Miconia alypifolia* (Fig. 36A) it is striate. In the latter species, bundles of striae are separated by large channels at the poles (Fig. 36A–C). In *Tibouchina* (Fig. 32C), it is smooth-punctate with a very faint striate pattern which in some grains is quite prominent at the poles. The finely rugulate surface in *Mouriri* (Fig. 31F) and *Votomita* (Fig. 32E, F) is composed of fine, elongate, branched, often overlapping muri that form a compact mesh with punctae. In *Miconia hondurensis* it is smooth-punctate (Fig. 35D, E). The surface of *M. caesia* (Fig. 36D) is distinctive in possessing a mesh of short, branched, cylindrical elements. In *Tococa broadwayi* (Fig. 36F), it is perforate.

Colpi are long (some grains are syncolpate in *Dissotis, Acanthella,* and *Dissochaeta*), with acute ends, and a smooth surface except in *Acanthella, Marumia,* and *Dissochaeta* where the surface is granular. In *Votomita,* the colpus surface is covered with bead-like elements. Endoapertures are lalongate (not clearly defined in *Dissochaeta*) and elliptic (circular to elliptic in *Votomita*). Extensions of the mesocolpia over the endoapertures are present (Figs. 32A, D, 33E, 36A). A horizontal bar is often persistent over the open endoapertures (Figs. 32C, 33A, D). Subsidiary colpi are long except in *Tococa broadwayi* (Fig. 36F), narrow, and have either a smooth, scabrate, or granular surface (Fig. 33B). They are usually

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FIGURE 32. Scanning electron micrographs of Melastomataceae pollen.—A. *Trembleya phlogiformis.* Lateral view showing extensions of the mesocolpia over the endoaperture (at center) and two subsidiary colpi. The exine surface is striate.—B. *Osbeckia polycephala.* Lateral view. The exine surface is rugulate.—C. *Tibouchina urvilleana.* Sublateral view with a subsidiary colpus at center. A horizontal ektexinous bar appears to divide the endoapertures into two parts (see legend discussion to *Sonderothamnus petraeus,* Fig. 19F).—D. *Tristemma littorale.* Polar view. Extensions of mesocolpia are apparent over the endoapertures (arrows). E, F. *Votomita monadelpha.*—E. Lateral view with a subsidiary colpus at center. Although not evident in this figure there are four colpi alternating with four subsidiary colpi.—F. The fine, elongate, branched surface units of the mesocolpia contrast with bead-like units of the colpus. This surface is somewhat similar to the pollen of *Boisduvalia* (Onagraceae, Fig. 52B, C, E) although it does not appear to be perforate. Scales equal 1 μm.

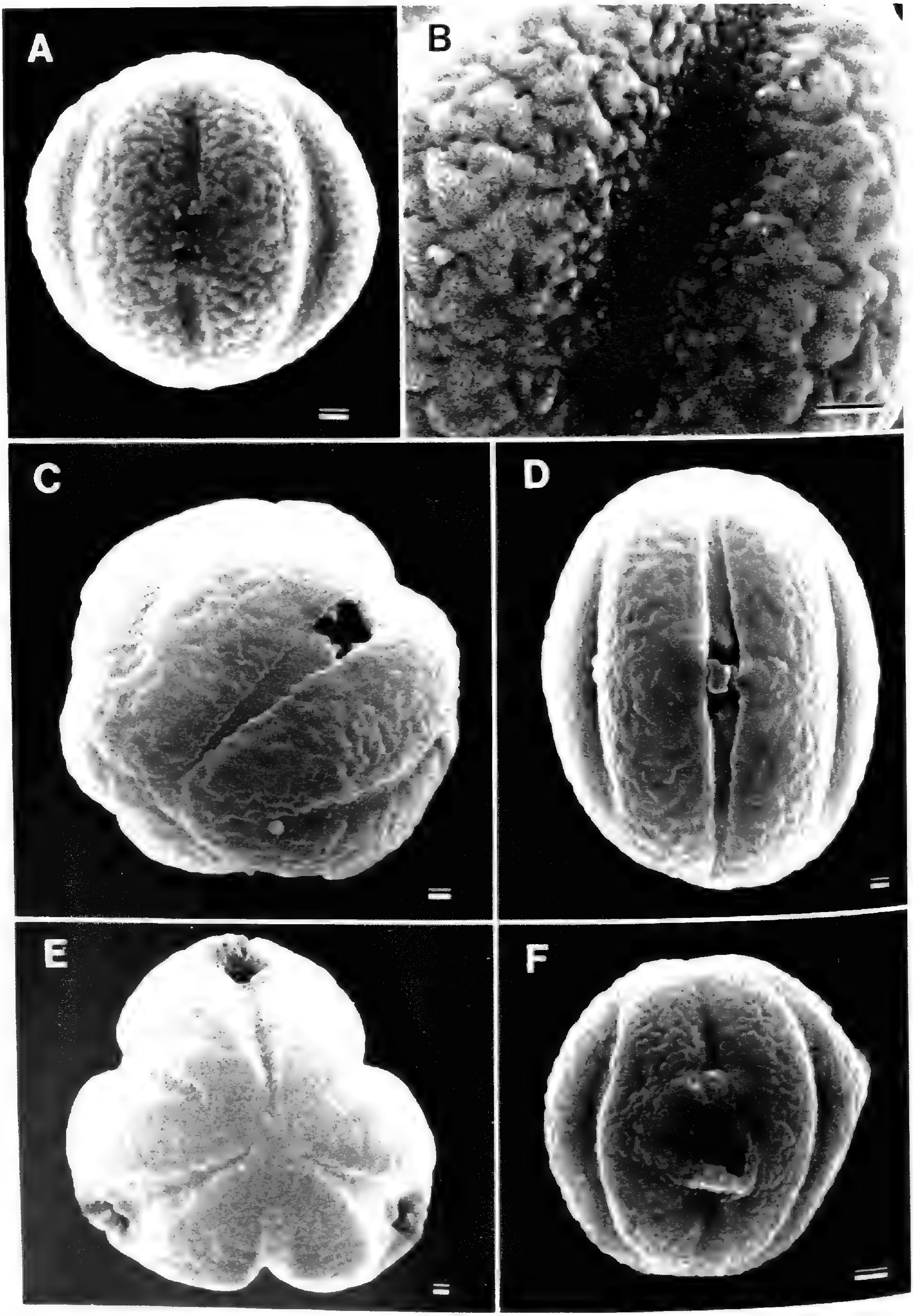

FIGURE 33. Scanning electron micrographs of Melastomataceae pollen. A, B. *Marumia nervosa*.—A. Latera view showing horizontal bar over endoaperture as described for Figure 32C. The exine surface is rugulate.—B Details of the granular subsidiary colpus and surrounding rugulate mesocolpia. C, D. *Dissotis brazzae*.—C Subpolar view. The colpi are united at the pole. The surface is rugulate.—D. Lateral view. See discussion Figure 32C concerning horizontal bar over endoaperture.—E. *Acanthella sprucei*. Polar view. The surface smooth with a few channels and pits. Extensions of the mesocolpia over the endoapertures are prominent.—F *Dissochaeta celebica*. Lateral view. The surface is rugulate. Scales equal 1 μm.

shorter than the colpi but in *Marumia* and *Dissochaeta* they are as long as or longer than the colpi. Some grains of *Miconia hondurensis* (Fig. 35E) are bilateral, dicolporate, syncolpate with two large intercolpar concavities. In addition to the usual tricolporate-isopolar pollen of *M. alypifolia* there are present: (1) grains with various arrangements of colpi and subsidiary colpi (Fig. 36C), (2) heteropolar grains (Fig. 36C), and (3) grains with both subsidiary colpi and intercolpar concavities (occurring in pollen with more than three colpi, Fig. 36B).

In the second group, "heterocolpate" with intercolpar concavities, there are present on the mesocolpia three intercolpar concavities—large, elliptic, thin-walled, depressed areas. The remaining thick-walled portion of the mesocolpia forms a more or less narrow band around the intercolpar concavities. This type of pollen is illustrated by *Adelobotrys tessmannii* (Fig. 34A–C), *Allomorphia caudata* (Fig. 34D), *Bredia hirsuta* (Fig. 34F), *Astronia cumingiana* (Fig. 34E), *Oxyspora paniculata* (Fig. 34G, H), and *Miconia melanotricha* (Fig. 35A–C). The grains are spheroidal in lateral view and circular to triangular or hexagonal (*Oxyspora*) in polar view. Colpi are long and narrow with acute ends and a more or less smooth surface. Extensions of the mesocolpia are present over the lalongate, elliptic endoapertures (Figs. 34D, E, 35A, B, D, not clearly defined in *Allomorphia,* not examined in *Astronia*). *Adelobotrys* differs from the other taxa in having wide colpi that are united at the poles, and by a granular-verrucate surface. The colpus membrane is raised over the endoaperture (Fig. 34B, arrow). This raised membrane is vertically oriented and does not seem to be analogous with an operculum.

The surface of the meso- and apocolpia is variable: psilate in *Adelobotrys* (Fig. 34A–C), scabrate in *Allomorphia* (Fig. 34D, although not very clear), striate-rugulate in *Oxyspora* (Fig. 34G, H), fine rugulate-verrucate in *Bredia* (Fig. 34F), smooth-punctate in *Miconia* (Fig. 35C), and coarse with many channels and pits (rugulate ?) in *Astronia* (Fig. 34E). The intercolpar concavities differ in size and surface sculpture. In *Bredia* and *Astronia,* the surface sculpture of the concavities is similar to that of the rest of the grain except that it is finer. *Adelobotrys* and *Allomorphia* have a verrucate surface while *Oxyspora* has angular, flat, irregularly shaped units on the surface of the intercolpar concavities. In *Miconia* the surface is granular-verrucate.

Exine structure is similar in both pollen groups described above. In the meso- and apocolpia the foot layer is well developed and often dome-shaped (Figs. 37B, D, 38A, 39A). Here the endexine is less developed and often very thin (Fig. 38A, B). A "white line" between the foot layer and the endexine is often distinct (Figs. 37B, C, 38A). The columellae are short, erect, and distally branched. The tectum is thick, perforate, and has an undulating outer margin, although in *Adelobotrys* (Fig. 39A) perforations are rare and the outer margin of the tectum is smooth. *Acanthella* (Fig. 38D) differs from the other taxa in having a very thick tectum (rarely perforate) and thick foot layer that are separated by columellae that appear granular and have lateral extensions.

Toward the colpi and subsidiary colpi or the intercolpar concavities, the endexine becomes thicker whereas the ektexine layers taper. The foot layer is discontinuous and thinner at the margins of the mesocolpia: on the surface of the colpi, subsidiary colpi, and intercolpar concavities, it remains either as a very thin layer (Figs. 38A, 39A, B, D) or is absent. The tectum is thin, the columellae are short and fine, or they are both absent. In the intercolpar concavities, the verrucae (or the irregular elements in *Oxyspora*) show a thin, dome-shaped tectum below which one or more fine columellae are present (Fig. 39A, B, D). In *Astronia* the tectum is thin and columellae are irregular and short (Fig. 39C).

In the region of the endoaperture, the endexine is thick and granular and often lamellate (e.g., *Adelobotrys, Trembleya*). The tectum is thinner and the columellae are shorter. The foot layer is tapered leaving the columellae and tectum directly overlying the granular endexine (Figs. 38D, 39A, C, D). Around the endoaperture in *Astronia* (Fig. 39C) the columellae and tectum are separated from the endexine.

The third, tricolporate group, is represented by *Tococa stephanotricha* (Fig. 36E) and *T. formicaria* (Fig. 36G), which have a rugulate surface and very short colpi. In TEM of *T. stephanotricha* (Fig. 40B, C) the endexine is uniform in thickness except near the endoapertures where it is thicker, granular, and lamellate. The foot layer is also uniform in thickness. The columellae are short, erect or reclining, and rarely branched. The tectum is discontinuous with irregular dome-like units in section.

A third species of *Tococa, T. spadiciflora,* could not be assigned to any of the three groups described above. It consists of polyads which are composed of basic units of tetrahedral tetrads (Fig. 35F–I). Internal bridges on the proximal faces of individual pollen grains maintain tetrad unity while external bridges on the distal faces of the tetrads, frequently along the aperture margins, maintain polyad unity (Fig. 35G–I). Individual grains are usually tetracolporate but grains with five or more colpi have also been noted. Colpi are long with acute ends and have a smooth surface. Some grains appear to have colpi of unequal length. Endoapertures are lalongate and elliptic. The meso- and apocolpia surface is smooth-punctate. Subsidiary colpi are difficult to characterize and are either weakly developed or absent. In TEM (Fig. 40A), the endexine is more or less uniform in thickness except near the endoapertures where it is thicker and granular. The foot layer is uniform in some areas but in others it is highly irregular and discontinuous with many channels and gaps. Columellae are long, thick, and erect, and they split at their distal ends into fine, very short branches. The tectum is thick and uniform, with large perforations. The tectum as well as the columellae show fusion at the points of attachment between members of the polyads.

Discussion

As indicated earlier, Melastomataceae pollen has received little study above the light microscope level. Guers (1974) included scanning electron micrographs of *Dicellandra barteri, Calvoa orientalis,* and *Osbeckia decandra.* These were part of a light microscope study of eight genera and 20 species from tropical Africa. *Dicellandra* and *Calvoa* compare favorably with our second pollen group in possessing intercolpar concavities; in contrast, *O. decandra* compares with our first pollen group.

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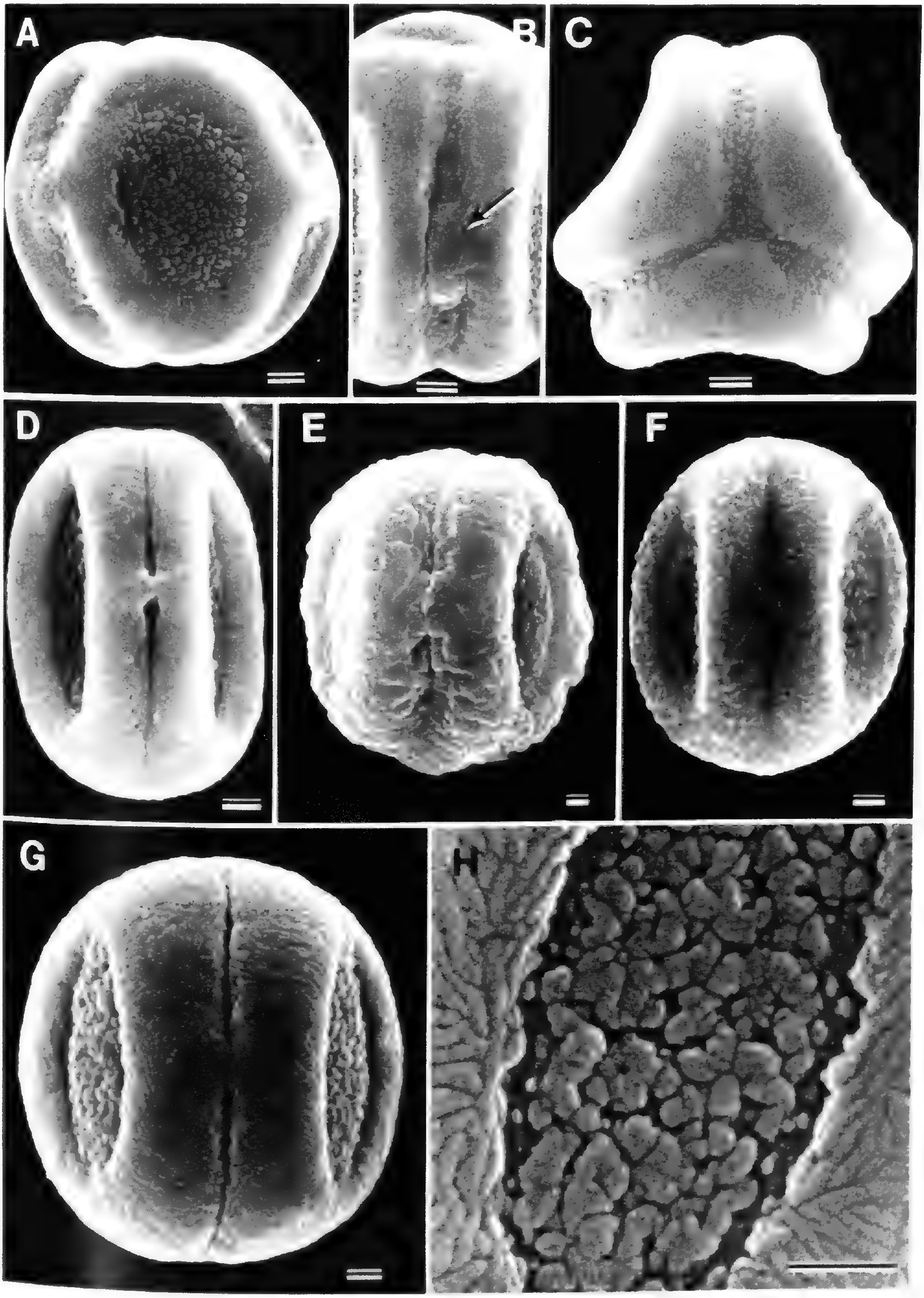
FIGURE 34. Scanning electron micrographs of Melastomataceae pollen. A–C. *Adelobotrys tessmannii.*—A. Lateral view showing an intercolpar concavity with a verrucate surface. The surrounding mesocolpia are narrow and have a psilate surface. The colpi are united at the poles (i.e., syncolpate).—B. Lateral view showing a colpus. The colpus membrane is raised over the endoaperture (arrow).—C. Polar view showing united colpi with a granular surface. The concave sides of the pollen grain are due to the thin-walled intercolpar concavities. In a wet grain they bulge, giving it a circular shape.—D. *Allomorphia caudata.* Lateral view. The colpus is narrow and wide extensions of the mesocolpia are present over the endoaperture. The intercolpar concavities have a verrucate surface. Elsewhere the surface is smooth.—E. *Astronia cumingiana.* Lateral view. The surface is coarsely rugulate. The colpus is very narrow. Note the large mesocolpial extensions (see Fig. 39C). The surface of the intercolpar concavities is also rugulate but not as coarse as the rest of the grain.—F. *Bredia hirsuta.* Lateral view. The surface is rugulate. The intercolpar concavities are also rugulate but with a finer surface. G, H. *Oxyspora paniculata.*—G. Lateral view. The surface is striate. The colpus is very narrow and long.—H. Enlarged view of the intercolpar concavity and the surrounding area. Irregular, flattened elements are present on the surface of the concavity. Scales equal 1 μm.

FIGURE 35. Scanning electron micrographs of Melastomataceae pollen. A–C. *Miconia melanotricha.*—A. A tetrahedral tetrad. Exine bridges connect tetrad members.—B. Three grains of a tetrad. The fourth grain is missing as indicated by broken bridges (arrow).—C. The bridges are narrow and have a smooth surface. The surface of the mesocolpia is smooth-punctate, that of the intercolpar concavities is granular-verrucate. D, E. *Miconia hondurensis.*—D. Polar view of a tricolporate grain. Three subsidiary colpi alternate with the colpi.—E. Sublateral view of a bilateral, dicolporate, syncolpate grain with two intercolpar concavities. Here the visible intercolpar concavity (large arrow) is meridionally elongated. In some dicolporate, syncolpate grains, it is laterally elongated similar to *Crypteronia* (Fig. 31B–D) pollen. The syncolpus circles the grain vertically. Small arrow indicates the position of an endoaperture. F–H. *Tococa spadiciflora* (*Archer 1976*).—F. A polyad.—G. A grain from a polyad showing bases of broken exine bridges on the margins of a colpus. The colpus at the center (arrowhead) appears to be shorter than the one on the right, and also at a slight angle to the polar axis. Two lines (top arrows) above the short colpus form a triradiate configuration. This phenomenon was observed in other grains, but pollen with meridionally arranged colpi appear to be more common.—H. An octad.—I. *T. spadiciflora* (*Forero et al. 5703*). An exine bridge between two grains. It is thick and has a punctate surface similar to that of the grains. Some punctae contain granules. Unless otherwise indicated, scales equal 1 μm.

FIGURE 36. Scanning electron micrographs of Melastomataceae pollen. A–C. *Miconia alypifolia.*—A. Lateral view. Note the striate-punctate surface near the equator. Toward the poles the surface becomes coarse.—B. Polar view of a six-colporate grain with subsidiary colpi (arrow) and intercolpar concavities (arrowhead). Such grains are rare.—C. Subpolar view of a heteropolar, conoidal (Muller, 1978b) grain. The two visible colpi (arrows) are united.—D. *M. caesia.* Polar view.—E. *Tococa stephanotricha.* Polar view.—F. *T. broadwayi.* Sublateral view. Subsidiary colpi are not as well developed as in other taxa of the family.—G. *T. formicaria.* Lateral view.—H. *Comolia stenodon.* Subpolar view. Scales equal 1 μm.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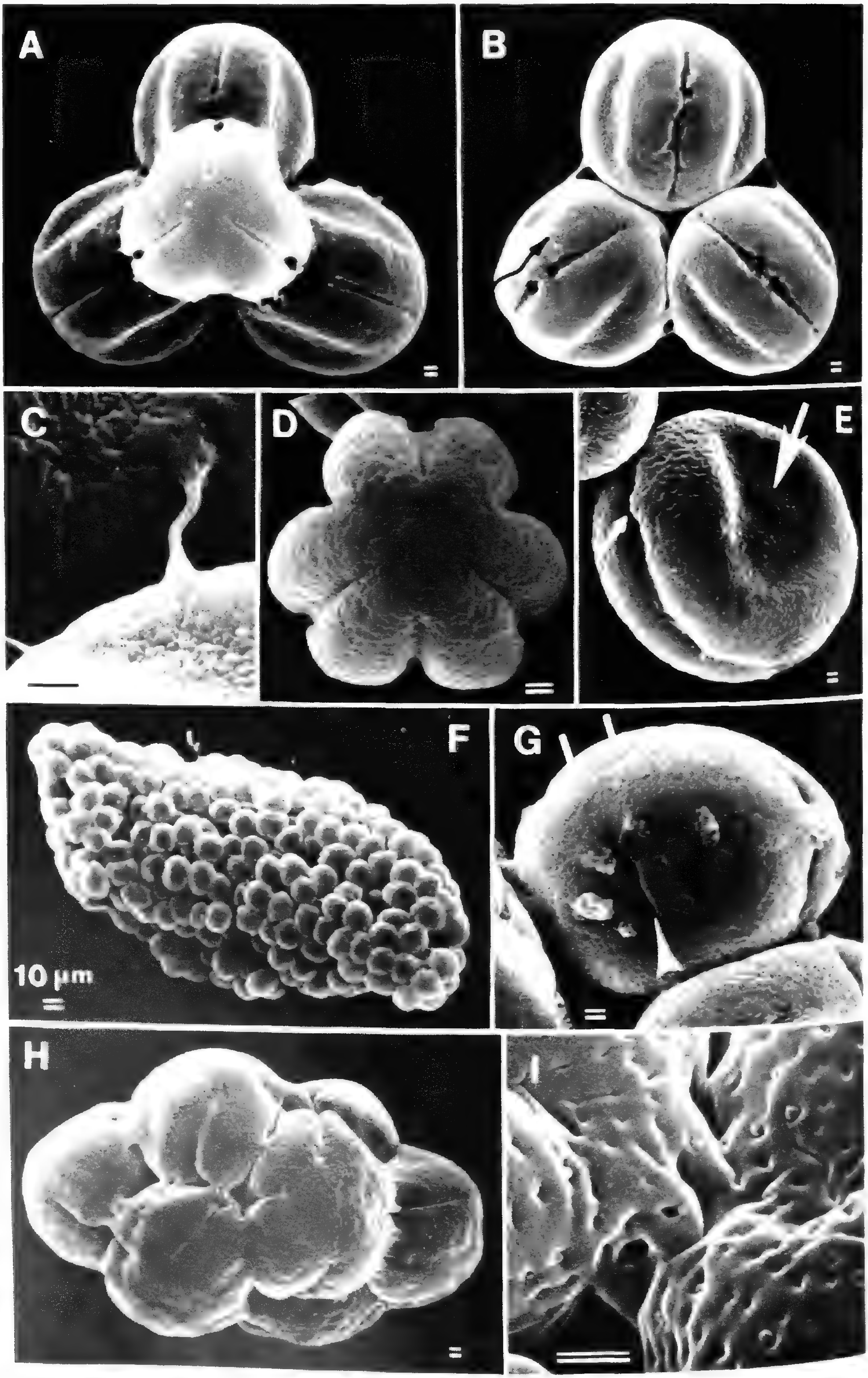
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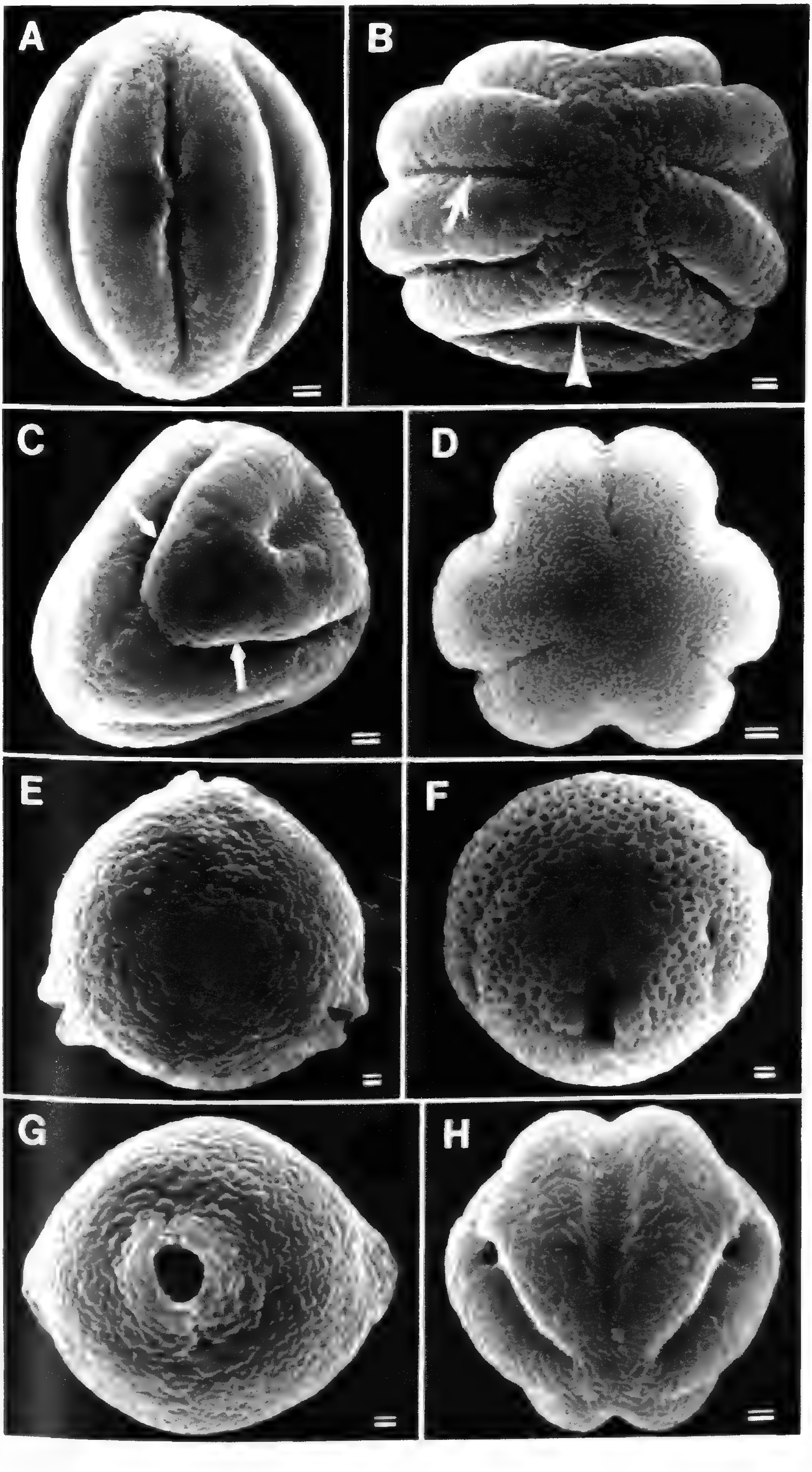
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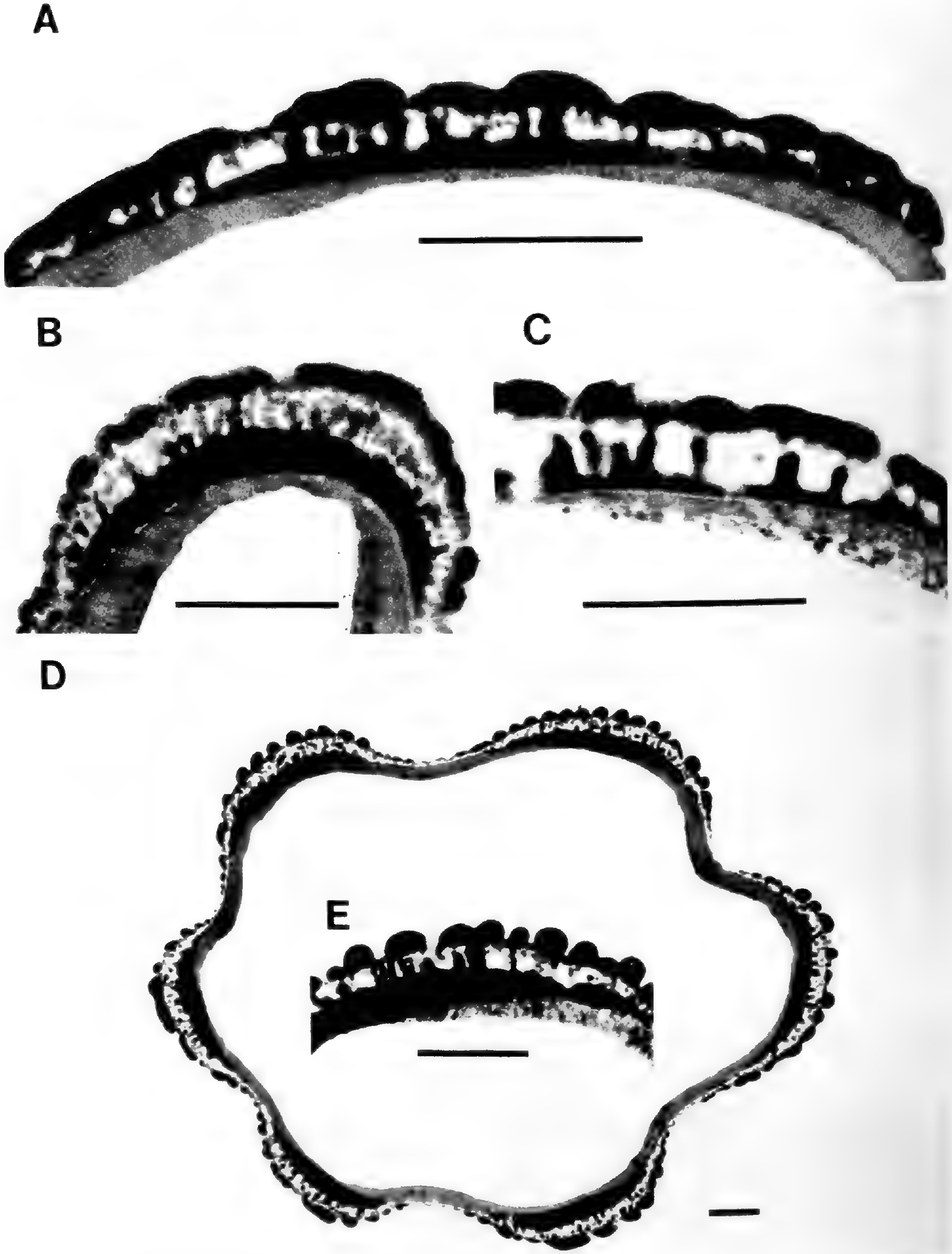


FIGURE 37. Transmission electron micrographs of Melastomataceae pollen.—A. *Tristemma littorale*. Section of a mesocolpium.—B. *Trembleya phlogiformis*. An oblique section of a mesocolpium which is folded due to the collapsed grain. The columellae are numerous and markedly branched.—C. *Tibouchina candolleana*. A portion of the mesocolpium near an endoaperture (not included here). The endexine is granular-lamellate. D. E. *Osbeckia polycephala*.—D. Cross section of an entire grain. Because the section does not include the equator or endoapertures, colpi and subsidiary colpi cannot be identified.—E. Mesocolpium near an endoaperture. The tectum is deeply lobed due to striae. Scales equal 1 μm.

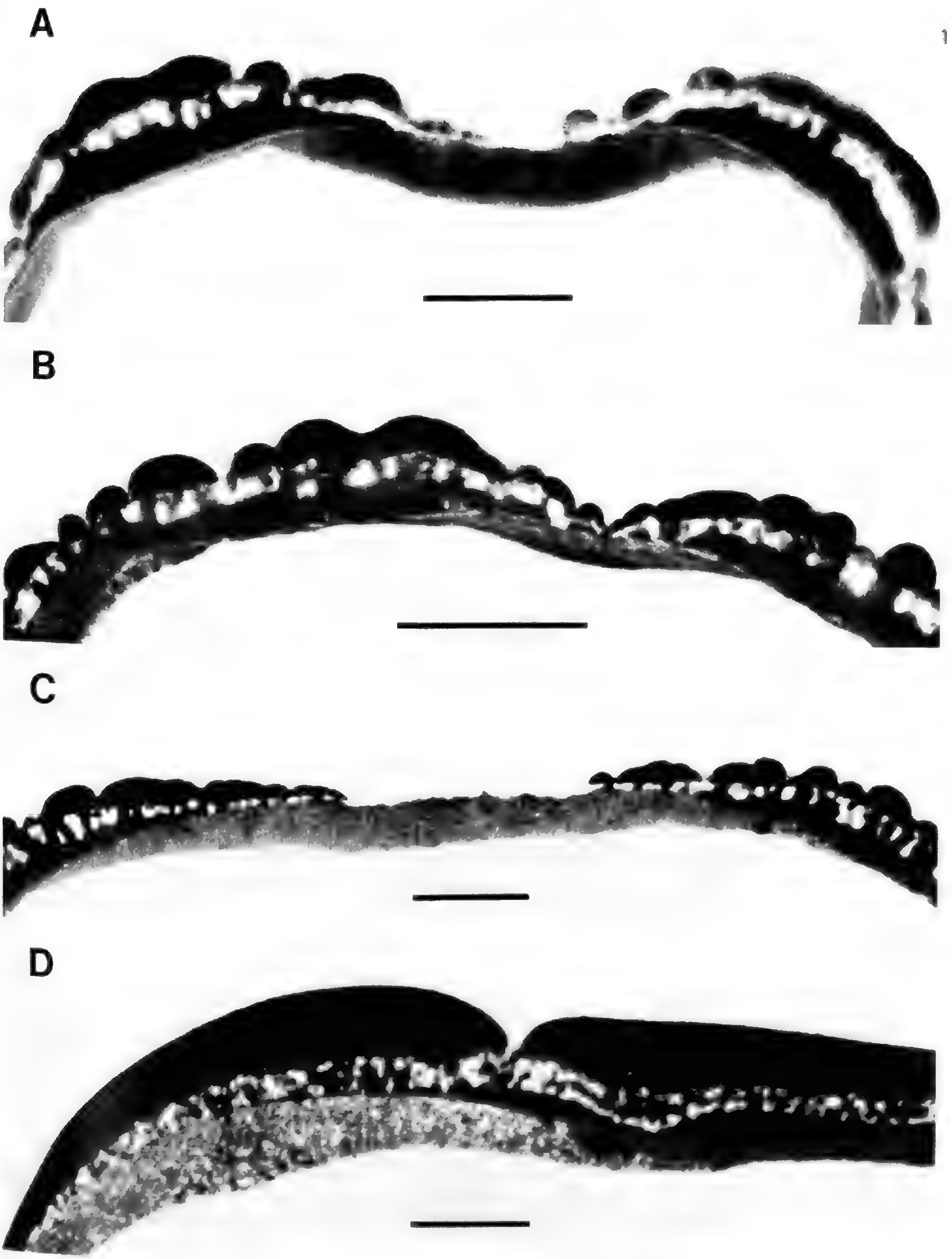
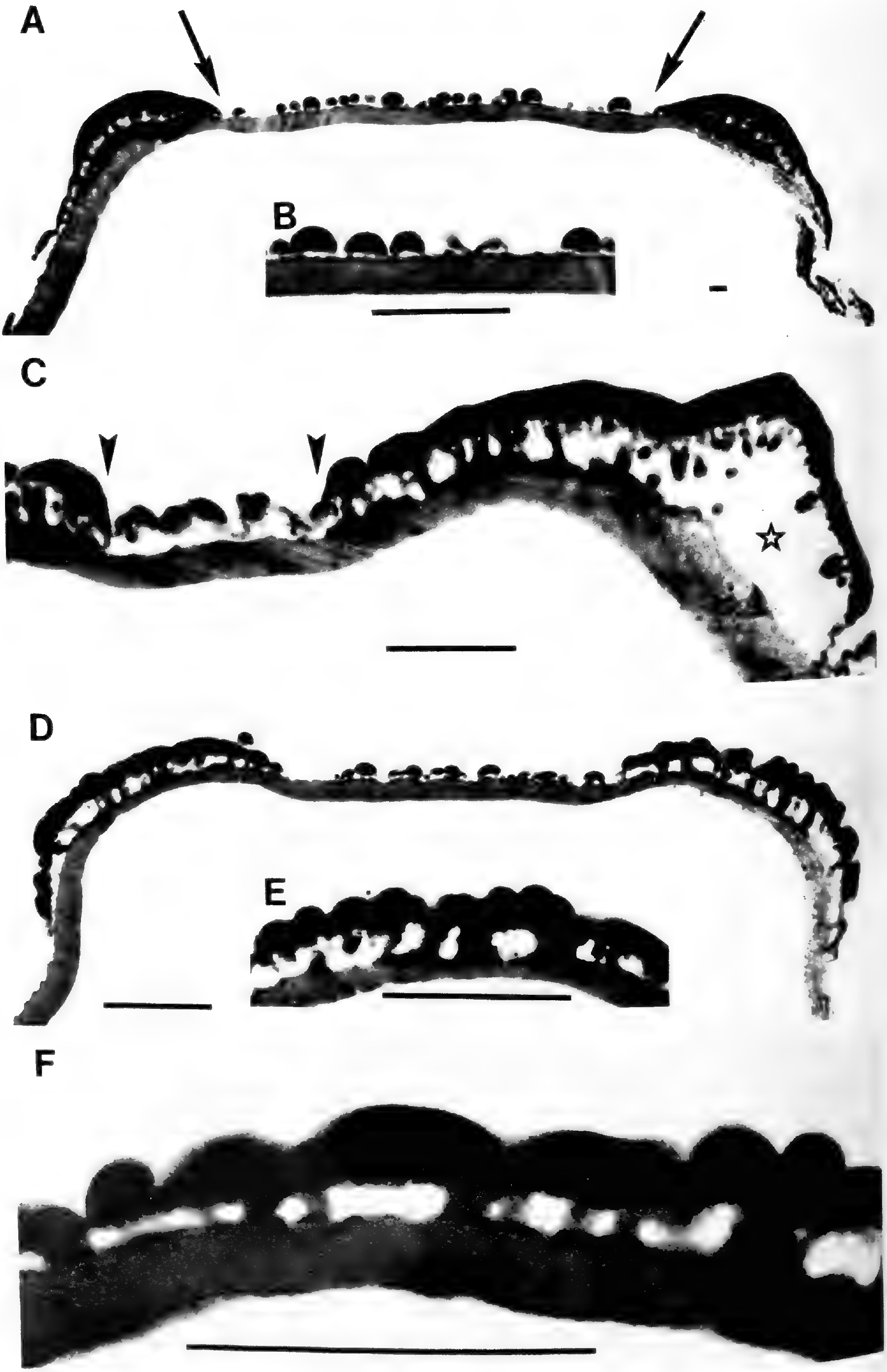


FIGURE 38. Transmission electron micrographs of Melastomataceae pollen.—A. *Marumia nervosa.* Section of two mesocolpia and a colpus or subsidiary colpus between them. The dome-shaped foot layer is similar to Combretaceae pollen (Fig. 20A, B, D, F).—B. *Dissochaeta celebica.* Similar to Figure 37A.—C. *Dissotis brazzae.* Similar to Figure 37A, B.—D. *Acanthella sprucei.* Mesocolpium in the region of an endoaperture. The tectum is very thick with rare perforations. The granular appearing columellae have lateral extensions. Toward the colpus the thick foot layer is reduced while the endexine increases in thickness and becomes granular. Note the general similarity to the pollen of Oliniaceae (Fig. 14B–E) and Penaeaceae (Fig. 26A, B, D). Scales equal 1 μm.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Among the genera examined here, *Mouriri, Votomita,* and *Memecylon* have often been segregated with several other genera from Melastomataceae sensu stricto as Memecylaceae or subfamily Memecyloideae (e.g., Dahlgren & Thorne, 1984; Johnson & Briggs, 1984). All three of these genera belong to the heterocolpate group, but they are not delimited as a group in any way from the other heterocolpate genera of Melastomataceae, although *Votomita* is unusual in having four colpi and subsidiary colpi, and a bead-like colpus surface. Further studies on this group, including *Lijndenia, Spathandra, Warnecka,* and more species of *Memecylon,* and particularly *Pternandra,* are essential to a proper understanding of the relationships between Melastomataceae sensu stricto and Memecyloideae.

Within the limited context of this study only those taxa in our first pollen type, that is, the heterocolpate type, show some similarities to other core families. At the SEM level some resemblance is evident with *Combretum* (Fig. 15A, B), *Bucida* (Fig. 17A), *Conocarpus* (Fig. 17B), *Pteleopsis* (Fig. 17C), *Terminalia* (Fig. 17D), *Ramatuella* (Fig. 17E), *Guiera* (Fig. 18E), *Poivrea* (Fig. 19C), and *Lumnitzera* (Fig. 19D) of Combretaceae; and *Sonderothamnus* (Fig. 25E) of Penaeaceae. Some of the bilateral, dicolporate, syncolpate grains in *Miconia hondurensis* (Patel et al., unpub. data) recall *Crypteronia.* At the TEM level the striking dome-shaped foot layer of the heterocolpate type (Figs. 37, 38, except *Acanthella* Fig. 38D) compares with that in Combretaceae (Fig. 20). TEM of *Acanthella* (Fig. 38D) is notably distinctive in Melastomataceae, resembling to some extent *Penaea* (Fig. 26A), *Sonderothamnus* (Fig. 26B, D), *Saltera* (Fig. 27D), and *Stylapterus* (Fig. 27E) of Penaeaceae; and *Olinia* (Fig. 14B–E) of Oliniaceae.

TEM of the other two pollen types (Figs. 39, 40) does not reveal any significant comparisons other than those already mentioned in the plate legends and pollen descriptions. Clearly, pollen in this family must be investigated in greater depth.

MYRTACEAE (INCLUDING PSILOXYLACEAE AND HETEROPYXIDACEAE)

In general, the pollen is tricolporate (triporate in *Tristania nereifolia*), radially symmetrical, and isopolar or heteropolar. In lateral view the pollen is oblate, elliptic with obtuse or truncate sides (Reitsma, 1970). In polar view it is triangular, goniotreme with straight or curved sides (convex or concave), and with acute or obtuse corners. Colpi vary in length, are either syncolpate or parasyncolpate, and generally have a smooth surface. Endoapertures are lalongate. Intercolpar concavities are present in some species. Heteropolar grains are due either to the nature of the colpi (e.g., long on one pole and syncolpate on the other pole), or to the different shapes (concave, convex, straight) of the two polar faces. In *Eugenia capuli,* and in some grains of *Luma chequen, Chamelaucium unciniatum, Temu divaricatum,* and *Ugni molinae,* one polar face is concave (or straight, in *Chamaelaucium*) and the other is convex. The pollen is free except in *Myrtus communis* (Fig. 48D) and *Psidium littorale* (Fig. 46B), where tetrahedral tetrads are present along with the monads.

Based on the nature of colpi, Pike (1956) recognized three pollen types in the Myrtaceae from the southwest Pacific area: (1) longicolpate grains; (2) syn- or parasyncolpate grains, and (3) brevi- or brevissimicolpate grains. All three types are present in the taxa examined in this study.

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FIGURE 39. Transmission electron micrographs of Melastomataceae pollen. A, B. *Adelobotrys tessmannii.*—A. Section including approximately one-third of an entire grain. Colpi and mesocolpia are on the sides of a large intercolpar concavity (between arrows). The mesocolpia consist of a thick imperforate tectum, short columellae, and a thick foot layer. In the intercolpar concavity, the verrucae of scanning electron micrograph (Fig. 34A) are dome-shaped and are supported by fine columellae and a thin foot layer. The endexine is thicker below the intercolpar concavity than below the mesocolpia.—B. Detail of a portion of the intercolpar concavity as described for A.—C. *Astronia cumingiana.* Section of a mesocolpium near a colpus (right) and an intercolpar concavity (between arrowheads). In the intercolpar concavity the tectum is folded or undulated while columellae and foot layer are not apparent in this plane of section. In the colpus region the area marked with a star is equivalent to the wide mesocolpial extensions noted in scanning electron micrograph (see Fig. 34E). D, E. *Oxyspora paniculata.*—D. Cross section of approximately one-third of an entire grain including two colpi (on the sides), two mesocolpia, and an intercolpar concavity.—E. Enlarged area of a mesocolpium.—F. *Bredia hirsuta.* Section of a mesocolpium. Scales equal 1 μm.

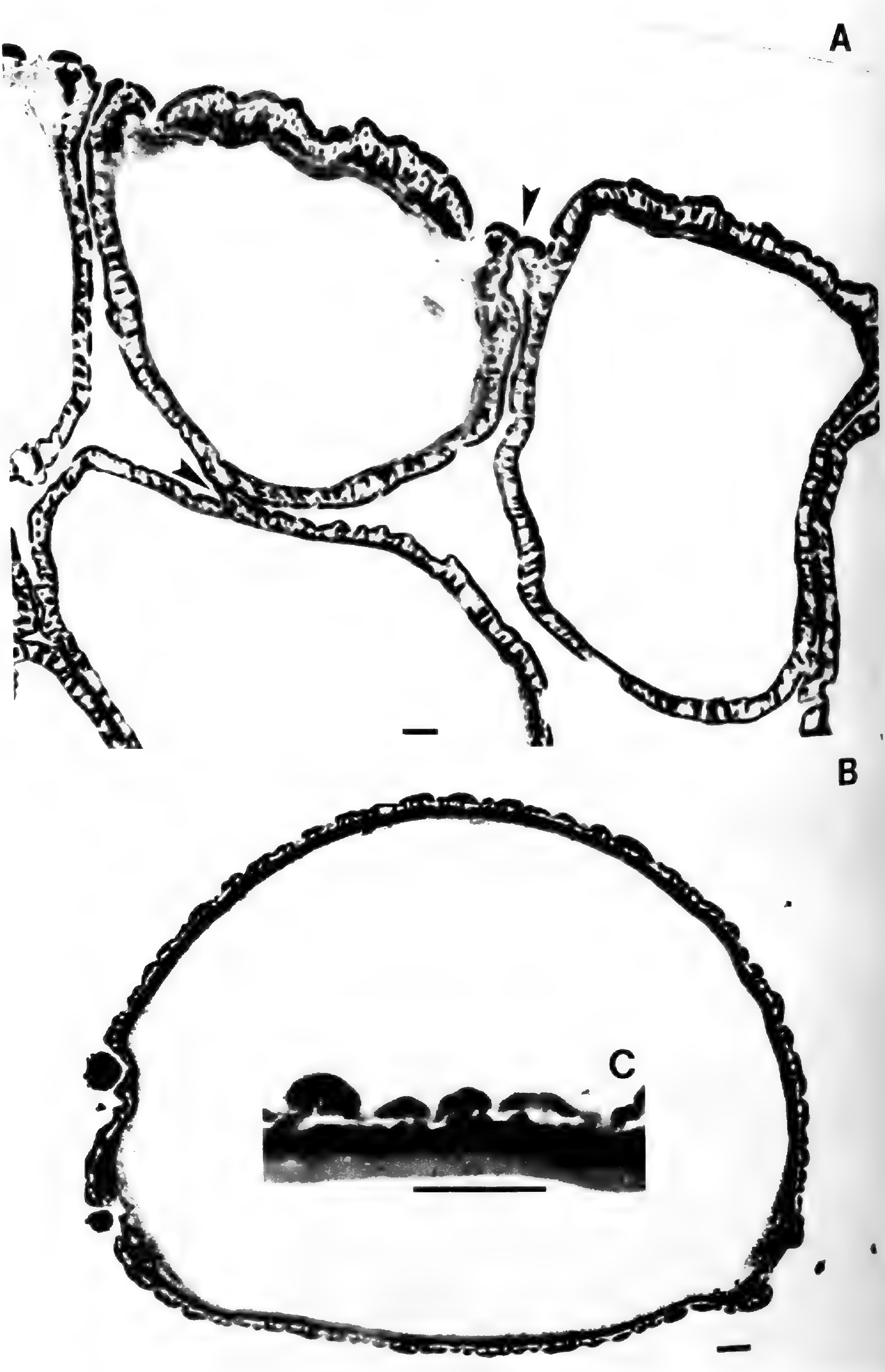

FIGURE 40. Transmission electron micrographs of Melastomataceae pollen.—A. *Tococa spadicifolia*. Section of a polyad. Fusion of tecta of two adjacent members (arrowheads). B, C. *Tococa stephanotricha*.—B. Section of an entire grain including two apertures. The tectum appears discontinuous due to the verrucate sculpturing.—C. Exine at a higher magnification. Note that foot layer and endexine are approximately equal. Scales equal 1 µm.

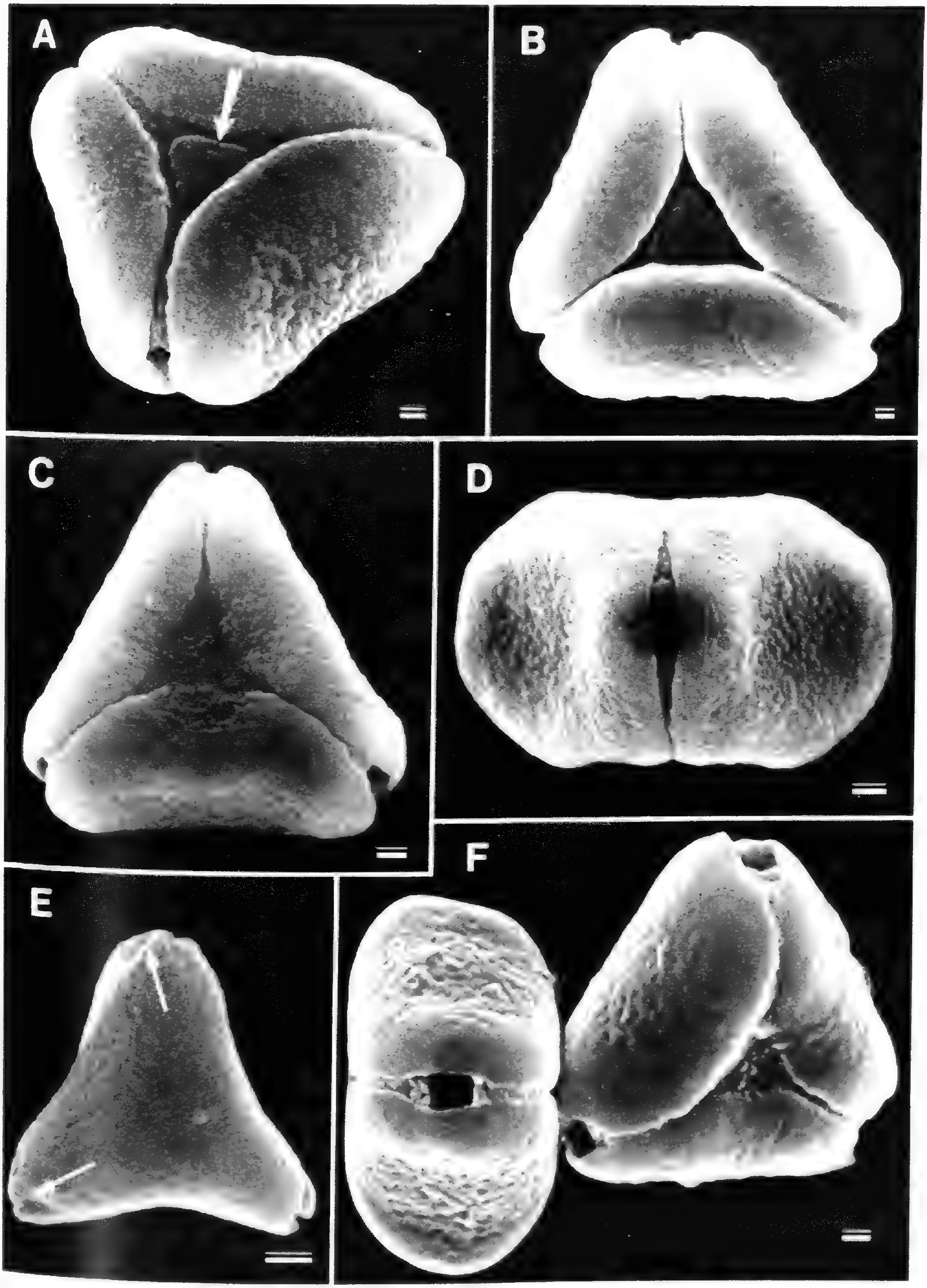

FIGURE 41. Scanning electron micrographs of Myrtaceae pollen.—A. *Metrosideros polymorpha.* Subpolar iew. Colpi are parasyncolpate forming a triangular apocolpium (arrow) at the pole. The intercolpar concavities ave a rugulate surface. Elsewhere the surface is smooth.—B. *Metrosideros nervulosa.* Polar view. The apocolpium and the triangular thin-walled area formed around it by the parasyncolpate colpi are somewhat collapsed. C, D. *Tristania conferta.*—C. Subpolar view. Syncolpate colpi form a thin-walled triangular area at the pole on hich are scattered some granular ektexinous elements.—D. Lateral view showing the outline of a lalongate. ptic endoaperture and two intercolpar concavities.—E. *Tristania nereifolia.* Polar view. Note the smooth- brate surface. The exine has irregular folds (arrows) over the apertures. Note close agreement with the scanning tron micrograph of Gadek and Martin (1981, fig. 1D).—F. *Tristania lactiflua.* Lateral (left) and subpolar ght) views. The psilate exine has punctae and channels in the intercolpar concavity areas. The grains are colpate. Scales equal 1 μm.

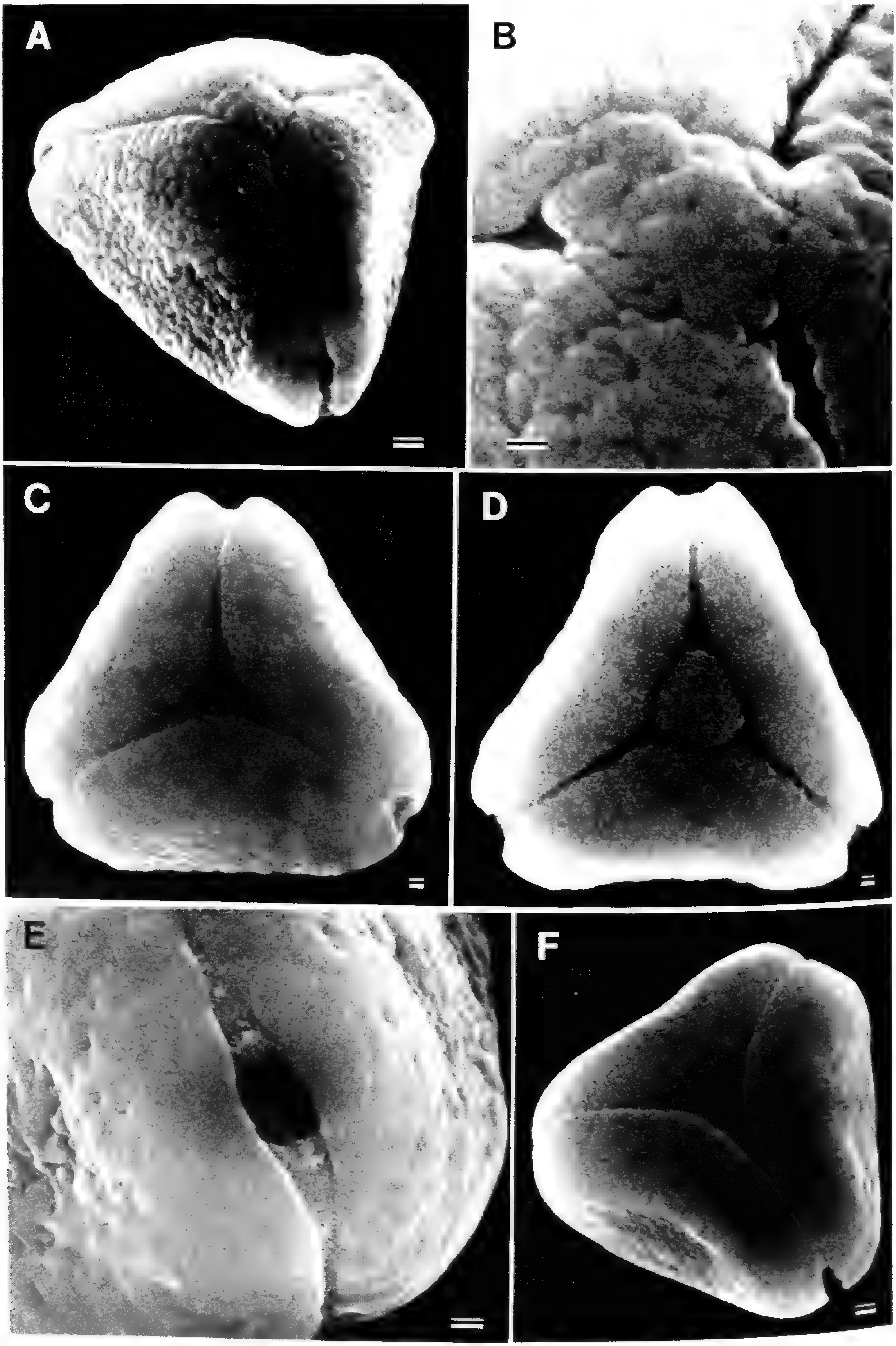

FIGURE 42. Scanning electron micrographs of Myrtaceae pollen. A, B. *Heteropyxis natalensis*. —A. Sublateral view. The surface is rugulate on the entire grain. Note distinct intercolpar concavities. The colpus at center bifurcated at the pole and fused with the other two colpi. The latter colpi do not appear to be united with eac other. Different combinations of colpi configurations, that is, syncolpate, parasyncolpate, or longicolpate, ar found on different grains of *Heteropyxis*. —B. Magnified portion of an apocolpium and surrounding area. I contrast to Figure 41A, none of the colpi appear to be united at the pole. Figure 41A is similar to the scannin electron micrograph of Schmid (1980, fig. 7) except that in the latter the bulging of material at each apertu

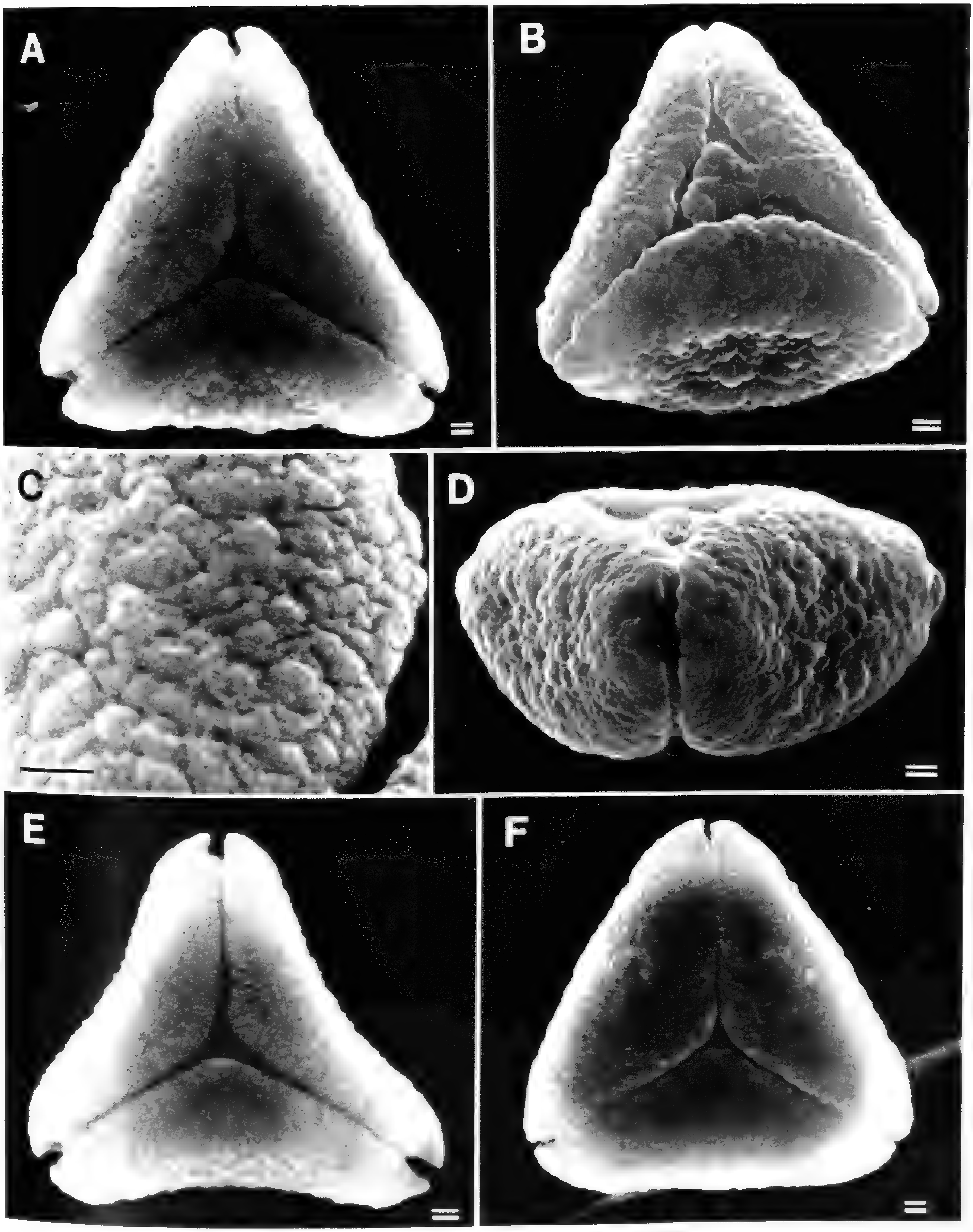

FIGURE 43. Scanning electron micrographs of Myrtaceae pollen. A, C. *Callistemon teretifolius.*—A. Polar view. Syncolpate grain. Intercolpar concavities are distinct and have a coarse rugulate-verrucate surface.—C. The mesocolpia surrounding the concavities have a fine rugulate-verrucate surface as shown here on an area near the pole. Dark areas on the right are parts of two colpi. B, D. *Callistemon citrinus.*—B. Subpolar view. The surface is rugulate. An intercolpar concavity is clearly visible (at the bottom margin). The triangular apocolpium is connected to the mesocolpium at the right (see also *Heteropyxis,* Fig. 42A).—D. Lateral view showing two intercolpar concavities.—E. *Calothamnus validus.* Polar view. The smooth surface has fine channels. The intercolpar concavities are granular-verrucate.—F. *Eremaea pauciflora.* Polar view. Intercolpar concavities appear to be absent. The surface is more or less uniform on the entire grain with fine granular, verrucate, rugulate elements. Scales equal 1 μm.

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probably represents the cytoplasmic contents of the unacetolyzed (?) pollen grain. C–E. *Eucalyptus ficifolia* —D. Polar views of two grains from the same sample. In C the grain is syncolpate, in D it is parasyncolpate.—Magnified area near the equator (and endoaperture).—F. *Eucalyptus robusta.* Subpolar view. Syncolpate grain. Intercolpar concavities have a granular surface. Elsewhere the surface is smooth. Scales equal 1 μm.

(1) Longicolpate type

The colpi are long; "colporate grains are longicolpate when the colpi are longer than the distance between their apices and the poles" (Pike, 1956: 51). *Hypocalymna angustifolium* (Fig. 44E, G), *Myrceugenella apiculata* (Fig. 47F), and *Ugni molinae* (Fig. 46D, E) belong to this type. In addition to the long colpi, pollen shape is also similar in *Myrceugenella* and *Ugni*: the triangular grains have convex sides and slightly protruding apertures in polar view and an elliptic shape with acute ends in lateral view. The surface in *Myrceugenella* is verrucate-granular with some larger verrucate elements at the poles (Fig. 47F). *Ugni* shows a unique surface pattern with multiangular units that have acute corners (Fig. 46E). These units are large and scattered at the poles but become smaller and more tightly packed toward the equator. The surface appears to be granular around the endoapertures. In *Hypocalymna,* the grains are triangular with straight sides in polar view and elliptic with acute corners in lateral view. The surface has a pebbly appearance, with large units of different shapes, separated by deep, narrow spaces. This pattern becomes finer at the margins of the colpi and at the poles. The colpi in all three taxa are very narrow, with a smooth surface except in *Myrceugenella* which has a granular surface.

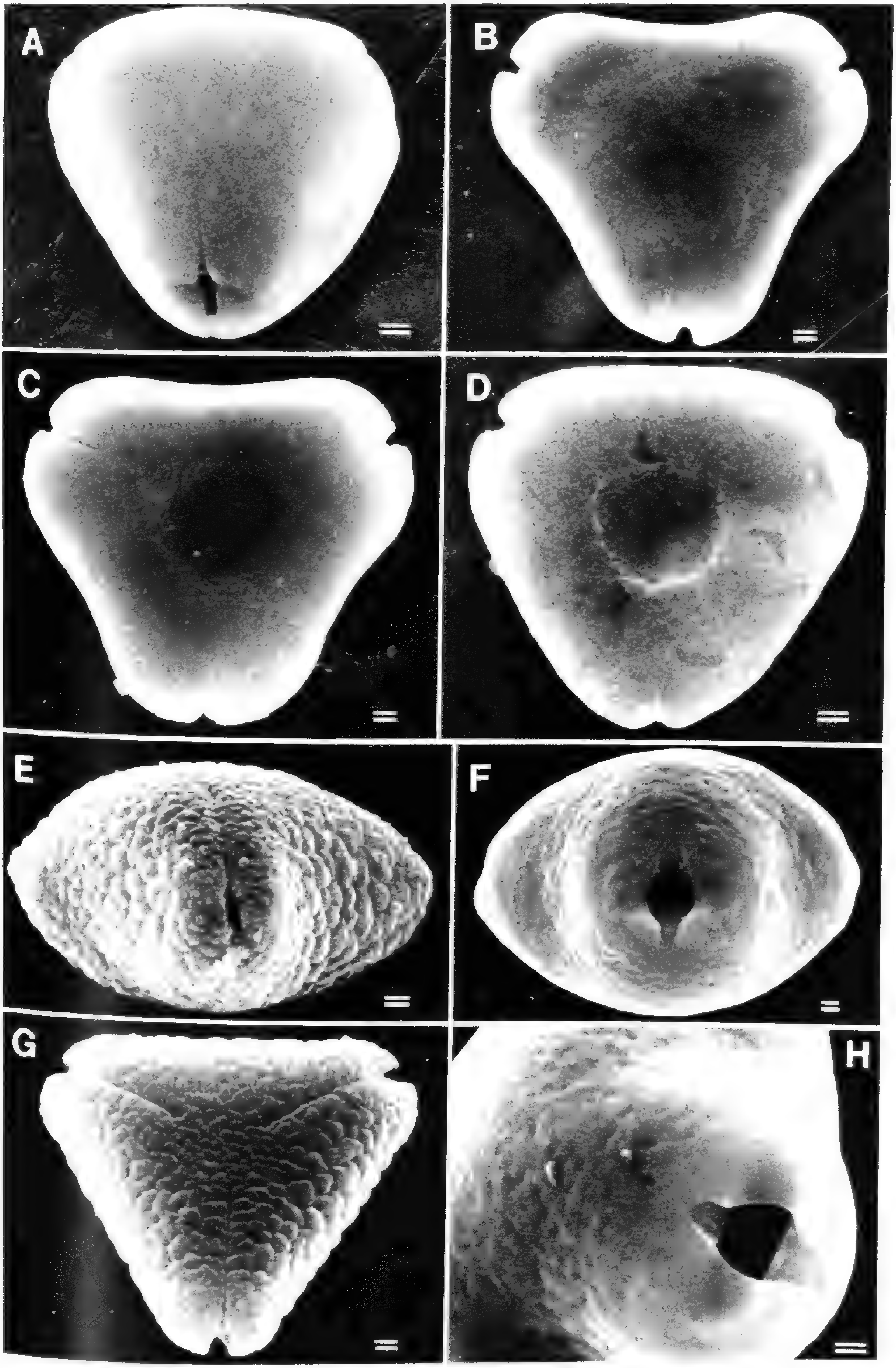
(2) Syncolpate and parasyncolpate type

In syncolpate grains, the colpi are either straight, that is, meeting at the poles without becoming wider, or curved where they are wider at the poles and form a triangular area. In parasyncolpate grains, the colpi bifurcate at the poles and their branches meet and outline a triangular apocolpium. Not all grains are strictly syncolpate or parasyncolpate; some are syncolpate on one pole and parasyncolpate on the other pole (i.e., syn/para), while others also combine with longicolpate grains and result in long/syn and long/para forms. These combinations were found in *Myrtus communis, Psidium littorale, Eucalyptus ficifolia* (Fig. 42C, D), *E. robusta, Heteropyxis natalensis, Temu divaricatum,* and *Eugena elliptifolia.* The taxa included in the syncolpate and parasyncolpate type are further grouped according to the presence or absence of intercolpar concavities.

Pollen with intercolpar concavities. Since the Myrtaceae pollen examined is oblate in lateral view, the intercolpar concavities are equatorially elongated and elliptic in shape. They are clearly defined in *Acmena smithii* (Fig. 47B), *Callistemon citrinus* (Fig. 43B, D), *C. teretifolius* (Fig. 43A), *Calothamnus validus* (Fig. 43E), *Eucalyptus ficifolia* (Fig. 42C–E), *E. robusta* (Fig. 42F), *Heteropyxis natalensis* (Fig. 42A, B), *Melaleuca hypericifolia* (Fig. 45A, B), *M. rhaphiophylla* (Fig. 45E), *Tristania conferta* (Fig. 41C, D), and *T. lactiflua* (Fig. 41F). In *Cleistocalyx operculata* (Fig. 47A), *Eugenia elliptifolia* (Fig. 47D), *Metrosideros nervulosa* (Fig. 41B), and *M. polymorpha* (Fig. 41A) they are not as markedly "depressed" as in the above mentioned taxa. In *Acmena, Eucalyptus ficifolia, E. robusta,* and *Tristania lactiflua,* the intercolpar concavities have many punctae with fine, irregular channels on a smooth surface while the surrounding areas of the mesocolpia are psilate. Similar surface sculpturing is present in *Eugenia elliptifolia* and *Cleistocalyx. Melaleuca hypericifolia* has a verrucate-granular surface in the intercolpar concavities and the surrounding areas are scabrate. In *Callistemon teretifolius, C. citrinus,* and *Heteropyxis,* the surface of the mesocolpia is rugulate, and it is regulate-verrucate in the intercolpar concavities. In *Melaleuca rhaphiophylla, Tristania conferta,* and perhaps *Calothamnus* (Fig. 43E) it is granular-verrucate in the intercolpar concavities and finely rugulate with fine channels on the mesocolpia. In *Metrosideros nervulosa* and *M. polymorpha* the intercolpar concavities have a coarse, rugulate-verrucate surface. On the mesocolpia, it is finely rugulate in the former and psilate in the latter (Fig. 41A, B).

Pollen without intercolpar concavities. Here, the surface is more or less uniform over the entire

FIGURE 44. Scanning electron micrographs of Myrtaceae pollen.—A. *Baeckea virgata.* Sublateral view. The surface is psilate, colpi are short.—B. *Homoranthus wilhelmii.* Polar view showing a psilate surface.—C. *Balaustion microphyllum.* Polar view. Psilate surface, short colpi. Note the circular, thin-walled area at the pole.—D. *Thryptomene calycina.* Polar view. Similar to C. E, G. *Hypocalymna angustifolium.*—E. Lateral view. Surface is pebbly, rugulate-verrucate.—G. Polar view. The grain is longicolpate. F, H. *Chamaelaucium uncinatum.*—F. Lateral view. The surface is smooth and with pits. The colpus is short and wide.—H. Close-up of the aperture. Colpus is shorter than the lalongate, elliptic endoaperture below it. Scales equal 1 μm.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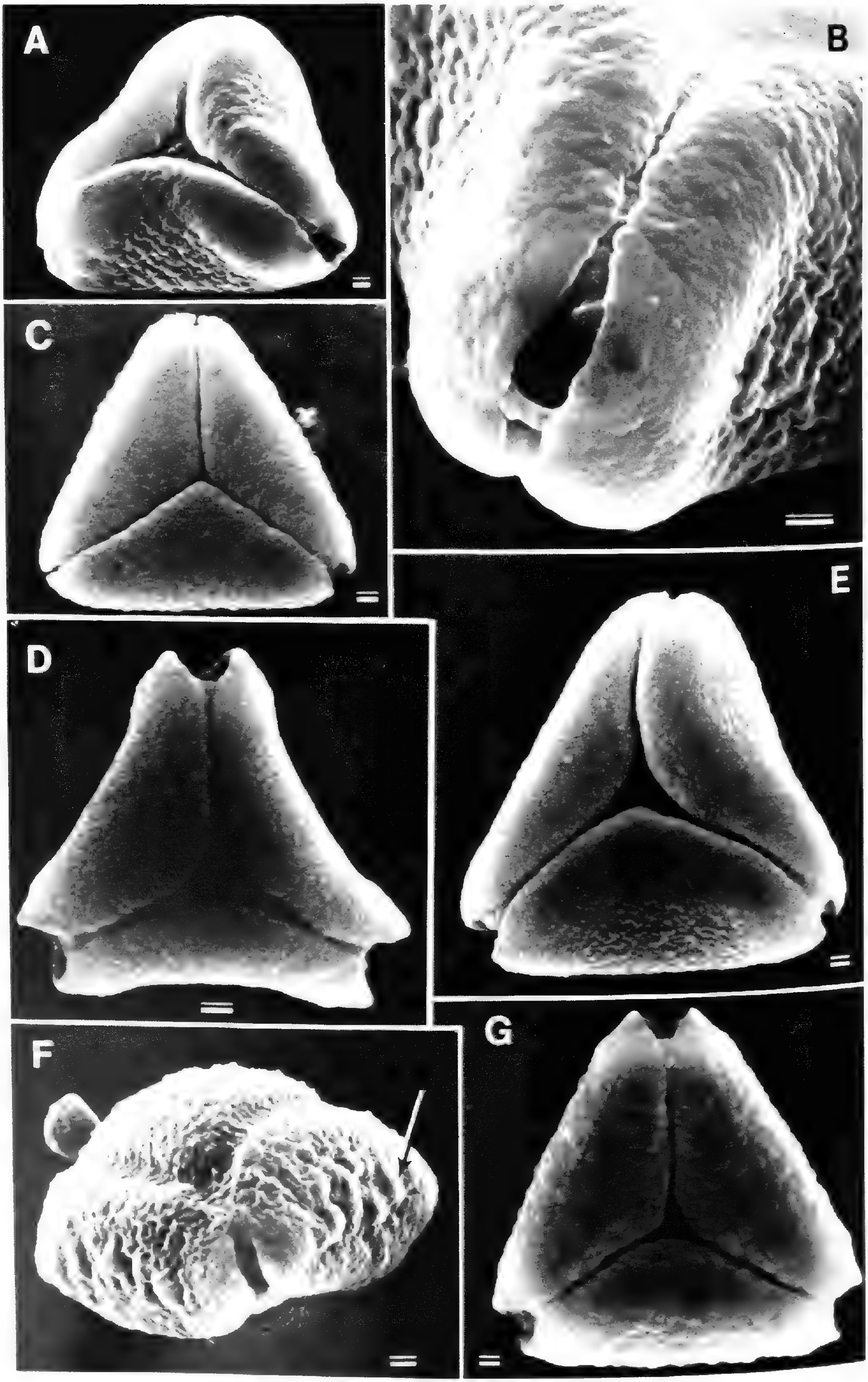
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grain. The surface in *Myrtus communis* (Fig. 48B–D), *Psidium littorale* (Fig. 46A–C), *Eremaea pauciflora* (Fig. 43F), *Melaleuca preissiana* (Fig. 45D), and *M. decussata* (Fig. 45C) is similar: granular-verrucate-rugulate. There are fine, branched, irregular channels separating the surface elements. In *M. communis* (Fig. 48C), minute lines and dots are seen on the surface elements.

The surface in *Luma chequen* (Fig. 47E), *Pilidiostigma glabrum* (Fig. 46F), and *Rhodamnia argentea* (Fig. 48E) is verrucate-granular. In *Luma,* the colpi are curved and form a large thin-walled triangular area at the poles that has irregularly scattered verrucae and granules on it. In *Pilidiostigma,* at the parasyncolpate pole, scattered granules form a triangular apocolpium. The surface is smooth near the endoapertures in both of these taxa. In *Rhodamnia,* larger verrucate elements are present along the margins of the mesocolpia, even near the endoapertures.

Austromyrtus bidwillii (Fig. 48F), *Temu divaricatum* (Fig. 48A), *Melaleuca pulchella* (Fig. 45G), and *Psiloxylon mauritianum* (Fig. 45F) show a coarsely rugulate pattern. In *Austromyrtus,* isolated rugulate and verrucate elements are present on the apocolpia. In *Psiloxylon,* the rugulate elements are larger on the equator. This genus has large apocolpia and differs from the rest of the parasyncolpate taxa in this respect. *Eugenia capuli* (Fig. 47C) has a slightly less coarse rugulate surface. In all the rugulate taxa, the surface near the endoapertures is smooth.

In TEM, the cross section of the *Myrtus communis* monad (Fig. 49C, D) shows that the endexine is uniform except near the endoapertures where it increases in thickness and becomes granular. The thin foot layer has an irregular upper margin and is discontinuous. The short columellae support a thick, infratectal granular layer. The tectum is also thick, with an irregular upper margin, and shows many perforations. The section of the tetrad (Fig. 49A) indicates in places a discontinuous dome-shaped tectum with a granular layer below it. Figure 49B shows the fusion of tecta between two members of the tetrad.

(3) Brevicolpate and brevissimicolpate type

In the brevicolpate grains the length of the colpi is equal to or less than the distance between their ends and the poles (Erdtman, 1971). In the brevissimicolpate grains, the colpus length is less than that of the underlying endoaperture (Erdtman, 1971). *Chamaelaucium uncinatum* (Fig. 44F, H) has brevissimicolpate grains. The surface is smooth with minute pits. The ends of the very short colpi are rounded.

(4) Uncertain type

Due to the lack of sufficient data the following taxa could not be assigned to any of the above pollen types. *Baeckea virgata* (Fig. 44A) and *Osbornia octodonta* (Fig. 46G) appear to have curved syncolpi. However, they are often partially obscured or not well developed and then appear as short colpi which outline a faint triangular thin-walled area at the pole. Moreover, *Baeckea* appears to have intercolpar concavities. *Homaranthus wilhelmii* (Fig. 44B) and *Thryptomene calycina* (Fig. 44D) seem to be brevissimicolpate. The surface is psilate in both taxa and *Thryptomene* shows a circular, thin-walled area at the pole. *Balaustion microphyllum* (Fig. 44C) appears to be brevicolpate with a psilate surface and a circular, thin-walled area on the pole. Intercolpar concavities may be present. *Tristania nereifolia* (Fig. 41E) differs from all the taxa of the family. The triangular pollen has

FIGURE 45. Scanning electron micrograph of Myrtaceae pollen. A, B. *Melaleuca hypericifolia.*—A. Sublateral view. Distinct intercolpar concavities have a verrucate-granular surface. Elsewhere the surface is psilate. Colpi are curved (arcuate) and united at the pole.—B. View near the endoaperture.—C. *Melaleuca decussata.* Polar view. The fine granular-verrucate-rugulate surface sculpture is essentially uniform over the entire grain. In contrast to A the colpi are straight and united at the pole. Intercolpar concavities are absent.—D. *Melaleuca preissiana.* Polar view. The surface is fine granular-verrucate-rugulate and more or less uniform over the entire grain. Colpi are curved (see A). Intercolpar concavities are absent.—E. *Melaleuca rhaphiophylla.* Subpolar view. The intercolpar concavities are not as distinct as in *M. hypericifolia.*—F. *Psiloxylon mauritianum.* Lateral view. The syncolpi form large apocolpia on both poles. The arrow indicates coarse rugulate elements on the equator: this is not believed to be a regular characteristic as other grains of *Psiloxylon* have an essentially uniform sculpture. Comparison should be made with the scanning electron micrograph of Schmid (1980, fig. 5).—G. *Melaleuca pulchella.* Polar view. Surface is rugulate. Scales equal 1 μm.

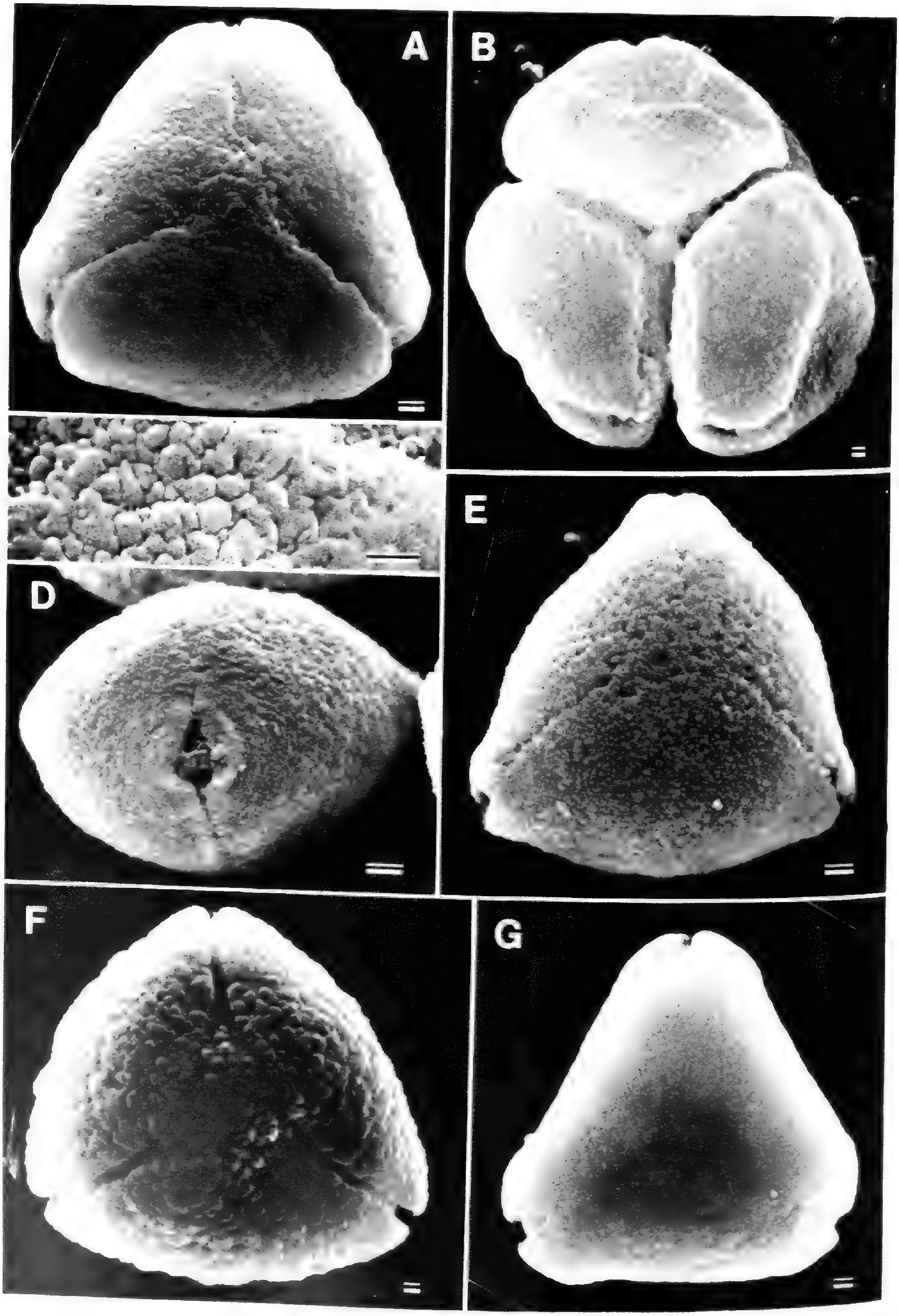

FIGURE 46. Scanning electron micrographs of Myrtaceae pollen. A–C. *Psidium littorale.*—A. Subpolar view of a monad. The grain is longicolpate (parasyncolpate and syncolpate grains are also present in sample) Int colpar concavities are absent.—B. A tetrahedral tetrad (fourth grain is at the back).—C. Surface details of A nea the pole showing the surface to be granular-verrucate-rugulate. D, E. *Ugni molinae.*—D. Lateral view show elliptic shape.—E. Polar view. Colpi are long. Note angular surface elements near the pole.—F. *Pilidio glabrum.* Polar view. The surface is verrucate-rugulate. The arcuate colpi are parasyncolpate. The apocolpi

deeply concave sides. The surface is scabrate and the nature of the three apertures is difficult to interpret but the pollen appears to be triporate.

Discussion

In his extensive bibliography of myrtalean palynology, Thanikaimoni (1984) lists only three references that allude to electron microscopy of Myrtaceae pollen, making it obvious that SEM-TEM investigations are greatly needed in the family, although, as discussed below, taxonomic investigations by Gadek and Martin (1981, 1982) are currently in progress. Since our intent in this study is the presentation of a broad overview of the Myrtales core families we shall not attempt a review of the extensive Myrtaceae pollen references, but shall only briefly mention a few of the more recent/pertinent ones. The most comprehensive taxonomic light microscope study was that of Pike (1956), which included 71 genera and 300 species from the southwestern Pacific area. Some of the conclusions reached from this study were:

(1) although the pollen in Myrtaceae is essentially uniform, in some taxa minor differences make it possible to recognize particular genera or species;

(2) within the family (following Niedenzu's classification, 1893) "There appears to be no particular feature that separates pollen of the Myrtoideae from that of the Leptospermoideae, but pollen of the tribe Chamaelaucieae (placed by Niedenzu in the Leptospermoideae) differs markedly from that of all other tribes in the family" (Pike, 1956: 46);

(3) within a tribe the taxa usually are similar, "... e.g., Myrtinae, Chamaelaucieae, but it is possible for closely related genera to have quite distinct pollen, e.g., *Metrosideros* and *Spermolepis*, *Leptospermum* and *Agonis*, *Baeckea* and *Balaustion*, *Wehlia* and *Pileanthus*. On the other hand, grains of widely separated genera may show certain similarities, e.g., those of *Regelia ciliata* are difficult to distinguish from those of some species of *Eucalyptus*, and those of *Astartea* and *Agonis* are ± similar" (Pike, 1956: 46);

(4) "grains of different species of the same genus are usually indistinguishable, e.g., *Leptospermum*, or they may be similar in general features but show a comparatively large range in size, e.g., *Eucalyptus*. Rarely is it possible to make specific distinctions as in *Regelia*" (Pike, 1956: 47).

McIntyre (1963) examined the pollen of 18 New Zealand taxa and found that most genera could be recognized. Species within genera also could be recognized to some extent. As concerns fossil identification of Myrtaceae pollen, McIntyre (1963: 104) stated: "There is little or no difference between the pollen grains of many genera of the Myrtaceae. Identification of living genera and species from fossil pollen, therefore, can only be reliable if there are no grains of similar type, from extinct genera and species, in the sample under consideration .... When all factors are considered it is obvious that attempted identifications of fossil Myrtaceae pollen on the basis of pollen characters of the indigenous species should be restricted to a period of time where it is reasonably certain that no other species or genera of the family were present ...."

Most recently Gadek and Martin (1981) examined the pollen of 28 species and seven genera of subtribe Metrosiderinae with light microscope and SEM. They found a greater range of pollen morphology within the family than was heretofore recognized and in some instances pollen could be identified to the generic and specific levels. With the SEM they were also able to circumscribe three basic exine sculpture types: (1) Psilate to microscabrate, (2) microfossulate, and (3) microrugulate, rugulate.

Lugardon and van Campo (1978) examined pollen of *Tristania laurina* and *Myrtus communis* with TEM and apparently encountered, at least with the latter, the same problem as we did, that is, a lack of staining contrast between the endexine and the foot layer. They described the thin, often discontinuous foot layer above a "white line" and a thick endexine below it as constituting the nexine. They further described an infractectal granular layer between the tectum and nexine but did not recognize columellae. In contrast, our section of *M. communis* (Fig. 49D) indicates very short columellae below the infratectal granular layer. This section also shows a distinct foot layer and endexine. The most de-

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is formed by scattered verrucate, granular elements.—G. *Osbornia octodonta*. Polar view. The surface appears to be scabrate, colpi are short and at the pole form a weakly developed thin-walled triangular area. Scales equal 1 μm.

finitive TEM study is that of Gadek and Martin (1982: 75), in which pollen of *Eucalyptus* and *Tristania* were examined in great detail. Their general description for the pollen structure is as follows: "The species all show a typical angiosperm exine differentiation consisting of two chemically different layers, an electron dense ektexine and a less dense endexine divided by a very thin electron-transparent lamella. They all differ, however, from the typical angiosperm architecture by the presence of a somewhat unstructured, granulate infratectal layer and the presence of a granular/alveolate endexinous layer around the pores. Species differences relate to the granulate/columellate organization of the infratectal layer; the extent or density of tectal perforations; and the presence and thickness of a foot-layer around the grain."

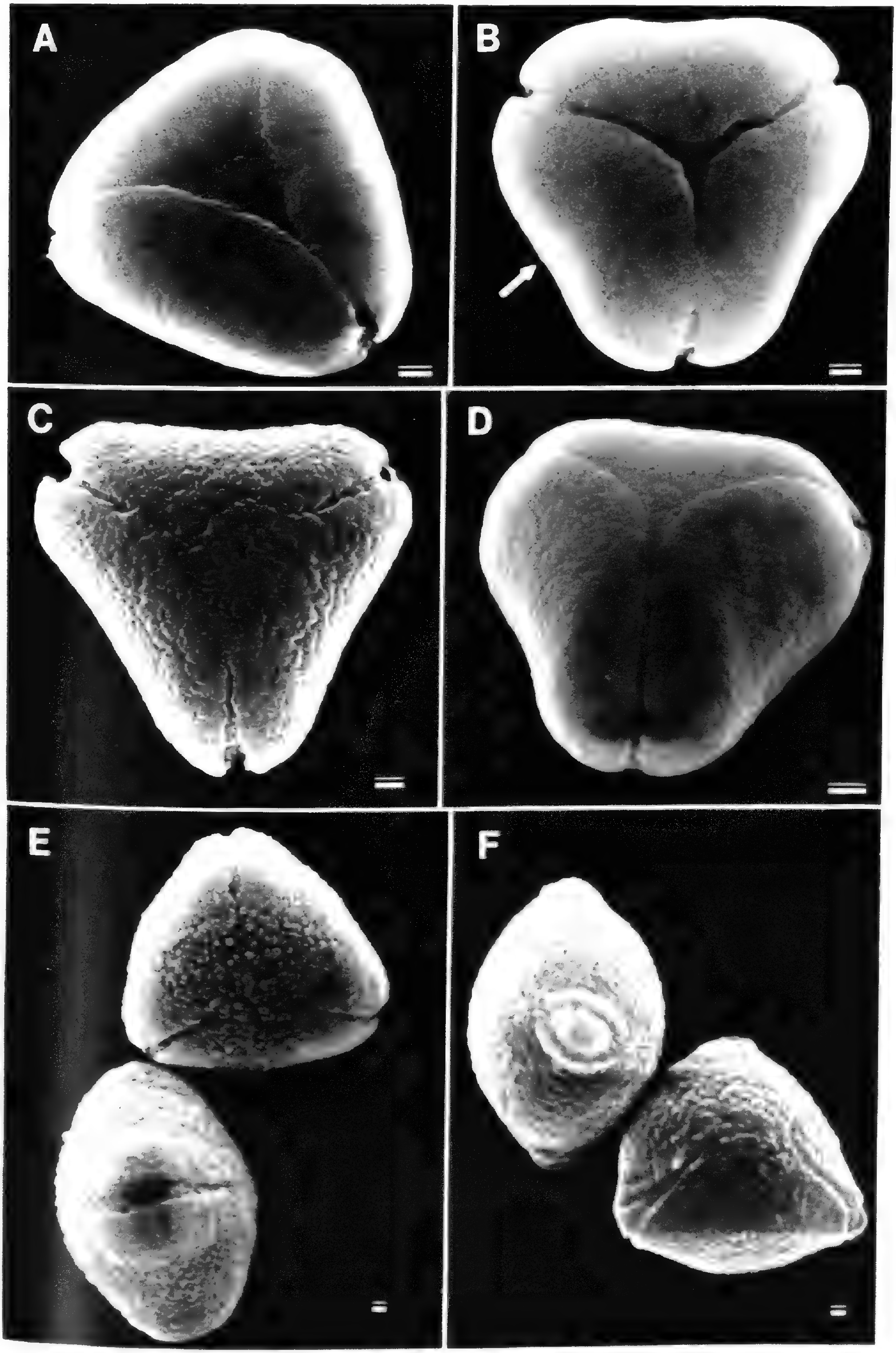
Dahlgren (in Dahlgren & Thorne, 1984) regards both *Heteropyxis* and *Psiloxylon* as segregate monotypic families. *Psiloxylon* differs from other parasyncolpate taxa of Myrtaceae by having unusually large apocolpia and larger rugulate elements on the equator, but otherwise is similar to the rest of the family. *Heteropyxis* is not easily distinguished from other genera in the syncolpate and parasyncolpate group with intercolpar concavities.

In summary, Myrtaceae pollen as documented with SEM does not appear to have any close similarities to taxa from the other core families of the Myrtales. Perhaps some superficial similarity exists with Onagraceae pollen but there is no mistaking the two families. Erdtman (1971) suggests similarity to Lythraceae (perhaps through *Cuphea*) but we have not been able to confirm it in this study. Furthermore, we do not have sufficient data to compare Myrtaceae pollen with families outside of the Myrtales as suggested by Erdtman (1971). It would be of interest to examine pollen of Cunoniaceae, Proteaceae, Lecythidaceae, and Sapindaceae in order to check Erdtman's (1971) observations. Pollen of Lecythidaceae and Sapindaceae have been examined in SEM (Muller, 1972, 1973; Muller & Leenhouts, 1976; Mori et al., 1980) and are not similar to Myrtaceae pollen. However, in Sapindaceae there are several taxa with triangular, parasyncolpate grains (Muller & Leenhouts, 1976).

FIGURE 47. Scanning electron micrographs of Myrtaceae pollen.—A. *Cleistocalyx operculata*. Subpolar view. The psilate surface has punctae and channels in the shallow and barely discernible intercolpar concavity areas.—B. *Acmena smithii*. Polar view. Surface is psilate; punctae and channels are present in the intercolpar concavities (arrow).—C. *Eugenia capuli*. Polar view of the convex face of the grain, the opposite face is concave. The surface is rugulate. Colpi are united (i.e., syncolpate) but are obscured by rugulate elements at the pole. The pole on the concave face usually has more distinct syncolpi.—D. *Eugenia elliptifolia*. Sublateral view showing syncolpi. The psilate surface becomes coarser and has fine channels and punctae in the intercolpar concavities.—E. *Luma chequen*. Polar (upper) and lateral (lower) views. The surface is smooth to slightly coarse in the area of the endoapertures. Toward middle part of the mesocolpia it becomes granular-verrucate. There is a large thin-walled area at the poles that has granules and verrucae scattered over it. The colpi merge with this thin-walled area, thus, the grains are syncolpate.—F. *Myrceugenella apiculata*. Lateral (left) and subpolar (right) views of unacetolyzed, glutaraldehyde-fixed pollen. The surface is granular-verrucate. Colpi are long. Scales equal 1 µm.

FIGURE 48. Scanning electron micrographs of Myrtaceae pollen.—A. *Temu divaricatum*. Polar view of a parasyncolpate grain. Other colpi combinations were found in the same sample. The surface is rugulate. B–D. *Myrtus communis*.—B. Polar view of a monad. All colpi are not united at this pole but different colpi combinations (i.e., parasyncolpate/syncolpate; syncolpate/syncolpate, etc.) are found within the same sample.—C. In this enlarged view of the surface, rugulate and verrucate elements contain fine electron dense lines and dots.—D. Tetrahedral tetrads are also common in the sample.—E. *Rhodamnia argentea*. Polar view. The syncolpate grain has straight colpi. The surface is verrucate-granular. Large verrucate-rugulate elements are present on colpi margins and at the pole.—F. *Austromyrtus bidwillii*. Subpolar view. Parasyncolpate grain shows rugulate surface. The apocolpium is formed by separate rugulate and verrucate elements. Scales equal 1 µm.

FIGURE 49. Transmission electron micrographs of Myrtaceae pollen. A–D. *Myrtus communis*.—A. Section of three members of a tetrahedral tetrad. The proximal faces of the grains have a discontinuous tectum (due to verrucate-granular sculpture), while the distal faces show a more or less continuous tectum. In the grain on the left, the apocolpium (the thin-walled triangular area where colpi unite) shows a thickened endexine (en). Several ektexinous connections (arrows) between adjacent grains are visible.—B. A close-up of a portion of A showing fusion of tecta.—C. Cross section of a single grain passing through the three apertures near the equator.—D. An enlarged area of C showing a thick tectum, an infratectal granular layer, short columellae, a thin discontinuous foot layer, and a well-developed endexine. The transmission electron micrograph of Lugardon and van Campo (1978, Pl. 1, figs. 1–6) differs from C and D in that columellae were not recognized. Scales equal 1 µm.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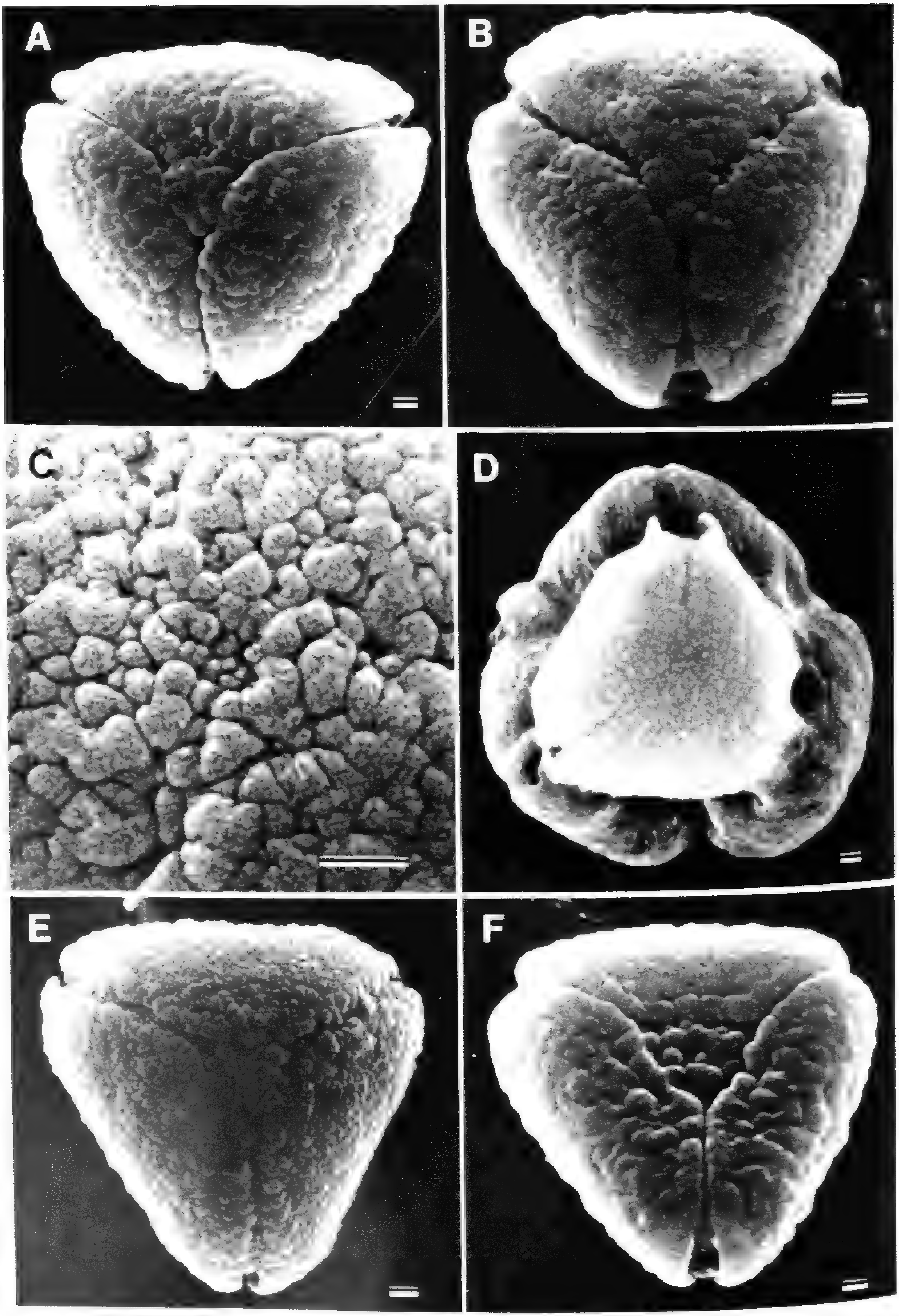
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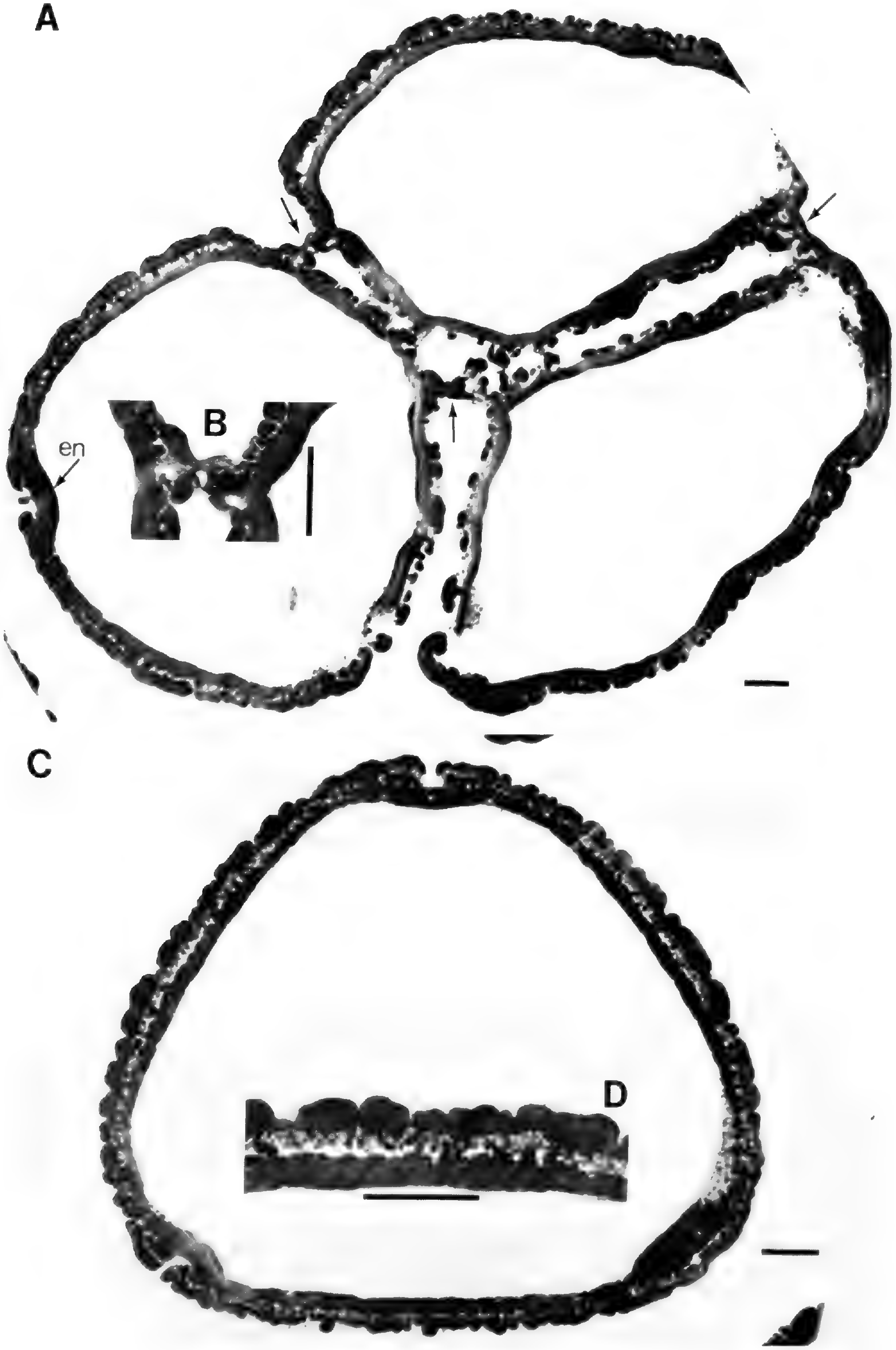
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The distinct SEM appearance of Myrtaceae pollen is countered by the TEM structure, which basically conforms with a typical post-and-beam organization of angiosperm pollen. The 'granular/alveolate' endexine of Gadek and Martin (1982) does appear somewhat similar to Onagraceae pollen but as further suggested by them it can also be found in other families, thus diminishing the uniqueness of the character. Furthermore, the infratectal granular layer has been observed in a number of core families in this study.

ONAGRACEAE

The scanning and transmission electron micrographs of Onagraceae pollen in Figures 50–63 and the data in Table 2 are intended as a general overview of the morphology of the family (forthcoming studies with Nowicke & Praglowski will be more inclusive). Pollen characterized by a dominant central body (Praglowski et al., 1983) with markedly protruding apertures is typical of *Fuchsia* (Fig. 50A, B), *Circaea* (Fig. 50C, D), *Clarkia* (Fig. 52A, B, D), *Gaura* (Figs. 52H, 53 A, B), *Heterogaura* (Fig. 54A, B), *Calylophus* (Fig. 55A, B), *Stenosiphon* (Fig. 55E), and *Oenothera* (Fig. 56A, C). In comparison, the apertural protrusions are less pronounced in *Xylonagra* (Fig. 54E, F), *Camissonia* (Fig. 57), *Ludwigia* (Fig. 58F, H), and *Hauya* (Fig. 50E), while in *Lopezia* (Fig. 51A, B, D, G), *Gayophytum* (Fig. 53E, F), *Gongylocarpus* (Fig. 56D), *Boisduvalia* (Fig. 58A), and *Epilobium* (Fig. 59A, B, E, J), the apertures are non-protruding. These latter genera, particularly *Lopezia* (Fig. 51A, D), have a triangular outline in polar view. While most Onagraceae pollen is three-aperturate, that of *Fuchsia* (Fig. 50A) is also characteristically two-aperturate in certain sections (Praglowski et al., 1983; Nowicke et al., 1984). Four-aperturate grains, as depicted for *Lopezia* (Fig. 51G) and *Heterogaura* (Fig. 54B), are less commonly represented, although occurring in many genera of the family.

Most genera of Onagraceae shed their pollen exclusively as monads, but some also shed the pollen in tetrads or polyads. Pollen tetrads characterize *Boisduvalia* (Fig. 58A), most species of *Epilobium* (Fig. 59E, J), and some species of *Camissonia* (Fig. 57A, F–H) and *Ludwigia* (Fig. 58A, F). In *Epilobium brachycarpum* (*E. paniculatum*), most individuals shed their pollen as monads (Fig. 59A, B), as do all species of sect. *Chamaenerion* (cf. Raven, 1976), while a few individuals are known to shed the pollen in tetrads (Fig. 59E), as do all other species of *Epilobium*. Polyads are found only in some species and sections of *Ludwigia* (Praglowski et al., 1983), including *L. longifolia* (Fig. 58H) in this study. The internal bridges (Fig. 58G) connecting adjacent tetrad members and the external bridges (Fig. 58I) connecting adjacent tetrads appear identical to each other as well as to their respective exine surfaces.

All taxa except *Circaea alpina* subsp. *imaicola* (Fig. 50D) are characterized by long ektexinous

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FIGURE 50. Scanning electron micrographs of Onagraceae pollen.—A. *Fuchsia thymifolia* subsp. *thymifolia*. Oblique lateral view with viscin threads associated with the proximal (top) pole. The arrow indicates a thickened area of threads showing a segmented-ropy morphology characteristic of this species (see Skvarla et al., 1978, Pl. 4, fig. 6). The apertural protrusion (AP) extends from the central body (CB). A portion of a second apertural protrusion is visible at the upper left. This two-aperturate condition is characteristic for the pollen of many species of *Fuchsia*.—B. *F. michoacanensis*. Apertural protrusion with crack extending from pore (at right) into the central body. The arrow indicates endexine lamellae. The exine surface consists of rod-like to elongate (almost rugulate) elements.—C. *Circaea cordata*. Portion of a pollen grain with apertural protrusion and a single smooth viscin thread. The surface is composed of globular and rod-like elements.—D. *C. alpina* subsp. *imaicola*. Lateral view showing three apertural protrusions. Note that the grain is essentially isopolar and in the absence of viscin threads (*C. alpina* is the only taxon in the Onagraceae without them) it is difficult, if not impossible, to determine the distal and proximal poles. E, F. Two collections of *Hauya elegans* subsp. *elegans*.—E. (*Moran 13387*). Two pollen grains in proximal polar view showing masses of viscin threads. In contrast to the pollen of *Fuchsia* (A) and *Circaea* (D) the apertural protrusions are considerably less prominent.—F. (*Rzedowski 9294*). Two groups of viscin threads exhibiting a segmented to coarsely beaded morphology. Each group consists of several individual threads aligned in parallel fashion. Attachment with the globular elements of the exine surface is partially evident in the thread group at the right.—G. *H. elegans* subsp. *barcenae*. Area of a fractured pollen grain showing thick, spongy ("paracrystalline") ektexine (ek) and solid, dense endexine (en). The short, irregular extensions at the lower margin of the ektexine are columellae (see Fig. 60C). The slightly lamellate upper margin of the endexine suggests a foot layer but it has not been confirmed in transmission electron micrograph with any degree of confidence (see Fig. 60C). The separation of ektexine from endexine is artificial, probably a result of processing. The scales equal 1 μm.

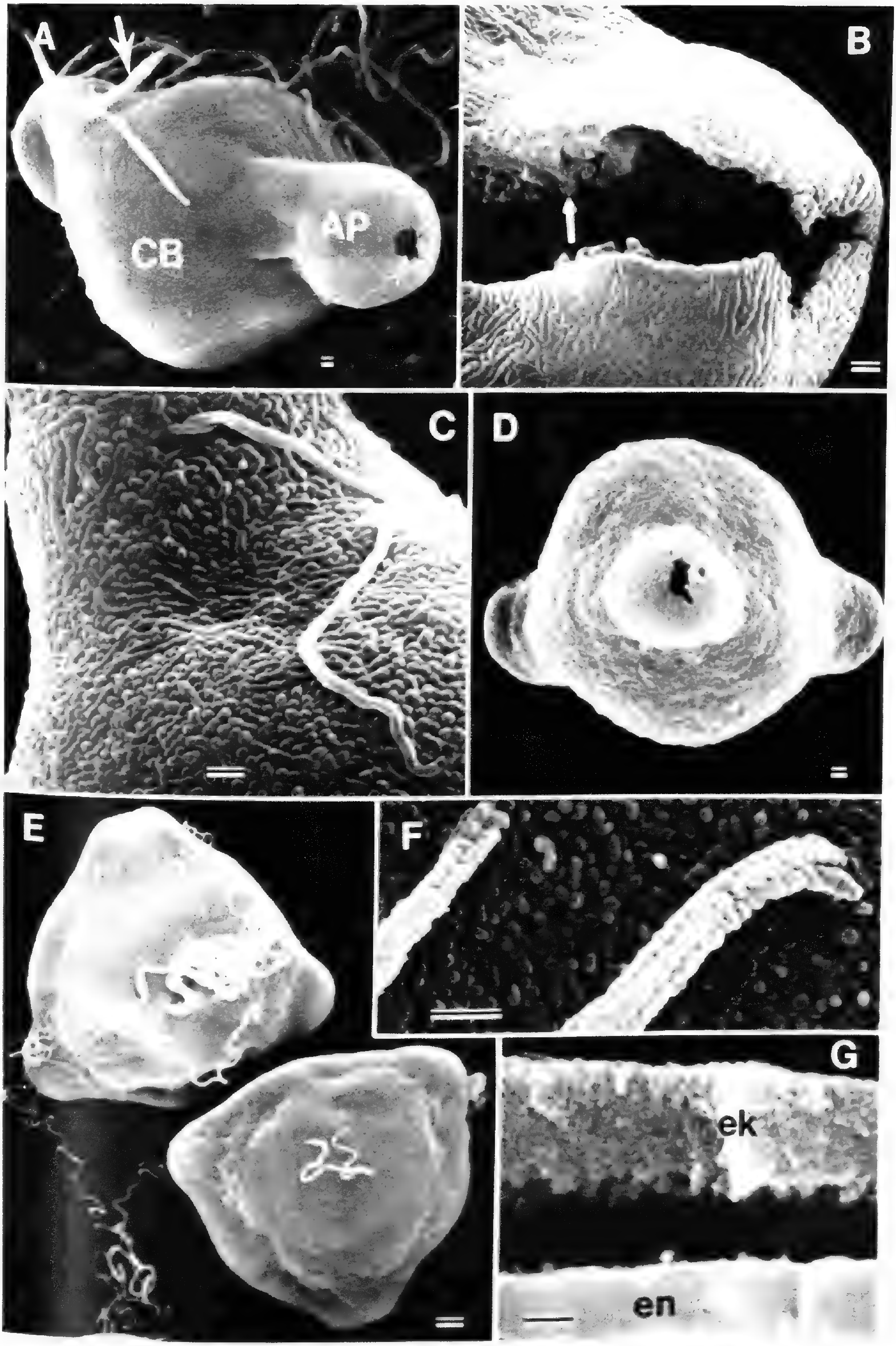
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TABLE 2. Summary of pollen characters in Onagraceae.[a]

	Pollen Type			Apertural Protrusions			Viscin Threads					Surface Texture				Columellae			Columellae/ Tectum			Endexine Granularity		
	M	T	P	P	NP	BCB	SM	B	R	TC	IC	G	R–E	RUG	P	P	I	A	C = T	C > T	C < T	P	NP	NE
Fuchsia	+			+					+			(+)	+	(+)				+						+
Lopezia	+					+		+				+			+	+			(+)		+			+
Circaea	+			+			+					+	+					+						
Camissonia	+	+			+		(+)		+			+				+			+			+		
Xylonagra	+				+				+			+	(+)			+					+	+		
Gongylocarpus	+					+			+			+	+				+				+		+	
Gayophytum	+					+	+		+			+	+					+						+
Hauya	+				+			+				+				+					+	+		
Calylophus	+			+				+				+	+			+			+					+
Gaura	+			+				+				+			(+)	+			+					+
Heterogaura	+			+			+					+						+						+
Clarkia	+			+			+					+	+					+						+
Oenothera	+			+				+				+	+		+		+				+			+
Stenosiphon	+			+						+		+	+			+				+				+
Ludwigia	+	+	+		+		+							+				+					+	
Boisduvalia		+				+	+			+	+			+	+		+	+	+					+
Epilobium	+	+				+				+	+		+	+	+	+	+		+	+			+	

[a] The data apply to the taxa listed in Table 1. Parentheses indicate that this observation was less common. Abbreviations for each category are:
Pollen type: M (monad), T (tetrad), P (polyad).
Apertural Protrusions: P (prominent), NP (not prominent), BCB (apertural protrusions blend into central body).
Viscin threads: SM (smooth), B (beaded), R (ropy), TC (tightly compound), IC (incised compound).
Surface texture: G (globular), R–E (rod-like to elongate), RUG (rugulate), P (porous underlying sheet).
Columellae: P (prominent), I (indistinct), A (absent).
Columellae/Tectum: C = T (columellae and tectum approximately equal), C > T (columellae of greater thickness than tectum), C < T (tectum of greater thickness than columellae).
Endexine granularity: P (prominent), NP (not prominent), NE (not evident in this study).

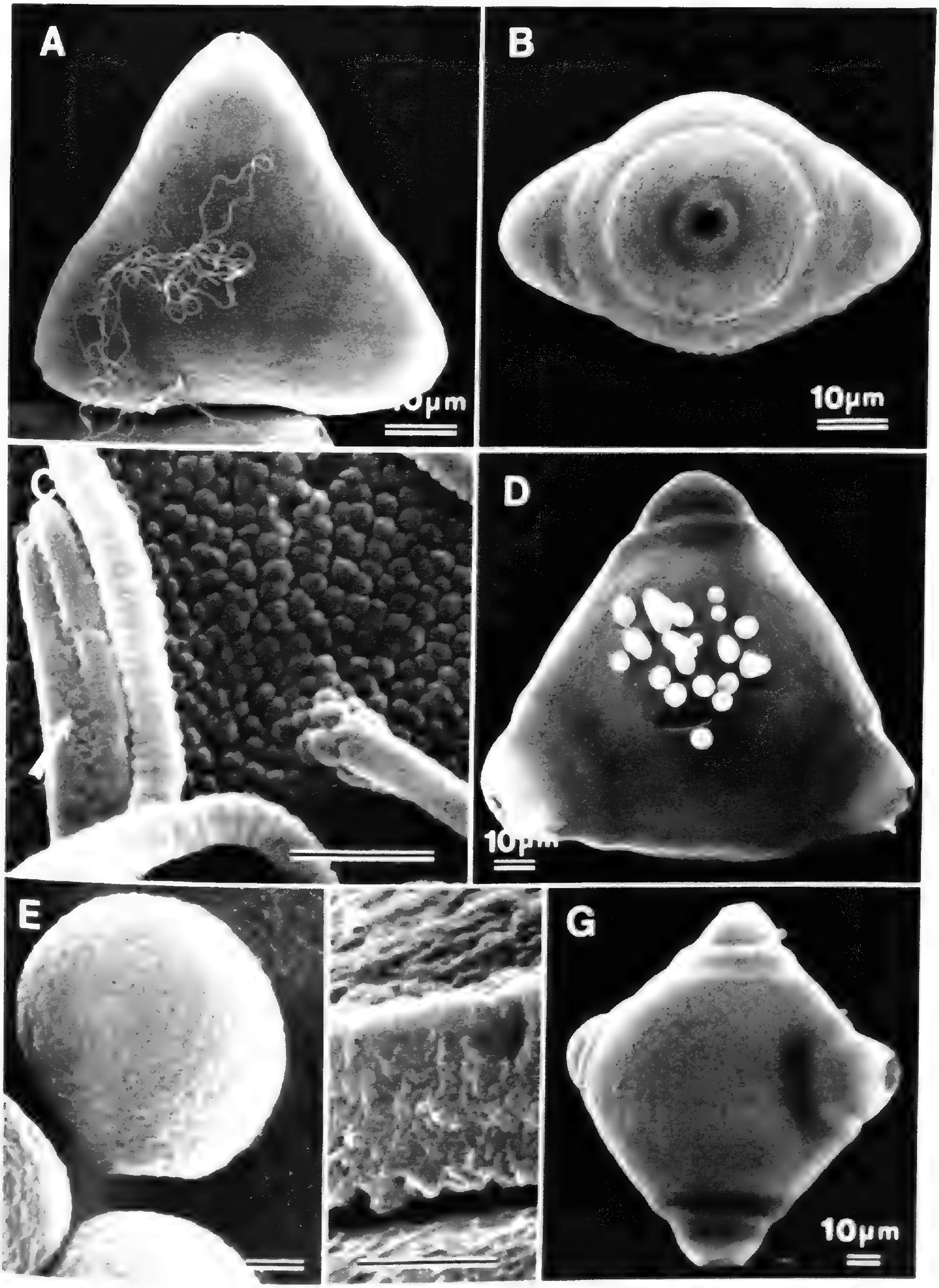
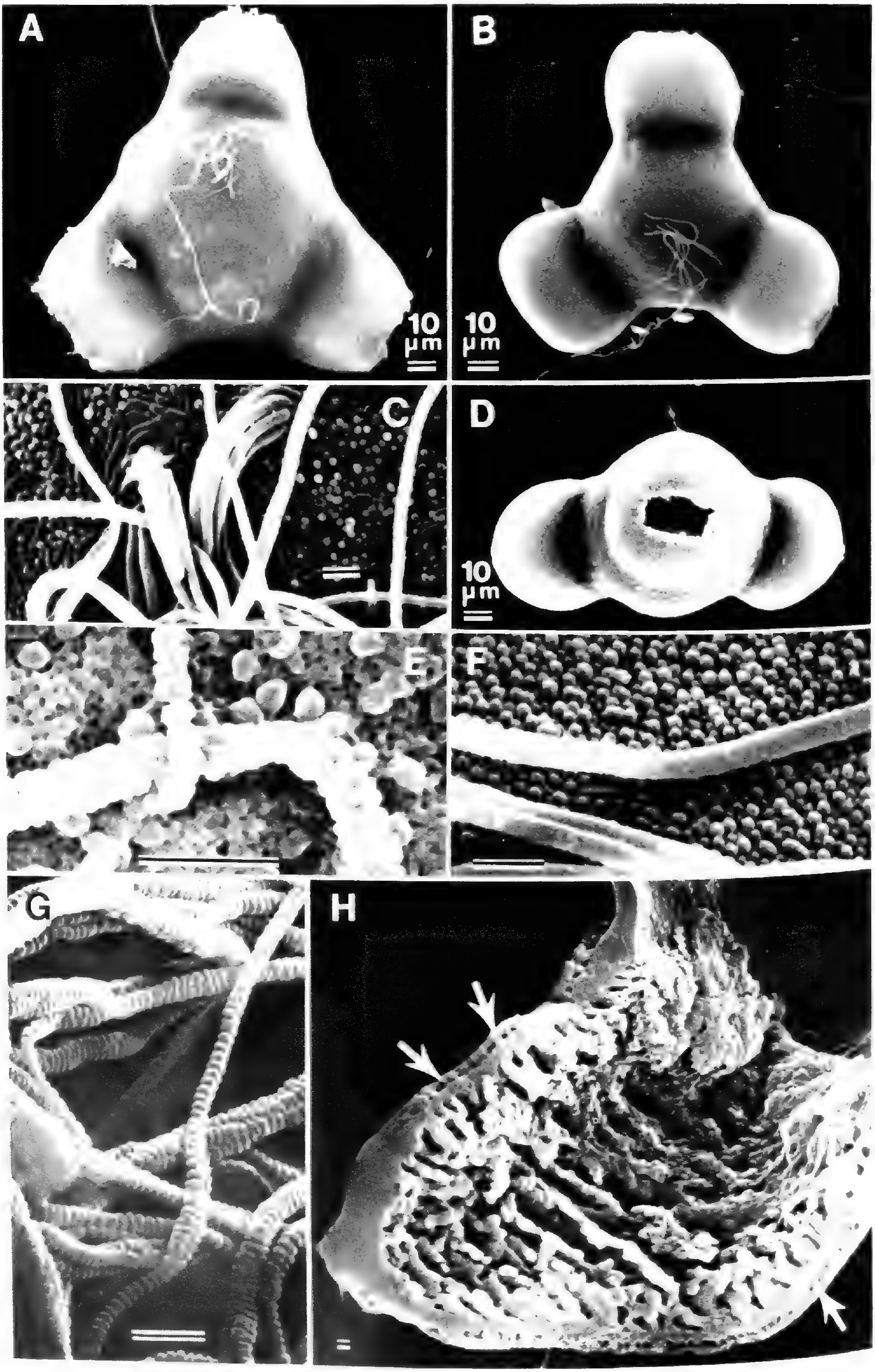


FIGURE 51. Scanning electron micrographs of Onagraceae (*Lopezia*) pollen. A–C. *L. racemosa* subsp. *race*—A. Proximal polar face with viscin threads.—B. Lateral view.—C. Surface detail showing tightly packed granular elements on a porous exine sheet. Viscin threads are beaded but some are smooth where they extend from the ektexine. Two or more threads are often united at the exine surface. Rarely a beaded-granular surface (arrow) is indicated where the two threads unite. D–G. *L. longifolia.*—D. Polar surface containing numerous granular-irregular elements, most probably Ubisch bodies. These bodies seem to be most commonly associated with pollen of *Lopezia*. Frequently, viscin threads are absent when Ubisch bodies are present.—E. Enlargement of Ubisch body. The surface of the Ubisch bodies and the exine is smooth rather than the more typically beaded appearance of *Lopezia*.—F. Fractured grain emphasizing the dense paracrystalline ektexine (cf. Fig. 50G of *uava*).—G. 4-aperturate pollen grain. Unless indicated otherwise, the scales equal 1 µm.


A
10 μm
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E
F
G
H

strands or viscin threads on the proximal polar face (*Hauya,* Fig. 50E; *Lopezia,* Fig. 51A; *Clarkia,* Fig. 52A, B, D; *Gaura,* Fig. 53B; *Gayophytum,* Fig. 53E; *Xylonagra,* Fig. 54F; *Stenosiphon,* Fig. 55E; *Gongylocarpus,* Fig. 56D; *Camissonia,* Fig. 57C; *Epilobium,* Fig. 59B). In thin section it is clear that they are extensions of the exine surface (*Fuchsia,* Fig. 60A; *Camissonia,* Fig. 61A; *Gaura,* Fig. 62A; *Clarkia,* Fig. 62D; see also Skvarla et al., 1976).

The threads have different surface patterns: smooth (*Circaea,* Fig. 50C; *Clarkia,* Fig. 52C, F; *Gayophytum,* Fig. 53H, I; *Heterogaura,* Fig. 54C; *Boisduvalia,* Fig. 58E; and *Ludwigia,* Fig. 58F, H, I); segmented (*Hauya,* Fig. 50F; *Lopezia,* Fig. 51C; *Gaura,* Figs. 52E, G, 53C, D; *Gayophytum,* Fig. 53G; *Calylophus,* Fig. 55C; *Oenothera,* Fig. 56B, E; and *Camissonia,* Fig. 57E); tightly compound-twisted (*Stenosiphon,* Fig. 55F; *Boisduvalia,* Fig. 58C; and *Epilobium,* Fig. 59F, H, I); and incised-compound (*Epilobium,* Fig. 58B). As discussed in a more comprehensive study (Skvarla et al., 1978), some patterns are difficult to categorize and may represent intermediate or transitional forms. For example, the obliquely inclined segmented-beaded threads of *Fuchsia* (Fig. 50A), *Xylonagra* (Fig. 54D), *Gongylocarpus* (Fig. 56D), and *Camissonia* (Fig. 57E) can also be considered as segmented-ropy. Sections through viscin threads (Figs. 60E, 61G, 62E, 63G) support the morphological patterns. *Lopezia longifolia* (Fig. 51D, E) commonly has prominent spherical particles on the polar face. These particles may represent Ubisch bodies. They have been observed most frequently on *Lopezia* pollen, particularly in certain collections of *L. longifolia.* When they occur, viscin threads are usually absent.

It must be stressed that we consider the viscin threads to be an integral part of the pollen grain wall, namely, the ektexine, and have documented this relationship clearly (Skvarla et al., 1975, 1976, 1978; Praglowski et al., 1983; Nowicke et al., 1984). The phrase "attachment point(s)" was used to indicate the specific area on the exine surface where the threads emerge. The area is a simple transition from ektexine surface elements to individually protruding threads or an enlarged region with several emerging threads. We now recognize that this phrase can be misleading and might be interpreted to mean that viscin threads are not an inherent part of the exine and instead are a later addition. Viscin threads form along with other exine units, as has been shown in developmental studies dating to the early twentieth century (Beer, 1905; Bowers, 1931). In order to avoid any existing or potential confusion, perhaps "attachment point(s)" should be replaced by a more appropriate syntactic unit such as "emergence area," "extension area," etc.

While viscin threads are evident in Onagraceae and some Ericaceae (Skvarla et al., 1978), equivalent structures have also been suggested in Leguminosae (Cruden & Jensen, 1979; Graham et al., 1980). In certain species of *Caesalpinia* and *Delonix,* randomly located strands termed "exinial connections" link pollen grains, and although they are without free ends they are thought to be similar to viscin threads and to facilitate pollination (Cruden & Jensen, 1979). In pollen of *Jacqueshuberia,* the linkages are markedly longer and fewer. They are considered to be viscin threads and to indicate an adaptation to entomophily (Graham et al., 1980). Recent study (Patel et al., 1985) of *Jacqueshuberia* threads shows that the thread ends are attached to different pollen grains, therefore indicating that they are long exinial connections rather than viscin threads.

Hesse has published a series of papers (summarized in Hesse, 1981) reviewing the well-known subject of pollen cement in Angiosperm families. He contrasts "pollenkitts" and "tryphine," the sticky, viscous, lipid-carotenoid adhesive substances that are synthesized in the tapetum (i.e., by plastids or endoplasmic reticulum)

FIGURE 52. Scanning electron micrographs of Onagraceae pollen. A, C. *Clarkia speciosa* subsp. *speciosa.*—A. Proximal polar view with several viscin threads extending from the exine surface.—C. View showing smooth viscin threads. Although not clearly indicated, the exine surface is composed of distinct globular and elongate elements. B, D, F. *C. unguiculata.*—B. Proximal polar view.—D. Lateral view with viscin threads in association with proximal (top) pole (compare with *C. alpina* subsp. *imaicola,* Fig. 50D).—F. View showing globular elements of exine surface and smooth viscin threads.—E. *Gaura lindheimeri.* The viscin threads are segmented-coarsely beaded. The exine surface has randomly dispersed globular elements on a perforate surface. G, H. *G. mutabilis.*—G. Segmented-beaded viscin threads.—H. Fractured apertural protrusion showing short columellae (arrows) and rows of lamellar endexine within the protrusion. Unless indicated otherwise, the scales equal 1 μm.

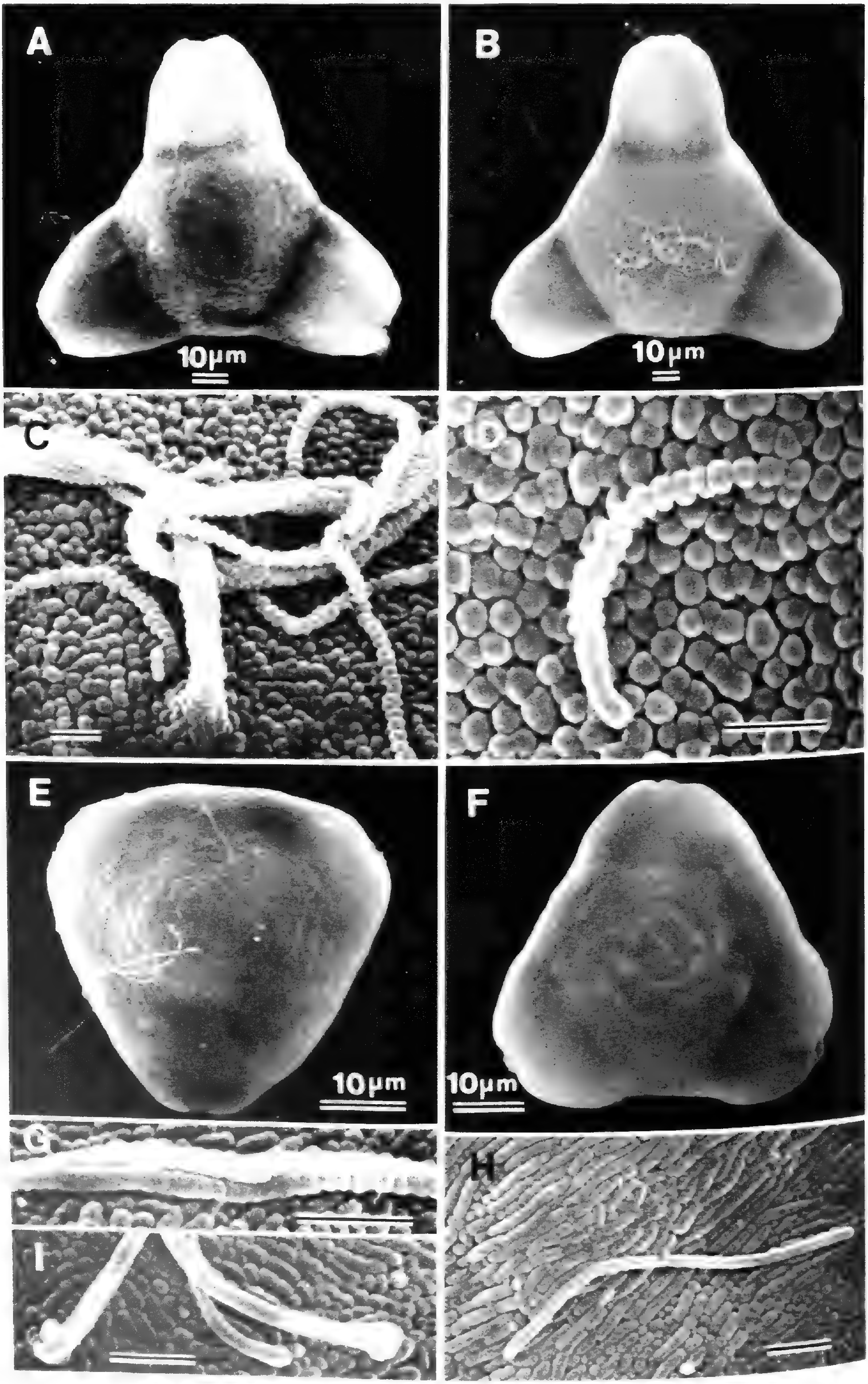

FIGURE 53. Scanning electron micrographs of Onagraceae pollen.—A. *Gaura calcicola.* Distal polar
emphasizing prominent apertural protrusions. B, C. *G. neomexicana.*—B. Proximal polar view with
threads.—C. Beaded viscin threads and exine.—D. *G. demareei.* This beaded viscin thread originates
apertural protrusions, rather than the proximal polar face. Viscin threads in the area of the apertures have
documented previously for *Lopezia* (Skvarla et al., 1978) and possibly for S_3S_4 genotype grains of

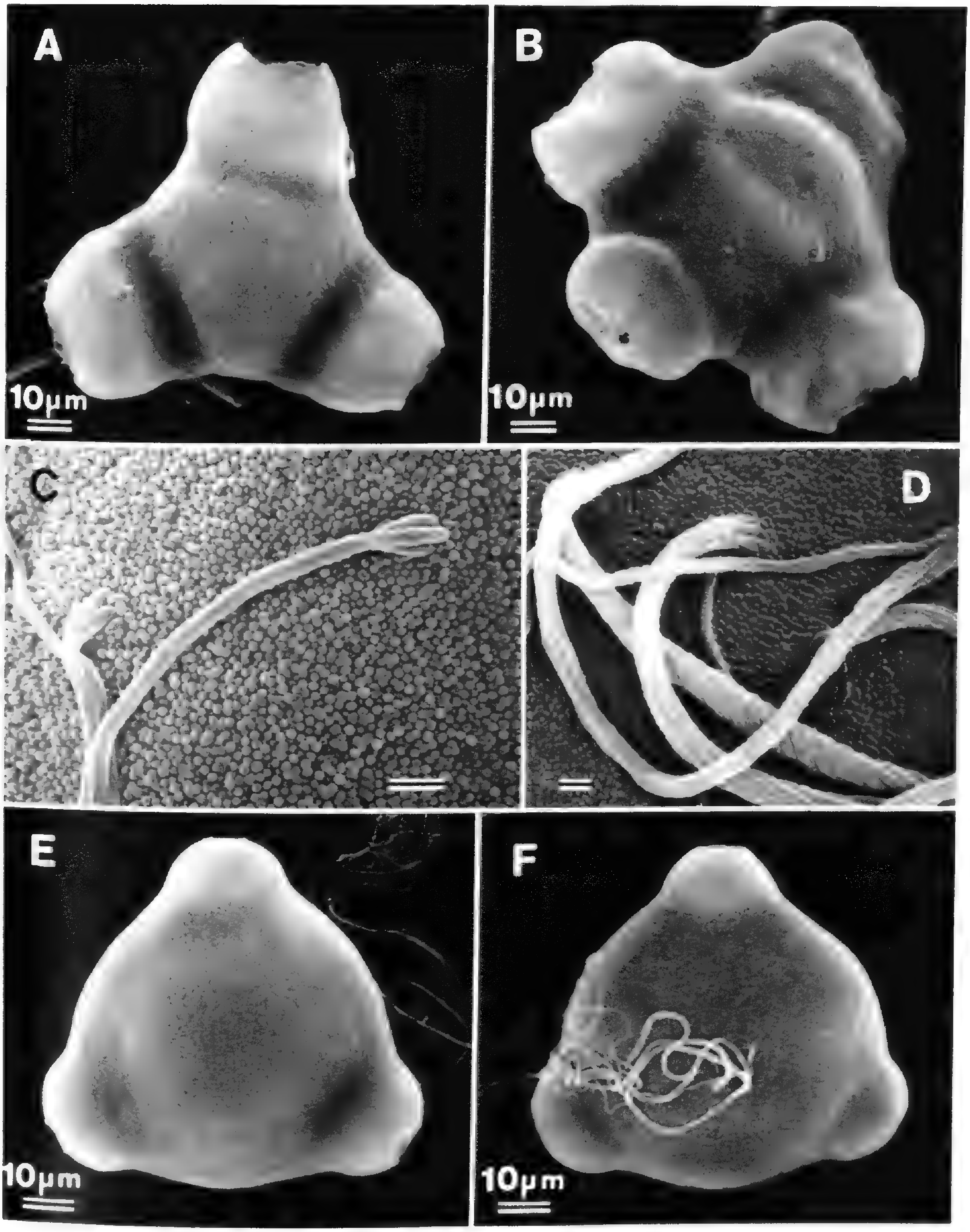

FIGURE 54. Scanning electron micrographs of Onagraceae pollen. A–C. *Heterogaura heterandra.*—A. Distal polar view.—B. 4-aperturate pollen grain in proximal polar view.—C. Smooth viscin threads with forked bases and a highly globular exine surface typically characterize the proximal face. D–F. *Xylonagra arborea* subsp. *wigginsii.*—D. Groups of twisted (segmented-ropy) viscin threads.—E. Distal polar face.—F. Proximal polar surface. Unless noted otherwise, the scales equal 1 µm.

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ganensis (Cresti et al., 1983). E, G, I. *Gayophytum ramosissimum.*—E. Proximal polar view.—G. A portion a branched viscin thread. In comparison with other areas of this thread which are smooth (not illustrated ere), this area is segmented-twisted (ropy).—I. Three viscin threads (see E) extending from an exine surface omposed of globular-elongate elements arranged in a striate pattern that is characteristic of this genus. Note hat one of the smooth threads appears lightly segmented-twisted (ropy) only at the point of attachment. F, H. *ayophytum micranthum.*—F. Distal polar view.—H. A smooth, short viscin thread on a markedly striate exine urface of globular-elongate elements. Numerous short threads, some appearing as partially sloughed off exine urface elements or striae (not illustrated here) also have been noted along with normal threads. Unpublished ata suggest that *G. micranthum* may also possess segmented-twisted threads (as shown for *G. ramosissimum*) nless indicated otherwise, the scale equals 1 µm.

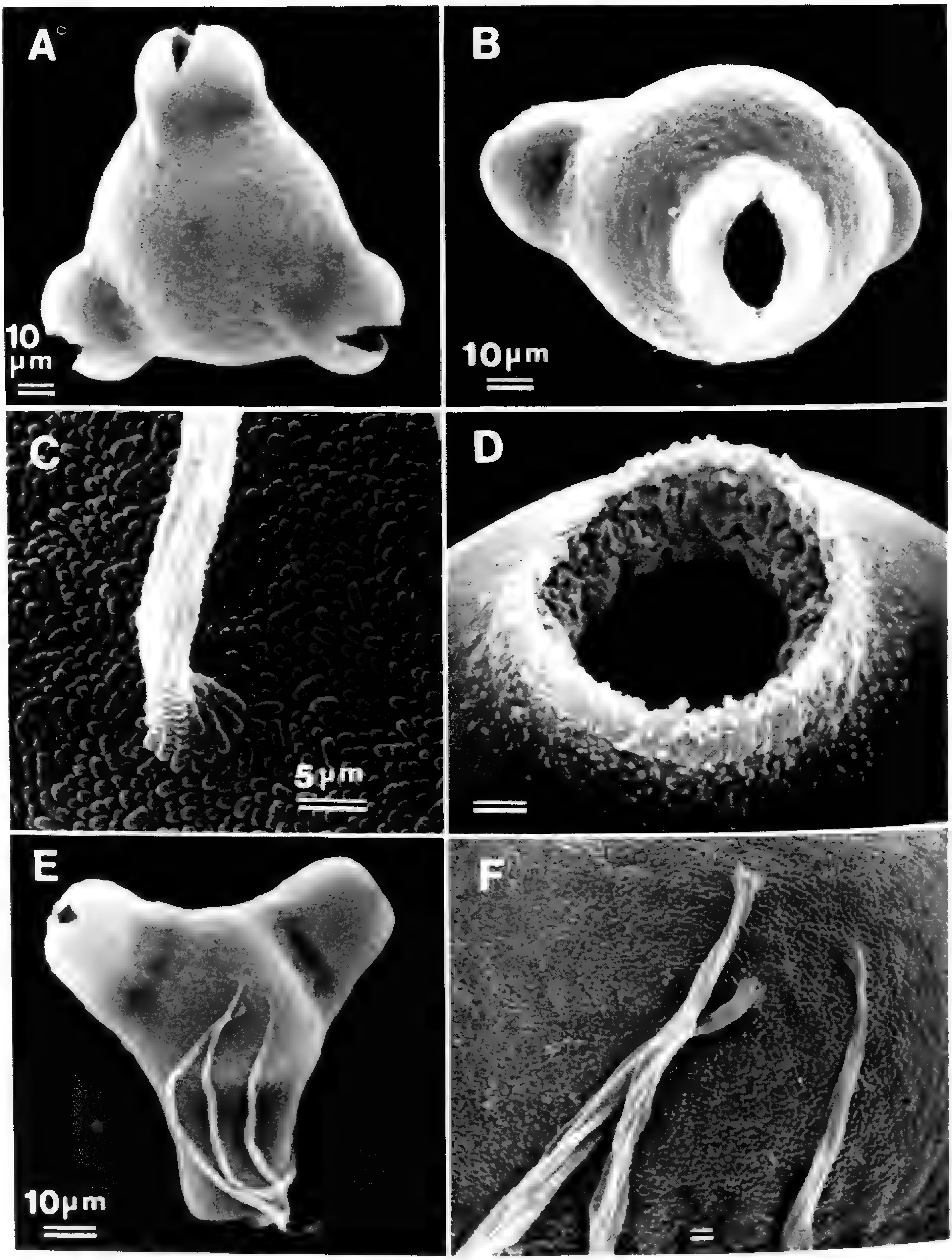
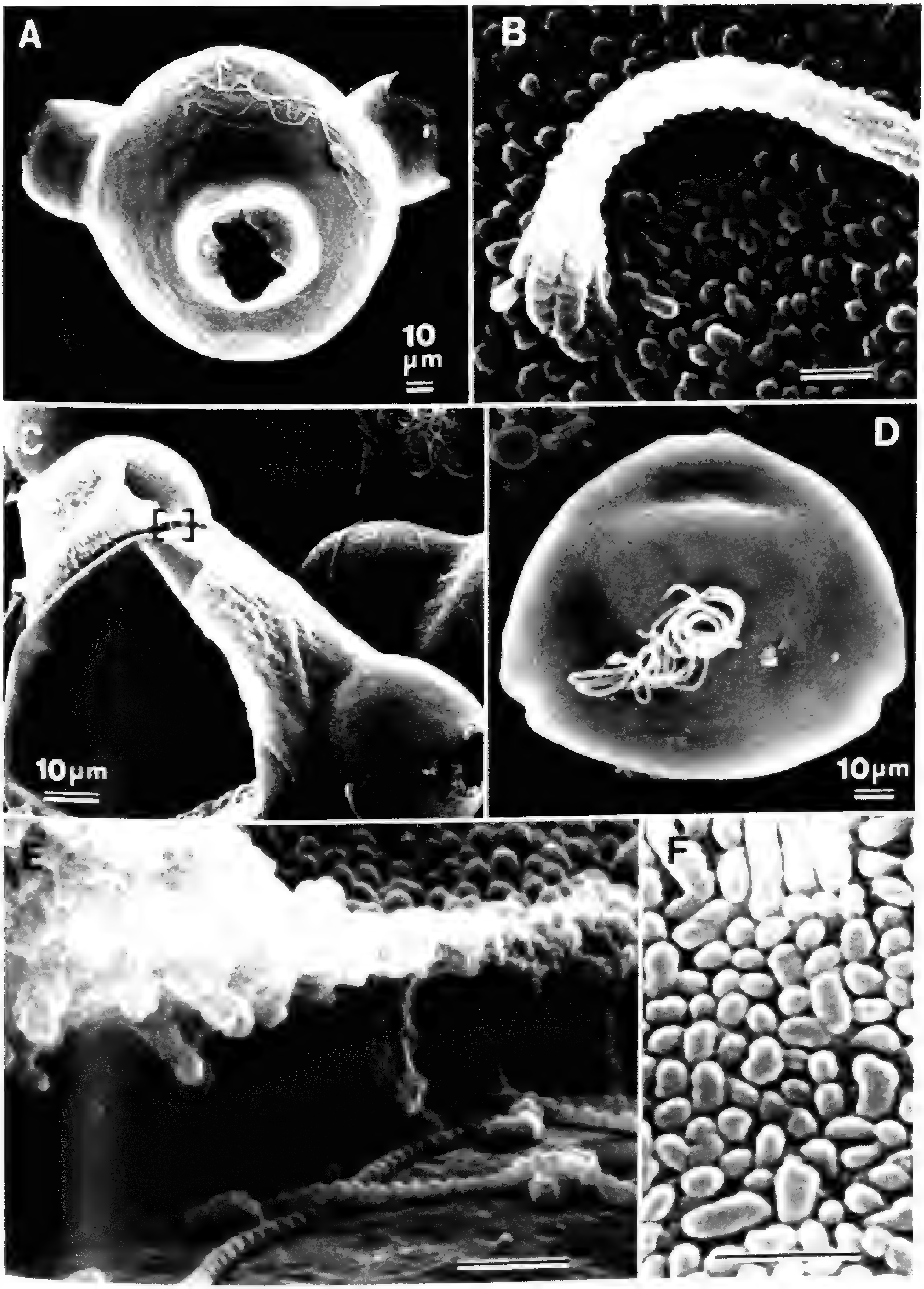


FIGURE 55. Scanning electron micrographs of Onagraceae pollen. A–D. *Calylophus toumeyi*.—A. Distal polar view.—B. Lateral view.—C. A group of beaded viscin threads extends from a surface which consists of globular-elongate elements.—D. Pore region showing internal construction of irregular sporopollenin. The ektexine has been peeled away leaving broken columellae on the endexine. Within the pore is lamellar endexine. E, F. *Stenosiphon linifolius*.—E. Proximal polar view with three groups of viscin threads.—F. Enlarged view of E showing smooth-twisted (tightly compound) viscin threads on a globular to rod-like polar surface. Unless indicated otherwise, the scales equal 1 µm.

FIGURE 56. Scanning electron micrographs of Onagraceae. A, B. *Oenothera brachycarpa*.—A. Lateral view similar to *Circaea alpina* subsp. *imaicola* (Fig. 50D) and *Clarkia unguiculata* (Fig. 52D).—B. A group of segmented-beaded viscin threads extends from a perforate exine surface composed of globular-elongate elements. C, E. *O. texensis*.—C. The pollen grain is collapsed as well as fractured. The apertural protrusion at the top is



mostly covered by exine material that has folded back to expose the columellae which appear as white dots. Randomly arranged viscin threads are intermingled with the columellae as well as with the exposed endexine urface, an artificial association resulting from collapse and fracture of the exine. The bracketed area appears in E.—E. Bracketed area of C emphasizing prominent spongy-perforate columellae and narrow tectum (compare with *H. elegans* subsp. *barcenae*, Fig. 50G). Several segmented-beaded viscin threads are on the surface of the endexine.—D. *Gongylocarpus rubricaulis* (*Sharp 44846*). Proximal polar view showing mass of viscin threads. In contrast to other Onagraceae taxa, apertural protrusions are considerably less conspicuous.—F. *G. fruticulosus* subsp. *glaber*. View of exine composed of short rod-like and globular elements of variable sizes. Unless indicated otherwise, the scales equal 1 µm.

or as tapetal breakdown products (Dickinson, 1973; Dickinson & Lewis, 1973), with viscin threads, which he considers to be non-sticky, non-viscous, and non-tapetally derived. He regards their development as beginning in a granular matrix of the anther loculus at the same time that an ektexine is developing on matrix-encased microspores. Hesse (1981) shows transmission electron micrographs in which he states that the threads approach the ektexine when it is almost completely formed and fuse with the surface. He further postulates that the viscin threads arose as a chance mutation.

Sculpturing of the exine surface is also variable throughout the family and is illustrated by globular elements (*Hauya,* Fig. 50F; *Lopezia,* Fig. 51C; *Clarkia,* Fig. 52F; *Gaura,* Figs. 52E, 53C, D; *Heterogaura,* Fig. 54C; *Xylonagra,* Fig. 54D;

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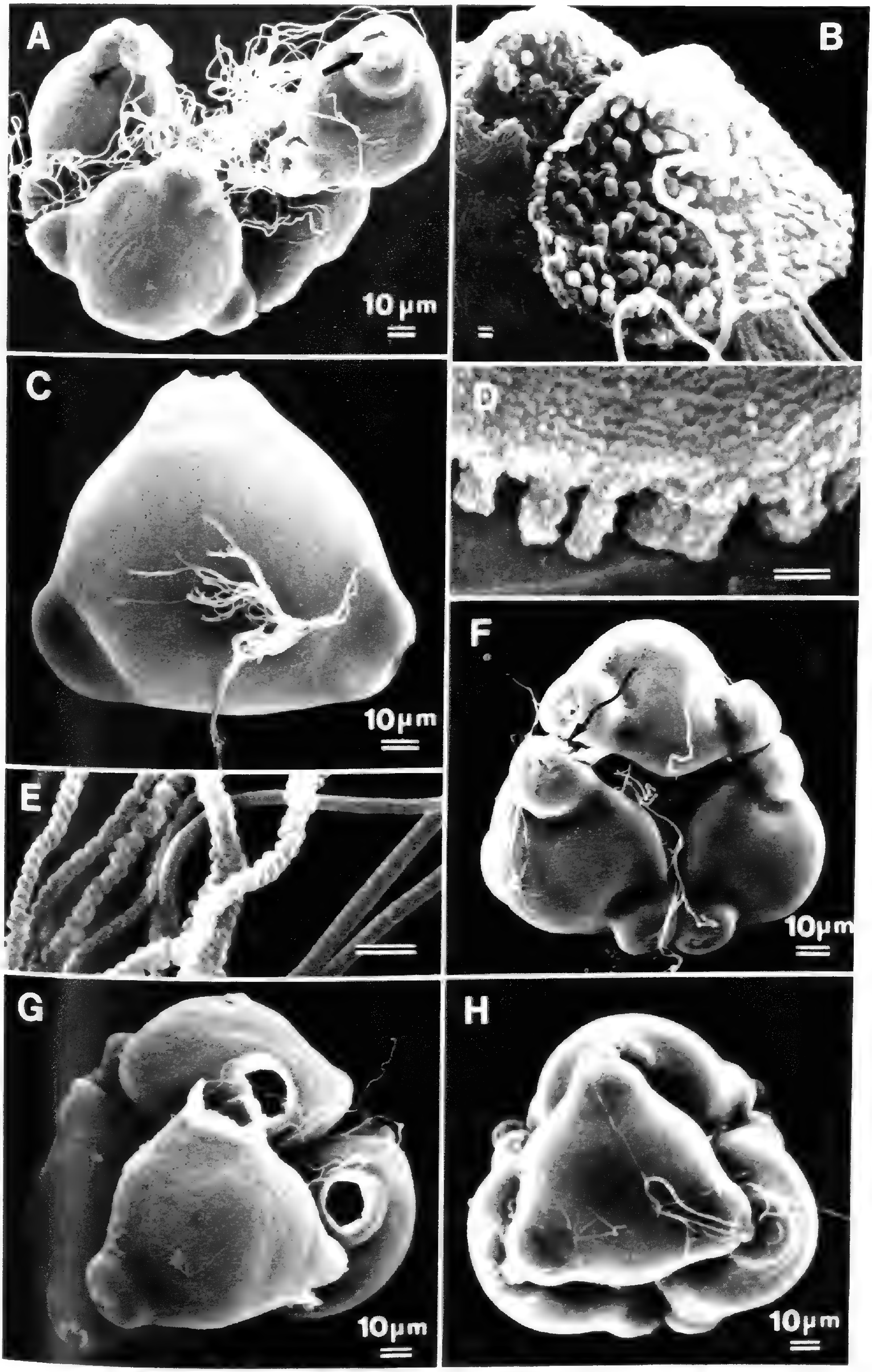
FIGURE 57. Scanning electron micrographs of Onagraceae (*Camissonia*) pollen. A, B, D, F. *C. arenaria.*—A. Tetrad (unacetolyzed) which is partially disrupted at two apertures. The arrowhead designates the aperture containing the exine fragment (i.e., "spur" of Skvarla et al., 1975) torn from the corresponding aperture designated by an arrow.—B. Enlargement of spur in A. The abundant short structures are the columellae which line the aperture protrusion. Also evident is a beaded viscin thread.—D. Fractured grain (acetolyzed) showing columellae structure at the junction of the central body and apertural protrusion.—F. Acetolyzed tetrad. The arrow indicates a partial disruption in one aperture region.—C. *C. tanacetifolia* subsp. *tanacetifolia.* Monad pollen grain. Numerous viscin threads extend from different areas of the proximal polar face. E, G. *C. cardiophylla* subsp. *robusta.*—E. The viscin threads are primarily beaded-ropy but a few are also smooth (see Skvarla et al., 1978).—G. Intact tetrad (acetolyzed).—H. *C. cardiophylla* subsp. *cardiophylla.* Intact tetrad (unacetolyzed). Unless indicated otherwise, the scales equal 1 μm.

FIGURE 58. Scanning electron micrographs of Onagraceae pollen.—A. *Boisduvalia stricta.* View of tetrahedral tetrad showing all four pollen members. B, C, E.—*B. densiflora.* These three scanning electron micrographs represent different collections and illustrate the diversity in viscin thread morphology which occurs on pollen in some Onagraceae taxa. In B (*Piper s.n.*), the morphology is clearly incised-compound, in C (*Thompson 5099*), it appears as tightly compound-twisted, and in E (*Piper s.n.*), it is smooth (see Skvarla et al., 1978 for detailed discussion). In all three examples, the associated exine surface appears to be rugulate-perforate. D, G. *Ludwigia goiasensis.*—D. The tetrad (fourth pollen member is not visible) is part of a polyad and is surrounded by parts of other tetrads. The bracketed area is enlarged below in G. Arrowheads indicate colpi.—G. Enlargement of bracketed area in D showing internal bridges (arrows) between adjacent pollen grains of the tetrad. The nature of the globular club-like structure associated with one of the bridges is unknown but may be related to viscin threads. The star represents union of adjacent pollen grain apertures.—F. *L. alternifolia.* Three members of a tetrad. The large open arrows indicate prominent meridional ridges characteristic of several *Ludwigia* species and which bifurcate at the equator to join with the equatorial ridges between the apertural protrusions. In contrast to *L. goiasensis* (D) and *L. longifolia* (H) the meridional ridges are best developed in *L. alternifolia* while the equatorial ridges are of equal prominence in all three species. The short, solid arrows show the colpi. H, I. *L. longifolia.*—H. Overall view of a polyad with basic tetrad composition. Arrow indicates an external bridge which connects adjacent distal tetrad pollen surfaces and maintains polyad unity. Arrowheads indicate colpi.—I. External bridge (not from H) with portions of adjacent exine surfaces and smooth viscin threads. Unless indicated otherwise, the scales equal 1 μm.

FIGURE 59. Scanning electron micrographs of Onagraceae (*Epilobium*) pollen. A–D. *E. brachycarpum.*—A. In distal polar view the pollen outline is nearly circular. The surface is composed of numerous randomly arranged short rod-like elements.—B. Viscin threads (smooth and incised compound, see Skvarla et al., 1978) originate from the center of the proximal polar surface. The sculpturing at the proximal pole shows thin-elongated elements. The surface becomes more coarse toward the equator and consists of rod-like or rugulate elements (see also Skvarla et al., 1978, Pl. 45). The remainder of the proximal polar face is also composed of rod-like or rugulate elements but they are not densely organized.—C. Enlarged view of exine surface showing that the rod-like or rugulate elements are underlain by a highly porous layer or sheet.—D. Fractured exine showing a channeled endexine (indicated by a bracket) and a "columellae" layer composed of randomly arranged porous sheets (arrows) which appear to be vertically oriented. The tectum is a continuous porous sheet (see C) upon which rod-like or rugulate elements are scattered. E–G. *E. brachycarpum.* This collection documents the rare occurrence of tetrads.—E. A tetrad.—F. Smooth and incised compound viscin threads occur on a surface similar to Figure 50B.—G. View of fractured exine surface. The arrows indicate the porous sheets as described above (see D).—H. *E. glaberrimum.* This view documents the only observation of a viscin thread (tightly compound) originating from an exine bridge connecting adjacent members of a tetrad.—I. *E. rigidum.* Numerous exine bridges show the same morphology (tightly compound) as the viscin thread at the left margin (see also Skvarla et al., 1978, Pl. 48).—J. *E. hectorii.* In this view exine bridges between adjacent tetrad members are clearly illustrated (arrows). Unless designated otherwise, the scales equal 1 μm.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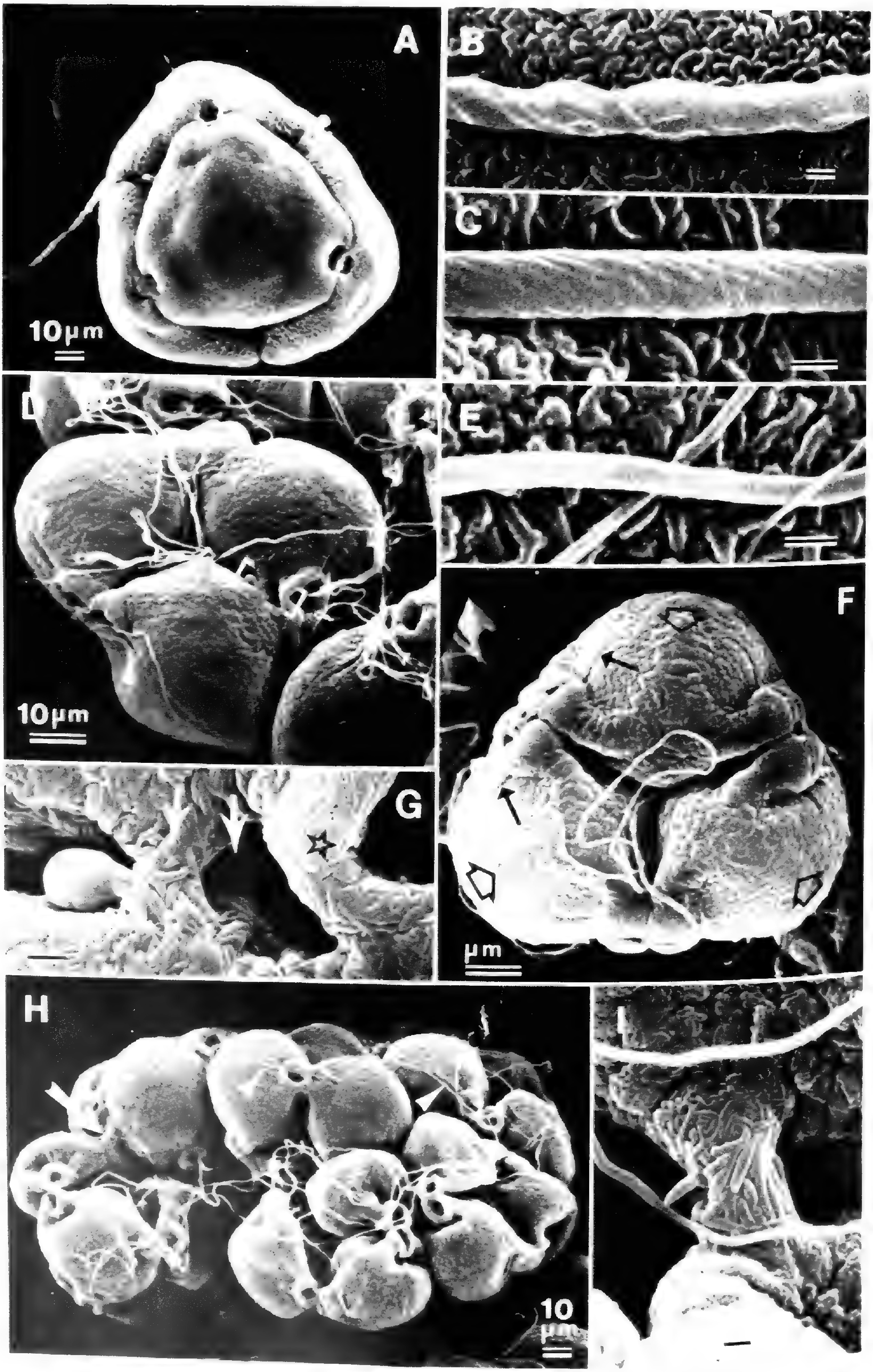
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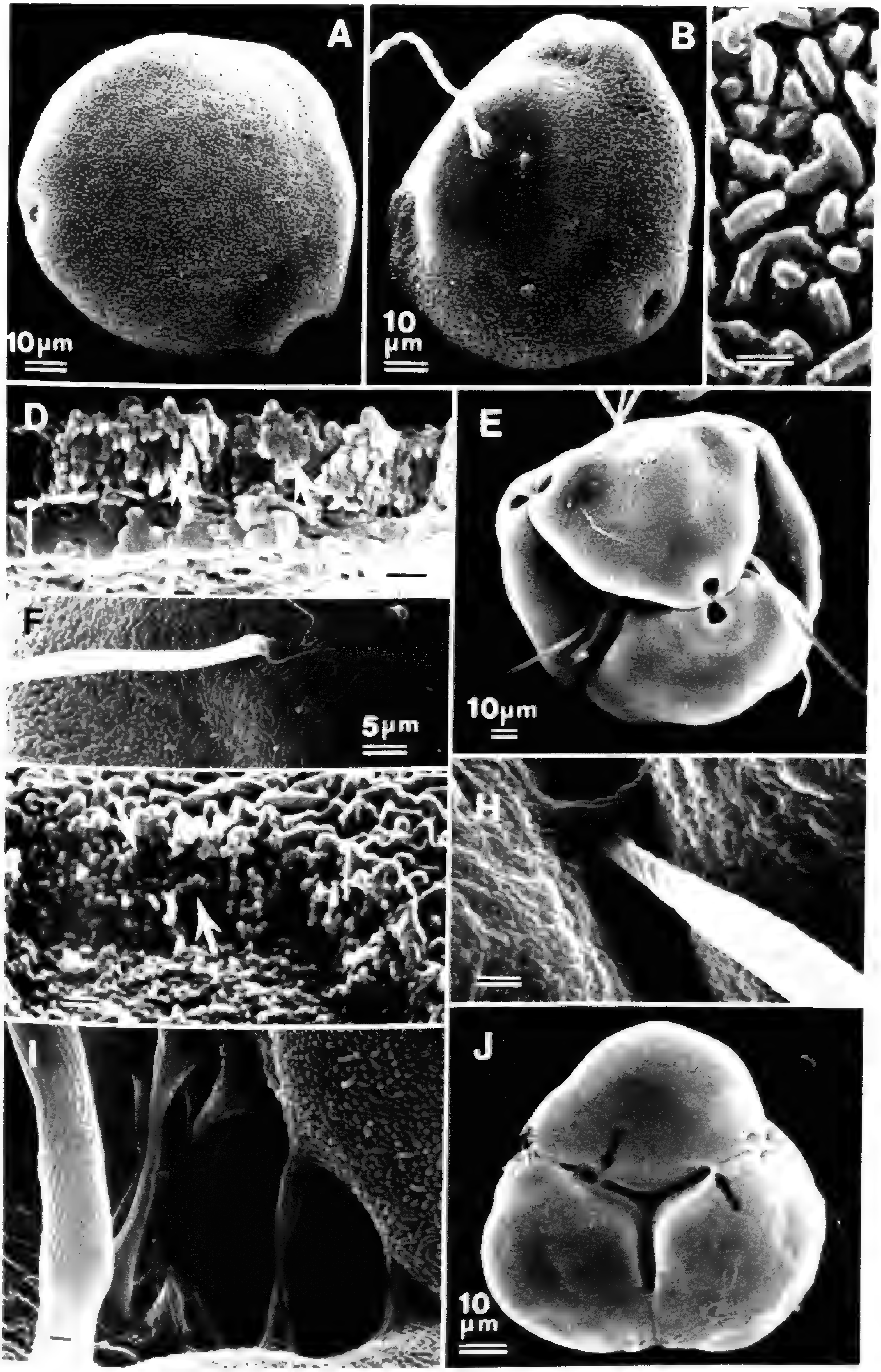
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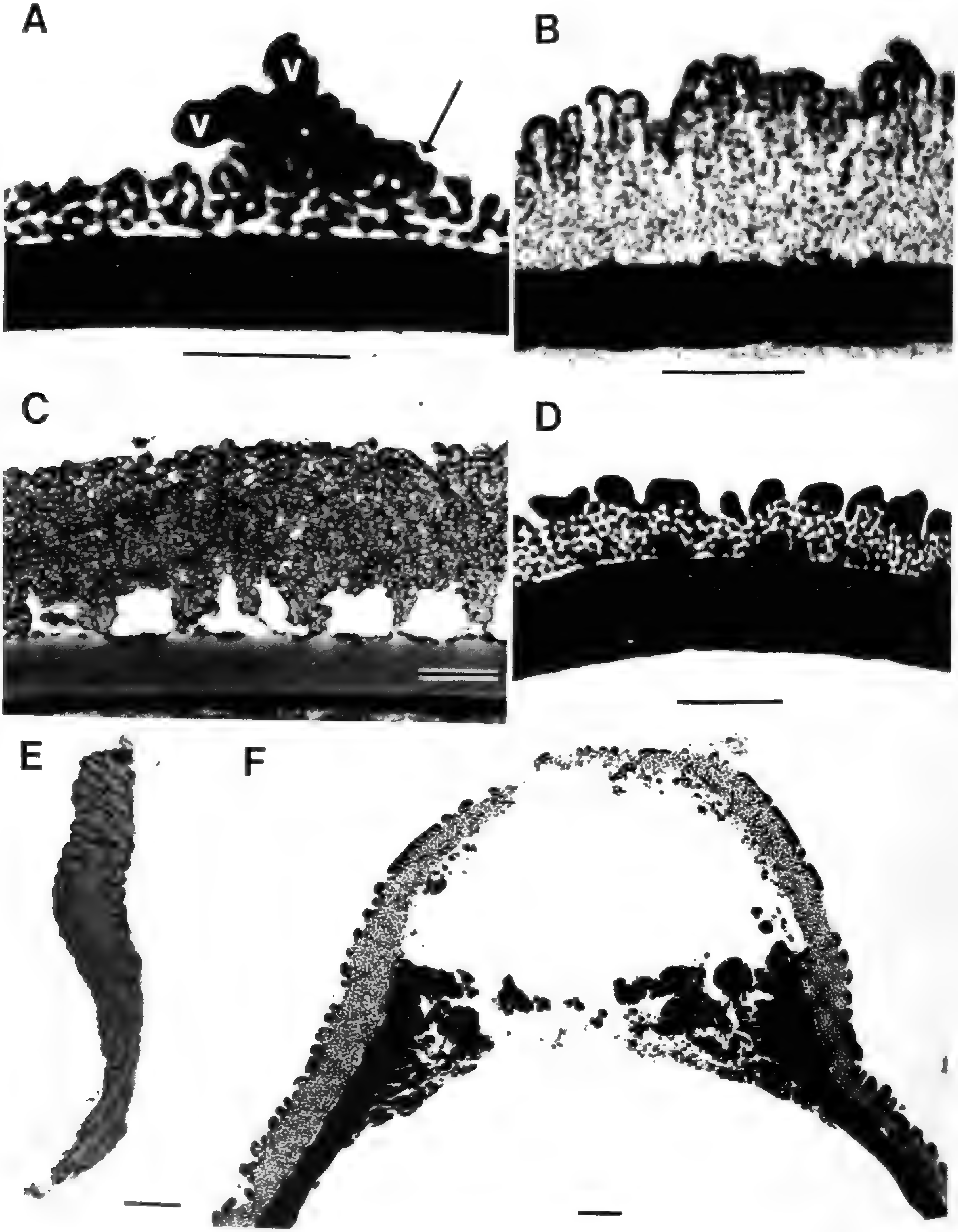

FIGURE 60. Transmission electron micrographs of Onagraceae pollen.—A. *Fuchsia garleppiana.* Section at proximal pole showing irregular and coarse spongy-paracrystalline ektexine attached (without columellae) to the uniform and solid endexine. The arrow indicates extension of viscin threads (v) from the ektexine.—B. *Ludwigia brevipes.* Section is through the distal face. The ektexine is massive and spongy-paracrystalline and the surface is markedly undulate. The endexine is uniform and solid and has a thin granular basal area. C, E. *Hauya heydeana.*—C. This sample represents fresh pollen prepared in glutaraldehyde and osmium tetroxide (acetolysis has been omitted). It is very similar to the fractured grain of *Hauya elegans* subsp. *barcenae* (Fig. 50G) but clearly emphasizes the short but prominent columellae. Although not clearly distinguished because of the cytoplasm, the endexine has a granular basal component.—E. Section through a group of viscin threads showing serrated margins indicative of a segmented morphology (see Skvarla et al., 1978, Pl. 20, 21). D, F. *Circaea mollis.*—D. The surface elements on the highly undulate exine surface appear as irregularly shaped isolated islands in sectional view. Also note that the upper surface of the endexine is irregular and appears to "outpocket" into the ektexine network.—F. Section through apertural protrusion showing apertural chamber underlain by a thickened zone of lamellar endexine. Scales equal 1 μm.

and *Camissonia,* Fig. 57D); rod-like or elongate elements (*Fuchsia,* Fig. 50B; *Boisduvalia,* Fig. 59C); rugulate or coarsely elongate elements (*Fuchsia,* Fig. 50B; *Boisduvalia,* Fig. 58B, C, E; *Ludwigia,* Fig. 58F, G, I; *Epilobium,* Fig. 59G); and combinations of globular and rod-like elongate elements (*Circaea,* Fig. 50C; *Clarkia,* Fig. 52C; *Gayophytum,* Fig. 53H, I; *Calylophus,* Fig. 55C; *Stenosiphon,* Fig. 55F; *Oenothera,* Fig. 56B; *Gongylocarpus,* Fig. 56F; and *Epilobium,* Fig. 59I). As discussed for viscin threads, some of the patterns are difficult to precisely categorize and therefore are amenable to considerable subjectivity. For example, slightly enlarged globular elements could be interpreted as rod-like to elongate, and extension of the latter could be interpreted as rugulate. Obviously, it is more important to be cognizant of these differences rather than being overly concerned with their exact categorization. Similarly, there should be no conflict when other descriptive terms—granular for globular and vermiculate for elongate and rugulate—are employed (Daghlian et al., 1984). Frequently, the surface elements are underlain by a highly perforate sheet or layer (*Lopezia,* Fig. 51C; *Gaura lindheimeri,* Fig. 52E; *Oenothera,* Fig. 56B; *Boisduvalia,* Fig. 58B, C, E; *Epilobium,* Fig. 59C).

Other surface features of significance are the long colpi and prominent ridges in *Ludwigia* (Fig. 58D, F, H). The latter are of two types: meridional ridges, which occur over the polar faces and extend to the "equator" in the area midway between the apertural protrusions, and lateral ridges, which occur between the apertural protrusions and are joined with the meridional ridges (*L. alternifolia,* Fig. 58F). Of the two, the lateral ridges seem to be the most consistent. In contrast, the meridional ridges are prominent in *L. alternifolia* (Fig. 58F) but poorly developed in *L. goiasensis* (Fig. 58D) and *L. longifolia* (Fig. 58H). Long colpi also were noted in *Calylophus* (Fig. 55A), although of less prominence than in *Ludwigia.*

Exine structure as observed in TEM as well as in fractured grains in SEM (Figs. 50G, 51F, 56E, F, 57B, D, 59D, G) indicates that it is composed of a network of spongy-paracrystalline ektexine and a dense, uniform endexine that frequently has a thin, granular, basal component (*Ludwigia,* Fig. 60B; *Camissonia,* Fig. 61A; *Xylonagra,* Fig. 61C; *Gongylocarpus,* Fig. 61H; *Epilobium,* Fig. 63D), and less frequently an irregular upper surface (Figs. 60B, D, F, 62D, 63E). The ektexine is without a foot layer and the columellae and tectum units are not always clearly recognized. Several ektexine structural patterns are evident. In *Hauya* (Fig. 60C), *Camissonia* (Fig. 61A), *Lopezia* (Fig. 61B), *Xylonagra* (Fig. 61C), *Calylophus* (Fig. 61E), *Gaura* (Fig. 62A), *Stenosiphon* (Fig. 62F), and *Epilobium cylindricum* (Fig. 63F), columellae and tectum are evident. In *Fuchsia* (Fig. 60A), *Ludwigia* (Fig. 60B), *Circaea* (Fig. 60D), *Gayophytum* (Fig. 61D), *Heterogaura* (Fig. 62C), *Clarkia* (Fig. 62D), and *Boisduvalia macrantha* (Fig. 63A, B), columellae and tectum are absent and the ektexine is composed of the spongy-paracrystalline-beaded sporopollenin network. In fractured exines of *E. brachycarpum* (Fig. 59D, G), this network appears to consist of porous sheets. *Clarkia* (Fig. 62D) is further distinguished by a partial separation of ektexine from endexine and their subsequent union in the apertural protrusions. In *Gongylocarpus* (Fig. 61H), *Oenothera* (Fig. 62E), *Boisduvalia densiflora* (Fig. 63C), *Epilobium hirsutum* (Fig. 63E) and *E. collinum* (Fig. 63G) extremely short columellae are present, although this is a highly subjective interpretation and it may be more accurate to regard this group as transitional. It is clear that Onagraceae pollen does not possess typical columellae, if indeed any columellae at all, and it might be more useful to consider the ektexine to be without them. This lack of columellae, coupled with the absence of a tectum and foot layer, leads to an interpretation of the Onagraceae ektexine as being without the tripartite units that characterize Angiosperm exines.

Also subject to redefinition is the layer we regard as endexine. Whereas in previous studies we defined as endexine the dense, massive layer underlying the spongy-paracrystalline ektexine, we now might redefine it as the foot layer to the ektexine. Support for this interpretation can be found in the aperture protrusions, where the so-called endexine has the spongy-paracrystalline appearance of the ektexine (Figs. 60F, 61F, 62B), and indeed is continuous with it (see also Skvarla et al., 1976; Nowicke et al., 1984). By this interpretation the narrow, granular layer that was regarded as a basal endexine component is now the endexine. The endexine in Onagraceae pollen would be defined then as extremely narrow, sporadic, and best developed in the apertures where coarse granules are evident (Nowicke et al., 1984). We do not necessarily support this explanation, but discuss it as an illustration of the complexity and multiplicity of interpretations amenable for Onagraceae pollen.

It is apparent from observation of the exine sections in Figures 60–63 that there are differences in the texture of ektexine sporopollenin network. *Fuchsia* (Fig. 60A) has a coarse, irregularly shaped network while *Clarkia* (Fig. 62D) has a considerably finer network, and in *Boisduvalia* (Fig. 60A, B) the network appears to consist of finely connected beads and porous sheets. This has yet to be critically analyzed. Perhaps this type of study, in conjunction with analysis of ektexine "porosity," would be of value in distinguishing the various taxa.

In the apertural protrusions, the apertural chamber is usually overlain by spongy ektexine and underlain by thick layers of endexine lamellae (*Circaea,* Fig. 60F; *Calylophus,* Fig. 61F). The lamellae usually have fine channels and a spongy-paracrystalline composition similar to the ektexine. In *Gaura* (Fig. 62B), the apertural chamber is remarkable in that lamellae line the entire chamber. Grains fractured through the apertural protrusions also clearly show these endexine lamellae (*Fuchsia,* Fig. 50B; *Gaura,* Fig. 52H; *Calylophus,* Fig. 55D).

Table 2 summarizes some of the pollen wall characters of Onagraceae discussed above.

Discussion

Onagraceae pollen has been the object of studies using light (Mitroiu, 1961–1962; Ting, 1966; Brown, 1967) and electron microscopy (Skvarla et al., 1975, 1976, 1978). These studies have shown that the pollen of the 17 genera and approximately 650 species possess the following distinctive features: viscin threads, a spongy-paracrystalline ektexine, apertural protrusions, and a large central body; tetrads and/or polyads

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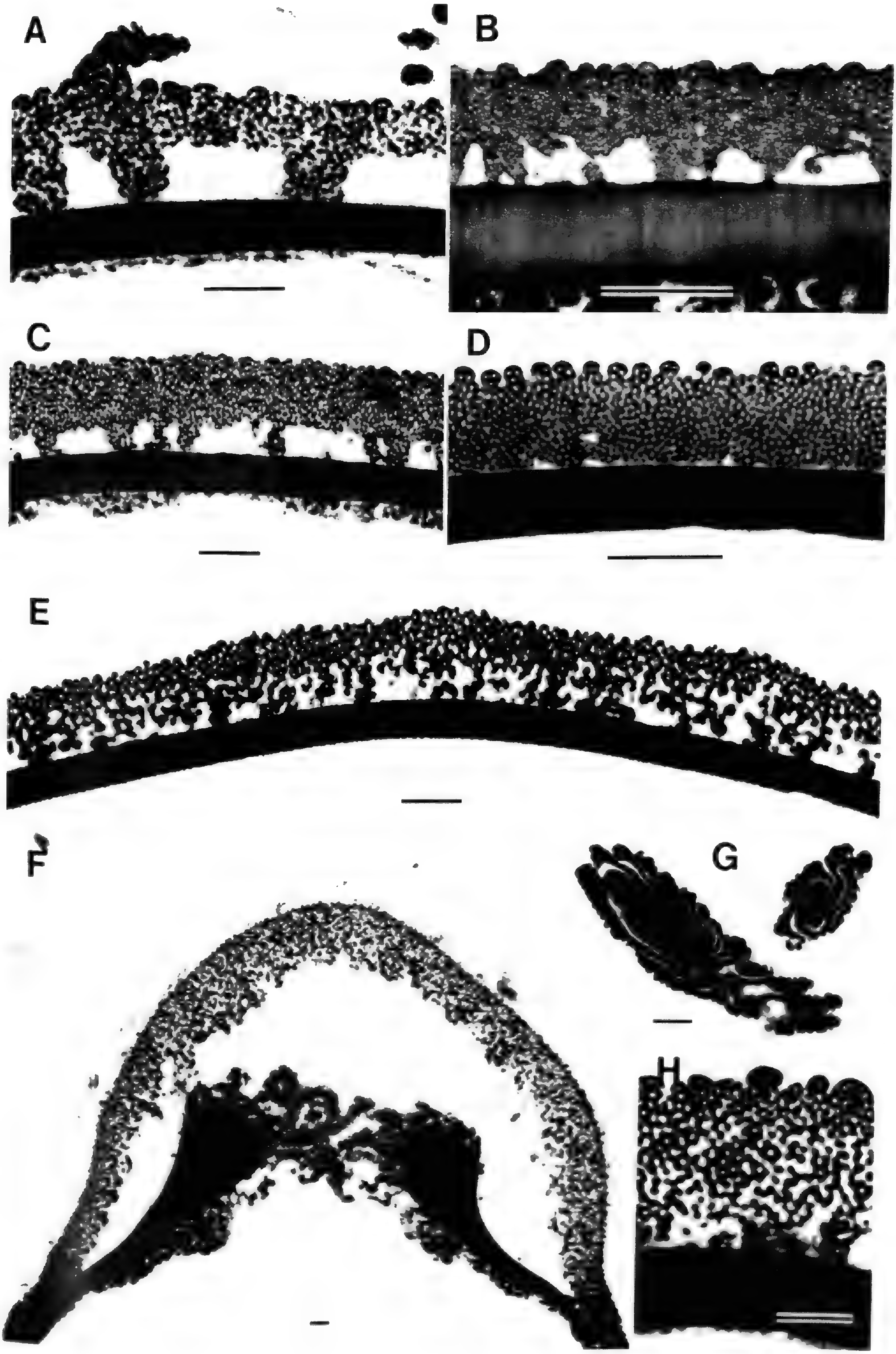
FIGURE 61. Transmission electron micrographs of Onagraceae pollen.—A. *Camissonia arenaria.* View at proximal face showing origin of viscin thread from the ektexine surface. Paracrystalline columellae are broad and nearly as thick as the overlying paracrystalline tectum. The lower margin of the endexine is composed of an irregular granular sheet.—B. *Lopezia grandiflora.* Fresh (unacetolyzed) pollen. Columellae are less pronounced than in *C. arenaria.*—C. *Xylonagra arborea* subsp. *wigginsii.* View at center of either the polar or lateral face. Pollen of this taxon is typically characterized by an irregular granular component at the lower portion of the endexine.—D. *Gayophytum micranthum.* View at center of distal polar face. Columellae are absent and the ektexine is in direct contact with the endexine. E, F. *Calylophus berlandieri* subsp. *berlandieri.*—E. Section through center of either lateral or polar face. Columellae development is somewhat intermediate between *Lopezia* (B) and *Camissonia* (A).—F. Section through aperture chamber. Note similarity to *Circaea* (Fig. 60F) and dissimilarity to *Gaura* (Fig. 62B). G, H. *Gongylocarpus rubricaulis* (*Davidse 9790*).—G. Section through two viscin threads showing the segmented-ropy morphology.—H. Columellae are only slightly developed. Scales equal 1 μm.

FIGURE 62. Transmission electron micrographs of Onagraceae pollen. A, B. *Gaura coccinea.*—A. Section at proximal face. Note short columellae and viscin thread origin from the ektexine.—B. Section through apertural protrusion. Note close similarity to fractured apertural protrusion of *Gaura mutabilis* (Fig. 52H).—C. *Heterogaura heterandra.* Fresh pollen. Columellae are absent (cf. *Gayophytum micranthum,* Fig. 61D).—D. *Clarkia breweri.* Section at proximal face. The ektexine is characteristically without columellae and separated from the endexine (see Skvarla et al., 1976, Pl. 2F). Two groups of viscin thread are evident. The upper ektexine surface suggests a faint "outpocketing."—E. *Oenothera maysillesii.* Section at proximal face showing markedly undulate ektexine, virtually indistinguishable columellae and viscin thread extension of the ektexine.—F. *Stenosiphon virgatus.* Section through center of either the polar or lateral face. Long, slender columellae are prominent. Scales equal 1 μm.

FIGURE 63. Transmission electron micrographs of Onagraceae pollen. A, B. *Boisduvalia macrantha.*—A. Section includes the flank of one apertural protrusion as well as an oblique view of an attached aperture margin of a second pollen grain. The ektexine is composed of thin, beaded, porous elements (see Skvarla et al., 1976, Pl. 8D, F, 9C, F).—B. Section through the center of a lateral face. Note the characteristically highly channeled endexine.—C. *B. densiflora* (*Abrams 6675*). View on proximal surface in middle of the tetrad. There is considerable similarity with the proximal views of *Boisduvalia subulata* and *Epilobium* (see Skvarla et al., 1976, Pl. 8E, 9B, G). D, E. *Epilobium hirsutum.*—D. View through center of the lateral or polar face. The ektexine appears to consist of slender columellae which support a compact and uniform tectal zone (arrow).—E. Section at proximal face showing extension of viscin threads (arrow) from the ektexine. The upper surface of the endexine immediately beneath the area of viscin threads may represent "outpocketing"; however, it is not clear if this irregularity is actually a portion of the ektexine.—F. *E. cylindricum.* Section beneath aperture protrusion showing two tetrad bridges. Note the granular lower portions of the endexine, characteristic of the aperture region.—G. *E. collinum.* Section on proximal face as well as a cross sectional view of a tightly compound viscin thread. Unless indicated otherwise, the scales equal 1 μm.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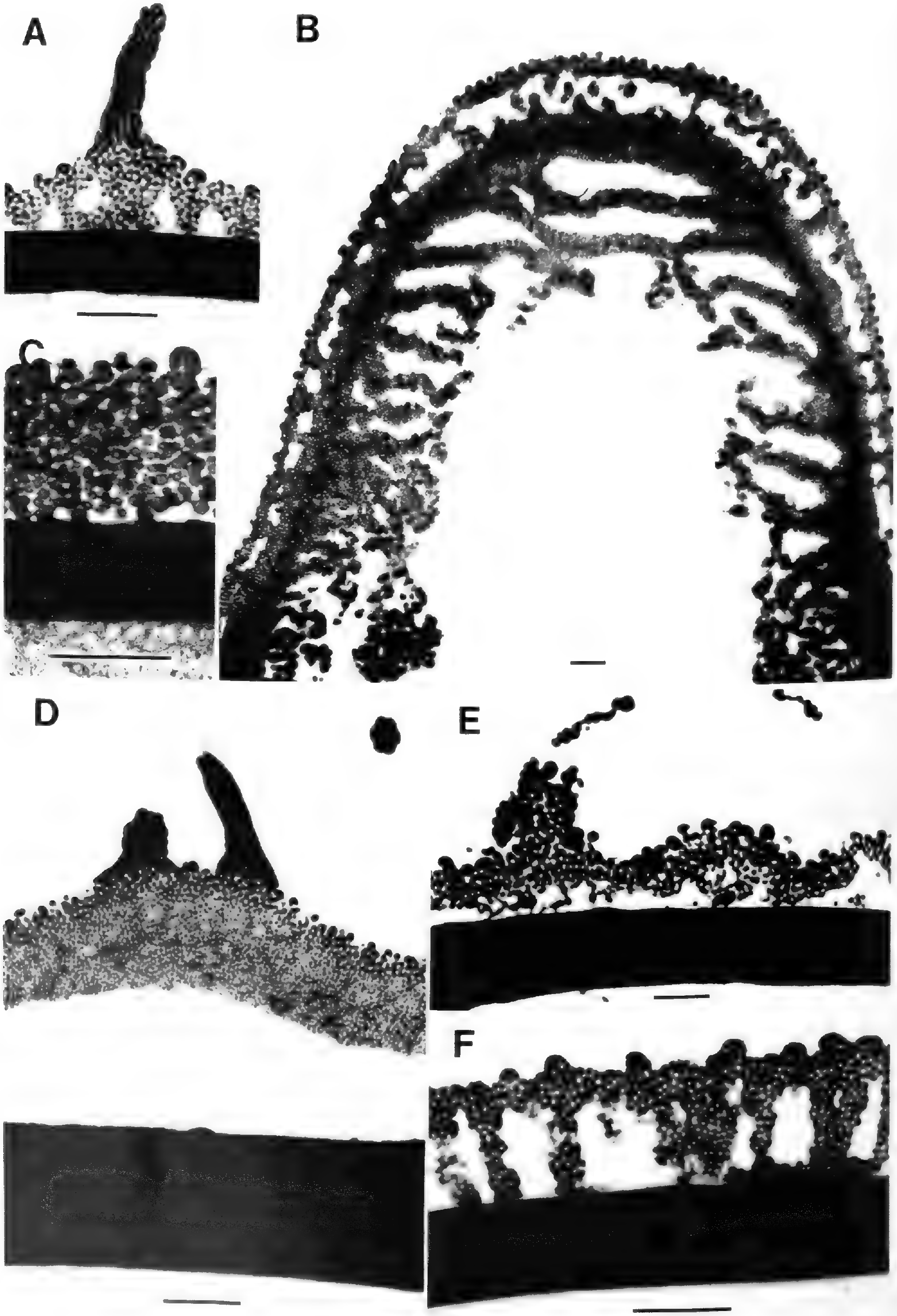
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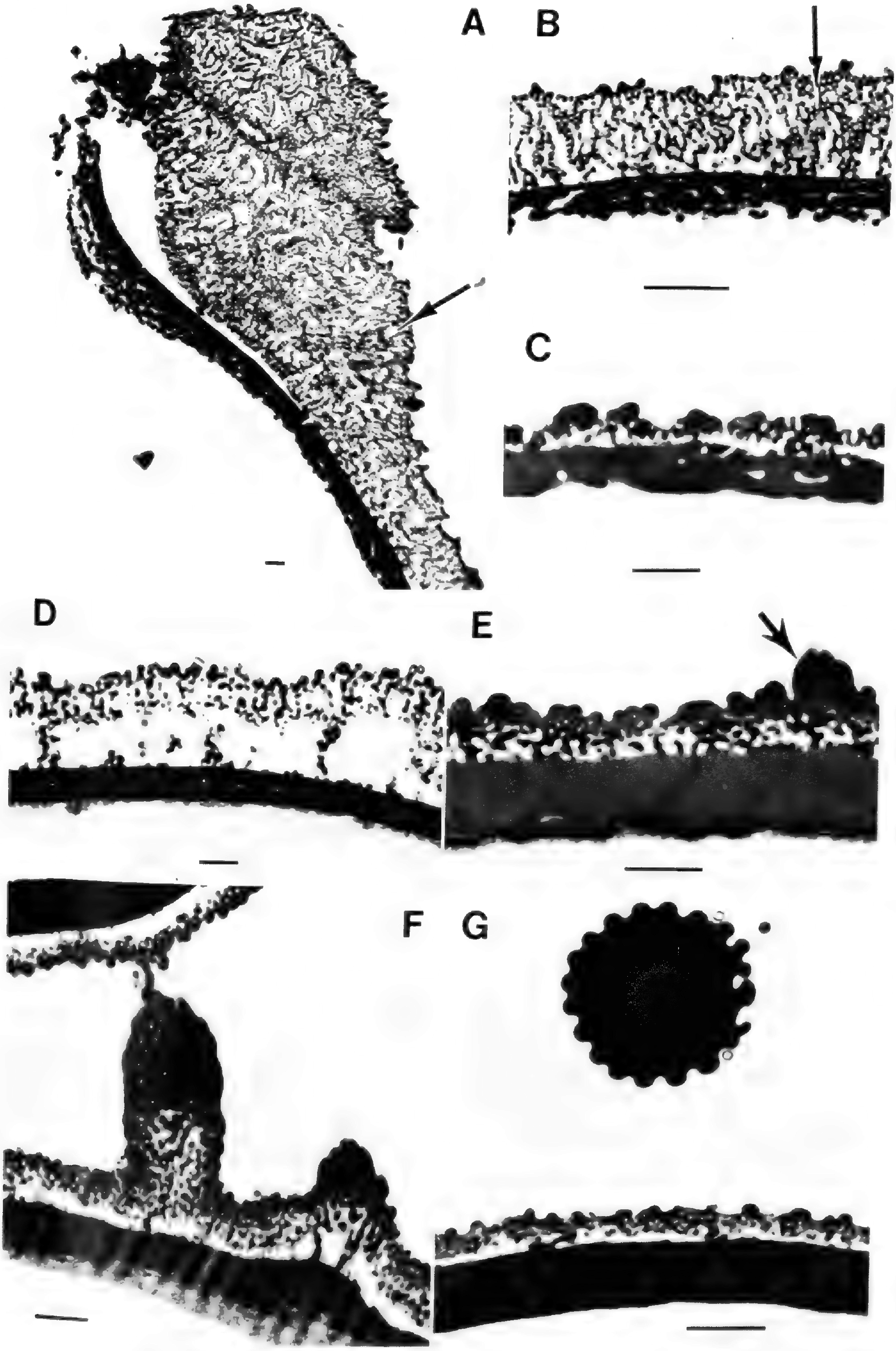
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in certain groups; and an exine surface composed of circular, globular, and elongate or rod-like elements. Prior to this study our feeling was that Onagraceae pollen was unique in the angiosperms, being easily recognizable and difficult to confuse with other groups. After this survey of Myrtales pollen our ideas have not changed: Onagraceae pollen morphology is distinctive in the order. In a remote sense—that is, by considering the extremely thick endexine, surface sculpturing, and protruding apertures—the pollen of *Ludwigia* resembles *Trapa* (see discussion in Trapaceae), although there are no difficulties in recognizing these taxa. A distant similarity between Myrtaceae and Onagraceae pollen exists, particularly in those grains having short colpi (compare *Hauya,* Fig. 50E; *Gongylocarpus,* Fig. 56D; and *Boisduvalia,* Fig. 58A; as well as *Lopezia* of Skvarla et al., 1976, with Myrtaceae SEM on Figs. 41–48). In addition, cross-sections of the subsidiary colpus of *Sonderothamnus* (Fig. 26C, D) of Penaeaceae show a remarkable similarity to those of some taxa of Onagraceae having the spongy ektexine residing directly on the endexine. Lastly, although meridional ridges have been observed on *Ludwigia* pollen (*L. alternifolia,* Fig. 58F), there is no confusing this genus with other taxa in the Myrtales also possessing meridional ridges.

SUMMARY AND CONCLUSIONS

Based on pollen morphology, the families that are considered to be the core members of the Myrtales (Dahlgren & Thorne, 1984) form a relatively cohesive group with the exceptions of Trapaceae, Myrtaceae, and Onagraceae. Each family is summarized below.

1. Lythraceae. The taxa examined from this family show the greatest amount of variation in pollen morphology in the entire order, with diversity evident at all levels: (1) shape (in lateral view: oblate-suboblate, spheroidal-subprolate, or spheroidal; in polar view: triangular-goniotreme, triangular-pleurotreme, triangular to hexagonal, or circular); (2) apertures (tricolpoidorate, tricolporate, tricolporate-syncolpate, or porate); (3) subsidiary colpi (0, 3, or 6); (4) sculpture (striate, striate-spinulate, psilate, or verrucate-rugulate); and (5) structure (normal ektexine-endexine layers, highly reduced or complex columellae). *Punica granatum* (subfam. Punicoideae) is similar to *Lagerstroemia* (Lythroideae) in the triangular shape (polar view) resulting from three meridional ridges. *Punica protopunica* has faint subsidiary colpi, meridional ridges and apertural fields, and thus resembles *Crenea* (Lythroideae). *Sonneratia* (subfam. Sonneratioideae) and *Duabanga* (subfam. Duabangoideae) are characterized by meridional ridges and apertural fields (true subsidiary colpi are absent). *Sonneratia* is similar to *Lafoensia* (Lythroideae), and *Duabanga* to *Diplusodon* (Lythroideae).

2. Trapaceae. This family is unique in having colpi hidden within the protruding, swollen aperture domes of sharply triangular pollen grains (in polar view) and in having three meridional ridges that are united at the poles. The ridges pass over the apertures and in this respect, as well as in structure, they differ from the meridional ridges found elsewhere (e.g., in *Lafoensia, Lagerstroemia,* or *Ludwigia*). *Trapa* remotely resembles *Ludwigia* (Onagraceae) in having a granular-beaded surface sculpture, and Onagraceae in general in exine structure (very thick endexine and indistinct foot layer and columellae), but overall *Trapa* is sharply distinct from Onagraceae and from other Myrtales. One sample of *T. natans* showed linked pollen grains indicating possible polyads.

3. Oliniaceae. The five taxa examined all show two unique features: asymmetrical colpi with unequal arms extending into the opposite polar faces and half subsidiary colpi that are present on only one polar face. *Olinia* resembles some Penaeaceae in having a psilate pollen surface, and in exine structure (a very thick foot layer and tectum, and a thin columellae-infratectal granular layer).

4. Combretaceae. The taxa examined have diverse morphology and five groups are recognized: (1) heterocolpate, (2) heterocolpate with a distinct echinate surface sculpture, (3) echinate surface without subsidiary colpi, (4) punctate surface without subsidiary colpi, and (5) reticulate surface without subsidiary colpi. Pollen in the heterocolpate group indicates general similarities to some Penaeaceae, Crypteroniaceae, and Melastomataceae.

5. Alzateaceae. *Alzatea verticillata* is similar in pollen characteristics to *Axinandra* and *Dactylocladus* (Crypteroniaceae) and *Rhynchocalyx* (Rhynchocalycaceae). Indistinct subsidiary colpi or intercolpar concavities appear to be present. In fine structure some resemblance is shown to Chrysobalanaceae.

6. Rhynchocalycaceae. The pollen of *Rhynchocalyx lawsonioïdes* is tricolporate and heterocolpate with three subsidiary colpi. In these and other characteristics the pollen of *Rhynchocalyx* is similar to that of Alzateaceae, *Dactylocladus* and *Axinandra* (Crypteroniaceae), *Dissocheata* (Melastomataceae) and *Lumnitzera* (Combretaceae).

7. Penaeaceae. The taxa examined are heterocolpate with tri- and tetracolporate pollen; *Glischrocolla* has 5-colporate pollen. Exomorphic resemblances are with Melastomataceae (*Tristemma, Dissotis*), Combretaceae (*Combretum, Quisqualis*), and Crypteroniaceae (*Dactylocladus*). Endomorphic resemblance is striking with Oliniaceae and *Dactylocladus* of Crypteroniaceae.

8. Crypteroniaceae. *Dactylocladus* and *Axinandra* are heterocolpate and can be favorably compared with some Lythraceae, Melastomataceae, Combretaceae, Penaeaceae, and perhaps in a general way with much of the Myrtales. *Crypteronia* differs from most Myrtales in having dicolporate pollen with two intercolpar concavities.

9. Melastomataceae. Pollen of the taxa can be divided into three basic types: (1) heterocolpate with subsidiary colpi alternating with colpi, (2) "heterocolpate" with intercolpar concavities alternating with colpi, and (3) tricolporate. The first group resembles several of the heterocolpate Combretaceae. Also in this first group are several genera often segregated as Memecylaceae, but they are not delimited as a group within the heterocolpate Melastomataceae. *Tococa spadiciflora* occurs as polyads, the only member of the family to the present time found to occur this way, and along with some *Ludwigia* of Onagraceae (and perhaps *Trapa natans* as discussed above), the only taxa with polyads in the Myrtales. Similarly, *Miconia melanotricha* is the only species in the family reported to have pollen in tetrads.

10. Myrtaceae. An essentially consistent morphology is found in all taxa examined. The markedly triangular (in polar view) pollen is divided, based in part on previous reports, into three groups defined by colpus morphology: (1) longicolpate (no intercolpar concavities), (2) syn- and parasyncolpate with and without intercolpar concavities, and (3) brevi- or brevissimicolpate (no intercolpar concavities). Pollen of *Myrtus communis* and *Psidium littorale* is found frequently as tetrads, the only other record in Myrtales other than Onagraceae (some species of *Ludwigia, Epilobium, Boisduvalia, Zauschneria,* and *Camissonia*) and *Miconia melanotricha* of Melastomataceae. *Psiloxylon* has large apocolpia but overall is similar to most Myrtaceae pollen in group (2). *Heteropyxis* likewise is not distinguished within the second group. Pollen of Myrtaceae is not clearly comparable with any other pollen in the Myrtales.

11. Onagraceae. The pollen of the taxa examined is variable within the family but, like Myrtaceae, is without any close similarity in the Myrtales. The distinctive characters are circular to triangular central body with markedly to slightly protruding apertures; globular (granular), rod-like (elongate), or rugulate surface elements; tetrads and polyads in addition to monads; viscin threads, and thick endexine and essentially spongy-paracrystalline ektexine usually lacking columellae and always lacking a foot layer.

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PRINCIPAL WORKS ON THE POLLEN MORPHOLOGY OF MYRTALES

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Introduction

The following list covers 454 references to works based on replica, scanning, and transmission electron microscopic studies, and covers 320 genera and 23 families. These encompass not only the core families of the order Myrtales sensu Dahlgren and Thorne and others, but also those families now not included in the order but that have been affiliated with it according to various earlier ordinal delimitations. This list has been drawn mainly from the comprehensive bibliographic indices of angiosperm palynological literature by G. Thanikaimoni (1972, 1973, 1976, 1980), and supplemented by more recent publications.

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Studies in *Fuchsia*

This special issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN (Vol. 69, no. 1, 1982) is devoted to several papers on the systematics of the genus *Fuchsia* (Onagraceae). The large section *Fuchsia,* which contains such horticulturally important species as *F. corymbiflora, F. triphylla,* and *F. fulgens,* contains 61 species, about 60% of the entire genus. Paul Berry's monograph treats the section in detail; extensive descriptions of flowers, blooming periods, habitats, and distribution are given. These are supplemented with beautiful color plates of several species. In addition to traditional keys to all the species, principal morphological differences between similar species and hybrids are treated in table form.

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ANNALS
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VOLUME 71 1984 NUMBER 4

LISIANTHIUS POLLEN FROM THE EOCENE OF PANAMA[1]

ALAN GRAHAM[2]

ABSTRACT

Fossil pollen similar to the extant genus *Lisianthius* (Gentianaceae) has been recovered from the middle(?) to late Eocene Gatuncillo formation, Panama. The genus presently extends from Mexico, through the Antilles and Central America, into northwest Colombia. The oldest fossil record for the family is from the Paleocene (pollen) and early Eocene (flowers) of the northern hemisphere. The distribution of modern Gentianaceae, and the meager fossil record, suggests the possibility of a northern origin for the family, migration of at least one member as far south as central Panama by the end of the Eocene, with subsequent introduction into northern South America. Since the Gentianaceae is relatively well represented in South America, it has been suggested the family is probably not a recent arrival. The occurrence of *Lisianthius* pollen in deposits as early as the Eocene in the region of present-day central Panama is consistent with this suggestion. The genus has not previously been reported in the fossil record.

During the Eocene the present region of Central America consisted of a series of volcanic islands trailing southward from the North American continent (Dengo, 1973). Extensive vulcanism is reflected in the Tertiary formations of Panama by the widespread occurrence of agglomerates (angular volcanic ejecta), tuffs (water-lain volcanic ash), and basalts (Stewart et al., 1980). Tectonic activity resulting from the interaction of the east Pacific (Cocos), North American, and developing Caribbean plates (Coney, 1982; Plafker, 1976) is equally evident throughout Cenozoic deposits in Central America. Along the Las Cascadas Reach of the Panama Canal, more than 113 faults have been observed in a distance of ca. 3 km (Stewart, pers. comm.). In the same region, left-handed fault motions total 4 km of displacement in a distance of 4 km. This tectonic activity resulted in the uplift of the isthmian region in latest Tertiary and Quaternary times (Marshall et al., 1976, 1981, 1982; Webb, 1976). The biogeographic consequences of this event have been widely discussed (e.g., Gentry, 1982; Graham, 1973; Raven & Axelrod, 1974; Woodring, 1966).

Around the periphery of these islands mangrove swamps developed and their remains contributed to the formation of bands of lignite containing fossil pollen of *Rhizophora, Pelliceria,* and other genera. One such deposit is the Eocene Gatuncillo formation of Panama.

The Gatuncillo formation outcrops in south-central Panama east of the former Canal Zone. Near Alcalde Díaz, exposures consist of lignites interbedded between layers of claystone, siltstone, and fine-grained sandstone. Samples were collected from a 30-foot roadcut section and processed for plant microfossils. The lignites contained a diverse and well-preserved assemblage of fossil pollen and spores representing remnants

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[1] Research supported by NSF grants GB-5671, GB-11862, DEB-8007312, and DEB-8205926. SEM photomicrographs were kindly provided by Dr. Joan Nowicke (Smithsonian Institution). Field work was facilitated through the cooperation of Robert and Joanne Stewart and their assistance is gratefully acknowledged.

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of a vegetation that occupied the region ca. 40 million years ago.

The collecting locality is reached by a gravel road off the Boyd-Roosevelt Highway. The general area is shown on the Alcalde Díaz (Peñocito) quadrangle map (sheet 4243 11 NE) of the Army Map Service, and the specific collecting site at coordinates 100.8 × 660.8 on the recently compiled "Geologic Map of the Panama Canal and Vicinity" (Stewart et al., 1980).

The sediments near Alcalde Díaz represent a classic sequence of near-shore depositional environments. At other sites in the region the section is capped by a marine limestone, and marine limestones surround the locality. Thus the Gatuncillo lignites were deposited along an ancient shoreline that can be traced on the geologic map as the contact between the Gatuncillo formation and strata mapped as pre-Tertiary (Stewart et al., 1980).

The age of the Gatuncillo is late Eocene, although lower in the section some middle(?) Eocene sediments may locally be included. The age assignment is based on larger foraminifera reported by Cole (1952) and is accepted on the most recent version of the geologic map of Panama (Stewart et al., 1980). Almost all the species reported by Cole (1952) are upper Eocene foraminifera, but two (of 21) were known elsewhere only from the middle Eocene. These are *Yaberinella jamaicensis* Vaughan from the middle Eocene of Jamaica, and *Fabiania cubensis* Cushman & Bermúdez from Cuba and Florida. Consequently the age of the entire Gatuncillo sequence is regarded as middle(?) to late Eocene.

MATERIALS AND METHODS

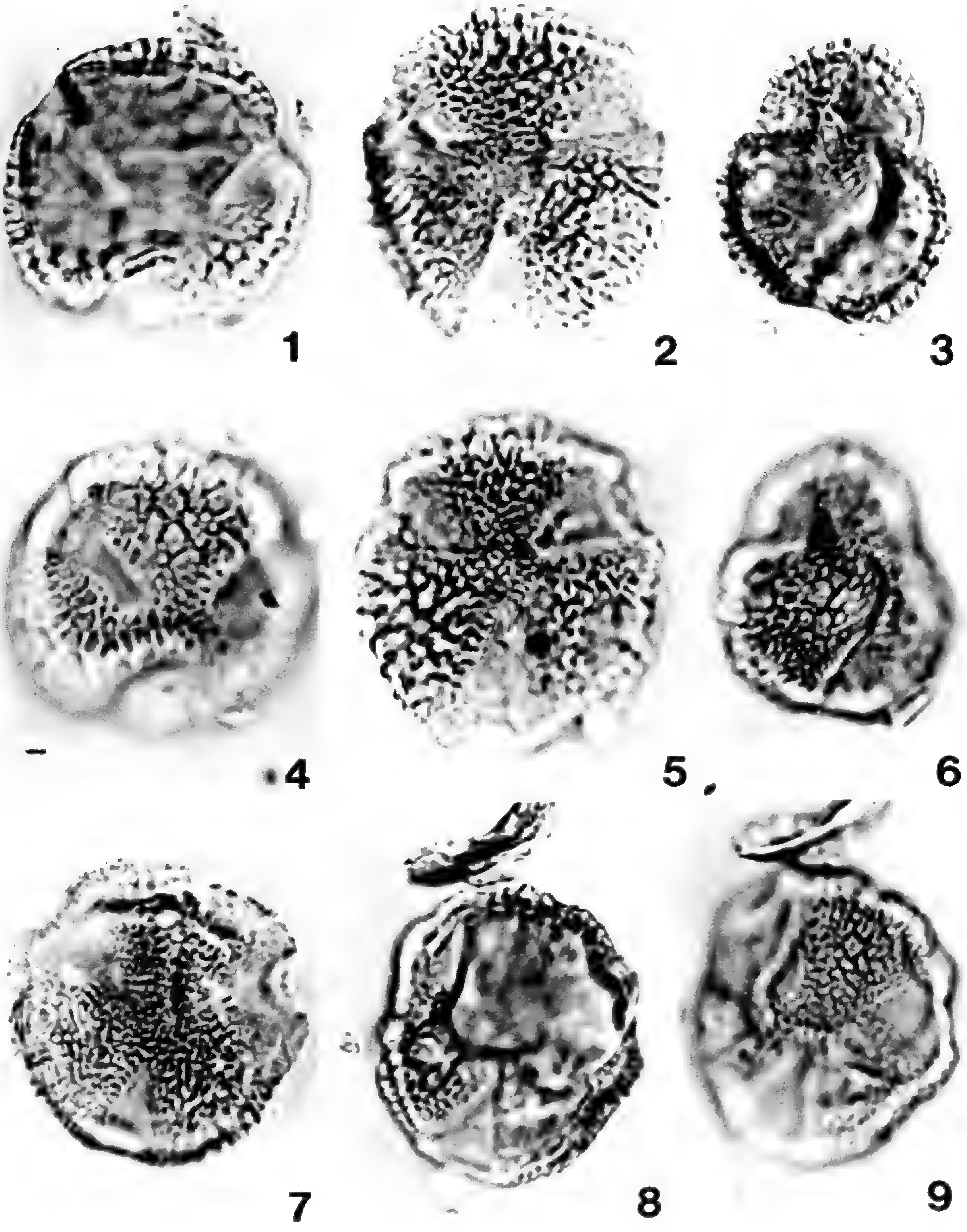
Lignite samples were macerated in a mortar and pestle then passed through HCl, HF, HNO_3, KOH, and acetolysis (one part concentrated H_2SO_4 to nine parts acetic anhydride). The palynomorphs were mounted unstained in glycerine jelly and sealed with CoverBond. Light photomicrographs were taken with a Wild microscope equipped with a Nikon 35 mm camera using Panatomic X film. SEM photomicrographs of extant pollen grains were prepared at the Smithsonian Institution. Acetolyzed samples were sputter-coated with gold-palladium and photographed with a Cambridge Stereoscan Mark IIA. The specimens are deposited in the palynology collections at Kent State University.

RESULTS

The fossil pollen and spores presently identified from the Eocene Gatuncillo formation of Panama include *Selaginella, Ceratopteris, Pteris,* Bromeliaceae, Palmae, cf. *Campnosperma, Ilex,* cf. *Arrabidaea,* cf. *Protium,* cf. *Tetragastris, Combretum/Terminalia, Casearia,* cf. *Tontalea, Alfaroa/Engelhardtia, Crudia,* Malpighiaceae, cf. *Ficus, Eugenia/Myrcia, Coccoloba, Rhizophora, Faramea, Cardiospermum, Serjania, Paullinia,* cf. *Chrysophyllum, Pelliceria,* and *Mortoniodendron.* Also recovered were pollen grains described as follows (description of the microfossils is based on light microscopy at 400× and 1,000× oil immersion magnifications): Pollen oblate to oblate-spheroidal, amb circular; tricolporate, colpi meridionally elongated, equatorially arranged, equidistant, tapering to acute apex, margin entire to slightly diffuse, faint margo formed by gradual diminution of reticulum near colpus margin, ca. 18 μm long (equator to apex), extending within 6–7 μm of pole (polar index 0.2), pore circular, situated at midpoint of colpus, margin diffuse, 4–5 μm diam.; reticulate, reticulum somewhat irregular, diameter of lumen ca. 2–3 μm in equatorial mesocolpal region, diminishing toward poles and margins of colpi, muri tall (ca. 2.5 μm) in equatorial mesocolpal area, giving somewhat deep, boxwork effect to reticulum, muri surface psilate, margins entire; exine tectate-perforate, height of columellae 2.5 μm in equatorial mesocolpal region, diminishing toward poles and margins of colpi; size 35–45 μm.

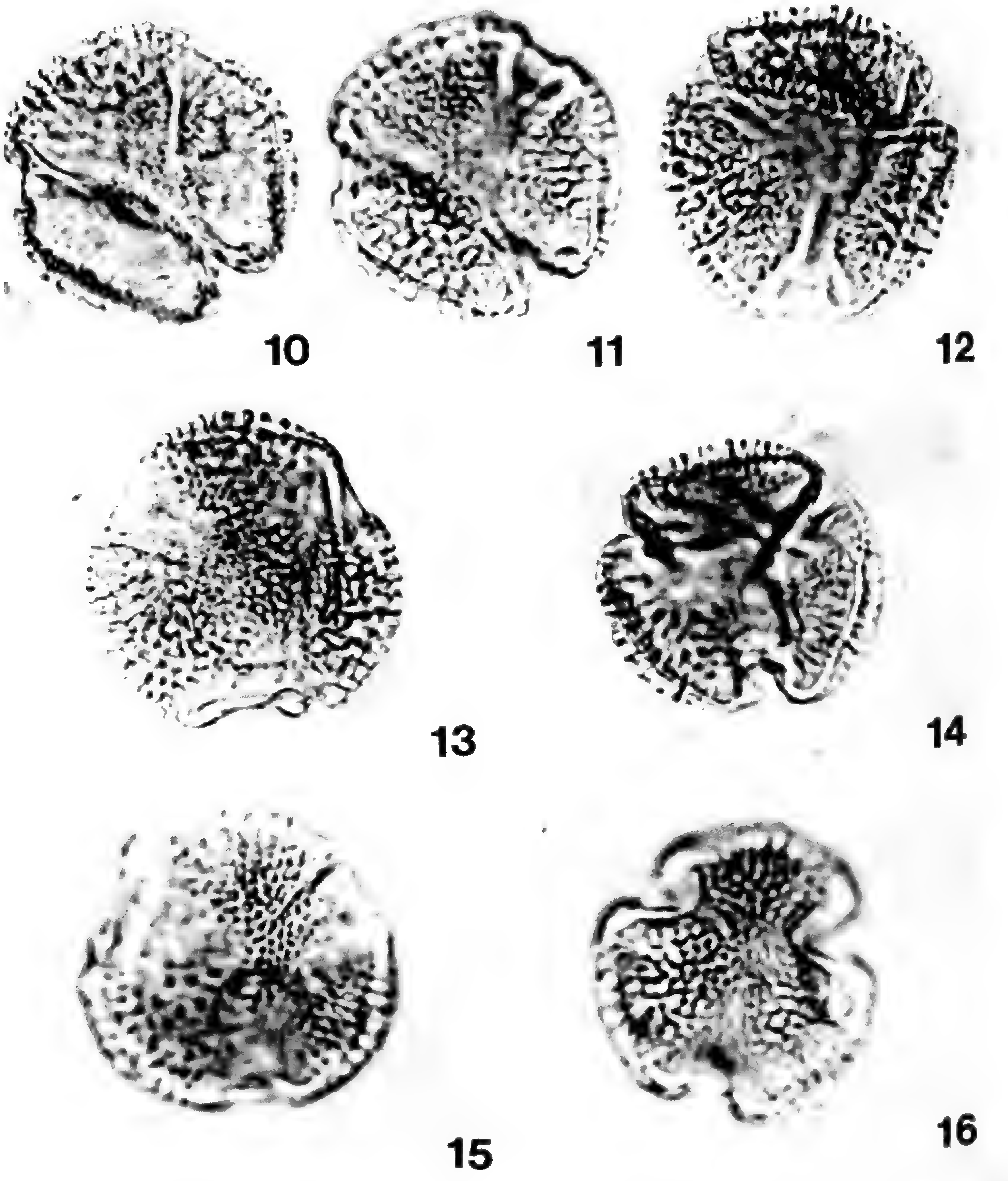
A second microfossil similar to the one described above was recovered and differs only in having a slightly finer and more regular reticulum. The microfossils have a low but consistent frequency on the four slides counted, and constitute ca. 0.5% of the total assemblage. The description is based primarily on five well-preserved specimens from our Locality D (the Alcalde Díaz locality), sample 4 (near the base of the roadside section), slide 1 (slides labeled Pan D, 4-1), although other specimens were examined to establish size ranges in quantitative features. Specimens with the coarser reticulum were more common than those with the finer more regular reticulum (ca. 4:1).

The modern genus in our pollen and spore reference collection most similar to the microfossils is *Lisianthius* P. Browne (sensu stricto). The collection includes all New World genera and most Old World genera of the Gentianaceae,



FIGURES 1–9. Fossil pollen of *Lisianthius* from the middle(?) to late Eocene Gatuncillo formation, Panama.—1, 4. Pan D 4-1, England Slide Finder coordinates X-23, 36 μm.—2, 5. Pan D 4-1, ESF V-34,1, 45 μm.—3, 6. Pan D 4-1, ESF Q-41,3, 41 μm.—7. Pan D 4-1, ESF Q-45, 45 μm.—8, 9. Pan D 4-1, ESF O-39, 1-2, 38 μm.

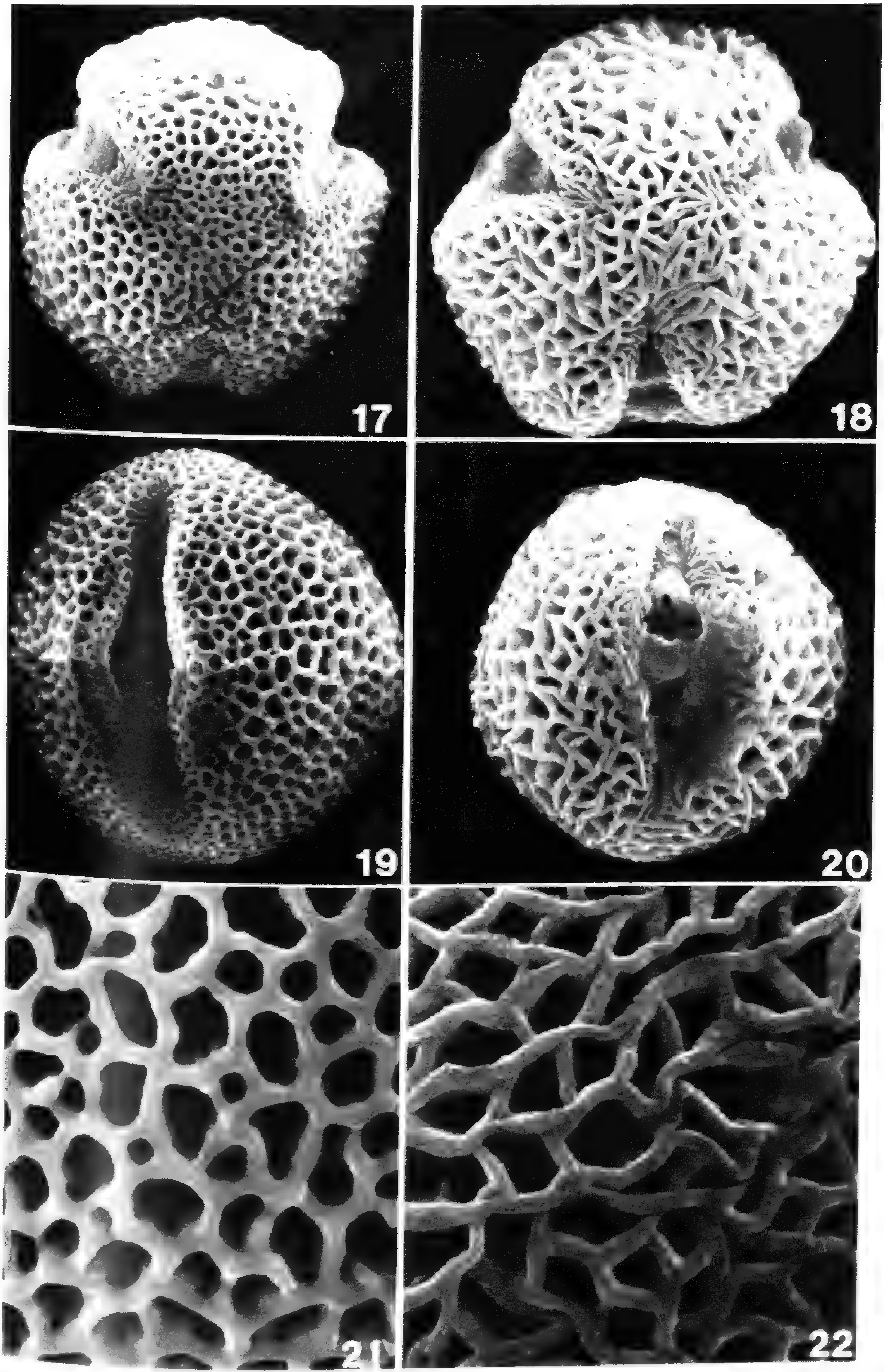
and multiple collections for virtually all species of *Lisianthius*. The microfossils conform in all major morphological features to pollen of the modern genus, but differ slightly in shape. All the microfossils were encountered in polar or near-polar view, reflecting their oblate to oblate-spheroidal shape. Most pollen grains of the modern species orient in equatorial view reflecting a prolate to slightly prolate-spheroidal shape. Also, the margo formed by diminution of the reticulum along the colpus margin is more pronounced in the modern pollen. These are minor, quanti-



Figures 10–16. Light photomicrographs of modern *Lisianthius* pollen.—10–12. *L. glandulosus* A. Rich. (*Ekman 1613,* Cuba, K; *Morton & Alain 9000,* Cuba, K).—13–16. *L. nigrescens* Cham. & Schlect. (*Breedlove 6477,* Mexico, F; *Ghiesbreght 702,* Mexico, BM).

tative differences, however, and given both the overall close morphological similarity, and the age of the fossils (upper Eocene), the specimens are considered within the range of variation of extant *Lisianthius* pollen (cf. Figs. 1–9 and 10–16). SEM photomicrographs of extant pollen (Figs. 17–22) proved useful in confirming details of morphology and relating these to interpretation and identification of the microfossils.

The modern pollen of *Lisianthius* (sensu lato) has been studied by Nilsson (1970a, 1970b; Nilsson in Elias & Robyns, 1975) and Weaver (1972). Among the species with pollen similar to the microfossils are *Lisianthius auratus* Standley, *L. capitatus* Urban, *L. dominensis* Urban, *L. glandulosus* A. Rich. (Figs. 10–12, 17, 19, 21), *L. nigrescens* Cham. & Schlect. (Figs. 13–16, 18, 20, 22), and *L. umbellatus* Sw. The variation in



FIGURES 17–22. Scanning electron photomicrographs of modern *Lisianthius* pollen.—17, 19, 21. *L. glandulosus* A. Rich. (*Morton & Alain 9000*, Cuba, US).—18, 20, 22. *L. nigrescens* Cham. & Schlect. (*Weaver 2183*, Mexico, US).

fineness of the reticulum noted for the fossils is matched among the pollen of modern species of *Lisianthius*. Pollen of *L. nigrescens* is similar to the more coarsely reticulate microfossils, and *L. glandulosus* represents the more finely reticulate type.

Both Nilsson (1970a, 1970b; Nilsson in Elias & Robyns, 1975) and Weaver (1972) agreed that *Lisianthius* pollen can be distinguished from other genera of the Gentianaceae, and this finding is consistent with our survey of the family. For example, in the related segregate genus *Macrocarpaea* the grains are either in tetrads, or if in monads, they differ from *Lisianthius* by the presence of conspicuous gemmae, or by a more open reticulum (viz., greater diameter of the lumen) and/or slightly coarser columellae.

DISCUSSION

Lisianthius is a New World genus of 27 species and two varieties of perennial herbs, shrubs, and small trees distributed from south-central Mexico, through the Antilles and Central America, into northwest Colombia (Weaver, 1972). The genus has been monographed by Weaver (1972), and treated floristically by Elias and Robyns (1975) for the Flora of Panama. Recently Sytsma et al. (1983) have studied the phylogenetics of the *L. skinneri* complex by endonuclease DNA mapping, morphology, flavonoids, and allozymes. The plants are entomophilous, but small percentages of pollen are quite likely to enter depositional basins. The conspicuous flowers are borne in clusters of about 15 to 30, and there may be between six and ten clusters per plant. At maturity the anthers extend beyond the corolla. *Lisianthius seemannii* (Griseb.) Perkins is especially floriferous with 100 or more flowers per plant, and *L. skinneri* (Hemsl.) O. Kuntze, the most common Central American species, also flowers profusely. Furthermore, several species of *Lisianthius* form thickets that locally dominate the habitat. As noted by Germeraad et al. (1968), outwashing is an important means of pollen transport in tropical environments and accounts for the greater representation of pollen from entomophilous species in tropical sediments than in deposits from temperate regions.

Lisianthius occurs from near sea level to about 1,800 m and is found in a wide variety of habitats. For example, *L. saponarioides* Cham. & Schlect. grows from 600 to 1,200 m on rocky limestone hillsides and in secondary scrub; *L. meianthus* Donn. Sm.—near sea level to 1,500 m in pine forests, limestone thickets, and roadsides; *L. oreopolus* Robins.—100 to 1,800 m in dry to moist pine or mixed forests; *L. peduncularis* L. O. Williams—dense moist forests at 1,000 m; *L. jefensis* Robyns & Elias—850 to 900 m in cloud forests; and *L. auratus* Standley—sea level to 1,800 m in pine forests or savannahs. Thus the floral features of *Lisianthius*, its occurrence in dense thickets, and its widespread distribution at moderately low elevations throughout Central America are consistent with the high-frequency, low-percentage recovery of microfossils from the Gatuncillo formation.

The presence of *Lisianthius* pollen in the late Eocene Gatuncillo formation, and earlier records of the Gentianaceae in the Paleocene and lower Eocene of the northern hemisphere (Crepet & Daghlian, 1981), is consistent with a northern origin for the family, one member of which had reached the area of present-day central Panama by late Eocene times. Its occurrence there at least raises the possibility of an early introduction from North America into South America prior to the more extensive exchange at the end of the Tertiary. This possibility parallels the similar impression of Raven and Axelrod (1974:629) based on the affinities and biogeography of modern taxa: "Judging from their affinities, the following taxa may also have gone from North America to South America. They are so well represented there it seems probable that they are not very recent arrivals: Boraginaceae, Clethraceae, Gentianaceae, Hydrophyllaceae, Loganiaceae—*Buddleia*, Onagraceae—*Fuchsia*, Plantaginaceae, Polemoniaceae, Scrophulariaceae, Theophrastaceae, Viscaceae."

Further consideration of the historical biogeography of *Lisianthius* and the Gentianaceae should await results of studies currently underway on other fossil microfloras from Central America. These include the lower Miocene Culebra, Cucaracha, and La Boca formations of Panama; the upper Miocene to Pliocene Gatun formation of Panama; and the Gatun formation in Costa Rica (Graham, unpubl. data). To date only the Culebra assemblage has been surveyed and *Lisianthius* pollen has not been recovered. Fossil representatives of other Gentianaceae have been discussed by Crepet and Daghlian (1981). This is the first report of *Lisianthius* in the fossil record.

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STEYERMARKOCHLOA UNIFOLIA, A NEW GENUS FROM VENEZUELA AND COLOMBIA (POACEAE: ARUNDINOIDEAE: STEYERMARKOCHLOEAE)[1]

GERRIT DAVIDSE[2] AND R. P. ELLIS[3]

ABSTRACT

Steyermarkochloa unifolia Davidse & Ellis, gen. et sp. nov. and **Steyermarkochloeae** Davidse & Ellis, trib. nov. are described. This species occurs in seasonally inundated white-sand soils in the Territorio Federal Amazonas, Venezuela, and Comisaria Guainía, Colombia. It has dimorphic culms and leaves. Only a single developed leaf is produced per vegetative culm. The morphology of this leaf is unique in the Poaceae in its cylindrical, solid sheath with flattened blade and absence of a ligule. Plants are polygamo-monoecious but most spikelets are unisexual. All spikelets are 3-flowered with the terminal floret always rudimentary. Male and bisexual spikelets usually have two fully developed florets, the lower usually male in bisexual spikelets, and are borne basally in the inflorescence. Female spikelets have the lower floret sterile and the second fertile. Lodicules are absent and the stamens and stigmas are terminally exserted. Anatomical studies indicate that the plant is arundinoid in all epidermal characteristics except the absence of microhairs and in most diagnostic characteristics of the blade anatomy. *Steyermarkochloa* is unusual in possessing vascular bundles inserted at different levels in the blade. The blades, sheaths, and roots have an extensive system of lacunae, a feature typical of aquatic plants. Although anatomical features clearly point to an arundinoid affinity, the many anomalous morphological features indicate an isolated position within the subfamily that is best recognized at the tribal level.

During his intensive studies of the savannas in the Territorio Federal de Amazonas, Venezuela, Otto Huber collected an unusual grass along the Río Temi in 1978 that could not be identified with any known Venezuelan species. A thorough search in the national herbarium of the Dirección de Investigaciones Biológicas (VEN) led to the discovery of an earlier unidentified collection of the same species made by E. Foldats in 1960 along the Río Atabapo, also in Amazonas. In 1980, the remaining unstudied grass collections of the New York Botanical Garden's expeditions to the Guyana Highlands became available to Davidse. Discovered among these collections was a unicate specimen of this grass collected by B. Maguire, J. J. Wurdack, and G. S. Bunting near Cerro Yapacana, Amazonas, in 1953, which represents the first collection of this species.

At the invitation of Huber, Davidse had the opportunity in 1979 to join an expedition to west-central Amazonas in the Departamento of Atabapo where several new populations of this interesting grass were located. Subsequent studies indicated that this species was undescribed, but because of the many anomalous morphological features, thorough anatomical studies were required to clarify the systematic position and relationships of this grass within the family. These studies were undertaken by Ellis and are reported here.

Based on these studies, we conclude that this unusual grass represents a new monotypic genus and new tribe of the Arundinoideae.

The genus is named in honor of Dr. Julian A. Steyermark, the most prolific botanical collector of all time, discoverer of hundreds of new taxa of plants and animals, author of numerous botanical publications, and a valued personal friend and field companion of Davidse.

TAXONOMY

Steyermarkochloeae Davidse & Ellis, tribus nov. TYPE: *Steyermarkochloa* Davidse & Ellis.

Gramina perennia culmis et foliis dimorphis; folium evolutum singulare in quoque culmo ve-

---

[1] Support for fieldwork was provided by NSF INT 76-14750 and CONICIT (Venezuela). Davidse thanks Dr. Otto Huber for providing him with the opportunity to join his expedition. Drs. Stephen S. Tillett (MFY) and Julio Cerda Cordero also participated in the expedition and contributed mightily to its success. We are grateful to Dra. Zoraida Luces de Febres (VEN) and Dr. Bassett Maguire (NY) for making specimens available to us and to Dr. John D. Dwyer for assistance with the Latin. Ellis acknowledges the excellent technical assistance by H. Botha and S. Perold.

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getativo vagina cylindrica solida lamina complanata ligula non evoluta. Inflorescentia spicata cylindrica; spiculae masculinae et/vel bisexuales infimae in inflorescentia, spiculae femineae summae. Spiculae solitariae, 3-florae, interdum unisexuales plerumque bisexuales, compressae dorsales; disarticulatis sub glumis; glumae 2; flosculus summus rudimentalis; flosculus inferior spiculae femineae sterilis; palea flosculi feminei spongiosa curvata (5–)7–11-nervis lemmate longior; lodiculae 0; stigmata 2, stylus 1; caryopsis fusiformis hilo lineari.

Perennial grasses with dimorphic culms and leaves; developed leaf solitary on each vegetative culm, the sheath solid, cylindrical, the blade flattened, a ligule not differentiated. Inflorescence spicate, cylindrical with male and/or bisexual spikelets lowermost and female spikelets uppermost. Spikelets solitary, 3-flowered, usually unisexual, sometimes bisexual, dorsally compressed; disarticulation below the glumes; glumes 2; uppermost floret rudimentary; lower floret of the female spikelet sterile; palea of the female floret spongy, curved, (5–)7–11-nerved, longer than the lemma; lodicules 0; stigmas 2, the style 1; caryopsis fusiform, the hilum linear.

Steyermarkochloa unifolia Davidse & Ellis, gen et sp. nov. TYPE: Venezuela. Amazonas: Departamento Casiquiare, sabana cerca de Yavita, a lo largo del Río Temi, lat. 3°0′, long. 67°25′, ca. 110 m, hasta 2 m de alto, formado densas colonias al borde del matorral, 25 Aug. 1978, *O. Huber 2620* (holotype, MO; isotypes, US, VEN). Figures 1–3.

Gramen perenne caespitosum. Culmi non ramosi, dimorphi; culmus vegetativus non elongatus ferens aliquot vaginas sine laminis et 1 folium evolutum; culmus reproductivus elongatus nodis 3–8, cavus, ferens vaginas sine laminis. Vaginae sine laminis marginibus liberis; folium evolutum vagina cylindrica solida lamina complanta; ligula non evoluta. Inflorescentia spicata cylindrica ferens spiculas inaequaliter verticellatas brevipedicellatas unisexuales vel bisexuales; spiculae masculinae et bisexuales portatae basin versus inflorescentia, spiculae femineae aliter apicem versus. Spiculae infra glumas disarticulantes, 3-florae, flosculo supremo rudimentali; glumae 2, subequales, lemmatibus breviores; spiculae masculinae rectae plerumque flosculis inferioribus staminatis, paleis lemmatibus subequalibus staminibus 2 per flosculum; spiculae bisexuales rectae plerumque flosculo inferiore masculino et flosculo secundo bisexuali, paleis lemmatibus subequalibus; spiculae femineae curvatae flosculo inferior sterili palea plerumque absenti, flosculo secundo femineo palea (5–)7–11-nervi spongiosa lemmate longiore; lodiculae 0; stigmata 2, stylus 1; caryopsis fusiformis; hilum lineare; embryo ⅕-plo caryopside longior.

Perennial, caespitose in dense clumps. *Culms* dimorphic; *vegetative culms* with the internodes not elongated, erect, the lower nodes bearing bladeless, stramineous sheaths much longer than the internodes, the sheaths progressively longer from the base upwards, the uppermost to 20 cm long, clasping the developed leaf, rounded on the back, glabrous adaxially, abaxially prominently tessellate-veined, densely beset with prickles along the veins towards the tip, the prickles often enlarged at the junction of the sheath and apicule, the margins free, overlapping, the midrib not well differentiated, slightly raised on the adaxial surface near the tip and excurrent as an apiculum 0.5–11 mm long, 0.1–0.3 mm wide with tightly curved margins, the uppermost node bearing a single, developed leaf 80–300 cm long, the sheath cylindrical, 2–5.2 mm diam., glabrous, solid, internally with conspicuous longitudinal lacunae regularly divided by cross-partitions, without a conspicuous midrib, ca. half-way splitting on one side into a narrow furrow, this opening into a flattened, glabrous blade, the blade 2.8–6.5 mm wide, differentiated into a narrow midrib, flanked on each side by a narrow line of bulliform cells and a thickened lamina, plano-convex in cross-section, the adaxial surface planar, the margins glabrous, the laminae abruptly narrowed and folded towards the tip, the distal 1–2 cm completely fused to form a blunt, navicular tip, a ligule not differentiated in the region of blade expansion; *reproductive culms* 40–350 cm tall, 3–13 mm diam., strictly erect, hollow, glabrous, often covered with a conspicuous, greyish waxy bloom, the basal internodes not elongated, the upper 3–8 internodes conspicuously elongated, all bearing bladeless sheaths similar to those of the vegetative culms, the sheaths clasping the culm with overlapping margins, the lower sheaths stramineous, the upper green, mostly 13–40 cm long, often with a waxy bloom, the uppermost shorter than the internodes. *Inflorescences* 7–49 cm long, cylindrical, spicate, bearing densely arranged, solitary, short-pedicellate spikelets in irregular whorls, the spikelets irregularly spirally arranged toward the base of the inflorescence, male or bisexual in the lower part, female in the upper part; peduncle exserted at maturity, glabrous; rachis ridged by the decurrent pedicels, densely covered by a waxy excrescence, the pedicels 0.4–1 mm long in the middle of the inflorescence, 4–13 mm long at the base, 4-angled, covered with a waxy excrescence except at the glabrous tip, the abscission point shallowly discoid. *Spikelets* dorsally compressed to rounded, 3-flowered, sometimes 2-flowered in male spikelets towards the base of the inflorescence, the uppermost floret always rudimentary in all spikelets and borne on a distinct rachilla segment; *male spikelets* with 2 functional male florets; *bisexual spikelets* usually with the lower floret male and the second floret bisexual; sometimes both lower florets bisexual; *female spikelets* with the lower floret sterile and the second floret female; glumes, lemmas and paleas scaberulous toward their tips with the tips dark brown and with single transverse veins between the nerves; *glumes* 2, equal or subequal, the lower glume 2.2–4.7 mm long, broadly lanceolate, 2-keeled, the keels scaberulous in the upper half, flattened between the keels, hardened and thickened between and on the keels, especially at maturity, 3–7-nerved, only the keel nerves well developed, the midnerve often not evident or well developed, the margin herbaceous, sharply incurved, nearly clasping at the base, the tip obtuse or narrowly truncate, the upper glume 2.1–3.7 mm long, lanceolate, rounded on the back or sometimes slightly flattened, 3–6-nerved, the tip obtuse to erose-truncate; *male and bisexual spikelets* mostly 4.5–7.5 mm long, straight, the lower lemma 4.3–7 mm long, broadly lanceolate, herbaceous, 3–7-nerved, the nerves, except for the lateral pair, conspicuous, the tip broadly acute, the palea subequal to the lemma, membranous, 2-keeled and usually 2-nerved, rarely with a few additional nerves, the male flowers without lodicules, the stamens 2, basifixed, exserted terminally through an orifice made by the lemma and palea, the anthers 2.2–3.8 mm long, the filaments free or fused along their entire length, the second floret similar to the lower floret but somewhat smaller in all its parts, when bisexual the stamens posterior, the 2 styles separate to the ovary or nearly so, lodicules absent, the rudimentary upper floret including the rachilla segment rarely longer than 1.5 mm; *female spikelets* mostly 9–17 mm long, curved, the lower floret sterile, the lemma 4.8–7 mm long, broadly lanceolate, herbaceous, 5–9-nerved, the nerves conspicuous, the apex obtuse, the lower palea usually not developed, rarely present as a hyaline bract to 2 mm long, the second floret female, the lemma 6.1–9 mm long, broadly lanceolate, curved, (5–7–)9–11 (–13)-nerved, the nerves conspicuous in the upper parts, the internerves sulcate, herbaceous along the margin, spongy-thickened in the middle along the midnerve, membranous at the very base, obtuse to truncate at the tip, the palea 8.5–14 mm long, always longer than the lemma at maturity, convolute, conspicuously spongy-thickened at maturity except for the herbaceous tip and somewhat membranous base, (5–)7–11-nerved, curved and slightly twisted, the apex forming a distinct orifice for stigma exsertion, truncate, the pistillate flower without lodicules and with 2 posterior staminodia, the ovary fusiform-cylindrical, the style 1, the stigmas 2, plumose, exserted terminally, the rudimentary upper floret 0.3–3 mm long, the rachilla 1.8–5 mm long; *caryopsis* ca. 5 mm long and 1 mm wide, ca. fusiform but broadest below the middle, the hilum linear, ca. 3.5 mm long, the embryo ca. one-fifth as long as the caryopsis.

Paratypes. COLOMBIA. GUAINÍA: near Coitara, ca. 7 km S of San Fernando de Atabapo (Venezuela), W bank of the Río Atabapo, 67°43′W, 3°55′N, 95 m, 28 Apr. 1979, *Davidse 16848* (BM, CANB, CAY, COL, F, INPA, ISC, K, L, MEXU, MO, NY, PRE, SP, US VEN). VENEZUELA. AMAZONAS: Depto. Atabapo, ca. 20 km S of San Fernando de Atabapo, E bank of the Río Atabapo, 67°39′W, 3°50′N, 95 m, 29 Apr. 1979, *Davidse, Huber & Tillett 16850* (VEN); Depto. Atabapo, Santa Cruz, margen del Río Atabapo cerca de la desembocadura del Río Atacavi, 10 Sept. 1960, *Foldats 3848* (MO, VEN); Depto. Atabapo, lower part of Caño Caname, 67°23′W, 3°41′N, 95 m, 2 May 1979, *Davidse, Huber & Tillett 17089* (MO, VEN); Depto. Atabapo, Cerro Yapacana, savanna I, 125 m, 20 Nov. 1953, *Maguire, Wurdack & Bunting 36621* (NY); Depto. Atabapo, sabanes al pié W del Cerro Yapacana, 10 Aug. 1983, *Huber & Kral 7973* (MO, VEN); Depto. Atabapo, between the W base of Cerro Yapacana and the headwaters of Caño Cotúa, 66°52′W, 3°38′N, 120 m, 8 May 1979, *Davidse, Huber & Tillett 17196* (MBM, MG, MO, PRE, VEN, WIS); Depto. Atabapo, middle part of Caño Yagua at Cucurital de Yagua, 66°34′W, 3°36′N, 120 m, 8 May 1979, *Davidse, Huber & Tillett 17382* (BRI, COL, MG, MO, PRE, UB, VEN); Casiquiare, orilla del alto Caño Pimichín, 67°42′O, 2°54′N, 10 m, 1 Mar. 1980, *Huber 4896* (MO, VEN).

MORPHOLOGICAL DISCUSSION

Steyermarkochloa grows in dense tufts along the margins of large or small streams in seasonally water-logged or inundated white-sand soils.

It is most commonly found as a component of savanna scrub or sabaneta (cf. Huber, 1982) or along the margins of white-sand savannas and morichales. Huber (pers. comm.) defines sabaneta as a "dense but low scrub formation with a rather dense herb layer and a more or less irregular shrub or treelet formation, the trees with open, irregular crowns rarely exceeding 4–5 m in height and their crowns not forming a continuous canopy. Sabanetas are inundated during most of the rainy season, normally from May to November, the inundation generally reaching 30–60 cm." Flowering plants (*Davidse, Huber & Tillett 17382*) have been observed to grow in water to 1 m deep early in the rainy season, March 1980 (Davidse, pers. observ.), and to 2 m deep at the height of the rainy season in the same locality, August 1983, (Huber, pers. comm.). In both cases only the inflorescence was emergent. The system of lacunae in the roots and leaves is a well-known feature of plants adapted to life in such aquatic or semiaquatic habitats.

The area inhabited by *Steyermarkochloa* is part of the Amazonas Savanna Refuge described by Steyermark (1982) and is well known for its high degree of endemism. This high endemism, as noted by Steyermark, is probably due in large part to the special edaphic requirements imposed on plants by the nutritionally extremely poor, highly acid sand soils with low water-holding capacity.

The basal internodes of both vegetative and reproductive culms are short and close together as is typical in grasses. Single buds enclosed in an inconspicuous prophyllum are borne distichously at the nodes. Only the lowermost buds are active and form new vegetative and reproductive culms. Branches at the upper nodes of reproductive culms have never been observed.

Over 300 vegetative culms in five populations were examined in the field, and, in all but one culm, they bore solitary developed leaves. In the one exception two leaves were observed. The consistent production of a single developed leaf per vegetative culm (alluded to in the specific epithet) is quite rare among grasses. Previously described examples of such a condition are in the bambusoid species *Sucrea monophylla* Soderstrom from Brazil (Soderstrom, 1981a) and *Puelia schumanniana* Pilger from Cameroon (Clayton, 1967).

The blade is normally twisted in living plants. This is an excellent field character to distinguish these otherwise inconspicuous plants from the accompanying herbaceous species, dominated by *Duckea, Monotrema, Lagenocarpus, Rhynchospora,* and *Scleria.*

The morphology of the fully developed leaf in *Steyermarkochloa* is unique in the Poaceae. The differentiation of a sheath into a solid, cylindrical stem-like structure that does not clasp the culm has not been reported previously. Based on dissection of plants in the field and on herbarium specimens, it appears that the terminal meristem becomes inactive and all further growth is channelled into the production of the basally stem-like leaf borne at the uppermost node. The exact details of the ontogeny and differentiation will be reported upon later, on the basis of anatomical studies of the apical region of vegetative culms.

This highly specialized leaf sheath is analogous to a culm in its cylindrical shape, solid parenchymatous interior (interrupted extensively, however, by lacunae), and the possession of two concentric rows of vascular bundles at different levels, as explained below. Functionally it means that the expanded blade is presented at a higher level and at a presumably more advantageous position for photosynthesis and light competition.

Cylindrical, solid blades in grasses are well known and, according to Böcher (1972), are probably primarily an adaptation to xeric habitats. Examples that have been anatomically studied are *Miscanthidium teretifolium* (Stapf) Stapf (Metcalfe, 1960) and *Sporobolus rigens* (Trin.) Desv. (Böcher, 1972). In such species the sheaths possess the normal, hollow cylindrical construction typical of all grasses. In *Steyermarkochloa,* the sheath may be an unusual adaptation to the seasonally flooded habitats it favors. The elongated, stem-like sheath may be a means of allowing the most important photosynthetic organ, the blade, to be fully functional at high water levels.

The reduction of all other leaves to simple, essentially bladeless, clasping sheaths with overlapping margins is unusual in aerial culms of nonbambusoid grasses. Similar sheaths, usually with rudimentary blades, are a characteristic feature of woody bamboo culms (McClure, 1966). As in the bamboos, it seems likely that the primary function of these sheaths is structural support of young, tender, rapidly elongating culms. However, the fact that the upper sheaths retain their green color for a long period of time indicates that photosynthesis is also an important function.

The apicula usually borne on the "bladeless"

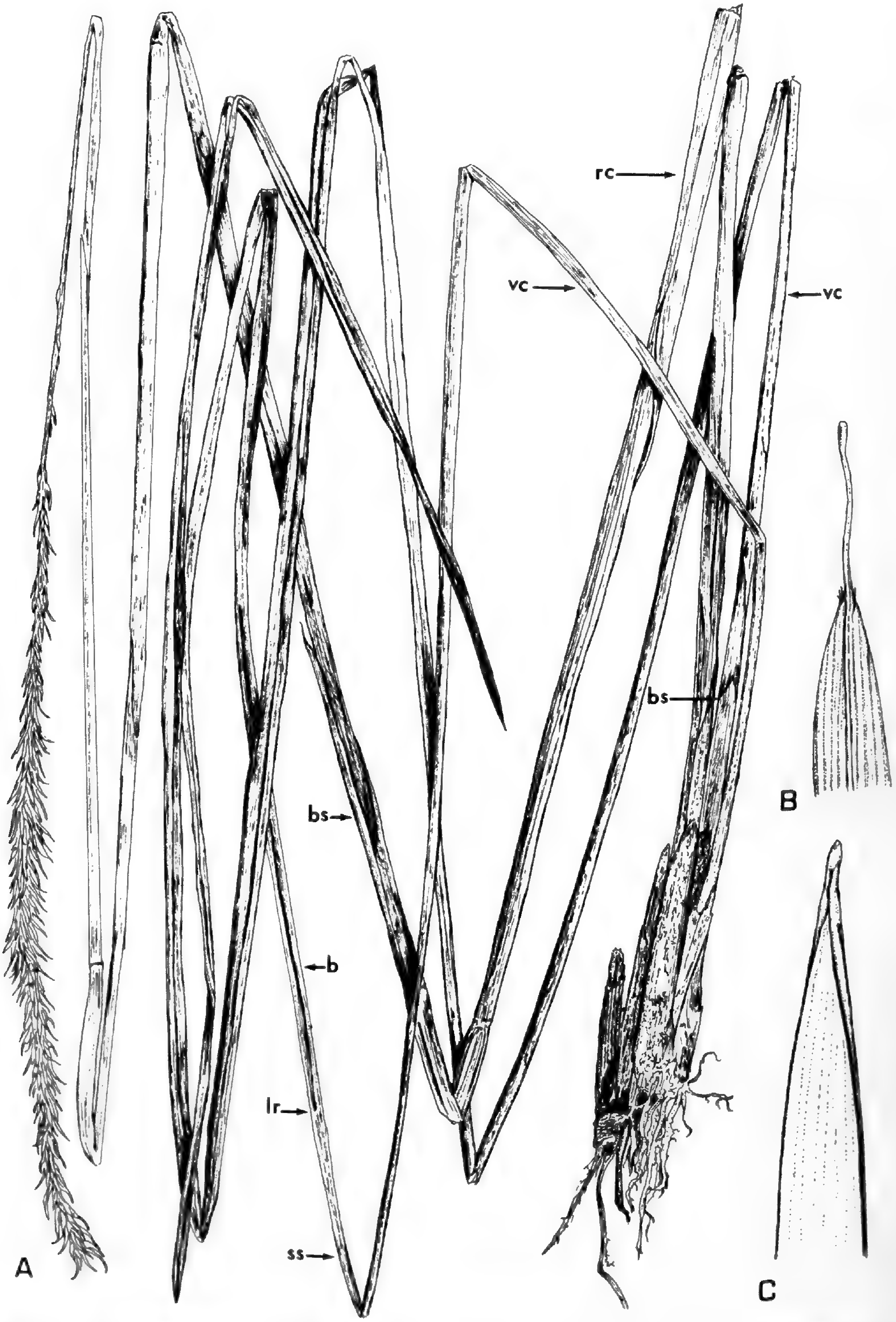


FIGURE 1. *Steyermarkochloa unifolia* Davidse & Ellis.—A. Habit; plant with one fertile culm and two vegetative culms each bearing one developed leaf. Note the bladeless sheaths at the nodes of the fertile culm and at the base of the vegetative culms; ×0.5.—B. Apiculum of a bladeless sheath, abaxial view; ×6.—C. Tip of a developed leaf, adaxial view; ×5. b = blade; bs = bladeless sheath; lr = ligular region; rc = reproductive culm; ss = solid, cylindrical sheath; vc = vegetative culm. [Based on *Davidse 16848* (CANB).]

sheaths (Fig. 1B) are presumed to represent vestigial blades because of their position and differentiation from the sheath. They appear to be thickened extensions of the midrib of the sheath that are tightly incurved. Ligules are not distinguishable at the junction of the apicula and sheaths. Ligules are also lacking in the developed leaves. Absence of ligules occurs sporadically throughout the family, and little taxonomic importance can be ascribed to this character at the generic level or above. The prominent scabrosity on the inner surface of the leafless sheaths is unusual. It is due to large prickle hairs disposed in regular rows on the uppermost part of the sheath where it does not entirely encircle the culm and where it is somewhat looser. This scabrosity could be a deterrant to small insects, including potentially damaging herbivores, that might utilize the space between the sheath and the culm. McClure (1966) noted that all bamboo sheaths have a lustrous inner surface in common. In most other grasses this also seems to be the normal condition.

Leaf dimorphism with some leaves reduced to simple sheaths without blades is a common feature of rhizomatous grasses in all major taxonomic groups. Typically they form a stiff, pungent tip on the growing point of the rhizome, enabling it to pierce the soil.

Steyermarkochloa resembles some genera and species of bambusoid affinity in producing inflorescences on specialized, bladeless culms. This is characteristic of the genera *Glaziophyton* (McClure, 1973), *Piresia, Diandrolyra, Mniochloa,* and *Ekmanochloa,* and certain species of *Olyra, Cryptochloa, Pariana,* and *Eremites* (Calderón & Soderstrom, 1980). In nonbambusoid grasses this feature is found only in those few genera and species known to produce subterranean, cleistogamous inflorescences, as in *Amphicarpum* (Hitchcock & Chase, 1950), *Chloris chloridea* (Presl) Hitchc. (Anderson, 1974), and *Paspalum amphicarpum* Ekman (Chase, 1929).

Spikelets are borne singly on simple, short pedicels. Although the appearance is spicate, the inflorescence is a raceme. The spikelet arrangement seems to be fundamentally spiral, but because of congestion in the central part of the inflorescence, a nearly whorled pattern is attained.

Spikelets are typically 3-flowered but occasional staminate spikelets toward the base of the inflorescence may be only 2-flowered, and several female spikelets with an extra empty lemma were observed in *Davidse, Huber & Tillet 17089.* The spikelets are largely unisexual with the female spikelets borne above the male spikelets (Fig. 2A). In most of the observed inflorescences female spikelets predominate, typically constituting 70% or more of the total. Certain specimens of *Davidse 16848* are entirely female. However, in most populations there is a great deal of variation in the proportion of male and female spikelets in an inflorescence, as shown by the fact that in another specimen of *Davidse 16848,* 70% of the spikelets in the inflorescence are male.

Although unisexual spikelets are by far the most common, certain plants bear spikelets with anthoecia morphologically similar to those of male spikelets but containing bisexual flowers. In such plants the lowest spikelets in the inflorescence may be entirely male, followed by a few whorls of bisexual spikelets, and topped by numerous whorls of female spikelets. The bisexual spikelets may bear two bisexual flowers or only the second floret may be bisexual with the lower floret male. We do not know with certainty whether the gynoecium of bisexual florets is really functional since no developed caryopses have been seen in such florets. The gynoecium seems to be of functional size, but the styles are usually completely separate to the top of the ovary (Fig. 3D), whereas they are united approximately one-half their length in female spikelets (Fig. 3C). This may be functionally related to the larger size of female florets (8.5–14 mm) compared to that of the bisexual florets (4.8–7 mm). Similar style-stigma dimorphism was reviewed by Connor (1979), who noted its occurrence in three genera (*Cortaderia, Bouteloua,* and *Eriochrysis*).

The androecium is always present as a posterior pair of stamens, whether fully developed as in male (Fig. 3B) or bisexual spikelets (Fig. 3D) or as staminodia as in female spikelets (Fig. 3E). Staminodia are always present in the second floret of female spikelets. In some female florets the staminodia are clearly differentiated into filaments and anthers, but they are never functional and do not exceed 0.3 mm in length. Rather unusual is that the two filaments in the male florets may be free (Fig. 3A) or fused nearly along their entire length (Fig. 3B) with the anthers always free. Both conditions can be found in the same inflorescence, but fused filaments were not observed in bisexual florets. Fused filaments are quite rare in the family, being known only in the Bambusoideae, in which they may be partially fused, as in some species of *Bambusa,* or mon-

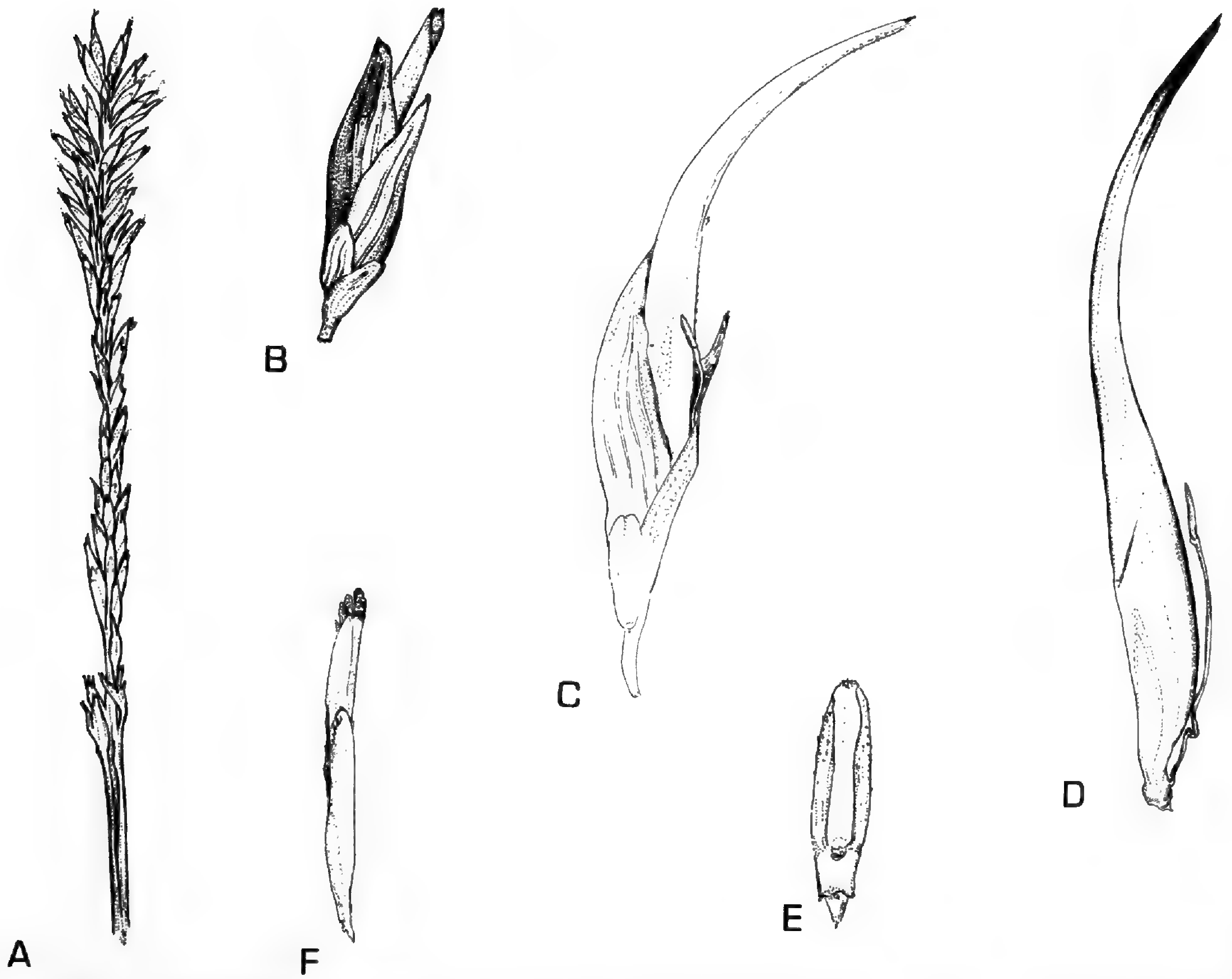


FIGURE 2. Inflorescence and spikelets of *Steyermarkochloa unifolia* Davidse & Ellis.—A. Inflorescence bearing male spikelets in the lower part and female spikelets in the upper part; ×0.5.—B. Young female spikelet; ×6.—C. Nearly mature female spikelet with prominently curved palea and small rudiment; ×5.—D. Curved, convolute palea of the second floret of a female spikelet with an elongated rachilla and rudimentary upper floret; ×6.—E. Lower glume of female spikelet, adaxial view; ×6.5.—F. Male spikelet at early anthesis, dorsal view with the lowest bract the back of the upper glume; ×6.5. [A, B: based on *Maguire, Wurdack & Bunting 36621* (NY); C–F: based on *Huber 2620* (holotype, MO).]

adelphous and completely fused into a tube, as in *Schizostachyum, Oxytenanthera,* and *Gigantochloa* (McClure, 1966), *Froesiochloa, Streptochaeta,* and *Dendrocalamus* (Soderstrom, 1981b).

As in many grasses with predominantly unisexual spikelets, there is a strong dimorphism between the male and female spikelets, although the glumes are identical in each kind of spikelet (Fig. 2). In *Steyermarkochloa,* the female spikelets differ most significantly from the male spikelets in that the former lack a flower and usually a palea in the lower floret, and the lemma and palea of the second floret are greatly enlarged, curved, more abundantly nerved, and spongy-thickened (Fig. 2C, D). Nervation of the lemmas and paleas, although somewhat variable, differs significantly in the different types of spikelets. In male and bisexual spikelets, the lemmas of the male florets are predominantly 3–5-nerved. In female spikelets, the lower lemmas are 5–9-nerved and the second lemmas are predominantly 9–11-nerved and only rarely 5–7- or 13-nerved. The differences are even more pronounced in the paleas which are almost always of the normal 2-keeled, 2-nerved type in male and bisexual florets, but convolute and (5–)7–11-nerved in female spikelets.

Although we have made no direct observations of this in the field, we believe that the spongy-thickened lemma and, especially, palea of the female spikelets are adaptations for dispersal of the fruits by water. It is likely that the spongy tissue provides enough buoyancy to the fallen spikelet to enable it to float for some time. We presume that fruit production and dispersal would

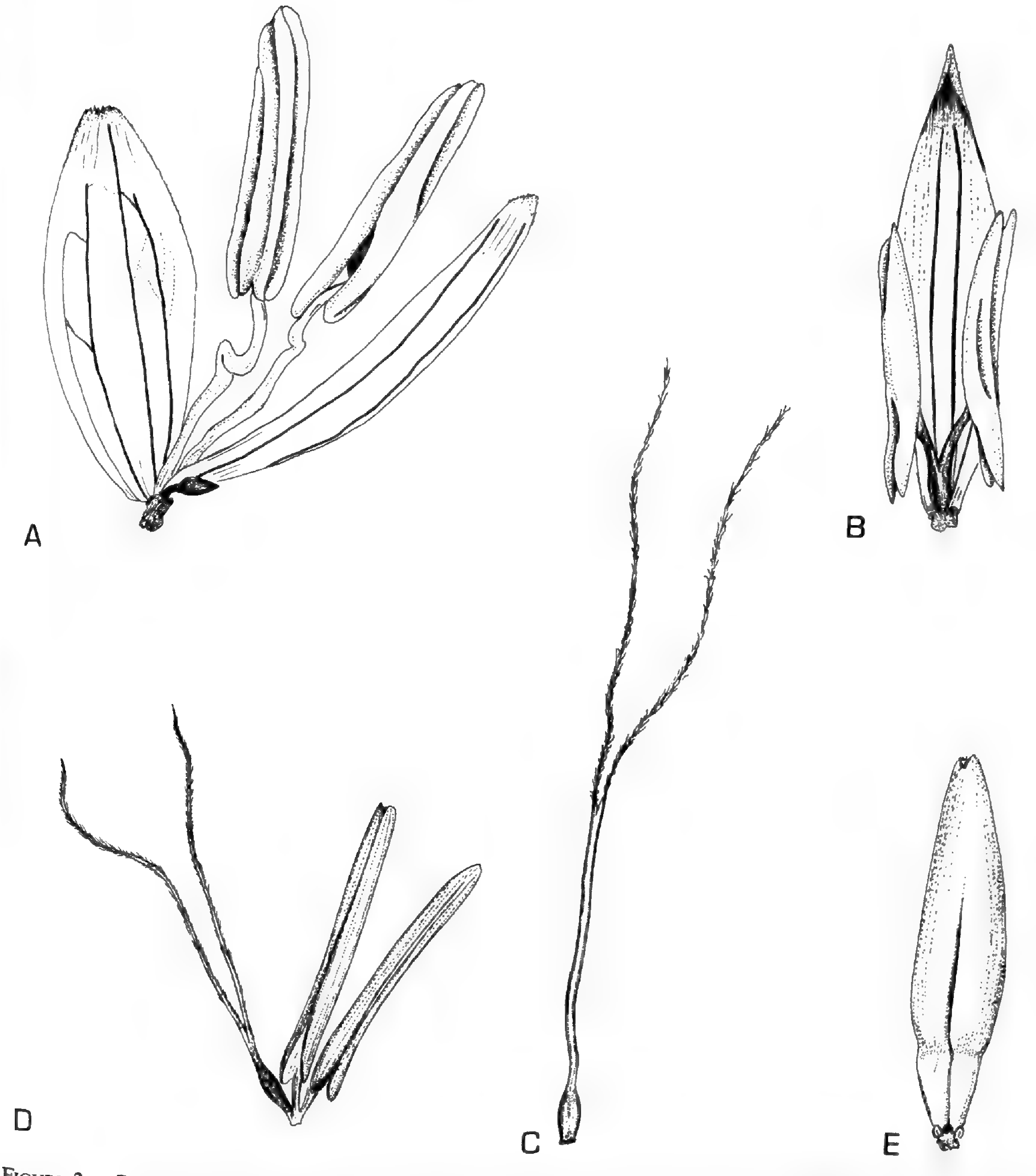
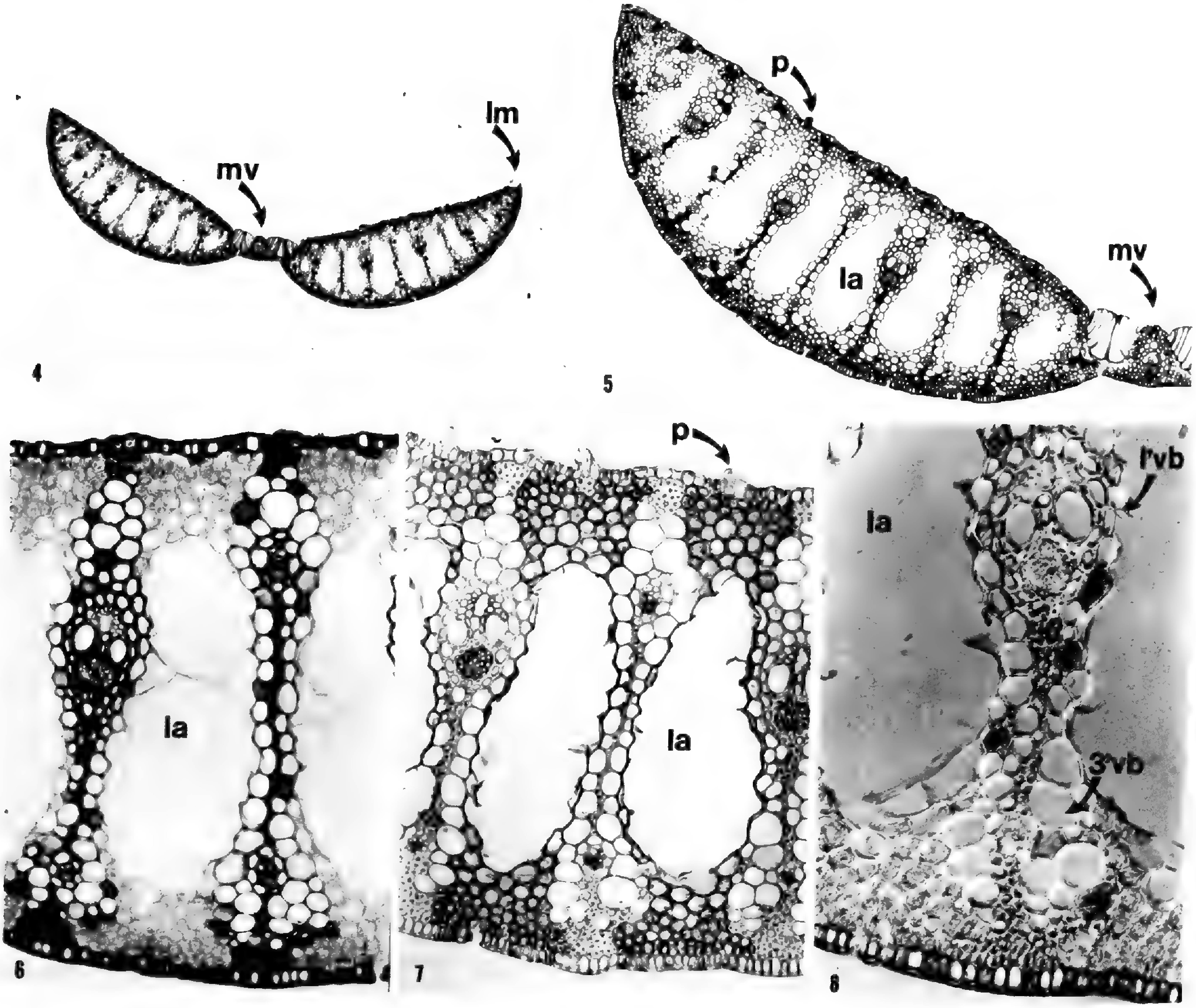


FIGURE 3. *Steyermarkochloa unifolia* Davidse & Ellis.—A. Male floret just before anthesis with lemma and palea flattened and separated; stamens two with separate filaments; rudimentary upper floret at the base; ×13.—B. Young male floret with the lemma removed; stamens two with united filaments; ×9.5.—C. Gynoecium of female spikelet at anthesis with a long united style; ×6.5.—D. Young flower of a bisexual floret; stamens with separate filaments; style short; ×11.5.—E. Caryopsis with linear hilum and staminodia at the base, the tip broken; ×9. [A–D: based on *Davidse 16848* (MO); E: after *Huber 2620* (holotype, MO).]

usually take place during the latter part of the rainy season while the habitat is still flooded but direct observations are lacking.

Unfortunately, only one mature caryopsis was found in all specimens presently available (Fig. 3E). For this reason the important internal embryo characteristics (Reeder, 1957) could not be determined. In its overall shape, the caryopsis most closely resembles the type found in terete, 1-flowered spikelets such as *Aristida.* The linear hilum is the normal type found in the Arundinoideae, but the relatively small embryo is unusual for that subfamily, although not unknown. Also unusual is that the embryo appears to occupy the entire lower portion of the caryopsis rather than only the abaxial face, as is typical for



Figures 4–8. Leaf blade anatomy of *Steyermarkochloa unifolia* Davidse & Ellis as seen in transverse section.—4. Leaf blade outline; ×40.—5. One-half of the lamina, note the alternating first order vascular bundles and third order vascular bundles in the adaxial part of the blade and the third order vascular bundles near the abaxial surface; ×100.—6. Detail of the vascular bundles and lacunae; lignified tissue black; ×250.—7. Detail of the adaxial and abaxial chlorenchyma groups separated by lacunae; note the adaxial epidermal prickles; ×250.—8. Adaxial first order vascular bundle (1'vb) and associated abaxial third order vascular bundles (3'vb); interference contrast; ×400. la = lacuna; lm = leaf margin; mv = midvein; p = prickle. [Based on *Davidse 16848*.]

grasses. However, the demarcation of the embryo in the single caryopsis available to us is not sufficiently clear to establish the morphology unambiguously. It will need to be confirmed when better material becomes available. The combination of a linear hilum and small embryo is most characteristic of the Pooideae and Bambusoideae.

Leaf Anatomy

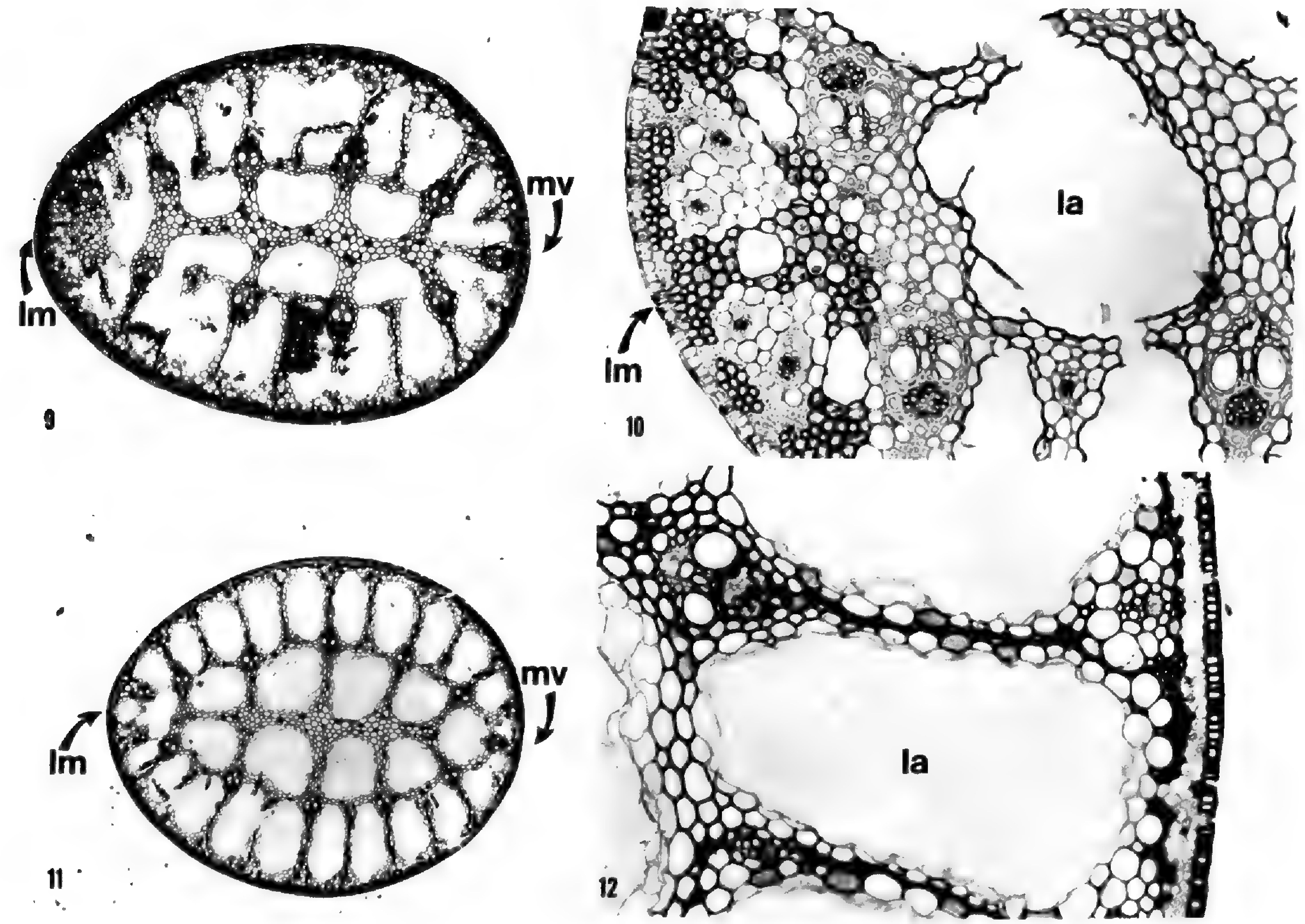
leaf in transverse section

Leaf blade (Figs. 4–8)

Outline: infolded leaf type but capable of opening to 180° (Fig. 4); outline elliptical in infolded condition—each half of the lamina with a flat adaxial surface and a rounded, outwardly bowed abaxial surface (Fig. 5); when infolded, adaxial channel with very deep, vertical sides—the two halves of the lamina becoming closely juxtaposed. Twenty-one costal zones in section, but due to the arrangement of many lateral vascular bundles in two planes, the total number of vascular bundles in section is 39 (Fig. 5). Leaf blade narrow (2.8–6.5 mm) but thick (> 0.5 mm). *Ribs and furrows:* no adaxial or abaxial rib or furrow development except in association with the median vascular bundle. *Median vascular bundle:* distinguishable by location only; structurally identical to the lateral first order vascular bundles; closely associated with two groups of bulliform cells. *Vascular bundle arrangement:* two distinct rows of vascular bundles positioned at different levels or planes in the lateral part of the leaf section; abaxial row composed of third order vascular bundles only but the adaxial row consists of alternating first order vascular bundles and third order vascular bundles (Fig. 5.). First order vascular bundles slightly more centrally located than third order vascular bundles which are more adaxially located (Figs. 6, 7); abaxial third order vascular bundles all equidistant from the epidermis; 11 first order vascular bundles in section; no second order vascular bundles. *Vascular bundle structure:* first order vascular bundles elliptical; metaxylem vessels wide, somewhat angular with slightly thickened walls (Fig. 8); lysigenous cavity and protoxylem vessel present; phloem adjoins the inner bundle sheath; divided by intrusion of sclerotic fibers (Fig. 6). Third order vascular bundles irregular in shape but generally vertically elongated; xylem and phloem distinguishable (Fig. 7). *Vascular bundle sheaths:* first and third order vascular bundles completely surrounded by an inner bundle sheath; composed of relatively large and rather thin-walled cells (Fig. 8). Outer bundle sheath parenchymatous; cells with slightly thickened (Fig. 8) and lignified (Fig. 6) walls; chloroplasts entirely absent (Fig. 7). Outer bundle sheath continuous but with well-developed adaxial and abaxial extensions consisting of parenchyma cells on either side of the sclerenchyma fibers (Figs. 6, 7); triseriate arrangement in the center of the blade (Fig. 7); a vertical girder is formed by these extensions running the full thickness of the leaf blade in which are located the adaxial and abaxial pairs of vascular bundles. *Sclerenchyma:* small abaxial girders present; fibers form a continuation of the fibrous center of the bundle sheath extensions (Fig. 7); smaller adaxial strands present; in contact with parenchymatous bundle sheath extensions (Fig. 7); no sclerenchyma developed between the vascular bundles. *Mesophyll:* chlorenchyma not radiately arranged; cells rounded, tightly packed and increase in size from the epidermides inward (Figs. 7, 8); seldom in contact with the outer bundle sheath cells—usually in contact with bundle sheath extensions (Figs. 6, 7); located between vertical bands containing vascular bundles; divided into adaxial and abaxial groups by central lacunae (Figs. 6, 7). Lacunae separate each successive vertical pair of vascular bundles; cavities distinct without aerenchyma cells although diaphragms of stellate cells are present at regular intervals along the length of each lacuna; 8–10 lacunae in each half of the leaf blade. *Colorless cells:* absent, except those forming bundle sheath extensions. *Adaxial epidermal cells:* bulliform cells absent except for a single, well-developed group on either side of the median vascular bundle (Fig. 5); restricted groups of tall and narrow cells project slightly above the level of the epidermis. Epidermal cells with slightly thickened outer tangential walls; intercostal prickles present (Fig. 7), barbs not well developed; no macrohairs or papillae visible. *Abaxial epidermal cells:* no bulliform cells developed. Epidermal cells large, very regular in shape and size with noticeably thickened outer tangential walls (Fig. 8); no prickles, macrohairs or papillae.

Leaf sheath (Figs. 9–12)

Outline: terete, solid cylinder (Figs. 9, 11); 39 vascular bundles in section with 21 vascular bundles associated with the continuous epidermis and the remaining 18 vascular bundles in two centrally situated rows (Figs. 9, 11); vasculature identical to the leaf blade except that no adaxial surface is developed. *Ribs and furrows:* not developed. *Median vascular bundle:* a single first order vascular bundle equivalent to the median vascular bundle of the leaf blade distinguishable, as is the region corresponding to the leaf margin (Figs. 9, 11). *Vascular bundle arrangement and structure:* the same as for the leaf blade. *Vascular bundle sheaths:* identical to those in the leaf blade except that the abaxial extensions are not in contact with the epidermis (Fig. 12); in the region of the ligule this contact is made (Fig. 10); adaxial extensions of the central vascular bundles not in contact with an epidermis but with a system of additional lacunae in the center of the fused leaf sheath. *Sclerenchyma:* no strands or girders in the sheath proper (Figs. 11, 12) but there is a tendency for the development of a hypodermal sclerenchyma layer (Fig. 12). Closer to the ligule, however, there are girders developed (Fig. 10) that are similar to those of the leaf blade. No "adaxial" sclerenchyma developed. *Mesophyll:* chlorenchyma not radiately arranged; cells rounded and tightly packed (Fig. 12); confined to narrow, continuous ring immediately adjacent to the epidermis (Figs. 11, 12); not in direct contact with the outer bundle sheath cells; no chlorenchyma associated with centrally located vascular bundles. In the vicinity of the ligule the continuous chlorenchyma ring becomes subdi-



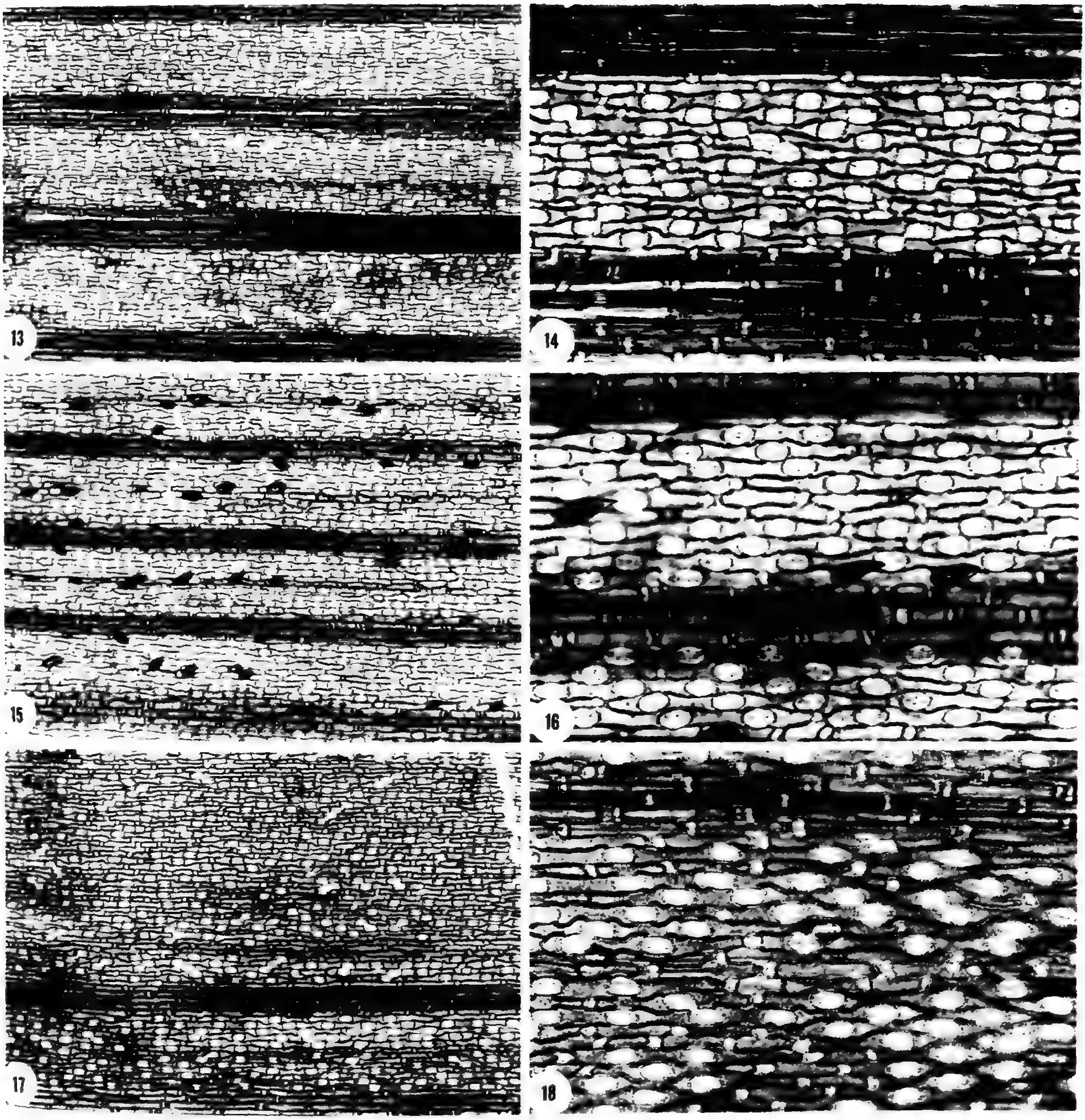
FIGURES 9–12. Anatomy of the leaf sheath of *Steyermarkochloa unifolia* Davidse & Ellis as seen in transverse section. 9, 10. Sections taken from the region of the ligule.—9. Circular outline of the fused sheath; ×40.—10. Detail of the region corresponding to the leaf blade margin; note the vascular bundle arrangement and distribution of the lacunae; ×250. 11, 12. Sections of the leaf sheath taken midway between the ligule and the base.—11. Circular outline; note absence of culm; ×40.—12. Detail of the lateral vascular bundles showing the arrangement in two different planes and a continuous chlorenchyma band adjacent to the epidermis; ×250. la = lacuna; lm = region of sheath corresponding to the margin in the leaf blade; mv = region of sheath equivalent to the midvein of leaf blade. [Based on *Davidse 16848.*]

vided by sclerenchyma girders in contact with the epidermis (Fig. 10). Lacunae developed as in the leaf blade (Fig. 12) with an additional nine air canals being located in the central core of the cylindrical sheath (Figs. 9, 11). *Colorless cells:* absent. *Adaxial epidermal cells:* adaxial epidermis not developed. *Abaxial epidermal cells:* no bulliform cells (Figs. 9, 11). Epidermal cells large, very regular in shape and size (Fig. 12); no macrohairs, prickles or papillae.

LEAF EPIDERMAL STRUCTURE

Abaxial epidermis of the leaf blade
(Figs. 13, 14)

Intercostal long cells: elongated cells with side walls more or less parallel (not angled outwards); anticlinal walls heavily thickened and pitted (Fig. 14); undulations irregular and slight; individual cell shape and size somewhat irregular but, nevertheless, constant throughout each and all intercostal zones (Figs. 13, 14); successive long cells never abut one another but are always separated by stomata or short cells. *Stomata:* consistently low dome-shaped (Fig. 14); as many files of stomata as there are files of cells in each intercostal zone (Fig. 14). All intercostal long cells actually function as interstomatal long cells and either are in contact with stomata at both ends or sometimes only one end; usually only one interstomatal long cell between consecutive stomata in a file (Fig. 14). *Intercostal short cells:* single or silico-suberose couples; cork cells rounded (Fig. 14); irregular occurrence throughout intercostal zones. *Papillae:* absent. *Prickles:* not observed. *Microhairs:* not seen. *Macrohairs:* absent. *Silica bodies:* costal bodies tall, saddle-shaped (Fig. 14); present throughout costal zones. Intercostal silica bodies irregularly rounded. *Costal zones:* composed of long cells longer than



FIGURES 13–18. Epidermal structure of the leaf of *Steyermarkochloa unifolia* Davidse & Ellis. 13, 14. Abaxial epidermis of the leaf blade.—13. Costal and intercostal zone distribution and arrangement; ×160.—14. Cellular detail of the costal and intercostal zones; note the intercostal stomata and short cells and the costal silica bodies; ×400. 15, 16. Adaxial epidermis of the leaf blade.—15. Costal and intercostal zone distribution; ×160.—16. Note presence of adaxial prickles in the intercostal zones; ×400. 17, 18. Epidermal structure of the leaf sheath.—17. Costal zones virtually absent due to the development of a hypodermal band of chlorenchyma; ×160.—18. Stomatal distribution and structure; pitted thickening of cell walls; ×400. [Based on *Davidse 16848.*]

those of the intercostal zones but equally as wide; all separated by paired short cells; six files per costal zone (Fig. 13); all files of similar composition.

Adaxial epidermis of the leaf blade (Figs. 15, 16)

Intercostal long cells: same as for the abaxial surface but tend to be slightly longer (Fig. 16). *Stomata:* regularly low dome-shaped (Fig. 16); arrangement as in the abaxial epidermis. *Intercostal short cells:* paired as in the abaxial epidermis (Fig. 16) but may give rise to prickles. *Papillae:* absent. *Prickles:* irregular intercostal prickles do occur (Fig. 15); small with the bases shorter than the stomata; barbs developed basally from the apex to the base; barb longer than the base (Fig. 16) usually not staining well. *Mi-*

crohairs: none visible. *Macrohairs:* absent. *Silica bodies:* tall, saddle-shaped as in the abaxial surface (Fig. 16). *Costal zones:* narrower than on the abaxial surface (Fig. 15), consisting of only four files of cells; costal cells somewhat shorter and more inflated than on the abaxial surface (Fig. 16).

Abaxial epidermis of the leaf sheath
(Figs. 17, 18)

Intercostal long cells: as for the leaf blade but pitting very evident (Fig. 18). *Stomata:* as in the leaf blade. *Intercostal short cells:* identical to those of the leaf blade but the intercostal zones much wider (Fig. 17). *Papillae:* absent. *Prickles:* very few asperites seen without development of barbs (Fig. 18). *Microhairs:* none seen. *Macrohairs:* absent. *Silica bodies:* tall, saddle-shaped as in the leaf blade (Fig. 18). *Costal zones:* largely absent (Fig. 17) and only present in the region equivalent to the leaf margin in that part of the sheath closer to the ligule.

Scanning electron microscopy of the leaf blade
(Figs. 19–26)

Leaf outline: narrow midrib region connecting the two symmetrical halves of the lamina (Figs. 19, 20). Slight ribs and furrows noticeable; associated with the lateral vascular bundles. *Long cells:* rectangular abaxial cells with uniform width (Fig. 21); not distinguishable on the adaxial surface (Fig. 22). *Stomata:* low dome-shaped subsidiary cells on both surfaces (Figs. 25, 26) with the adaxial subsidiary cells being slightly wider (Fig. 26); not sunken or associated with papillae. *Papillae:* absent although reduced, unbarbed prickles on the adaxial surface may be mistaken for papillae (Fig. 22). *Microhairs:* no microhairs observed on any part of the leaf blade segments examined. *Prickles:* very few barbed prickles (Fig. 23) observed in the region of the midrib on the abaxial surface; adaxial prickles common (Fig. 22); ends are conspicuously blunted and not barbed (Fig. 24). *Macrohairs:* absent (Figs. 19, 20). *Silica bodies:* abaxial silica bodies only visible (Fig. 21); tall, saddle-shaped; indented in the leaf surface.

ANATOMICAL DISCUSSION

Steyermarkochloa is unique among the grasses in possessing a fused, solid, terete leaf "sheath." Morphologically the cylindrical "sheath" gradually grades into the dorsiventral blade without evidence of a ligule. An anatomical interpretation of this transition from sheath to blade is given in schematic form in Figure 27. The material available for anatomical study did not include blade segments taken close to the ligular region, and thus the exact manner of opening of the leaf blade could not be determined anatomically.

It will be noted that, even in the basal portions of the leaf "sheath," true radial symmetry does not exist and regions equivalent to the midrib and leaf blade margins can be distinguished by the configuration of the vascular bundles and lacunae. Near the ligular region this assymmetry is still evident and the vasculature pattern remains identical. Even in the leaf blade itself, one can observe homologous vascular bundles arranged in basically the same pattern as in the sheath. It must be noted that the diameter of the "sheath" decreases towards the ligule, a process that continues along the length of the blade. For comparative purposes this fact has not been incorporated in Figure 27 but should be borne in mind.

A comparison of the basal and ligular portions of the sheath reveal that the continuous clorenchyma cylinder present in the lower parts becomes subdivided by the development of sclerenchyma girders linking all the outermost vascular bundles with the epidermis. This epidermis is undoubtedly homologous with the abaxial epidermis of the leaf blade proper. In the leaf blade itself the continuous sclerenchyma band located internally to the chlorenchyma becomes reduced and eventually is lost, resulting in the chlorenchyma, lacunae, sclerenchyma girder, and epidermal configuration so typical of the leaf blade.

Although not anatomically studied in this study, an adaxial channel is rapidly established commencing in the region of the ligule in the area equivalent to the leaf blade margin. In order

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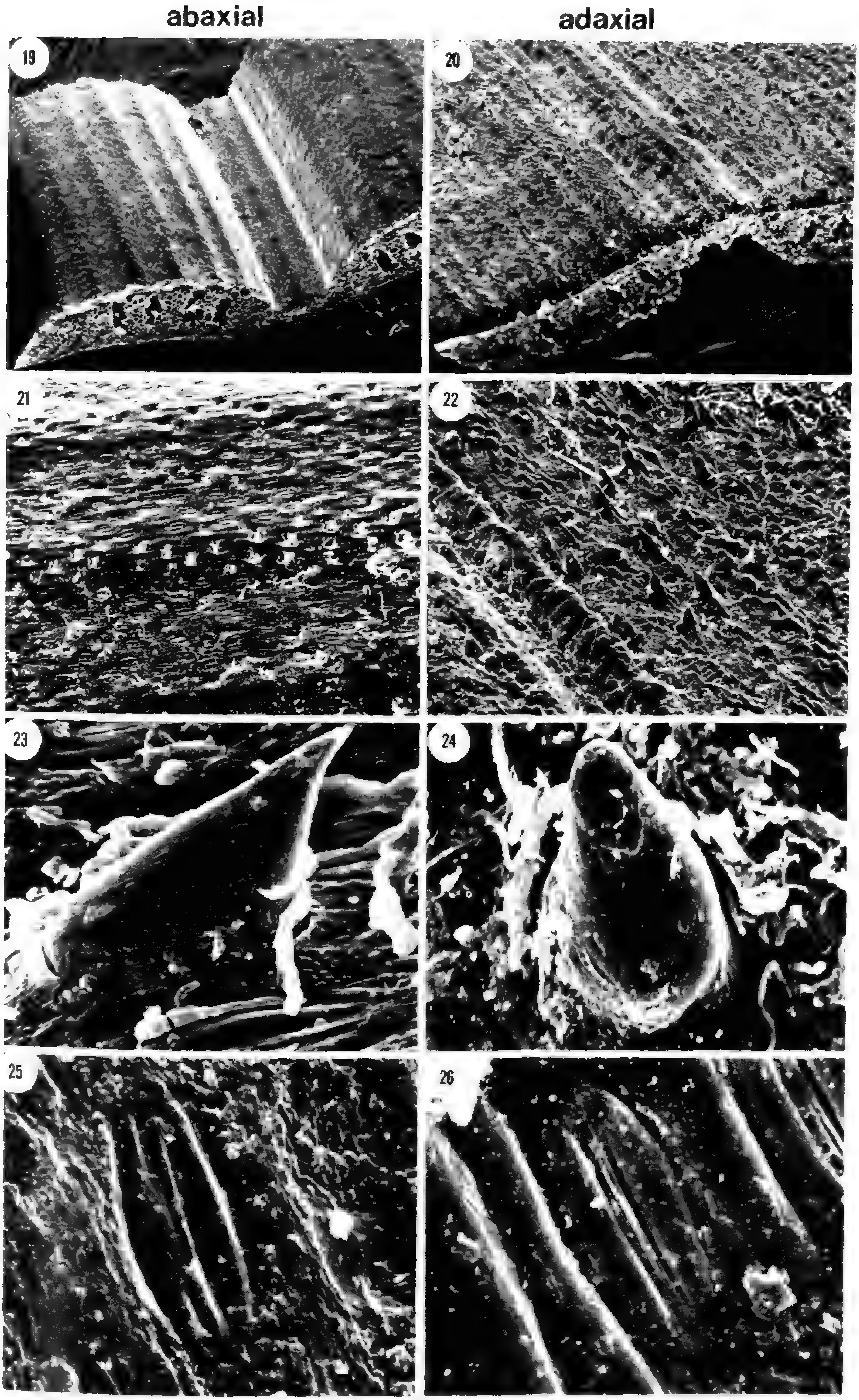
FIGURES 19–26. Scanning electron micrographs of the leaf blade of *Steyermarkochloa unifolia* Davidse & Ellis.—19, 20. Outline of the leaf lamina from the lower and upper surfaces; ×60.—21. Abaxial surface showing costal and intercostal zones; ×240.—22. Adaxial surface showing scattered prickles and files of bulliform cells adjacent to the midrib; ×240. 23, 24. Prickles; ×2,400.—23. Barbed prickle from the abaxial surface.—24. →



Truncated blunt prickle from the adaxial surface.—25, 26. Stomata from the abaxial and adaxial surfaces; ×3,600. [Based on *Davidse 16848*.]

for this to be effected an adaxial epidermis is laid down, chlorenchyma is developed in the parenchyma ground tissue, and the most centrally located lacunae are lost. Once the adaxial channel has reached its full depth then a pair of bulliform cell groups on either side of the median vascular bundle are developed and the anatomical structure of the blade is complete.

This unique leaf structure of *Steyermarkochloa* deserves further intense investigation, and ontogenetic studies, in particular, should be undertaken as soon as living material becomes available. This leaf structure probably represents a highly advanced and derived condition.

CONCLUSIONS

Agrostologists have recently recognized that leaf blade anatomical characters can be satisfactorily used as the principal means of defining the five subfamilies of the Poaceae (Renvoize, 1981). These five groups can be characterized according to the unique combination of anatomical features common to their constituent species, and the delimitation of subfamilies is now firmly based upon differences in leaf blade anatomy (Clifford & Watson, 1977). The anatomical diagnoses of these subfamilies (Renvoize, 1981) should, therefore, provide a sound basis for the classification of *Steyermarkochloa* into the correct subfamily. With this objective in mind, the various combinations of leaf blade anatomical characters that are diagnostic of the various subfamilies will be discussed and compared with the anatomy of *Steyermarkochloa* already described.

The presence or absence, and the shape of microhairs are constant features and provide valuable indications of subfamily relationships (Clifford & Watson, 1977). Microhairs are present in all subfamilies except the Pooideae, in which they have not been recorded. In this respect *Steyermarkochloa* resembles the Pooideae. However, a few exceptions are known. In *Pseudopentameris* of the Arundinoideae microhairs are absent. *Cortaderia selloana* is the only recorded species

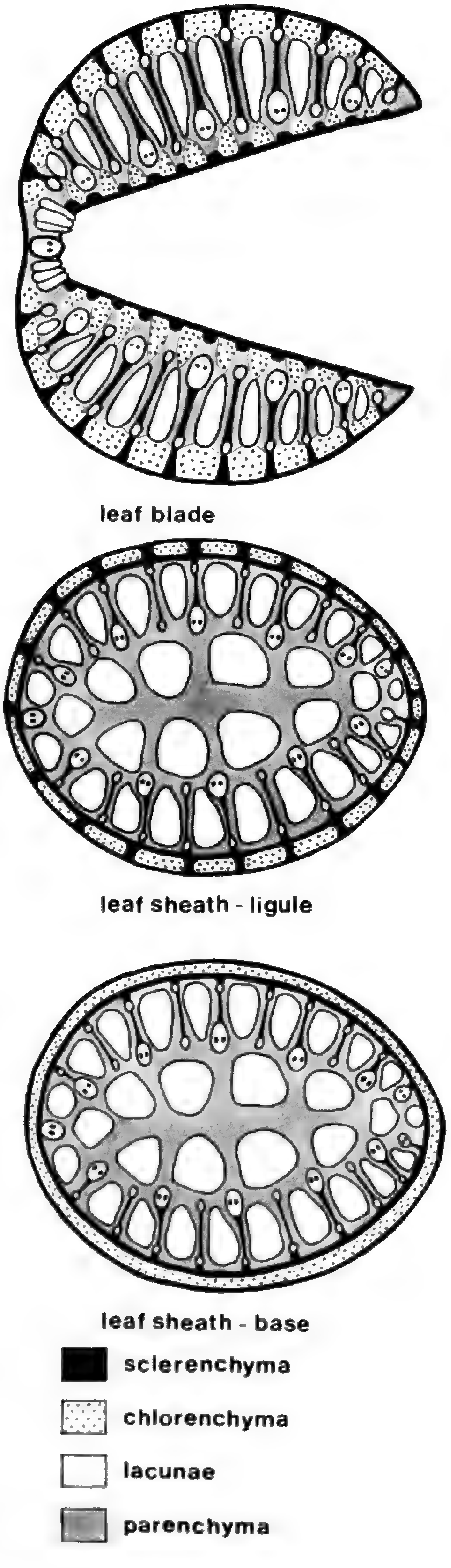


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FIGURE 27. Diagrammatic representation of the leaf anatomy of *Steyermarkochloa unifolia* Davidse & Ellis illustrating the distribution of comparable tissues in different parts of the leaf sheath and blade. Left-hand side of diagram is equivalent to the median vascular bundle of the leaf blade and the right-hand side corresponds to the leaf margin.

which may vary for the presence or absence of microhairs (Metcalfe & Clifford, 1968) and, very often, microhairs may be lacking from the abaxial epidermis of the leaf blade in species with setaceous leaves such as many *Merxmuellera* species (Ellis, 1980a, 1980b).

No microhairs were observed on either the abaxial or the adaxial leaf epidermides or on the leaf sheath epidermis of *Steyermarkochloa* (Figs. 13–18). This finding was corroborated by a scanning electron microscopy examination of both surfaces of the leaf blade (Figs. 19–26). This total absence of microhairs on the leaf blade is significant and strongly indicates a relationship with the pooid grasses. An arundinoid relationship is not ruled out completely, however, but bambusoid, chloridoid, or panicoid connections are remote.

The shape of the stomatal subsidiary cells of *Steyermarkochloa* is clearly dome-shaped (Figs. 14, 16, 18, 25, 26)—a condition considered to be characteristic of arundinoid grasses and only sometimes present in bambusoid, chloridoid, and panicoid grasses (Renvoize, 1981). Dome-shaped subsidiary cells do not occur in the Pooideae, in which the subsidiary cells are parallel-sided. Stomatal shape, in contrast with the absence of microhairs, does not support pooid affinities for *Steyermarkochloa.*

The long cell walls of *Steyermarkochloa* are neither straight (as in the pooid grasses) nor clearly sinuous (as in the other subfamilies). However, the shape of these cells, together with the stomatal domination of the intercostal zones, closely resembles the condition in several of the arundinoid reed-grasses such as *Arundo, Phragmites,* and *Gynerium* (Gordon-Gray & Ward, 1971; Renvoize, 1981). An arundinoid relationship is again indicated. This similarity with the peripheral, reed-like genera of the Arundinoideae appears to be significant and agrees with the indications of several other anatomical criteria.

The silica bodies of *Steyermarkochloa,* which are tall, oblong or saddle-shaped, and often adjacent to crescent-shaped or oval cork cells, can also be accommodated in the arundinoid diagnosis of Renvoize (1981). They definitely do not resemble the pooid, panicoid, or bambusoid types, and the saddle-shaped silica bodies of the Chloridoideae are usually equidimensional, rather than elongated.

The characters of the epidermis, therefore, indicate affinities of *Steyermarkochloa* with the Arundinoideae, but this conclusion must remain somewhat tentative. The absence of microhairs makes a more definite decision impossible. A further search for microhairs on the sheaths of the fertile culms also proved negative.

From the leaf blade anatomy, as seen in transverse section, it can be confidently inferred that *Steyermarkochloa* is definitely not bambusoid because the chlorenchyma is not comprised of arm cells, and fusoid cells are not present. Serial sections of the leaf blade clearly show that the cavities between successive sclerenchyma girders (Figs. 6–8) arise from the breakdown of colorless cells and are, consequently, true lacunae and not fusoid cell cavities, because regularly spaced, transversely orientated fusoid cells are not present at intervals along the air canals. Stellate cells also occur in these cavities. Lacunae of this type are well known in the leaves of hygrophilous grasses but appear to be of little significance in indicating phylogenetic relationships. Thus, *Vetiveria,* of the Andropogoneae (Kammathy, 1969) superficially resembles *Steyermarkochloa* in the structure and distribution of the lacunae. In the Arundinoideae, lacunae have also been described in the midrib of the leaves of *Gynerium sagittatum* (Metcalfe, 1960; Conert, 1961) and the blade of *Merxmuellera cincta* (Ellis, 1982). Both these species are tall, reed-like grasses with *M. cincta* not conforming anatomically with the danthonoid grasses proper. In this respect *Steyermarkochloa* again resembles the arundinoid reed-grasses.

The chlorenchyma cells of *Steyermarkochloa* do not have inward projecting invaginations of the cell walls (Fig. 8) and, consequently cannot be considered arm cells, which are diagnostic of bambusoid grasses. Instead, the chlorenchyma consists of cells that are smooth-walled, tightly packed, and isodiametric in shape and arranged in a nonradiate pattern (Figs. 7, 8). This nonradiate arrangement rules out the possibility of chloridoid or panicoid relationships (Ellis, 1977). Tightly packed, isodiametric chlorenchyma cells are not typical of pooid grasses either. The mesophyll cell shape and arrangement in *Steyermarkochloa* again resembles the condition in some arundinoid grasses such as *Cortaderia selloana* (Conert, 1961) and *Merxmuellera cincta* (Ellis, 1982).

The bundle sheaths of *Steyermarkochloa* are double with the outer parenchymatous sheath devoid of chloroplasts. The absence of specialized Kranz chloroplasts in either bundle sheath, together with the nonradiate nature of the chlorenchyma cells, most of which are not directly in contact with a bundle sheath cell, is enough to predict with confidence that *Steyermarkochloa* has the C_3 photosynthetic pathway (Ellis, 1977). Once again, chloridoid affinities are ruled out and panicoid associations are most unlikely. All bambusoid and pooid grasses and most arundinoid grasses have the C_3 pathway (Renvoize, 1981).

Vascular bundles inserted at different levels in the leaf lamina, such as in *Steyermarkochloa* (Figs. 5–8), are very rare in the Poaceae and are only generally recorded from the midribs and keels of bambusoid grasses (Metcalfe, 1960). It is significant that in the bamboos and rices this complex system of vascular bundles is restricted to the keel and that the lateral vascular bundles are arranged in a single horizontal row. The only other grasses, in addition to *Steyermarkochloa,* in which the vascular bundles of the lamina have been reported to be in different planes in single sclerenchyma girders are *Porteresia coarctata,* a monotypic genus in the Oryzeae (Tateoka, 1965), *Gynerium saggitatum* of the Arundineae (Conert, 1961), and *Merxmuellera cincta,* an atypical member of the Danthonieae (Ellis, 1982). Possible affinities between *M. cincta* and some of the arundinoid grasses have been discussed by Ellis (1982). Significantly, *Gynerium,* also an arundinoid reed-grass, and *M. cincta* share many characteristics with *Steyermarkochloa.* Apart from the adaxially and abaxially located vascular bundles in single sclerenchyma girders in the midrib region, *Gynerium* also has similar lacunae and islands of chlorenchyma and, consequently, anatomically strongly resembles *Steyermarkochloa.*

The phylogenetic implications derived from leaf blade anatomy strongly corroborate those derived from features of the leaf epidermis. Arundinoid affinities are again suggested and anatomical evidence suggests that *Steyermarkochloa* is a peripheral genus of the Arundinoideae, and is best accommodated close to the reed-grasses such as *Gynerium, Arundo, Phragmites,* and *Thysanolaena.* All these genera are known to have some anomalous arundinoid anatomical characters, but Renvoize (1981) did not consider these to be sufficient to justify the exclusion of these genera from the subfamily. This observation further substantiates the placement of *Steyermarkochloa* in the Arundinoideae close to these other somewhat anomalous and peripheral genera.

As noted earlier, we are in agreement with the practical approach to grass classification advocated by Renvoize (1981), in which subfamilies are primarily based on anatomical characteristics of the leaves, and tribes on gross morphological characteristics supplemented by information from cryptic characters. Having established with reasonable certainty on the basis of anatomical evidence that *Steyermarkochloa* is arundinoid, it now remains to establish its tribal affinity. For this purpose it is most useful to compare *Steyermarkochloa* with Renvoize's (1981) classification in which one large tribe, Arundineae, and seven small ones are recognized.

In the Arundinoideae, *Steyermarkochloa* is unique in its combination of dimorphic culms, dimorphic leaves, solitary developed leaf with a cylindrical sheath lacking a ligule, polygamous breeding system, many-nerved, convolute palea, and 2-keeled glumes. On the basis of these important differences, *Steyermarkochloa* clearly stands alone in the subfamily, and therefore tribal status is warranted.

As noted earlier, *Steyermarkochloa* most closely resembles the Bambusoideae in having dimorphic culms and leaves, but the anatomy and morphology of the developed leaf definitively distinguish *Steyermarkochloa* from the bamboos. Developed bamboo leaves are usually flat, broad, lanceolate or linear-lanceolate, articulate with the blade, petiolate, and ligulate.

Grasses with a polygamous reproductive system are not known in the Arundinoideae and apparently not in the family. Connor (1979, 1981) in his extensive review of reproductive systems in the Poaceae did not list a single example. The predominance of unisexual flowers over bisexual flowers in *Steyermarkochloa* suggests that this represents a transitional stage in the evolution of unisexual from bisexual flowers. The breeding system in *Steyermarkochloa* is a good example of one of the intermediate steps in the model of the evolution of monoecism through a gynomonoecious pathway that was proposed by Charlesworth and Charlesworth (1978) and discussed by Connor (1981). It involves (1) a reduction in male fertility in some bisexual flowers to produce female flowers (gynomonoecism), followed by (2) a reduction in female fertility of the bisexual flowers to produce male flowers. In *Steyermarkochloa* step 1 of the model has been nearly completed. The lower florets of all female spikelets have completely lost all flowers, whereas the second floret has retained only female flowers accompanied by staminodia. Following the model to its logical conclusion, the staminodia would presumably be completely eliminated in the ultimate step of this differentiation. Because the staminodia are always very small and the female flowers occur only in morphologically differentiated female spikelets, we conclude that female unisexuality has been genetically firmly fixed in the genome of *Steyermarkochloa.* Step 2 of the model is apparently still in progress since all possibilities (2 bisexual flowers; 1 bisexual flower and 1 male flower; 2 male flowers) are known. That this system seems to be moving in the direction of male unisexuality is indicated by the predominance of male flowers over bisexual flowers and by the intermediate condition of one male and one bisexual flower being more common than two bisexual flowers.

Unisexuality is known in the Arundinoideae but is not very common. In the Arundineae, *Gynerium* and *Lamprothyrsus* are dioecious and *Cortaderia* is gynodioecious. A tendency toward floral simplification is also seen in *Neyraudia* and *Phragmites,* in which all florets are usually bisexual but the lowermost floret is sterile or sometimes male. In the Centosteceae, *Centosteca* is gynomonoecious whereas *Zeugites* and *Calderonella* are monoecious. Unisexuality in itself has little utility as a tribal character because it has evolved repeatedly in unrelated groups of grasses (Connor, 1981).

Two-keeled glumes are unknown in the Arundinoideae but are common in many genera of Andropogoneae and in *Myriocladus* of the Bambusoideae. This similarity must have evolved independently because there is no other resemblance among these taxa. *Steyermarkochloa* is also unique in the Arundinoideae in the combination of other characters relating to inflorescence and spikelet morphology, although when considered individually these characters are known in other genera. Especially important in this regard are rounded to somewhat dorsally compressed spikelets that disarticulate below the glumes, awnless lemmas, absence of lodicules, two stamens, united style (at least in female flowers), and fusiform caryopsis.

The lack of lodicules and the convolute, many-nerved palea of the female spikelet, which, together with the second lemma, forms a tubular structure, are correlated characters that are directly related to terminal stigma exsertion. Munro (1868) noted for the bamboos that there is a tendency for the palea to be rounded on the back and many-nerved, rather than 2-keeled and 2-nerved, when lodicules are lacking. Among elodiculate, nonbambusoid grasses, we are aware of only one species with a many-nerved palea, namely, *Micraira sublifolia* F. Muell., a moss-like grass from Queensland. In this species the palea is 5–7-nerved but remains 2-keeled. In the other seven described species of the genus, the paleas are 2-keeled and 2-nerved and also divided to the base into two equal halves (Lazarides, 1979).

Among all other elodiculate, nonbambusoid grasses, the tendency is for the paleas to be of the normal 2-keeled, 2-nerved type (e.g., *Munroa decumbens* Phil.), 1-nerved and rounded on the back (e.g., *Anthoxanthum odoratum* L.), or completely absent (e.g., *Alopecurus,* female plants of *Jouvea*).

Although *Steyermarkochloa* anatomically resembles the reed-grasses *Arundo, Gynerium, Phragmites,* and *Thysanolaena* most closely, it is morphologically distinct in almost all characters of the leaves, inflorescence, spikelets, and flowers. This reinforces our decision to classify *Steyermarkochloa* in its own tribe. As is evident from the preceding discussion, many of the morphological features of *Steyermarkochloa* correspond to those of the Bambusoideae, yet any close relationship with the Bambusoideae seems to be definitively ruled out on the basis of anatomical evidence. It seems likely, therefore, that the complex of bamboo-like characters—dimorphic culms and leaves, occasionally fused filaments, many-nerved paleas, lack of lodicules, terminal exsertion of stamens and stigmas, and possibly caryopsis type—represents an example of independent, parallel evolution, a process well established for other characters in the Poaceae. Furthermore, the highly specialized leaves and culms, spicate inflorescence, largely unisexual spikelets, lack of lodicules, and two stamens are undoubtedly specialized characters in the family, and it seems most likely that *Steyermarkochloa* is a highly derived, specialized genus of the Arundinoideae.

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OCCURRENCE OF CRYSTALS IN IRIDACEAE AND ALLIED FAMILIES AND THEIR PHYLOGENETIC SIGNIFICANCE[1]

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ABSTRACT

Styloid crystals, presumed to be calcium oxalate, seem to be a fundamental characteristic of Iridaceae based on previous reports of their presence in several genera of both major subfamilies, and supplemented here by further records in 75 of the ca. 85 genera of the family. Styloids have now been reported in some 300 species of Iridaceae, of about 320 examined. These elongated crystals are lacking in a few scattered species but perhaps significantly from *Sisyrinchium* and some closely allied genera. Families and isolated genera possibly related to Iridaceae, including *Geosiris* and *Isophysis,* were also examined for crystal types. Styloids are present in *Isophysis.* Tecophilaeaceae and Campynemaceae have raphides and three species of Colchicaceae and several of Uvulariaceae have crystal sand. A few of the latter have raphides, sometimes with crystal sand. Crystals are absent in *Geosiris.* The difference in crystal types taken together with some significant differences in morphology suggest that Campynemaceae and Colchicaceae are not immediately allied either to Iridaceae or to one another. We suggest that Campynemaceae may be better placed close to Melanthiaceae or Burmanniaceae. *Isophysis,* with three stamens but a superior ovary, is probably best treated in its own subfamily of Iridaceae. Tecophilaeaceae are no longer believed to be closely related to Iridaceae and their placement in a different order is supported.

Data on the kinds of crystals of the calcium oxalate type (raphides, styloids, and crystal sand) occurring in plant tissues are widely scattered in the literature and information concerning their distribution in the plant kingdom is not readily available to systematists. Although little is known about the function of such crystals in plants, their shape and location are often very characteristic at different taxonomic levels (Franceschi & Horner, 1980). A brief mention by Metcalfe (1961) that styloids (pseudoraphides) were particularly characteristic of Iridaceae seemed intriguing and worth further investigation to establish, as far as seems reasonable, the frequency of styloids and possibly other crystal types in the family. We have also surveyed the crystal characters in putative relatives of Iridaceae. These include the monotypic Madagascan Geosiridaceae; Colchicaceae (Liliaceae-Colchicoideae); Uvulariaceae (Liliaceae-Uvularioideae); the Tasmanian *Isophysis*; and the poorly known Australasian *Campynema* and *Campynemanthe.* The latter two genera are variously assigned to Hypoxidaceae, Colchicaceae (Dahlgren & Clifford, 1982), or to a separate Campynemaceae (Dumortier, 1829: 57–58; Dahlgren & Rasmussen, 1983) and have been suggested to be close to Iridaceae (Dahlgren & Rasmussen, 1983: 369–372). Uvulariaceae sensu Dahlgren & Rasmussen, postulated as ancestral to Colchicaceae and to Iridaceae (Dahlgren, pers. comm.), comprises *Hexacyrtis* and the *Disporum* group of Liliaceae and is largely North Temperate. A few members of Tecophilaeaceae were also examined because this family was proposed as close to the ancestral line of Iridaceae by Hutchinson (1973), although there is little current support for his view.

MATERIALS AND METHODS

Dry or FAA-fixed living leaf samples were gathered from at least one to a few species of many genera of Iridaceae from both subfamilies, Iridoideae (here including Sisyrinchioideae) and Ixioideae. Samples were examined at Missouri Botanical Garden (MO) and Royal Botanic Gardens, Kew (K). At MO samples were sometimes cleared in 5% NaOH for several hours or more until satisfactorily transparent or more often were cleared in household bleach. They were then

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mounted immediately in glycerin or dehydrated through an alcohol series and permanently mounted in Canada balsam. At K samples were sectioned using a Reichert sliding microtome. Sections were stained in safranin and alcian blue, dehydrated through an alcohol series and mounted in Euparal. The samples were viewed between polarizing filters to detect the presence and type of crystals in the tissue. The sole species of *Isophysis* and *Geosiris,* one each of *Campynema* and *Campynemanthe* and several of Colchicaceae, Uvulariaceae, Liliaceae (sensu Dahlgren & Clifford, 1982) and Tecophilaeaceae (Table 1) were treated in the same way at MO for comparison. The genera and species studied are listed in Table 1 together with the crystal types observed. Voucher or accession number information is available from the authors but is not reported here.

OBSERVATIONS

Slender styloids of the type first described for Iridaceae in *Iris, Crocus, Romulea, Witsenia,* and *Gladiolus* by Gulliver (1863a, 1863b, 1865) and later by Rothert and Zalenski (1899) (see Netolitsky, 1929 for an early review) and in several other genera more recently (see below) were found in the leaves of the majority of species examined but notably not in *Sisyrinchium* and some closely related genera. The styloids are typically long and slender, with pointed or forked ends (Figs. 1, 2, 7) or occasionally square ends (Figs. 3, 4). They are strongly birefringent and vary considerably in size, the length being 100 to 200 (to 300) μm or sometimes much longer.

In a few species (*Patersonia macrantha, P. sericea, P. umbrosa, Romulea atrandra*) short, more or less isodiametric crystals, 16 to 25 μm long, were observed (Fig. 8) of the type described by de Vos (1970) in *Romulea* and Rudall (1983) in *Dietes*. In transverse section styloid crystals appear more or less square (Fig. 6) or rectangular (Fig. 5), occasionally with the longer walls convex. They occur both in the outer vascular bundle sheaths (Fig. 6) where they are difficult to detect in cleared leaves, and in scattered crystal idioblasts in the mesophyll (Fig. 5), usually in the outer chlorenchymatous layers if the leaves are very thick, observed also by de Vos (1970, 1974).

Crystal sand was noted in only two of several species of *Sisyrinchium* examined. This is the only record of crystal sand in Iridaceae.

TABLE 1. Species examined for crystals: st = styloids; cs = crystal sand; rb = raphides; Ca carb = calcium carbonate; x = no crystal inclusions seen. Brackets indicate crystal type observed in some specimens, but not in others.

Campynemaceae	
Campynema linearis Labill.	rb
Campynemanthe viridiflora Baill.	rb
Liliaceae	
Calochortus tiburonense A. J. Hill	x
Erythronium albidum Nutt.	? Ca carb
Lilium canadense L.	? Ca carb
Colchicaceae	
Ornithoglossum sp.	cs
Baeometra uniflora (Jacq.) G. Lewis	cs
Gloriosa carsonii Baker	cs
Uvulariaceae	
Disporum hookeri (Torrey) Nicholson	rb & cs
D. maculatum (Buckley) Britt.	rb & cs
D. sessile Don	cs
Schelhammera pedunculata F. Muell.	x
Streptopus amplexifolius DC.	rb & ? cs
Tricyrtis affinis Makino	? Ca carb
T. latifolia Max.	? Ca carb
Uvularia sessilifolia L.	? cs
Geosiridaceae	
Geosiris aphylla Baill.	x
Tecophilaeaceae	
Cyanella lutea L. f.	rb
Walleria mackenzii Kirk	rb
Cyanastrum cordifolium Oliver	x
Iridaceae-Isophysidoideae	
Isophysis tasmanica (Hook.) T. Moore	x
Iridaceae-Ixioideae	
Anapalina caffra (Ker ex Baker) G. Lewis	st
Anomalesia cunonia (L.) N. E. Brown	st
A. saccata (Klatt) Goldbl.	st
Anomatheca fistulosa (E. Meyer ex Klatt) Goldbl.	x
A. laxa (Thunb.) Goldbl.	st
A. verrucosa (Vogel) Goldbl.	st
A. viridis (Aiton) Goldbl.	st
Antholyza ringens L.	st
Babiana erectifolia G. Lewis	x
B. odorata L. Bolus	st
B. patula N. E. Brown	st
B. stricta Ker	st
B. villosa Ker	st
B. virginea Goldbl.	x
Chasmanthe aethiopica (L.) N. E. Brown	x

TABLE 1. Continued.

C. bicolor (Gasp.) N. E. Brown	st
C. floribunda (Salisb.) N. E. Brown	st
Crocosmia aurea Planch.	st
C. masonorum (L. Bolus) N. E. Brown	st
C. pottsii (Baker) N. E. Brown	st
Crocus asturicus Herbert	st
C. banaticus J. Gay	st
C. cancellatus Herbert	st
C. candidus Clarke	st
C. carpetanus Boiss. & Reut.	st
C. etruscus Parl.	st
C. flavus Weston	st
C. hadriaticus Herbert	st
C. heuffelianus Herbert	st
C. malyi Vis.	st
C. pulchellus Herbert	st
C. speciosus M. Bieb.	st
C. tomasinianus Herbert	st
C. tournefortii J. Gay	st
C. veluchensis Herbert	st
C. vernus Hill	st
Dierama igneum Klatt	st
D. pictum N. E. Brown	st
D. pulcherrimum Baker	st
D. tysonii N. E. Brown	st
Freesia andersoniae L. Bolus	st
F. caryophyllacea (Burm. f.) N. E. Brown	st
F. fergusoniae L. Bolus	st
Geissorhiza aspera Goldbl.	st
G. exscapa (Thunb.) Goldbl.	st
G. heterostyla L. Bolus	st
G. inflexa (Delaroche) Ker	st
G. inaequalis L. Bolus.	st
G. longifolia (G. Lewis) Goldbl.	st
Gladiolus carmineus C. H. Wright	st
G. dalenii van Geel	st
G. debilis Ker	st
G. punctulatus Schrank	st
G. scullyi Baker	st
G. segetum Ker	st
G. stellatus G. Lewis	st
G. splendidus Rendle	st
G. watsonioides Baker	st
Hesperantha alpina (Hook. f.) Pax ex Engler	st
H. bachmannii Baker	st
H. falcata (L. f.) Ker	st
H. petitiana (A. Richard) Baker	st
H. radiata (Jacq.) Ker	st
Homoglossum guthriei (L. Bolus) L. Bolus	st
H. muirii (L. Bolus) N. E. Brown	st
H. priorii (N. E. Brown) N. E. Brown	st
Ixia maculata L.	st
I. orientalis L. Bolus	st

TABLE 1. Continued.

Lapeirousia anceps (L. f.) Ker	st
L. bainesii Baker	st
L. coerulea Schinz	st
L. corymbosa (L.) Ker	st
L. divaricata N. E. Brown	st
L. pyramidalis (Lam.) Goldbl.	x
L. rhodesiana N. E. Brown	st
Melasphaerula ramosa (Burm. f.) N. E. Brown	st
Micranthus plantagineus (Pers.) Ecklon	st
Oenostachys dichroa Bullock	st
O. schweinfurthii Baker	st
O. zambeziacus (Baker) Goldbl.	st
Pillansia templemanii (Baker) L. Bolus	st
Radinosiphon leptostachya N. E. Brown	st
Romulea atrandra G. Lewis	st
R. bulbocodium Sebast. & Maur.	st
R. flava (Lam.) de Vos	st
R. grandiscapa J. Gay ex Baker	st
R. phoenicea Mouterde	st
R. ramiflora Tenore	st
R. rosea (L.) Ecklon	st
Savannosiphon euryphylla (Harms) Goldbl. & Marais	x
Schizostylis coccinea Backh. & Harvey	st
Sparaxis grandiflora (Delaroche) Ker	st
Synnotia variegata Sweet	st
S. villosa (Burm. f.) N. E. Brown	st
Syringodea bicolor Baker	st
Thereianthus lapeirousioides (Baker) G. Lewis	st
T. spicatus (L.) G. Lewis	st
Tritonia crocata (L.) Ker	st
T. flabellifolia (Delaroche) G. Lewis	st
T. florentiae (Marl.) Goldbl.	x
T. laxifolia (Klatt) Benth. ex Baker	st
T. watermeyeri L. Bolus	st
Tritoniopsis parviflora (Jacq.) G. Lewis	st
T. ramosa (Ecklon ex Klatt) G. Lewis	st
Watsonia aletroides (Burm. f.) Ker	st
W. brevifolia Ker	st
W. meriana (L.) Miller	st
W. stenosiphon L. Bolus	st
Zygotritonia crocea Stapf	x
Iridaceae-Iridoideae (incl. Sisyrinchioideae)	
Alophia drummondii (Graham) R. Foster	st
Anomalostylus grandis (Kranzl.) R. Foster	x

TABLE 1. Continued.

Aristea alata Baker	st
A. compressa Buchinger	st
A. ensifolia Muir	st
A. lugens (L. f.) Hort.	st
A. macrocarpa G. Lewis	st
A. platycaulis Baker	st
Belamcanda chinensis (L.) DC.	st
Bobartia aphylla (L. f.) Ker	st
B. gracilis Baker	st
Calydorea campestris (Klatt) Baker	st
C. nuda Baker	st
C. xiphioides (Poepp.) Espinosa	st
Cardenanthus tunariensis R. Foster	st
Cardiostigma longispatha (Herbert) Baker	st
Chamelum frigidum (Poepp.) Ravenna	x
Cipura flava Ravenna	st
C. paludosa Aubl.	st
Cypella hauthalii (Kuntze) R. Foster	st
C. herbertii (Lindl.) Herbert	st
C. linearis (H.B.K.) Baker	st
Dietes bicolor (Steud.) Sweet ex Klatt	st
D. flavida Oberm.	(st)
D. robinsoniana (F. Muell.) Klatt	st
Diplarrhena moraea Labill.	st
Eleutherine bulbosa (Miller) Urban	st
Ennealophus euryandrus (Gris.) Ravenna	st
E. foliosus (H.B.K.) Ravenna	st
Fosteria guatemalensis (Standl.) Ravenna	st
F. oaxacana Molseed	st
Galaxia fugacissima (L. f.) Druce	st
Gelasine azurea Herbert	st
G. coerulea (Vell.) Ravenna	st
Herbertia lahue (Molina) Goldbl.	st
H. puchella Sweet	st
Hesperoxiphion peruvianum Baker	st
Homeria collina (Thunb.) Salisb.	st
H. elegans Sweet	st
H. marlothii L. Bolus	st
Iris pumila L.	st
Larentia linearis (H.B.K.) Klatt	st
Libertia caerulescens Kunth & Bouche	st
L. chilensis (Mol.) Gunckel	st
L. elegans Poepp.	st
L. formosa R. Graham	st
L. grandiflora (R. Br.) Sweet	st
L. ixioides (Forst. f.) Sprengel	st
L. paniculata (R. Br.) Sprengel	st
Mastigostyla johnstonii R. Foster	st
Moraea bellendenii (Sweet) N. E. Brown	st
M. fugax (Delaroche) Jacq.	st

TABLE 1. Continued.

M. neopavonia R. Foster	st
M. spathulata (L. f.) Klatt	st
M. tripetala (L. f.) Ker	st
Nemastylis tenuis (Herbert) Baker	st
Neomarica caerulea (Ker) Sprague	st
N. gracilis (Herbert) Sprague	st
N. heloysa-mariae P. Och.	st
N. northiana (Schneev.) Sprague	st
Nivenia corymbosa (Ker) Baker	st
N. stokoei N. E. Brown	st
Ona obscura (Cav.) Ravenna	x
Orthrosanthus chimboracensis (H.B.K.) Baker	(st)
O. laxus (Endl.) Benth.	(st)
O. multiflorus Sweet	st
O. polystachyus Benth.	st
Patersonia fragilis (Labill.) Asch. & Graeb.	st
P. glabrata R. Br.	st
P. graminea Benth.	st
P. juncea Lindl.	st
P. longiscapa Sweet	(st)
P. lowii Stapf	st
P. macrantha Benth.	st
P. occidentalis R. Br.	st
P. novoguineensis L. S. Gibbs	st
P. pygmaea Lindl.	st
P. sericea R. Br.	st
P. umbrosa Endl.	st
Phaiophleps biflora (Thunb.) R. Foster	x
Pseudotrimezia barretoi R. Foster	st
Sessilanthera citrina Cruden	st
S. heliantha (Ravenna) Cruden	st
Sisyrinchium acre Mann.	x
S. alatum Hook.	x
S. angustifolium Miller	x
S. cuspidatum Poepp.	x
S. chilense Hook.	x
S. elmeri Greene	x
S. fasciculatum Kl.	cs
S. filifolium Gaudich	x
S. grandiflorum Dougl. ex Lindl.	x
S. idahoense Bicknell	x
S. junceum E. Meyer	x
S. longipes (Bickn.) Kearney & Peebles	x
S. macrocarpum Hier.	x
S. micranthum Cav.	x
S. nashii Bickn.	st
S. pachyrhizum Baker	x
S. setaceum Kl.	?x
S. striatum Sm.	x
S. tinctorum H.B.K.	x
S. vaginatum Spreng.	cs
Solenomelus sisyrinchium (Gris.) Pax ex Diels	st

TABLE 1. Continued.

S. pedunculatus (Gill.) Johnston	st
Sphenostigma mexicanum R. Foster	st
S. sellowianum (Klatt) Baker	st
Tapeinia pumila (Forst. f.) Baill.	st
Tigridia bicolor Molseed	st
T. dugesii S. Wats.	st
T. huajuapanensis Molseed ex Cruden	st
T. meleagris (Lindley) Nichols.	st
T. pavonia (L. f.) DC.	st
T. orthantha (Lemaire) Ravenna	st
T. seleriana (Loesener) Ravenna	st
Trimezia martii (Baker) R. Foster	st
T. martinicensis (Jacq.) Herbert	st
T. sincorana Ravenna	st
T. steyermarkii R. Foster	st
Witsenia maura Thunb.	st

The unusual Tasmanian relict *Isophysis,* often associated with Iridaceae because of its equitant leaves and three stamens, but a superior ovary, also has styloids, although not in all specimens examined.

In contrast, *Campynema* and *Campynemanthe* have typical raphides and no styloids. Members of Colchicaceae examined lack true raphides but have crystal sand. Crystal sand (described by Netolitsky, 1929) consists of small and scattered globose to ovoid birefringent granules. Uvulariaceae are heterogeneous for crystals. Two species of *Disporum* and one of *Streptopus* have both raphides and crystal sand, while a third species of *Disporum* has crystal sand only. A single species of *Uvularia* examined has a few scattered crystals that may be crystal sand and in *Schelhammera* we found no crystalline inclusions at all. The two species of *Tricyrtis* and the single species each of *Erythronium* and *Lilium* (both Liliaceae) studied here, have what appear to be large round crystals of calcium carbonate (the tissue bubbles in bleach and even more when dilute hydrochloric acid is added). No crystals were seen in *Calochortus.*

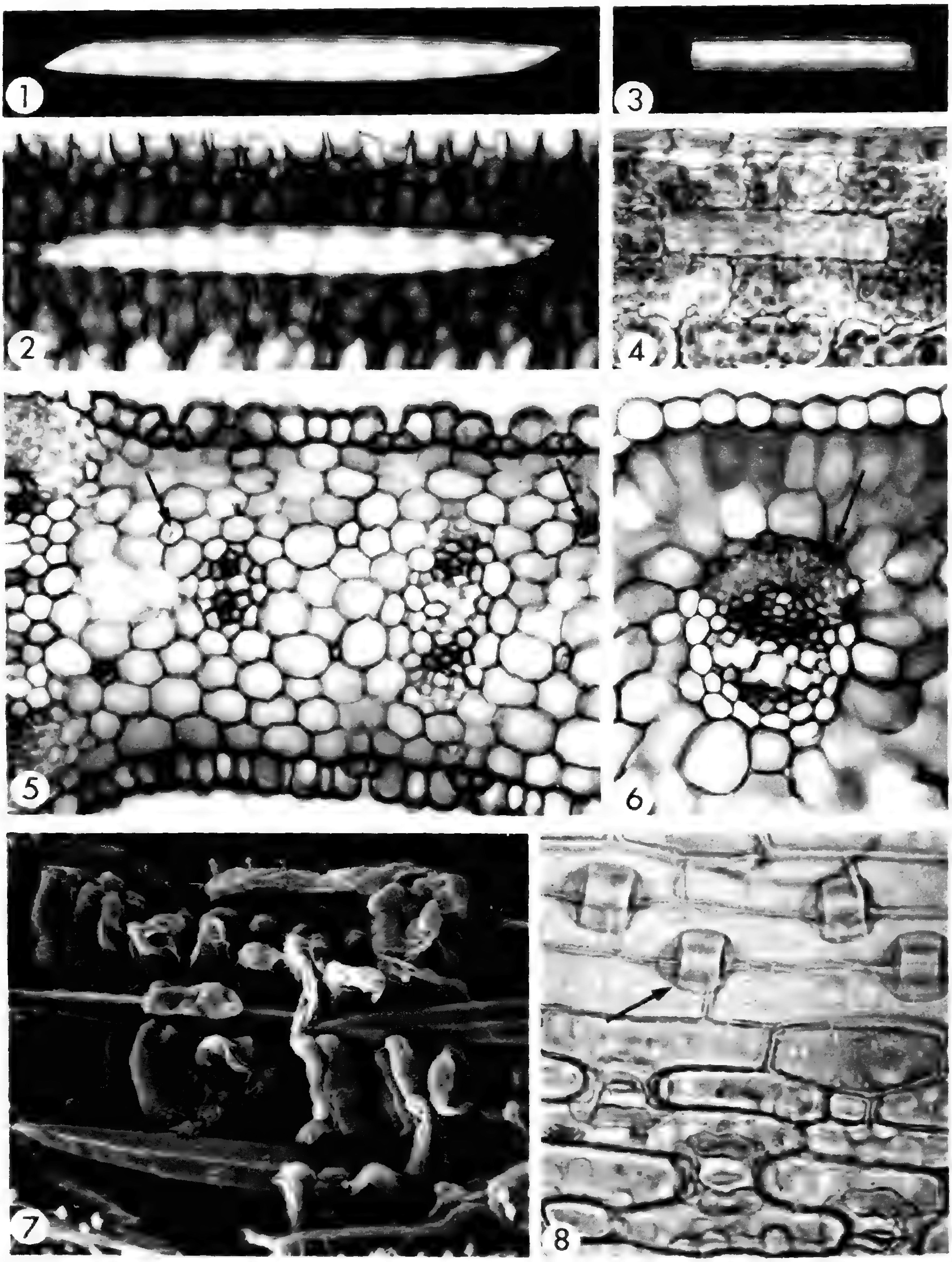
No crystals of any kind were detected in *Geosiris* but because this monotypic genus is a nongreen leafless saprophyte the comparison of its leaf scales with the green fully developed leaves of other species may not be valid.

Raphides were noted in *Cyanella* and *Walleria* (Tecophilaeaceae) but no crystals of any sort were seen in *Cyanastrum,* a genus often treated as a separate family, Cyanastraceae.

DISCUSSION

The occurrence of styloids already noted by Metcalfe (1961), Hegnauer (1963), Gibbs (1974), and others to be a peculiarity of Iridaceae, appears to be a fundamental and nearly universal characteristic of the family on the basis of a survey here of some 240 species in 75 genera. Our data supplements previous reports of styloids in the Ixioid genera *Crocus, Romulea,* and *Gladiolus* (Gulliver, 1863a, 1863b; Rothert & Zalenski, 1899) and in *Romulea, Syringodea, Homoglossum,* and *Tritonia* (de Vos, 1970, 1974, 1976, 1982: 30). In Iridoideae, styloids have been described in a few genera including *Iris, Witsenia,* and *Belamcanda* (Gulliver, 1863a, 1863b; Rothert & Zalenski, 1899; Frey, 1929; Wu & Cutler, in press), *Ferraria* (de Vos, 1979), and *Dietes* (Rudall, 1983). Styloids were described by Noel (1959) in *Bobartia* (also Iridoideae) (and possibly by Strid, 1974: 10–12 who observed square crystals in sectioned leaves). Chodat and Balicka-Iwanowska (1892) observed large styloids arranged longitudinally and surrounding vascular bundles in the leaves of many genera of Iridaceae. The absence of styloids in *Sisyrinchium* leaves was first noted by Gulliver (1865) in *S. anceps, S. striatum,* and *S. bermudianum* and later by Rothert and Zalenski (1899) in *S. bermudianum,* and confirmed in 20 out of 21 species in this study. The lack of styloids in *Sisyrinchium* and also the closely related genera *Phaiophleps* and *Chamelum* may well have some significance for the systematics of those genera, although styloids do occur in *Libertia* and *Tapeinia,* also close to this alliance. Rudall (in press) also found styloids completely lacking in rhizomes of *Sisyrinchium,* whereas they are present in underground stems of most genera of Iridaceae. Apart from this, the occasional absence of styloids in a few scattered species appears to have no systematic relevance. The size and shape of crystals in Iridaceae is also somewhat variable. The occurrence of cuboidal crystals (Fig. 8) in a few species has little obvious taxonomic significance; crystal shape may depend to some extent on the shape of the crystal idioblast enclosing it (Franceschi & Horner, 1980). However, Wu and Cutler (in press) have found that styloid shape and size in *Iris* may well be taxonomically useful at the species level.

Styloids are relatively rare in the monocotyledons but are also characteristic of Agavaceae, Phormiaceae, and a few other families or sub-



FIGURES 1–8. Crystals in Iridaceae.—1, 2. *Trimezia sincorana,* crystal with pointed ends in LS leaf. (1. Polarized. 2. Bright field). ×700.—3, 4. *Patersonia longiscapa,* crystal with square ends in LS leaf. (3. Polarized. 4. Bright field). ×700.—5. *Gladiolus daleni,* leaf TS. Crystals (arrowed) in scattered mesophyll cells. ×630.—6. *Crocus cancellatus,* leaf TS. Crystals (arrowed) in vascular bundle sheath. ×650.—7. *Geissorhiza aspera,* scanning electron micrograph. Crystals among mesophyll cells. ×500.—8. *Patersonia umbrosa,* leaf surface, showing cuboidal crystals (arrowed) immediately beneath epidermis, over veins. ×1,400.

families of Asparagales (Dahlgren & Clifford, 1982: 92). They have not, however, been recorded in any members of Liliales sensu stricto except Iridaceae.

The discovery of raphides in Campynemaceae appears to be the first report for the family and crystal sand appears not to have been recorded previously in Colchicaceae. Genera of Colchicaceae have long been known to lack raphides or styloids (Hegnauer, 1963; Gibbs, 1974). In Uvulariaceae, data for *Uvularia* are contradictory, Hegnauer reporting raphides here but both Gibbs (1974: 1915) and Sterling (1977) point out their absence, a condition we confirm. The few examples of the Uvulariaceae we examined indicate that the alliance as circumscribed to include *Tricyrtis,* and the *Disporum-Uvularia* group of genera, is heterogeneous for crystal types. Either raphides and scattered crystal sand occur (*Streptopus, Disporum*) or crystal sand alone (*Uvularia, Disporum*) or no calcium oxalate type crystals at all (*Schelhammera, Tricyrtis*) but possibly calcium carbonate in *Tricyrtis.* Gibbs (1974: 1915) has also reported raphides in *Streptopus.* The single species each of *Erythronium* and *Lilium* (both Liliaceae) studied here, also have what appear to be large round crystals of calcium carbonate.

The different crystal types found in Colchicaceae, Uvulariaceae, and Campynemaceae contribute little to our understanding of their relationships to Iridaceae but in our view, do constitute evidence for the continued separation of *Campynema* and *Campynemanthe* from Iridaceae. In general raphides may be considered a primitive feature in flowering plant groups (Tomlinson, 1962). The presence of styloids or crystal sand is rare and presumably derived and the styloids of Iridaceae are consistent with the specialized position of Iridaceae in Liliales.

The character of an inferior ovary in Campynemaceae presumably evolved independently in this family and in Iridaceae. Campynemaceae also differ from Iridaceae in the basic leaf form, having bifacial rather than monofacial equitant leaves, and in having six stamens. *Campynemanthe* also has a distinctive type of axile placentation in which the seeds remain attached to the vasculature of the central axis after dehiscence or disintegration of the capsule.

Isophysis shares with Iridaceae not only the peculiar but not unique character of monofacial and equitant leaves and an androecium of three stamens, but also the distinctive styloids that appear fundamental in the family. It differs notably from Iridaceae only in having a superior ovary. Early reports that the stamens of *Isophysis* are opposite the inner tepals (Bentham & Hooker, 1883) and hence not comparable with Iridaceae are incorrect. We have examined the limited material available to us and confirm the statement by Krause (1930: 260) that the stamens are opposite the outer tepals. It now seems desirable to include *Isophysis* in Iridaceae on the grounds mentioned above but it should probably be treated as a separate rather isolated subfamily, whose affinities to the other subfamilies are distant.

Similarities between Colchicaceae and Iridaceae, except for unspecialized characteristics shared with other families of the Liliales, seem restricted to the presence of a cormous rootstock in both families (Dahlgren & Rasmussen, 1983). However, we believe that it is very likely that a rhizome is the basic type of rootstock for Iridaceae and that corms evolved at least twice in the family. In Ixioideae, the corm is basal rooting and has a stele, whereas in some specialized Iridoideae (the predominantly African Homerinae) it is apically rooting and without a stele (de Vos, 1977; Goldblatt, 1976, 1982). Rhizomes occur in many genera of Iridoideae including those with predominantly unspecialized characteristics, several of which are often treated as a separate subfamily Sisyrinchioideae. We are uncertain whether the corm is basic in Colchicaceae, but its structure seems somewhat different from that of the corm types found in Iridaceae and, given our hypothesis that a rhizome is basic in Iridaceae, the presence of corms in other families appears irrelevant in questions of phylogenetic relationship. The absence of styloids and the presence of crystal sand in Colchicaceae seems to remove this family even further from a possible close affinity with Iridaceae. Dahlgren's suggestion (pers. comm.) that Colchicaceae and Iridaceae may be independently derived from Uvulariaceae has merit although it is more difficult to see similarities with Iridaceae than Colchicaceae. In this connection it seems significant that Uvulariaceae is heterogeneous for crystals and provides a possible link between ancestors with the primitive condition of raphides alone and derived lines with specialized crystal types.

Although Tecophilaeaceae are not seriously considered to be allied to Iridaceae, and have been assigned to Asparagales by Dahlgren and Clifford (1982) rather than Liliales, the family was included in this study. The finding of typical raphides, very common in Asparagales, is consistent with their placement in this order on the basis of their phytomelan encrusted seeds and introrse anthers. The absence of any crystals in *Cyanastrum,* already recorded by Dahlgren and

Clifford, in contrast to *Cyanella* and *Walleria,* lends some support to its treatment as a separate family, for example by Dahlgren and Clifford.

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A REVIEW OF *EUPHORBIA* (EUPHORBIACEAE) IN BAJA CALIFORNIA[1]

MICHAEL J. HUFT[2]

ABSTRACT

Study of the available collections from Baja California reveals that there are at least 13 species of *Euphorbia* (excluding *Chamaesyce*) there. *Euphorbia chersonesa* Huft, *E. lagunensis* Huft, and *E. pumicicola* Huft are described as new, *E. ceroderma* I. M. Johnston and *E. cyathophora* Murr. are reported from Baja California for the first time, and *E. humayensis* Brandegee, reported from Baja California when it was described, but omitted in the recent "Flora of Baja California," is reinstated. The taxonomy of subgenus *Poinsettia* is updated, and a key to all Baja California species of *Euphorbia* is provided.

In the recent "Flora of Baja California" (Wiggins, 1980), seven species of *Euphorbia* are recognized (excluding the 26 species of subg. *Chamaesyce* Raf., which I recognize as the genus *Chamaesyce* S. F. Gray, and which will not be further considered here). These are distributed among three subgenera, *Agaloma* (Raf.) House, *Esula* Pers., and *Poinsettia* (Graham) House. An examination of the available herbarium material shows that there are actually 13 species of *Euphorbia* in Baja California. Of the six additions reported here, two are species of western Mexico reported from Baja California for the first time, one was cited from Baja California when it was published but was not included in the Flora, two are described as new, and one was previously recognized as a variety of *E. heterophylla* L., a species to which it has no close relationship, and is here described as a new species. In addition, the treatment of subg. *Poinsettia* is updated to take into account the work by Dressler (1961) that cleared up much previous confusion in that group.

The following key will distinguish the species of *Euphorbia* now known from Baja California.

1. Glands of the involucre cup-like or bilabiate, usually 1 or 2 (3–5 in *E. pumicicola*) (subg. *Poinsettia*).
  2. Glands bilabiate.
    3. Bracts usually red at base; gland usually 1 per cyathium; seeds cylindrical, sharply tuberculate .... 1. *E. cyathophora* Murr.
    3. Bracts green or white at base; glands 3–5 per cyathium; seeds ovoid, angular, the tubercles low and blunt .... 2. *E. pumicicola* Huft
  2. Glands with circular opening, usually 1 per cyathium; bracts green, pale, or purple-spotted at base, never red; seeds ovoid, angular, coarsely tuberculate .... 3. *E. heterophylla* L.
1. Glands of the involucre flat or shallowly concave, usually 4 or 5.
  4. Glands appendiculate (appendages nearly obsolete in *E. chersonesa*); stipules minute, glanduliform; seeds ecarunculate (except in *E. eriantha*) (subg. *Agaloma*).
    5. Plants annual.
      6. Involucres and capsules glabrous; herbage glandular-pubescent; leaves alternate; appendages green, unlobed, ample .... 4. *E. humayensis* Brandegee
      6. Involucres and capsules pubescent; herbage not glandular; leaves alternate or opposite; appendages white or green, lobed, divided, or nearly obsolete.
        7. Appendages nearly obsolete; leaves alternate; seeds coarsely tuberculate .... 5. *E. chersonesa* Huft
        7. Appendages lobed or divided; leaves mostly opposite; seeds shallowly pitted or smooth and 4-angled.
          8. Plant delicate; appendages 3-lobed, green, spreading; seeds shallowly and coarsely pitted, ecarunculate; capsules broader than long, densely tomentose on the angles, otherwise glabrous .... 6. *E. lagunensis* Huft

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8. Plant robust; appendages 5–10-fid, white, arching over the glands; seeds smooth, 4-angled, carunculate; capsules longer than wide, densely white-tomentose all over .... 7. *E. eriantha* Benth.
5. Plants shrubs or leafless wax-coated perennials.
    9. Leaves scale-like or lacking; stems in dense clumps, erect, covered with a thick wax coat .... 8. *E. ceroderma* I. M. Johnst.
    9. Leaves fully formed; stems woody, highly-branched.
        10. Leaves verticillate; cyathia disposed in cymes .... 9. *E. xantii* Engelm. ex Boiss.
        10. Leaves alternate; cyathia occurring singly in axils of leaves.
            11. Herbage, involucres, and ovary pubescent .... 10. *E. misera* Benth.
            11. Herbage, involucres, and ovary glabrous.
                12. Petioles very slender, ca. 0.4 mm diam. or less, equalling or exceeding blade in length; leaf blade thin, dark green .... 11a. *E. californica* Benth. var. *californica*
                12. Petioles stouter, ca. 0.5–1 mm diam., shorter than blade; leaf blade thick, leathery, pale yellowish green .... 11b. *E. californica* var. *hindsii* (Benth.) Wigg.
4. Glands exappendiculate; stipules lacking; seeds carunculate (subg. *Esula*).
    13. Plant annual; glands elliptic, lacking horns; capsules verrucose; seeds reticulate .... 12. *E. spathulata* Lam.
    13. Plant perennial; glands with 2 short horns; capsules smooth; seeds pitted ... 13. *E. palmeri* Engelm.

SUBGENUS *POINSETTIA* (GRAHAM) HOUSE

1. Euphorbia cyathophora Murr., Comm. Götting. 7: 81. 1786.

This species is here reported from Baja California for the first time. It is the common weedy poinsettia of the eastern and central United States with red-based bracts and is also common in Mexico and Central America. It is often confused with the widespread tropical weed, *E. heterophylla,* but the two species are quite distinct, as was first clearly pointed out by Dressler (1961).

Specimens examined. MEXICO. BAJA CALIFORNIA SUR: Sierra San Lázaro, 10 Oct. 1893, *Brandegee s.n.* (NY, UC); San Bernardo, 13 Oct. 1893, *Brandegee s.n.* (UC).

2. Euphorbia pumicicola Huft, sp. nov. TYPE: Mexico. Baja California Sur: ca. 5 mi. N of Comondú, ca. 2,000 ft., 3 Oct. 1941, *Hammerly 175* (holotype, DS 293876, photograph at F—neg. no. 58289; isotype, CAS), distributed as *E. heterophylla* L. sensu latior.

Herba annua, glabra. Folia opposita, obovata, infra mediam leviter lobata, supra mediam serrata; stipulae obsoletae. Inflorescentia terminalis, compacta, cymosa; bracteae similes foliis caulinis, prope basin interdum discolores. Cyathia 2–2.7 mm alta, orificio 1.7–1.8 mm diam.; lobi 5, laciniati, excedentes glandulas; glandulae 3–5, exappendiculatae, bilabiatae. Flores masculae ca. 10; bracteolae obsoletae; styli 3, ca. 1 mm longi, indivisi vel parum furcati. Capsula ovoidea-deltoidea vel subglobosa. Semina ovoidea-angulata, ecarunculata, tuberculis humilibus obtusis.

Erect taprooted *annual,* 15–20 cm high, glabrous, sparsely branched. *Stem* 1.8–2.5 mm diam. at base. *Leaves* opposite, 2–4 pairs, the upper ones crowded below the inflorescence, the lowest ones above the middle of the stem; petiole slender, 1–1.5 cm long; blade obovate, green, shallowly lobed below the middle, serrate above the middle, 2–3.5(–4) cm long, 1–1.6 cm wide; base cuneate; apex obtuse to acute; stipules lacking. *Inflorescence* a compact terminal cyme; bracts similar to stem leaves but smaller, to 1.5 cm long, green, often white or pale toward base. *Cyathia* campanulate, green, 2–2.7 mm high, 1.7–1.8 mm diam. at orifice; lobes 5, 0.5–0.7 mm long, exceeding the glands, laciniate, white toward apex; glands 3–5, 0.2–0.3 mm high, ca. 0.5 mm wide, bilabiate, exappendiculate. *Staminate* flowers ca. 10; bracteoles lacking. *Styles* 3, ca. 1 mm long, undivided or very slightly bifid; gynophore exserted from the cyathium 1.5–3 mm, nutant. *Capsule* ovoid-deltoid to subglobose, 2.5–3.5 mm high, 3–4.5 mm diam., green; seeds truncate-ovoid, 2–2.3 mm long, 2–2.3 mm diam., angular, bluntly pointed at hilar end, covered with low blunt tubercles, ecarunculate, brown.

Euphorbia pumicicola may be distinguished from the other annual species of subg. *Poinsettia* by the combination of a glabrous plant body, opposite leaves, 3–5 bilabiate glands per cyathium, and angular, bluntly tuberculate seeds. In its small stature and possession of more than one gland per cyathium it is reminiscent of *E. inornata* (Dressler) A. Radcliffe-Smith of Peru, but that species differs by its more spreading habit, alternate phyllotaxy, nearly entire leaves, and more nearly smooth seeds.

Euphorbia pumicicola is known only from the type, which was collected on a plateau thickly strewn with lava rocks (whence the name). A more extended description of the habitat with a list of associated species is given by Johnson (1958: 235–236).

3. **Euphorbia heterophylla** L., Sp. Pl. 453. 1753.

Although Wiggins (1980) recognized three varieties of *E. heterophylla,* including the typical variety, there is no consistent basis for the recognition of infraspecific taxa. *Euphorbia heterophylla* var. *graminifolia* Engelm. is the most commonly recognized variety, based on a specimen of *E. cyathophora* with narrow leaves. Both *E. heterophylla* and *E. cyathophora* exhibit a wide range of leaf shapes, none of which have any geographical integrity or any correlation with other characters. It is worth pointing out that although the varietal name is often cited as *E. heterophylla* var. *graminifolia* (Michx.) Engelm. (e.g., in Fernald, 1950; Macbride, 1951; Radford et al., 1968; Standley & Steyermark, 1949; Wiggins, 1980), presumably based upon *E. graminifolia* Michx. (which is typified by another narrow-leaved specimen of *E. cyathophora*), Engelmann in fact named a new variety without reference to Michaux's name.

The other heterotypic variety recognized by Wiggins is *E. heterophylla* var. *eriocarpa* Millsp. The type specimen of this name does not even belong to subg. *Poinsettia,* as was pointed out by Dressler (1961), but rather represents an otherwise undescribed species of subg. *Agaloma* and is described below (*E. chersonesa*).

Euphorbia heterophylla, which is such an aggressive weed elsewhere in its range, does not seem to be very common in Baja California, and apparently occurs only in the southern quarter of the peninsula.

Specimens examined. MEXICO. BAJA CALIFORNIA SUR: Miraflores, 13 Oct. 1890, *Brandegee 517* (UC-2; 3 other sheets of this number, but collected nine and 11 days earlier, are *E. chersonesa*); San Bernardo, 13 Oct. 1893, *Brandegee s.n.* (UC); Cape region, Nov. 1902, *Brandegee s.n.* (UC); Sierra de la Giganta, Mesa del Potrero de San Javier (NE of Misión San Javier), ca. 25°52′N, 111°32½′W, ca. 800–850 m, 19 Sept. 1965, *Carter 4967* (UC); Sierra de la Giganta, W-facing mesa-like slope of Cerro Gabilán, ca. 25°50½′N, 111°24½′W, ca. 1,200 m, 4 Oct. 1965, *Carter 5108* (UC); Sierra de la Giganta, N slope above cliffs near summit, Cerro del Barreno, S side of Valle de los Encinos (S side of Cerro Giganta), ca. 26°03′N, 111°35′W, ca. 1,260 m, 30 Sept. 1967, *Carter & Moran 5341* (UC); Sierra de la Giganta, N- and NW-facing slopes S of Portezuela de Última Agua (crest of the Sierra de la Giganta NW of Puerto Escondido), ca. 25°50′N, 111°23′W, ca. 875–960 m, 5 Oct. 1970, *Carter & Moran 5539* (UC); Mts. W of Boca de la Sierra, near 23°23′N, 109°49′W, 390 m, 30 Sept. 1967, *Howe s.n.* (SD); San José del Cabo, 1 Apr. 1930, *Johansen 507* (DS); Borrego Ranch, 20 Sept. 1930, *Jones s.n.* (DS); Primer Agua, near Loreto, 19 Oct. 1930, *Jones s.n.* (UC).

SUBGENUS *AGALOMA* (RAF.) HOUSE

4. **Euphorbia chersonesa** Huft, sp. nov. TYPE: Mexico. Baja California Sur: ca. 1.5 mi. S of Mission Dolores landing, near 25°05′N, 110°54′W, ca. 275 ft., E-facing slope, rhyolite, 4 Dec. 1959, *Wiggins, Carter & Ernst 270* (holotype, UC 1303223, photograph at F—neg. no. 58288; isotypes, DS, US). Figure 1: d–f.

Euphorbia heterophylla L. var. *eriocarpa* Millsp., Proc. Calif. Acad. Sci., Ser. 2, 2: 230. 1889 non *E. eriocarpa* Bertol., 1839. TYPE: Mexico. Baja California Sur: Comondú, 21 Mar. 1889, *Brandegee 26* (holotype, F), *Brandegee s.n.* (probable isotype, UC).

Herba annua, erecta. Folia alternata vel opposita, inferiora saepe fugacia; petiolus gracilis; lamina ovata vel elliptica, raro parum lobata, rare pubescens vel glabrata, grosse dentata, sinuata, vel serrata; stipulae glanduliformes. Cyathia dense puberula; glandulae 4, aliquantum alveiformia; appendices glandularum valde minutae, integrae vel crenatae; flores masculos 10–15; bracteolae obsoletae; styli 3, profunde furcati, basi libri, vix divergentes. Capsula exserta, dense puberula; semina ovoidea-angulata, grosse tuberculata, ecarunculata.

Erect taprooted *annual,* 2–6 dm high. *Stem* terete, glabrous, with scattered short hairs, or minutely puberulent near the nodes, faintly glaucous, 1–4 mm diam. at base. *Leaves* alternate or opposite, often varying even on a single plant, often fugacious below the inflorescence; petioles slender, 5–40 mm long, puberulent to glabrate, shallowly canaliculate; blade ovate or elliptic, rarely with a few shallow lobes, 1–10 cm long, 0.5–7.5 cm wide, 1.2–4.5 times as long as wide, thinly appressed-pubescent to glabrate above and below, the hairs to 0.5 mm long; base acute to broadly cuneate; apex obtuse, acute, or scarcely short-cuspidate; margin coarsely dentate to shallowly sinuate or serrate, rarely subentire; stipules glanduliform, 0.2–0.4 mm long. *Inflorescence* a terminal cyme, the bracts similar to the stem leaves. *Cyathia* campanulate, 0.9–1.5 mm high, 0.9–1.3 mm diam. at orifice, green, densely puberulent; lobes 5, deltate, ca. 0.5 mm long; glands 4, stalked, reniform, green, somewhat creased longitudinally, ca. 0.5 mm long parallel to the

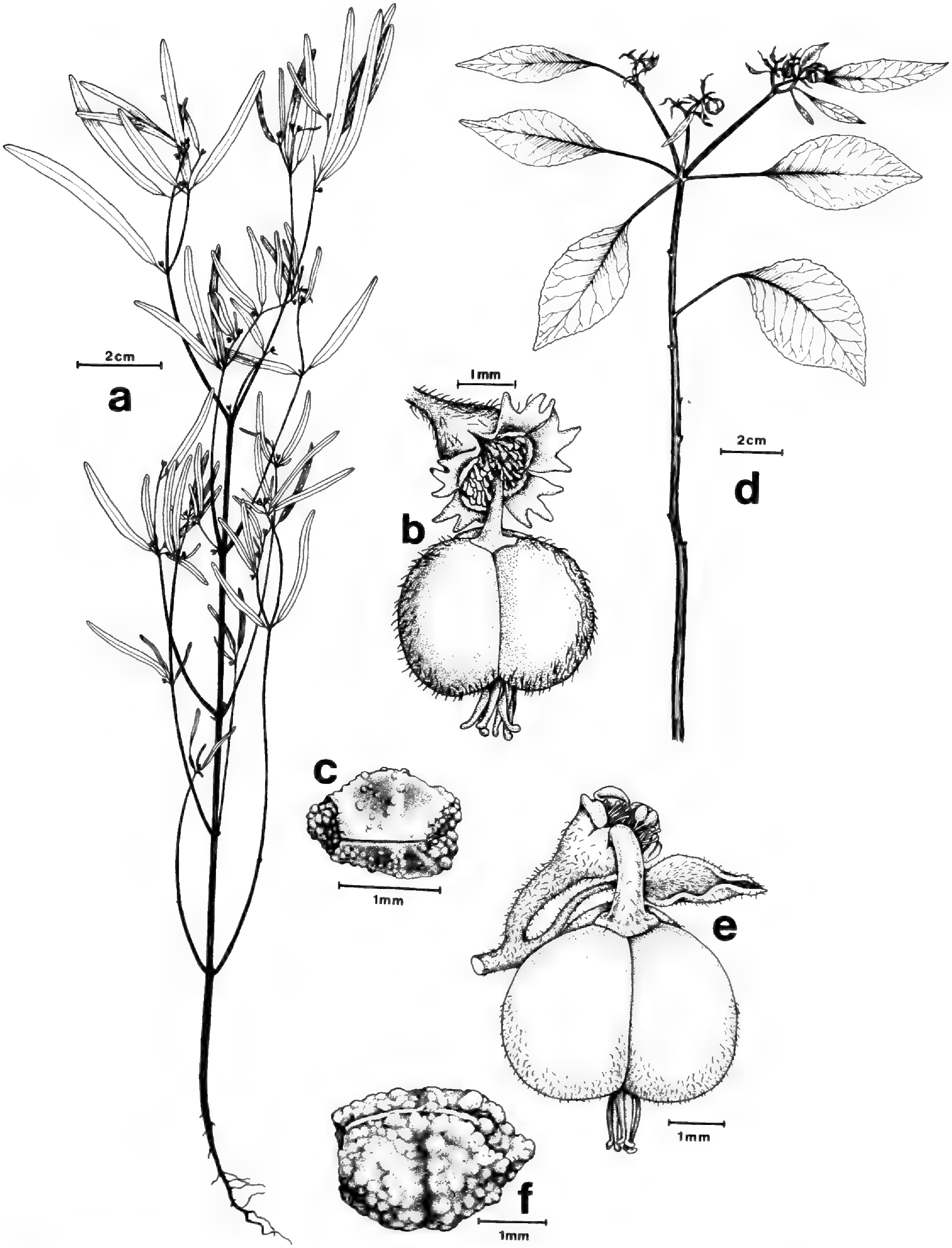

Figure 1. a–c. *Euphorbia lagunensis* Huft.—a. Habit, *Jones 27509.*—b. Cyathium and mature capsule, *Jones 27509.*—c. Seed, *Brandegee 12.* d–f. *Euphorbia chersonesa* Huft.—d. Habit, *Moran 18927.*—e. Cyathium and mature capsule, *Wiggins et al. 270.*—f. Seed, *Wiggins et al. 270.*

rim of the cyathium, 0.1–0.2 mm wide; appendages forming a minute rim around the gland, entire or crenate. *Staminate* flowers 10–15; bracteoles obsolete. *Styles* 3, 0.6–0.9 mm long, free to the base, divided nearly their entire length, only slightly divergent; stigmas capitate; gynophore glabrous or sparsely pilose, exserted from the cyathium 1.5–3 mm, nutant. *Capsule* depressed-globose, strongly 3-lobed, 3–3.5 mm high, 4–6 mm diam., densely puberulent; seeds ovoid-angular, 3–3.5 mm long, 1.8–2.2 mm in diameter, light gray to brown, coarsely tuberculate, the tubercles white-tipped, ecarunculate.

This distinctive species is certainly not a member of subg. *Poinsettia,* much less is it related to *E. heterophylla,* as is clear from the flat or somewhat creased, rather than bilabiate or cup-shaped, glands, and the presence of petaloid appendages. The presence of glanduliform stipules and minute appendages dictates its placement in subg. *Agaloma,* where it would seem most at home in sect. *Cyttarospermum* Boiss., based on the annual habit, slender petioles, absence of bracteoles between the staminate flowers, and styles that are deeply bifid and free to the base. The sectional classification of subg. *Agaloma,* however, is in great need of revision (Johnston, 1974; Buck & Huft, 1977), so its placement here must be provisional. *Euphorbia chersonesa* does not seem to have any close relatives and can be easily distinguished from other species of sect. *Cyttarospermum* by the densely puberulent cyathium and capsule, the nearly obsolete appendages of the cyathial glands, the short, erect styles, and the coarsely tuberculate seeds that are not pitted.

Euphorbia chersonesa is apparently restricted to the southern quarter of the Baja California peninsula. Only two of the collections provide elevational data (275 m, 940 m), and little ecological data is available. *Gentry 4096* was collected in "moist soil in shade of basaltic cliffs," and the associates of *Wiggins et al. 270* include "*Lysiloma candida, Ruellia, Colubrina glabra* [= *C. viridis*], *Aeschynomene, Olneya tesota,* and *Bursera microphylla.*"

Additional specimens examined. MEXICO. BAJA CALIFORNIA SUR: Sierra de Laguna, 26 Jan. 1890, *Brandegee 8* (UC); Rancho Salada, 16 Jan. 1890, *Brandegee 9* (F, UC); San José del Cabo, 2–4 Oct. 1890, *Brandegee 517* (DS, GH, UC; 2 other sheets of this number, collected on 13 Oct. 1890, are *E. heterophylla*); Comondú, 5 Dec. 1938, *H. S. Gentry 4096* (DS); Sierra de la Giganta, N ridge of Cerro Mechudo, 24°48′N, 110°43′W, ca. 940 m, 3 Nov. 1971, *Moran 18927* (UC).

5. **Euphorbia humayensis** Brandegee, Zoe 5: 208. 1905. TYPE: Mexico. Sinaloa: Culiacán, 1 Oct. 1904, *Brandegee s.n.* (lectotype, UC 110009, here designated, photographs at F—neg. no. 58287 and MICH; isolectotype, F 196158).

This species was not included in Wiggins (1980), even though one collection from the Cape region of Baja California was cited by Brandegee in the protologue, and two additional collections by Brandegee from Baja California are deposited in the herbarium of the University of California at Berkeley. The species is otherwise known from tropical deciduous forest and thorn scrub in western Mexico, from Sinaloa south to Michoacán. Curiously, this species has recently been collected in the savannas of Venezuela (Guárico, 10 km NWN of Altagracia de Orituco along highway to Caucagua, 18 Nov. 1973, *Davidse 4171,* MO, distributed as *E. ocymoidea* L. vel sp. aff.). This and *E. chersonesa* are the only representatives in Baja California of sect. *Cyttarospermum,* a group of some 35–40 species that reaches its greatest development in western Mexico.

Additional specimens examined. MEXICO. BAJA CALIFORNIA SUR: W side of Cape region, Nov. 1902, *Brandegee s.n.* (UC); Todos Santos (Cape region), 4 Oct. 1899, *Brandegee s.n.* (UC); Sierra de Laguna, 21 Jan. 1890, *Brandegee 10* (F, UC), distributed as *Phyllanthus* sp.

6. **Euphorbia eriantha** Benth., Bot. Voy. Sulphur 51. 1844.

Poinsettia eriantha (Benth.) Rose & Standley, Contr. U.S. Natl. Herb. 16: 13. 1912.

The presence of five flat or convex cyathial glands, distinct petaloid appendages, and carunculate seeds requires that this species be placed in subg. *Agaloma,* as pointed out by Dressler (1961), and not in subg. *Poinsettia,* where Wiggins (1980) placed it. It belongs to sect. *Zygophyllidium* Boiss. where its closest relatives are *E. lacera* Boiss. of central Mexico and *E. jaliscensis* Robins. & Greenm. of western Mexico.

7. **Euphorbia lagunensis** Huft, sp. nov. TYPE: Mexico. Baja California Sur: The Laguna, Laguna Mountains, 22 Sept. 1930, *M. E. Jones 27509* (holotype, MO 1034346, photograph at F—neg. no. 58290). Figure 1: a–c.

Species haec ab *E. bilobata* Engelm. glandulae cyathii haud lobatis, appendicibus viridibus 2–4 lobatis, semine luteo-pustulato differt.

Erect taprooted *annual,* 1.5–3.5 dm high. *Stem* glabrous or with a few hairs at the nodes, (0.8–)1–2 mm diam. at base; nodes 3–4 below the inflorescence; internodes (1.5–)2.5–5 cm long. *Leaves* opposite, the lower ones fugacious; petioles (2–)3–8 mm long, appressed-pubescent; blade linear, 18–43 mm long, 1.8–5 mm wide, 7–12(–18) times as long as wide, sparsely to moderately appressed-pubescent above and below, the hairs to 0.5 mm long; base cuneate; apex obtuse; margin entire; stipules glanduliform, minute, less than 0.1 mm long. *Inflorescence* a terminal cyme, the bracts similar to the stem leaves, the cyathia thus appearing solitary in the forks. *Cyathia* campanulate, green, villous to pilose, 0.7–0.9 mm high, 0.8–0.9 mm diam. below the glands, 1.2–1.5 mm across the appendages; lobes 5, erose, 0.3–0.4 mm long, 0.4–0.5 mm wide; glands 4, green, reniform, 0.6–0.8 mm long parallel to the rim of the cyathium, ca. 0.3 mm wide; appendages green, (2–)3–4-lobed (rarely merely crenate), exceeding the gland by 0.3–0.5 mm; gynophore glabrous, exserted from the cyathium 0.3–1 mm, erect or nutant. *Staminate* flowers ca. 15. *Styles* 3, ca. 0.7 mm long, free to the base, nearly erect or only slightly divergent, divided nearly their entire length. *Capsule* subglobose, 1.7–2.2 mm high, 2–2.2 mm diam., densely white-tomentose on the angles, otherwise glabrous; seeds ovoid-angular, 1.4–1.5 mm long, 0.8–0.9 mm diam., with 2 transverse ridges, grayish to brown, covered with yellow pustules, ecarunculate.

This species belongs to sect. *Zygophyllidium,* a group of ten species of the United States and Mexico that is characterized by an annual habit, opposite leaves, and tuberculate seeds. Its closest relative is *E. bilobata* Engelm. of extreme western Texas, southern New Mexico, and southeastern Arizona, but it differs from that species in its entire, rather than deeply bilobed, glands, appendages that are green and 2–4 lobate, rather than white and completely divided, and seeds that are yellow-pustulate, rather than bluntly and sparingly tuberculate. Most of the specimens of *E. lagunensis* were identified and distributed as *E. bilobata* and were found under that name in several herbaria. *Hammerly 387A* is cited as *E.* cfr. *bilobata* in Johnson (1958), but the species is not included under any name in Wiggins (1980).

Euphorbia lagunensis is apparently confined to high elevations of the Sierra de Laguna and Sierra de San Francisquito, where it occurs on rocky banks and in canyons, or in open grassy meadows (cf. descriptions of collecting localities in Jones, 1935: 93–94, Goldman, 1951: 59–61, and Johnson, 1958: 246–249, as well as a photo of the meadow at Sierra de Laguna in Johnson, 1958: 235).

Additional specimens examined. MEXICO. BAJA CALIFORNIA SUR: Sierra de Laguna, 23 Jan. 1890, *Brandegee 12* (F, UC); Sierra de San Francisquito, 14 Oct. 1890, *Brandegee s.n.* (F); Saucito, 14 Oct. 1893, *Brandegee s.n.* (UC); El Taste, 14 Sept. 1893, *Brandegee s.n.* (US); El Taste, Nov. 1902, *Brandegee s.n.* (UC); *Quercus devia-Pinus cembroides* association, canyon W of cabin, La Laguna, Sierra de Laguna, E of Todos Santos, 1,700 m, 24 Dec. 1947, *Carter et al. 2309* (MO, duplicates to be distributed to K, MEXU, MICH, UC, US); from San Jorge to San Francisquito and La Chuparosa, E side of Sierra de la Victoria, "Rancho Encenoso," headwaters of Arroyo de San Francisquito, 23°29–31′N, 109°47–55′W, 12 Apr. 1955, *Carter & Ferris 3343-A* (DS); shady, rocky bank above stream near the meadow on Sierra de la Laguna, ca. 5,000 ft., 13 Oct. 1941, *Hammerly 387A* (CAS); Laguna Mts., 2 Mar. 1928, *Jones 24513* (NY).

8. **Euphorbia ceroderma** I. M. Johnston, Proc. Calif. Acad. Sci., Ser. 4, 12: 1066. 1924. TYPE: Mexico. Sonora: San Pedro Bay, 7 July 1921, *Johnston 4304* (holotype, CAS, photograph at F—neg. no. 57898).

This distinctive species is here reported from Baja California for the first time. It is known only from the collections in Baja California cited below and from San Pedro and San Carlos Bays near Guaymas, Sonora, where, according to the protologue, it is abundant.

Euphorbia ceroderma belongs to sect. *Trichosterigma* (Kl. & Gke.) Boiss., where its two closest relatives are *E. antisyphilitica* Zucc. of the Chihuahuan Desert region and *E. rossiana* Pax of the Tehuacán Valley area of Puebla and Oaxaca, Mexico. These three species are remarkable in their peculiar habit of forming dense clumps of erect, leafless, yellow-green stems. *Euphorbia antisyphilitica* has by far the greatest range of the three and is much more widely known, as it is a characteristic component of the Chihuahuan Desert flora and is the source of a widely used wax (Hodge & Sineath, 1956). The three species may be separated by means of the following key.

1. Cyathia 0.7–1 mm high; appendages acute, entire; bracts 10–20 mm long, whip-like .... *E. ceroderma*
1. Cyathia 2–3 mm high; appendages rounded or erose; bracts 1–2 mm long.
    2. Appendages entire, rounded; cyathia 1–3

per glomerule; bracts linear to linear-lanceolate, entire .... *E. antisyphilitica*

2. Appendages conspicuously erose or irregularly dentate; cyathia 3–8 per glomerule; bracts broader, fimbriate .... *E. rossiana*

In the protologue, Johnston distinguished *E. ceroderma* from *E. antisyphilitica* by the wax-coated stems and much smaller glabrous cyathia of the former, but of these characters, only the size of the cyathia holds up. All three species in this group have wax-coated stems, the heaviness of which apparently varies with the season, and the cyathia of *E. ceroderma* are not glabrous, but are puberulent, although not quite as densely so as in the other two species.

Additional specimens examined. MEXICO. BAJA CALIFORNIA SUR: Sierra de la Giganta, vic. of Rancho San Ignacio, Arroyo Santo Domingo, ca. 12 km E of Santo Domingo jct., 25°38′N, 111°37′W, ca. 200 m, 11 Nov. 1962, *Carter 4452* (SD, UC); Sierra de la Giganta, Arroyo Santo Domingo, ca. 24 km SSW of San Javier, ca. 25°41′N, 111°35′W, ca. 200 m, 14 Oct. 1964, *Carter 4736* (MICH, MO, UC), 26 Oct. 1964, *Carter 4872* (UC), 1 June 1965, *Carter & Sharsmith 4928* (MICH, UC); Sierra de la Giganta, Arroyo Santo Domingo, ca. 34 km SSW of San Javier, 25°38′N, 111°37′W, ca. 200 m, 1 June 1965, *Carter 4928A* (MICH, UC); Arroyo Purísima, above Purísima, 31 Mar. 1951, *H. S. Gentry 10307* (MICH); 3 mi. N of San Juanico, near 26°16′N, 112°29′W, ca. 80 m, 14 Feb. 1973, *Moran & Reveal 20100* (SD); Magdalena Plain, 2 mi. S of Pozo Grande, near 25°43′N, 112°01′W, ca. 10 m, *Moran 21364* (SD).

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A REVISION OF *STENANDRIUM* (ACANTHACEAE) IN MEXICO AND ADJACENT REGIONS[1]

THOMAS F. DANIEL[2]

ABSTRACT

Nine species of *Stenandrium* Nees are recognized as occurring in the southern United States, Mexico, and northern Central America (Guatemala, Belize, El Salvador, Honduras, and Nicaragua). One of these species, **S. manchonense** T. F. Daniel from Guerrero, distinguished by its erect, caulescent habit and large, whorled leaves with undulate to angular margins, is described as new to science, and two new combinations, **S. nanum** (Standley) T. F. Daniel and **S. pilosulum** (Blake) T. F. Daniel, are made. *Stenandrium* is circumscribed in relation to its closest relatives, *Aphelandra* and *Holographis*. Each of the nine species is described, mapped, and distinguished from its relatives. Illustrations are provided for *S. manchonense, S. barbatum,* and *S. dulce.*

Stenandrium Nees is a genus of perennial herbs and subshrubs found in tropical and subtropical regions of the New World, from the southernmost regions of the United States to central Argentina and Chile. Over 50 species of *Stenandrium* have been described, largely from Brazil, the West Indies, and Mexico. The genus has not been the subject of any detailed study since Nees's treatment in DeCandolle's "Prodromus" (1847). Recent regional accounts of *Stenandrium* in North and Central America have been provided by Wasshausen (1966) for Texas and Gibson (1974) for Guatemala. Standley did not include an account of the genus in his treatment of Acanthaceae in "Trees and Shrubs of Mexico" (1926), undoubtedly due to the inconspicuousness of its woody nature.

During this study nine species were found to occur in Mexico. One of these is described as new to science and two new combinations in *Stenandrium* are made. Five of the species are endemic to Mexico. The range of *S. barbatum* extends into the western United States, and *S. pedunculatum* and *S. subcordatum* have ranges extending into northern Central America. These regions are covered by this revision for the sake of completeness. *Stenandrium dulce* has a broad geographic range, extending from the southern United States to Chile.

Vegetatively, plants of *Stenandrium* are often inconspicuous. Several of the species bear their leaves at or near ground level. Although these plants are commonly referred to as acaulescent, they have an underground rhizome that bears a cluster of leaves at its apex. *Stenandrium barbatum* is somewhat intermediate between these acaulescent species and those with elongate, leafy stems. In this species the rhizomes frequently become aerial, although the leaves of the current season are typically clustered at their apices. In many individuals of *S. barbatum,* there is slight internodal elongation as well. Leaves of *Stenandrium* are either opposite or whorled depending on the species. The blades are usually entirely green and membranous in texture. In *S. nanum,* however, they have a pale green or whitish coloration along the major veins (also present in some individuals of *S. subcordatum*) and a coriaceous texture. The inflorescence consists of a lax to dense, bracteate spike. The bracts are green and vary from small (ca. 2.5 mm long) and subulate to large (ca. 21 mm long) and obovate. The flowers consist of a five-parted calyx and corolla, four short, monothecous stamens, an inconspicuous staminode, and a bicarpellate gynoecium. The corolla is inconspicuously bilabiate and the limb usually appears somewhat actinomorphic, or at least the lobes are all similar in form. Only in *S. subcordatum* is the corolla distinctly zygomorphic with the lobes of the upper lip conspicuously reduced in size relative to the lobes of the lower lip. The fruit is an ellipsoid capsule bearing four pubescent seeds.

Lindau (1895) placed *Stenandrium* in his

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subfamily Acanthoideae, tribe Aphelandreae, an assemblage of tropical American genera with a corolla imbricate in bud and with an upper lip, an androecium of four monothecous stamens, and tricolpate pollen. Bremekamp (1965) maintained this status for *Stenandrium* in his suggested revision of infrafamilial classification in the Acanthaceae. He noted that members of this tribe are distinguishable by a distinctly bilabiate corolla. This is not the case in *Stenandrium,* however, which usually has a subactinomorphic corolla suggestive of Bremekamp's Stenandriopsideae. Because infrafamilial classification in the Acanthaceae is unclear at the present time, no change in tribal status is suggested for *Stenandrium.*

The closest morphological relatives of *Stenandrium* that occurr in the region covered by this revision are *Aphelandra* (Mexico through South America) and *Holographis* (endemic to Mexico). These three genera appear to be extremely closely related. In Mexico, where each genus has been thoroughly studied, they can be distinguished by the following key:

1a. Corolla subactinomorphic, the lobes more or less similar in form (or the upper lip considerably reduced in size with respect to the lower lip in *S. subcordatum*), the upper lip divided nearly to its base into two prominent, obovate lobes greater than 2.5 mm long; plants acaulescent (the leaves clustered at or near the ground) or caulescent; corolla pinkish or purplish (rarely white); anthers included in corolla tube; stigma funnelform ____ *Stenandrium*

1b. Corolla zygomorphic, the lobes dissimilar in form, the upper lip entire to emarginate, or if bilobed with lobes greater than 2 mm long, the lobes not obovate and usually not more than one-half the length of the upper lip; plants caulescent; corolla yellow, orange, red, pinkish, purplish, or white; anthers usually partially or completely exserted from corolla tube; stigma bilobed or funnelform.

  2a. Corolla red or yellow, 30–70 mm long; bracts conspicuous, 9–50 mm long, (3–)5–15 mm wide, often tinged with pink or purple and sometimes toothed ____ *Aphelandra*

  2b. Corolla yellow, pinkish, purplish, or white, 7–18 mm long; bracts inconspicuous, 1–5(–11) mm long, 0.5–2.5(–5) mm wide, green, entire ____ *Holographis*

It is evident from the above key that the distinctions among these genera are subtle at best. Although I believe all three genera should be maintained as such, mutually exclusive characters are not well developed among them. The characters and trends separating *Aphelandra* and *Holographis* are discussed in more detail by Daniel (1983). The distinctions between *Stenandrium* and *Holographis* are further discussed by Daniel (1984). Despite their close relationship, *Stenandrium* and *Aphelandra* are usually readily distinguishable. The large, strongly zygomorphic corollas, usually well-exserted stamens, and conspicuous, often colored and/or toothed bracts of *Aphelandra* are not encountered in *Stenandrium.* Using these generic distinctions, however, several southern Central and South American species described in *Aphelandra* should be transferred to *Stenandrium.*

Stenandrium in the West Indies and South America has not been thoroughly studied yet. Cursory examination of the 15 or so species described from the West Indies reveals that none of the species of the North and Central American mainland occur there. Indeed, all species known from the West Indies have been described as endemic to that region. Although I examined a limited amount of material from South America in order to better understand species circumscriptions and application of names, species from this region are also in need of further study. Because species from South America are so poorly known and the relationships among them and to the Mexican species are still largely undetermined, I have used a conservative species concept in this revision.

TAXONOMY

Stenandrium Nees in Lindl., Introd. Nat. Syst. Bot., 2nd edition, 444. 1836, nom. cons. TYPE: *Stenandrium mandioccanum* Nees.

Gerardia L. Sp. Pl. 610. 1753, pro parte.

Acaulescent (arising from a woody rhizome or caudex) or caulescent perennial herbs or subshrubs to 5 dm tall. Leaves opposite or whorled (4 per node), sessile or petiolate. Inflorescence of axillary or terminal, elongate or head-like, usually pedunculate spikes, the flowers sessile, subtended by 2 paired, isomorphic bractlets and a bract; bracts green, variable in shape, conspicuously ciliate in several species; bractlets subulate to linear to lanceolate. Calyx 5-lobed, the lobes divided nearly to the base, usually lance-subulate, equal or subequal in size; corolla pink, purple, or white, glabrous or pubescent on the outer surface (the trichomes sometimes restricted to the lower-central lobe), imbricate, the lower-central lobe outermost in bud, the tube cylindric, apically ampliate into a short throat, the throat pubescent within, the limb bilabiate, 5-parted, appearing subactinomorphic to bilabiate, the upper lip bilobed, the lower lip trilobed, the lobes obovate, rounded to truncate at apex; androecium of 4 stamens and a staminode, the stamens subdidynamous, included, the filaments short (usually ca. 1 mm long), the anthers monothecous, pubescent, the staminode borne between the posterior pair of stamens, usually shorter than the filaments and lacking an anther; pollen prolate to spheroidal, tricolpate (in ours as examined); style terminal, filiform, flared at apex into an asymmetrically funnelform stigma. Capsule ellipsoid, glabrous or pubescent. Seeds 4 (or fewer by abortion), laterally flattened, suboval in outline, the surface variously pubescent, the trichomes often with barbs, or branches.

Distribution. Southern North America (from about Lat. 33°N southward), West Indies, Central America, and South America.

KEY TO THE SPECIES OF *STENANDRIUM* IN MEXICO AND ADJACENT REGIONS

1a. Plants caulescent (internodal elongation clearly evident, the leaves not clustered at or near the ground level).
  2a. Leaves whorled, 4 per node.
    3a. Plants sprawling; leaves 6–14 mm long; peduncles 0.5–7 mm long; bracts 1–1.5 mm wide; calyx 5.5–8.5 mm long, the lobes purplish near apex .... 1. *S. verticillatum*
    3b. Plants erect; leaves 11–25 mm long; peduncles 20–110 mm long; bracts 1.5–2 mm wide; calyx 3.5–5.5 mm long, the lobes not purplish near apex .... 2. *S. manchonense*
  2b. Leaves opposite.
    4a. Nodes callous; leaves coriaceous, the upper surface glabrous, pale green or whitish along major veins, the lower surface punctate-pitted; bractlets 0.7–1 mm wide .... 3. *S. nanum*
    4b. Nodes not callous; leaves membranaceous, the upper surface pubescent, concolorous, the lower surface not punctate-pitted; bractlets 0.3–0.7 mm wide.
      5a. Leaves congested, vertical or nearly so, oblanceolate to spatulate, 2–9 mm wide; capsule 9–14 mm long; seeds 3–5.5 mm long, 2.5–4 mm wide; plants of the Chihuahuan Desert .... 4. *S. barbatum*
      5b. Leaves not congested, horizontal or spreading, ovate to elliptic to obovate, 7–45 mm wide; capsule 5.5–9(–13) mm long; seeds 1.5–3.5 mm long, 1–2.5 mm wide; plants occurring south of the Chihuahuan Desert.
        6a. Bracts lance-subulate to subulate, 1–1.5 mm wide; seeds covered with rigid, papilla-like trichomes (rarely restricted to the margin) usually lacking branches or barbs .... 5. *S. chameranthemoideum*
        6b. Bracts obovate, 2.5–7(–12) mm wide; seeds covered with bristle-like trichomes bearing lateral barbs or branches .... 6. *S. pedunculatum*
1b. Plants acaulescent (leaves clustered at or near the ground level).
  7a. Bracts lance-subulate, 4.5–7 mm long, 0.5–1.5 mm wide; leaves truncate to cordate at base, not decurrent on the petiole .... 7. *S. subcordatum*
  7b. Bracts lanceolate to ovate to elliptic to obovate to strap-shaped, 6–21 mm long, 1.5–7.5 mm wide; leaves rounded to acute to attenuate at base, usually decurrent on the petiole, or plants leafless at anthesis.
    8a. Leaf blades glabrous (although usually inconspicuously glandular along the basal portion of lower surface) or plants leafless at anthesis; bractlets linear to linear-lanceolate, tapering from above the middle if at all; capsule entirely pubescent; plants of the northern Sierra Madre Occidental .... 8. *S. pilosulum*
    8b. Leaf blades pubescent (rarely glabrous or only ciliate near base) at anthesis; bractlets subulate to lance-subulate, tapering from or below the middle; capsule glabrous or pubescent only above the middle; plants occurring east and south of the northern Sierra Madre Occidental.
      9a. Internodes never elongated, plants strictly acaulescent, solitary; leaves spreading, ovate to elliptic (if oblanceolate or strap-shaped then 40–100 mm long and plants with peduncles 100–200 mm long), pubescent (rarely glabrous) with trichomes 0.2–1 mm long; seminal trichomes with flexuous or downward pointing lateral barbs or branches; plants not restricted to the Chihuahuan Desert .... 9. *S. dulce*
      9b. Internodes often with slight elongation evident, plants commonly forming dense mats; leaves vertical or nearly so, oblanceolate to spatulate (8–60 mm long and plants with peduncles 5–35 mm long), conspicuously pubescent with trichomes 1–4 mm long; seminal trichomes usually with conspicuously recoiled lateral barbs or branches; plants restricted to the Chihuahuan Desert .... 4. *S. barbatum*

1. **Stenandrium verticillatum** Brandegee, Zoe 5: 237. 1906. TYPE: Mexico. Puebla: El Riego, 18°26′N, 97°24′W, July 1905, *C. Purpus 1238* (holotype, UC!; isotypes, F!, GH!, MO!,

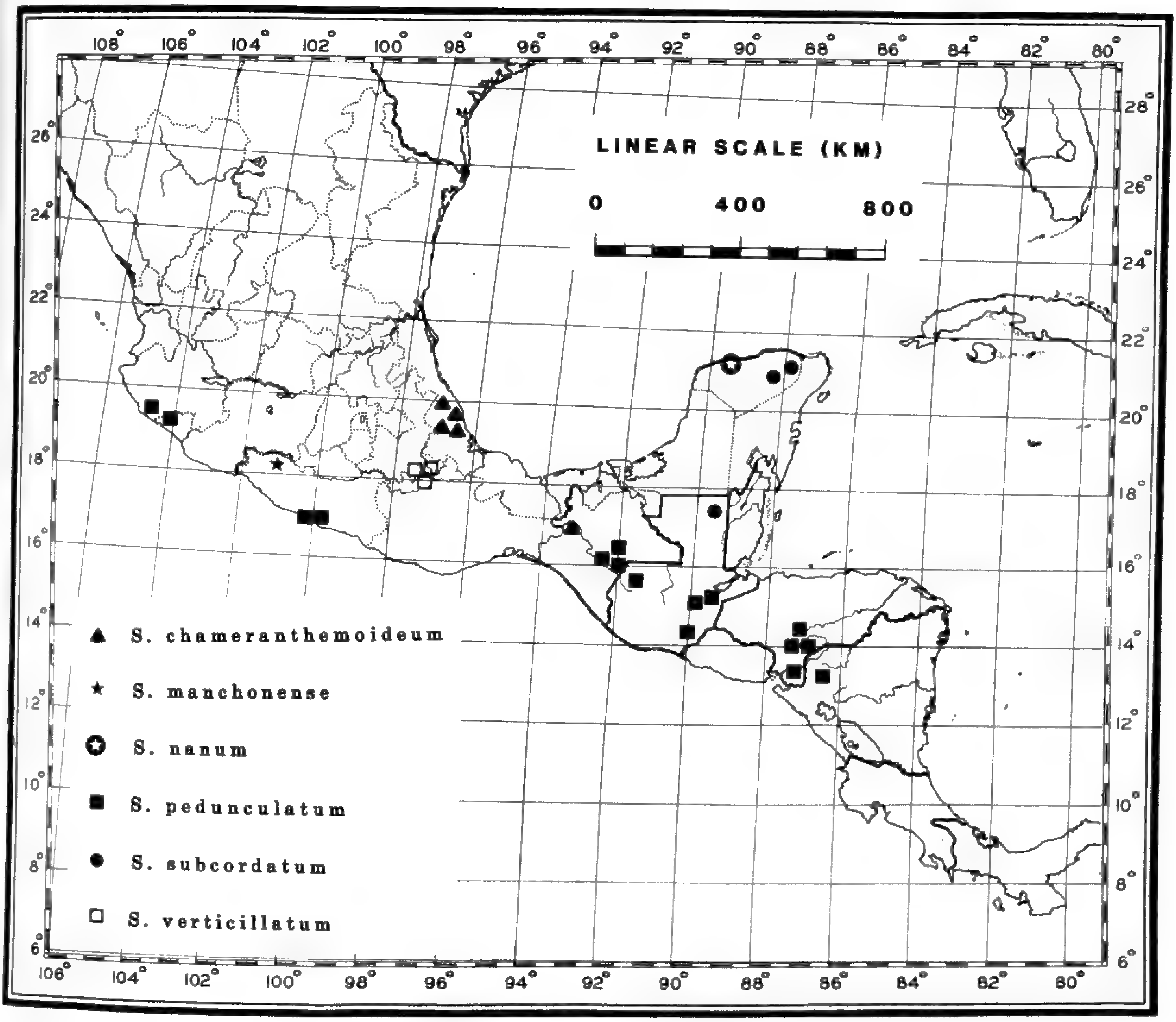

FIGURE 1. Distribution of *Stenandrium chameranthemoideum, S. manchonense, S. nanum, S. pedunculatum, S. subcordatum,* and *S. verticillatum.*

NY!, POM!, US!). *Gerardia verticillata* (Brandegee) Blake, Contr. Gray Herb. 52: 101. 1917.

Sprawling caulescent herb to 10 cm tall from a woody base. Stems subquadrate to terete, evenly pubescent with retrorse to flexuous trichomes 0.1–1.2 mm long. Leaves whorled, 4 per node, subsessile to short-petiolate, the petioles 0.5–5 mm long, the blades obovate to elliptic to suborbiculate, 6–14 mm long, 4–7.5 mm wide, 1.2–2 times longer than wide (the lowermost leaves often reduced in size or scale-like), rounded to acute at apex, attenuate at base, the surfaces pubescent, the lower more densely so, the margin ciliate. Inflorescence of axillary or terminal, sessile or pedunculate spikes to 1.5 cm long, the peduncles 0.5–7 mm long, the spike axes pubescent like the stems; flowers opposite to subopposite along the axes. Bracts lanceolate to lance-ovate, 4–7 mm long, 1–1.5 mm wide, pubescent like leaves. Bractlets linear to lance-subulate, 2–5.5 mm long, 0.5–0.8 mm wide, pubescent like leaves. Calyx 5.5–8.5 mm long, the lobes 5–8 mm long, purplish near apex, pubescent like leaves. Corolla rose-colored, 8–12 mm long, glabrous on outer surface, the tube 5–6 mm long, the upper lip 3–5 mm long with lobes 2.5–4 mm long, the lower lip 3–5.5 mm long with lobes 2.5–5 mm long. Stamens 1.5–2 mm long, the anthers 1.3–1.5 mm long. Capsules 7–8.5 mm long, sparsely pubescent to nearly glabrous; seeds 2.5–3 mm long, 2–2.5 mm wide, pubescent with bristle-like trichomes bearing lateral barbs or branches.

Distribution. Known only from the arid Tehuacán Valley (Fig. 1) of southern Mexico (Puebla and Oaxaca) where it was collected at eleva-

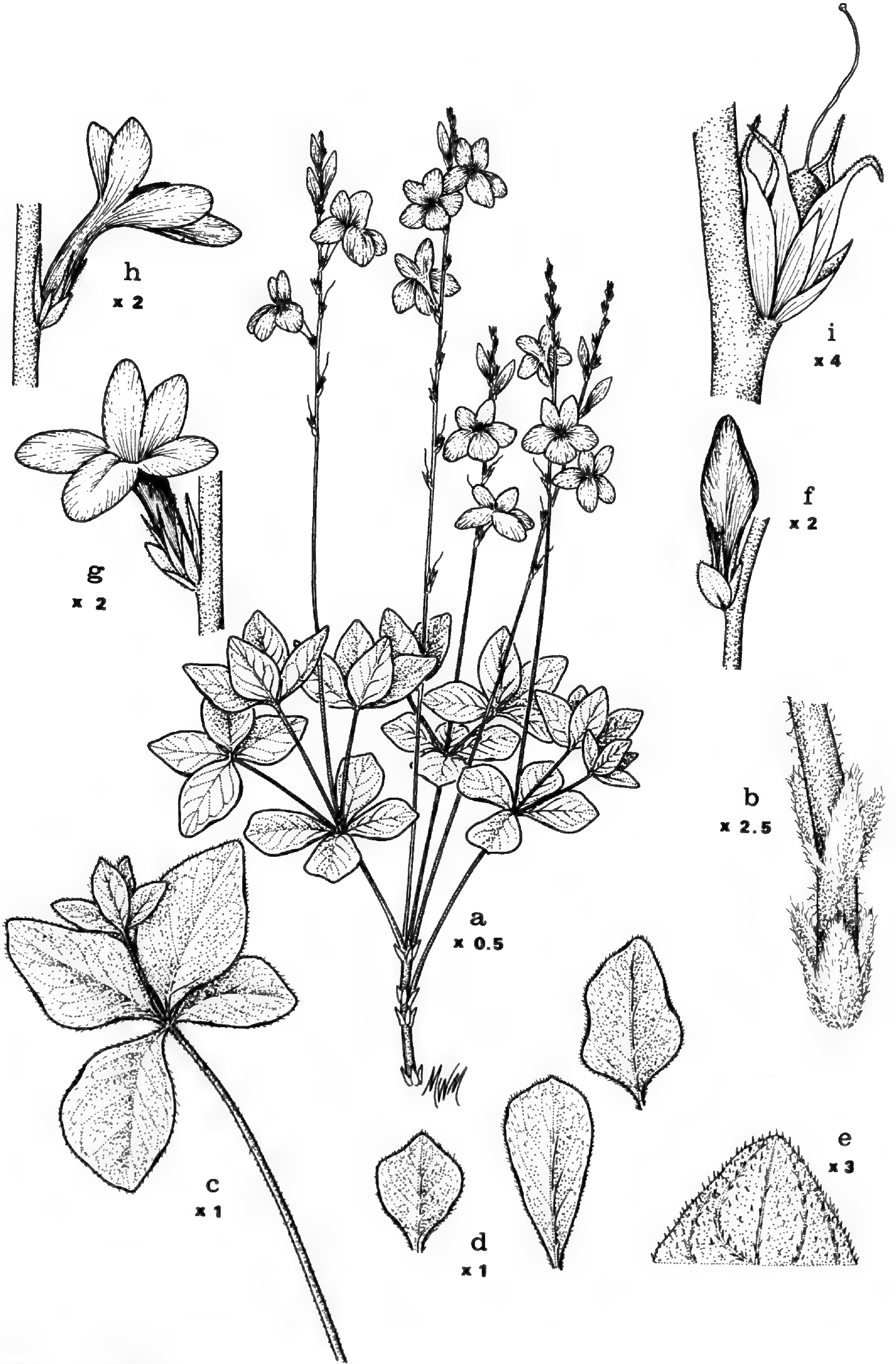

FIGURE 2. *Stenandrium manchonense.*—a. Habit.—b. Lower nodes showing scale-like leaves.—c. Upper node with whorled leaves.—d. Leaves showing variation in form.—e. Leaf apex.—f. Floral bud.—g. Flower.—h. Flower (side view).—i. Developing (immature) capsule.

tions between 2,000 and 2,700 meters (May–July).

Additional specimens examined. MEXICO. OAXACA: Los Naranjas, vic. of San Luis Tultitlanapa, Puebla, *C. Purpus 3083* (F, GH, MO, NY, UC, US). PUEBLA: Cerro de Castillo, *C. Purpus 2512* (UC); Acatitlán, *C. Purpus 3939* (UC).

This species is known from four collections of C. A. Purpus. It can be distinguished by its low, sprawling habit, short whorled leaves, and apically purplish calyx lobes. It is similar to *S. manchonense,* with which it shares a caulescent habit and whorled leaves with a low length to width ratio.

2. **Stenandrium manchonense** T. F. Daniel, sp. nov. TYPE: Mexico. Guerrero: Manchón, 18°07′N, 100°59′W, Distr. Mina, 10 June 1937, *G. Hinton et al. 10460* (holotype, US!; isotypes, DS!, ENCB!, F!, GH!, K!, LL!, MICH!, MO!, UC!). Figure 2.

Herba caulescens usque ad 2.5 dm alta; caules pubescentes trichomatibus 0.2–1 mm longis; folia verticillata, nodo quatuor, laminae ovatae vel suborbiculatae vel obovatae, 11–25 mm longae, 4–20 mm latae, 1–2.2-plo longiores quam latiores; inflorescentia spicata usque ad 11 cm longa; bracteae ovatae vel lanceolatae, 2.5–4 mm longae, 1.5–2 mm latae; bracteolae lanceolatae vel lanci-subulatae, 2–3.5 mm longae; calyx 3.5–5.5 mm longus; corolla 11–18 mm longa; capsula ignota.

Caulescent herb to 2.5 dm high. Stems subquadrate, pubescent with flexuous-crinkled trichomes 0.2–1 mm long. Leaves whorled, 4 per node, the lowermost leaves scale-like, sessile, elliptic to oblanceolate, 3–7 mm long, 2 mm wide, the upper leaves subsessile to short-petiolate, the petioles 0.5–3 mm long, the blades ovate to suborbiculate to obovate, 11–25 mm long, 4–20 mm wide, 1–2.2 times longer than wide, cuneate to attenuate at base, rounded to acute at apex, the margin ciliate, irregularly undulate, the undulations often somewhat angular, the surfaces pubescent. Flowers borne alternately in long-pedunculate, loose spikes to 21 cm long, the peduncles 2–11 cm long, the peduncles and rachis pubescent like the stems or the rachis lacking most of the longer trichomes. Bracts ovate to lanceolate, 2.5–4 mm long, 1.5–2 mm wide, the abaxial surface sparsely pubescent, the margin ciliate. Bractlets lanceolate to lance-subulate, 2–3.5 mm long, 0.5–0.8 mm wide, ciliate. Calyx 3.5–5.5 mm long, the lobes 3–5 mm long, sparsely pubescent to nearly glabrous on abaxial surface, the margins ciliate. Corolla color unknown, 11–18 mm long, the tube 5–7 mm long, the upper lip 6–8 mm long, the lower lip 8–11 mm long, the lobes subequal (or the lobes of the upper lip slightly shorter), 6–9 mm long, glabrous on the abaxial surface. Stamens 1.5–2 mm long, the anthers 1–1.2 mm long. Capsules not seen.

Distribution. Known only from the type, which was collected in southwestern Mexico (Guerrero) in oak woods at an elevation above 1,100 meters (June) (Fig. 1).

This species is readily distinguished from all other species of *Stenandrium* by its erect, caulescent habit and relatively large (11–25 mm long), whorled leaves with an undulate to angular margin. Its closest relative appears to be *S. verticillatum,* the only other caulescent species with whorled leaves in Mexico. *Stenandrium verticillatum* differs from *S. manchonense* by its scrambling, bushy growth form, smaller leaves and bracts, and longer calyx with purplish lobes. In addition, the inflorescence of *S. verticillatum* consists of a short (to 1.5 cm), few-flowered spike that is either sessile or borne on a peduncle 0.5–7 mm long. In *S. manchonense,* the inflorescences are longer (3.5–21 cm), many flowered, and borne on peduncles 2–11 cm long.

3. **Stenandrium nanum** (Standley) T. F. Daniel, comb. nov. *Pseuderanthemum nanum* Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 46. 1930. TYPE: Mexico. Yucatán: Silám, s.d., *G. Gaumer 1305* (holotype, F!).

Caulescent perennial herb to 10 cm tall, from woody rhizome. Stems subquadrate, multistriate, pubescent with straight trichomes 0.1–0.2 mm long, the nodes callous. Leaves opposite, petiolate, the petioles 3–6 mm long, pubescent like stem, the blades coriaceous, ovate to elliptic, 16–48 mm long, 10–27 mm wide, 1.6–2 times longer than wide, acute, sometimes unequal at base, acute to rounded at apex, the upper surface glabrous, pale green or whitish along the major veins, the lower surface punctate-pitted, with some trichomes along the midvein, the margin revolute. Inflorescence of axillary or terminal, sessile (or borne on peduncles to 1 mm long) spikes to 6 cm long. Bracts lanceolate, 6–7 mm long, 1.5 mm wide, pubescent like stem. Bractlets lanceolate, 4–5.5 mm long, 0.7–1 mm wide. Calyx 8–9 mm long, the lobes lance-subulate. Corolla 16–24 mm long, glabrous on outer surface, the tube 8–14 mm long, the lobes of the upper lip 5–6.5 mm long, the lobes of the lower lip 7–9 mm long. Stamens 2 mm long, the anthers 1.5 mm long. Capsule 8–9 mm long, glabrous. Seeds not seen.

Distribution. Known only from two collections from the Yucatán Peninsula of Mexico (Fig. 1).

Additional specimen examined. MEXICO. YUCATÁN: Progresso, s.d., *Gaumer 2295* (F).

Although Standley (1930) described this species in *Pseuderanthemum* and Leonard (1936) so maintained it, its proper position is in *Stenandrium.* Neither Standley nor Leonard discussed the androecial arrangement or capsular form of this species. In *Pseuderanthemum,* the androecium consists of two bithecous stamens containing tricolporate pollen and two staminodes and the capsule is stipitate. In *Stenandrium,* the androecium consists of four monothecous stamens with tricolpate (in ours as examined) pollen and the capsule lacks a stipe. Both specimens treated by Standley and Leonard have the diagnostic features of *Stenandrium.*

Stenandrium nanum is readily distinguished by the callous nodes and coriaceous leaves with a pale green or whitish coloration along the veins on the adaxial surface, and punctate-pitted abaxial surface. Its closest relative in Mexico appears to be *S. chameranthemoideum.* In addition to the above cited characters, it can be distinguished from *S. chameranthemoideum* by its longer, lanceolate bractlets and longer corollas. The ranges of these two species are not known to overlap.

4. **Stenandrium barbatum** Torr. & Gray, Pacific Rail. Rept. (Pope's Explor.) 2: 168. 1855. TYPE: United States. Texas: Pecos River, Mar. 1851, *C. Wright 1453* (holotype, GH!; isotypes, GH!, K!, NY!). *Gerardia barbata* (Torr. & Gray) Blake, Contr. Gray Herb. 52: 100. 1917.

Dwarf acaulescent or subcaulescent perennial herb to 12 cm tall from a stout woody rhizome, often forming small, dense mats. Leaves vertically oriented, sessile or short-petiolate, the petioles to 5(–25) mm long, the blades oblanceolate to spatulate, 8–60 mm long, 2–5(–9) mm wide, (3–)4–11 times longer than wide, tapering-attenuate at base, acute at apex, pubescent with a sparse to dense understory of erect or bent trichomes 0.1–0.2 mm long and an overstory (sometimes restricted to the margin) of flexuous trichomes 1–4 mm long, the margin entire. Inflorescence of leafy-bracteate, pedunculate spikes to 7 cm long, the peduncles to 35 mm long (not exceeding the leaves), pubescent with straight to retrorse trichomes 0.1–0.5 mm long and sometimes with flexuous trichomes 1–2 mm long as well, the spike axis pubescent with straight trichomes 0.1–0.2 mm long (sometimes very sparsely so), the flowers opposite to subopposite along the spike. Bracts oblanceolate to obovate to elliptic, 7–21 mm long, 2–4 mm wide, pubescent like the leaves. Bractlets subulate, 1.5–6 mm long, 0.3–0.6 mm wide, pubescent (sometimes sparsely so), usually with a mixture of eglandular trichomes and inconspicuous stipitate glands, the trichomes sometimes restricted to the margin and rarely consisting entirely of inconspicuous stipitate marginal glands. Calyx 4–8 mm long, the lobes subequal, lance-subulate, pubescent like bractlets. Corolla pinkish purple with white streaks on the lower lip, 13–21 mm long, glabrous or sparsely pubescent on the outer surface, the tube 4–5 mm long, the upper lip 5.5–9 mm long with lobes 4–8.5 mm long, the lower lip 6–11 mm long with lobes 6–9 mm long. Stamens 1.5–2 mm long, the anthers 1.5 mm long. Capsule 9–14 mm long, glabrous (rarely pubescent). Seeds 3–5.5 mm long, 2.5–4 mm wide, the testa densely pubescent with long, stiff, golden trichomes with usually conspicuously recoiled branches.

Distribution. Chihuahuan Desert regions of southern New Mexico, western Texas, eastern Chihuahua, and western Coahuila (Fig. 3) on limestone slopes and in arroyo gravel in desert associations of *Agave, Viguiera, Fouquieria, Larrea, Acacia, Dasylirion, Prosopis,* and *Yucca* up to pinyon-juniper communities at elevations from 750 to 1,350 meters (Mar.–Oct.).

Representative specimens examined. UNITED STATES. NEW MEXICO: Chaves Co., ca. 2 mi. W of Roswell, *Hinckley & Smith 4374* (SRSC); Doña Ana Co., 6 mi. W of El Paso, *Hanson s.n.* (TEX); Eddy Co., Carlsbad Caverns, *Nelson 11402* (DS, GH, POM, UC); Lea Co., Monument, *Castetter 70907* (UNM); Lincoln Co., 10 mi. NW of Riverside, *Goodman & Waterfall 4958* (GH); Otero Co., Sacramento Mts., *Van Devender & Betancourt s.n.* (ARIZ); Sierra Co., Elephant Butte Dam, *Nelson 6122* (UNM). TEXAS: Brewster Co., Terlingua Beds, on rd. to Agua Frio Ranch from 118, *Correll & Wasshausen 27843* (LL), *27897* (LL, UC); Culberson Co., Sierra Tinaja Pinta, San Antonio Peak, *Correll & Rollins 23873* (ENCB, LL); El Paso Co., Franklin Mountains W of El Paso, *Warnock 10328*

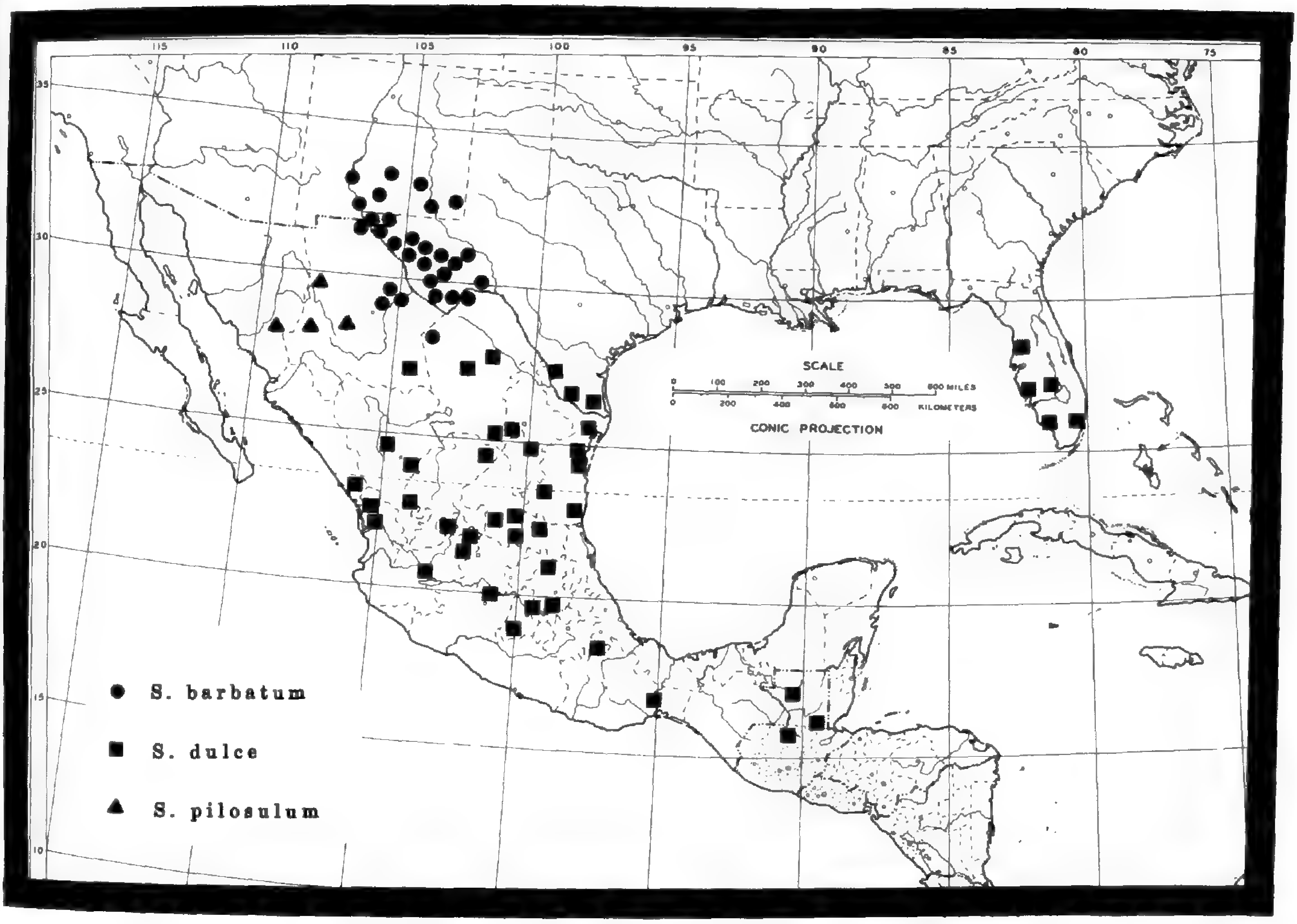

FIGURE 3. Distribution of *Stenandrium barbatum, S. dulce,* and *S. pilosulum.*

(LL), *Ferris & Duncan 2402* (CAS, DS), *Lundell & Lundell 16940* (LL), *Barlow s.n.* (UC), *Correll & Johnston 21834* (LL, UC), *Daniel 2713* (ASU, MICH, NY); Hudspeth Co., near summit of Hueco Mountains, 30 mi. E of El Paso, *McVaugh 8147* (CAS, DS, K, POM, TEX, UC); Jeff Davis Co., just W of Chispa summit, 30°43′N, 104°47′W, *Johnston et al. 10684* (LL); Pecos Co., NE side of Sierra Madera, ca. 25 mi. S of Ft. Stockton, *McVaugh 7914* (ASU, DS, TEX); Presidio Co., 2 mi. S of Shafter, *Warnock 46642* (SRSC); Reeves Co., 16 mi. NW of Toyahvale, Rt. 290, *Correll & Correll 38527* (ENCB, TEX); Terrell Co., 9⅓ mi. W of Dryden, *Cory 43864* (GH, TEX). MEXICO. CHIHUAHUA: near Cd. Juarez, *Pringle 8501* (ENCB, F, GH, K, MO, NY, POM, UC, US); ca. 9 mi. W of Ojinaga, *Henrickson & Lee 15821* (TEX). COAHUILA: just across river from mouth of Maravillas Creek, *Johnston et al. 10589.5J* (LL); Sierra de las Cruces, vic. of Santa Elena Mines, *Stewart 350* (GH, LL), *397* (LL).

Stenandrium barbatum is one of the better known and collected species due to its abundance in the United States and adjacent Mexico and its conspicuousness when in flower. The plants are usually copiously white hirsute and frequently form low, dense clumps with abundant pinkish purple corollas. Although the plants generally resemble other acaulescent species in habit, the woody rhizomes of *S. barbatum* are frequently aerial and often branch. The leaves and inflorescences are often clustered at the branch apices; however, slight internodal elongation during the growing season commonly results in a short (to 15 mm long) stem. Because of this unusual situation and because of some intergradation between the leaves and bracts, *S. barbatum* is listed in the key under both initial leads.

The closest relatives of *S. barbatum* appear to be *S. dulce* and *S. pilosulum.* The close relationship between *S. dulce* and *S. barbatum* is illustrated by a specimen from western Coahuila (*Stewart 397,* LL) which is treated as *S. barbatum* because of its narrow, oblanceolate to spatulate leaves, long trichomes, and glabrous corolla lobes. However in several characters, including the lance-elliptic bracts on some individuals, and often sparse pubescence, this collection is suggestive of *S. dulce,* which also occurs in western Coahuila.

Stenandrium barbatum (Fig. 4) is readily distinguishable from both *S. dulce* and *S. pilosulum* by its dense, mat-forming habit, nearly vertical, oblanceolate to spatulate leaves that are con-

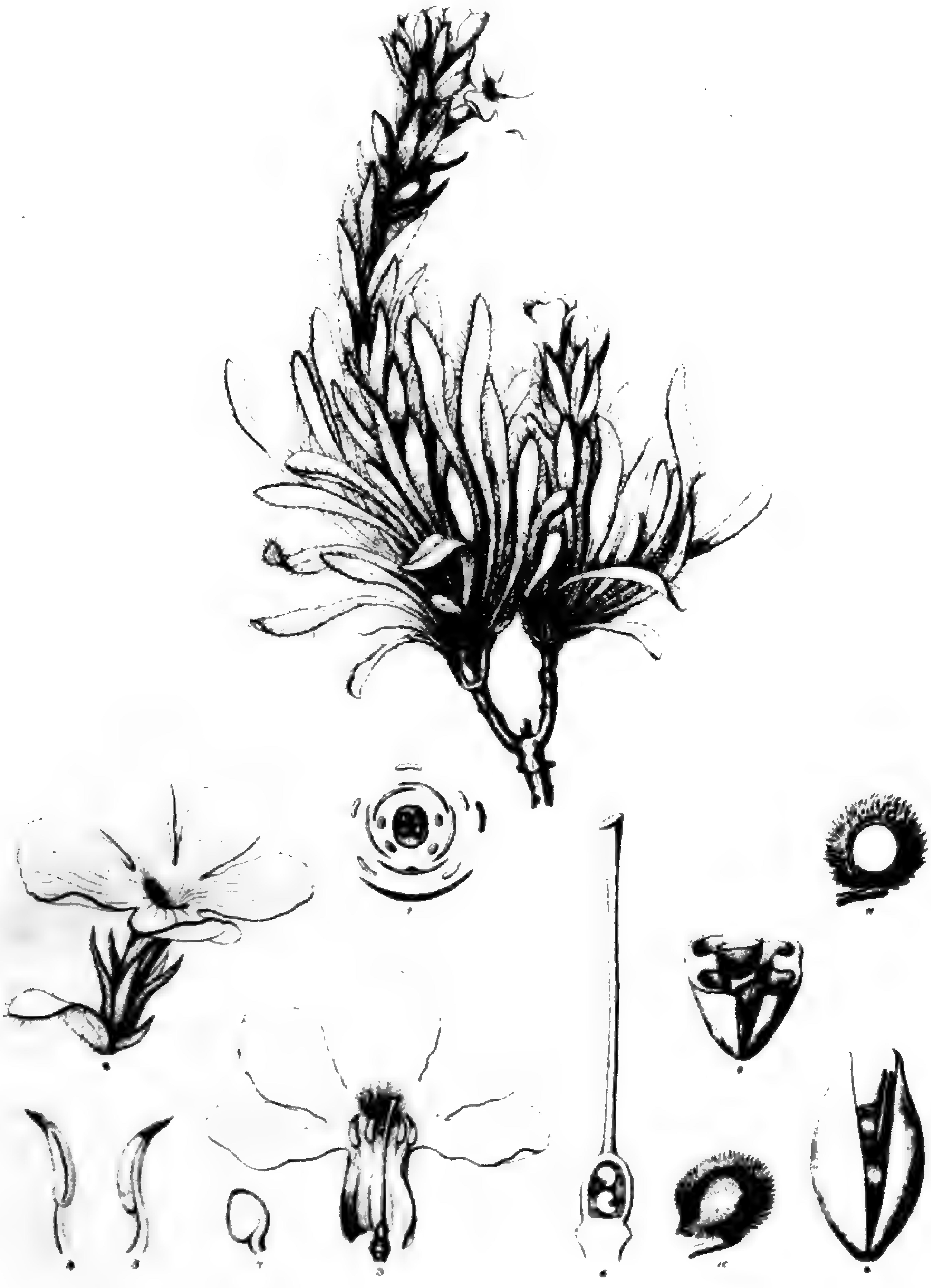

FIGURE 4. Illustration of *Stenandrium barbatum* from John Pope's report to the War Department in 1855.

spicuously pubescent with long (1–4 mm) stiff trichomes, leafy-bracteate spikes, and golden seminal trichomes that usually have recoiled lateral barbs or branches.

5. Stenandrium chameranthemoideum Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854: 139. 1854. TYPE: Mexico. Veracruz: Colipa, Mar. 1841, *F. Liebmann 10750* (lectotype, C!, here designated; isolectotype, US!). *Gerardia chameranthemoidea* (Oerst.) Blake, Contr. Gray Herb. 52: 100. 1917.

Caulescent perennial herb to 3 dm tall. Stems terete to subquadrate, pubescent with an understory of straight to retrorse trichomes 0.05–0.1 mm long and an overstory (sometimes sparse or absent) of flexuous trichomes 0.5–1 mm long or evenly pubescent with straight to retrorse trichomes 0.1–0.6 mm long. Leaves opposite, petiolate, the petioles 3–40 mm long, the blades ovate to elliptic to obovate, 16–82 mm long, 10–41 mm wide, 1.1–2.6 times longer than wide, attenuate-decurrent at base, rounded to acute at apex, the surfaces pubescent, sometimes sparsely so, the margin entire to irregularly undulate to subcrenulate. Inflorescences of axillary or terminal spikes to 10 cm long, the spikes sessile or borne on peduncles 2–15 mm long, the peduncles and spike axes pubescent like the stem or nearly glabrous, the flowers subopposite to alternate along the spike axes. Bracts lance-subulate to subulate, 2.5–7 mm long, 1–1.5 mm wide, the abaxial surface pubescent, the margin ciliate (or bracts very sparsely pubescent with short trichomes). Bractlets lance-subulate, 2–4 mm long, 0.5–0.7 mm wide, pubescent like bracts. Calyx 4–9 mm long, the lobes subequal, lance-subulate, 4–8.5 mm long, pubescent like bracts or nearly glabrous, the margin sometimes with inconspicuous glands as well. Corolla pinkish or whitish, 10–14 mm long, the tube 5–8 mm long, the upper lip 3.5–6 mm long with lobes 3.5–6 mm long, the lower lip 5–7 mm long with lobes 4.5–6.5 mm long, the anterior lobe pubescent or glabrous on abaxial surface, the other lobes glabrous. Stamens 2–2.5 mm long, the anthers 1.5–1.8 mm long. Capsule 6–9(–13) mm long, glabrous. Seeds 1.5–3.5 mm long, 1–2.5 mm wide, the testa covered with papilla-like trichomes (restricted to the margin in some plants) mostly lacking barbs.

Distribution. Eastern and southern Mexico (Veracruz and Chiapas) in canyons and on ridges at elevations from 250 to 1,000 meters (Sept.–Apr.) (Fig. 1).

Additional specimens examined. MEXICO. CHIAPAS: 13 km N of Berriozábal near Pozo Turipache and Finca El Suspiro, *Breedlove 31226, 39893* (CAS). VERACRUZ: Hac. de Sta. Barbara, *Liebmann 10749* (C); 22 km de Palma Sola Rumbo a Plan de Las Hayas, *Nevling & Gomez-Pompa 1026* (F); Zacuapan, *Purpus 5573* (UC); Cousoquitla, Zacuapan, *Purpus 8202* (GH, MO, NY, US); Pachuquilla, Puente Nacional, *Ventura A. 7364* (ENCB, MICH).

In the protologue of *S. chameranthemoideum,* Oersted (1854) cited two of Liebmann's localities in Veracruz, "Ved Colipa og Hacienda de Sta. Barbara." There are specimens on four sheets representing Liebmann's collections of this species at C. Three are from Colipa and bear the number *10750.* The other is from the Hacienda de Santa Barbara and is numbered *10749.* The lectotype is here designated as *Liebmann 10750* (specimen mounted on three sheets).

Unfortunately this species is not well represented in herbaria. The few known collections suggest that there is considerable variation in pubescence of *S. chameranthemoideum. Nevling & Gomez-Pompa 1026* contains three plants that differ markedly in pubescence of the stems, inflorescence axes, and bracts.

The plants from Chiapas differ from those collected in Veracruz by their cauline pubescence (evenly pubescent with straight to retrorse trichomes 0.1–0.6 mm long), somewhat longer capsules (8–13 mm), and testa ornamentation (papilla-like trichomes restricted to the margin). In all other characters, however, these collections closely resemble the more northerly ones.

The closest morphological relative of this species appears to be *S. nanum.* Both species have a caulescent habit, opposite leaves, and narrow bracts and bractlets. The distinctions between them are discussed under *S. nanum.*

6. **Stenandrium pedunculatum** (Donn.-Smith) Leonard, J. Wash. Acad. Sci. 32: 187. 1942. *Blechum pedunculatum* Donn.-Smith, Bot. Gaz. (Crawfordsville) 49: 457. 1910. TYPE: Guatemala. Zacapa: ca. 0.5 mi. on opposite side of river from Gualán, 15 June 1909, *C. Deam 6277* (holotype, US!; isotypes, GH!, MO!).

Erect or procumbent caulescent perennial herbs to 50 cm tall from a stout woody rootstock or rhizome. Stems pubescent with an understory of straight to retrorse trichomes, 0.2–0.5 mm long, and an overstory of flexuous trichomes, 0.5–1.5 mm long. Leaves opposite, petiolate, the petioles to 20 mm long, the blades ovate-elliptic to obovate, 12–90 mm long, 7–45 mm wide, 2–3.5 times longer than wide, subtruncate to long-attenuate at base, rounded to subacute at apex, pubescent on both surfaces (often sparsely so), margin entire to crenulate, usually ciliate. Inflorescence an axillary or terminal, often somewhat head-like, pedunculate spike to 35 mm long, the peduncles (0.5–)1.5–5 cm long, the flowers opposite or subopposite along the rachis. Bracts obovate, 5.5–14 mm long, 2.5–7(–12) mm wide, pubescent like leaves. Bractlets subulate, 1.5–5.5 mm long, 0.3–0.7 mm wide, glabrous or sparsely pubescent. Calyx 3–6.5 mm long, the lobes lance-subulate, 2.5–5.5 mm long, glabrous to sparsely pubescent. Corolla pink to white, 10–19 mm long, the tube 5–7 mm long, the upper lip 4–8 mm long, the lower lip 5.5–11 mm long, the lobes subequal, 4–10 mm long or lobes of the lower lip to 1.3 times longer than those of the upper lip, the lower-central lobe pubescent on abaxial surface. Stamens 1.5 mm long, the anthers 1 mm long. Capsule 5.5–8 mm long, glabrous or sparsely pubescent above the middle. Seeds 2–3 mm long, 1.5–2.5 mm wide, pubescent with long, bristle-like trichomes with lateral barbs or branches.

Distribution. Western and southern Mexico (Jalisco, Colima, Guerrero, and Chiapas) and northern Central America (Guatemala, Honduras, and Nicaragua) in forests, especially along streams, and on grassy slopes at elevations from near sea level to 1,350 meters (May–Dec.) (Fig. 1).

Representative specimens examined. MEXICO. CHIAPAS: Venustiano Carranza, above Finca Carmen, along rd. from Acala to Pugiltik, *Ton 2990* (F, LL, MICH, US); La Trinitaria, along rd. to Boqueron W of Hwy. 190 at point 18 km SW of La Trinitaria, *Breedlove 42253* (MO). COLIMA: ca. 16 mi. WNW of Santiago, *McVaugh 14972* (MICH), *15734* (MICH). GUERRERO: 20 mi. NE of Acapulco, *Barkely et al. 17M722* (TEX). JALISCO: Pueblo Careyitos, near Chamela, *Pérez J. 1739* (ASU). GUATEMALA. HUEHUETENANGO: Sierra de los Cuchumantes, between Santa Ana Hista and Netón, *Steyermark 51400* (F). JUTIAPA: vic. of Jutiapa, *Standley 75318* (F). ZACAPA: Sierra de las Minas, near electric plant of Río Hondo, *Standley 74009* (F). HONDURAS. CHOLUTECA: mountains near El Banquito, *Williams & Molina R. 10796* (F). EL PARAISO: Orillas del Río Lizapa, Llano de Lizapa, *Molina R. 3955* (F, MO). MORAZÁN: drainage of Río Yeguare near San Francisco, *Molina R. 218* (F, GH), *Williams 15911* (DS, F, GH, MO). NICARAGUA. ESTELÍ: Cerro de las Animas, NE of Estelí, *Standley 20325* (F).

This widely distributed species exhibits considerable variation in stem length, bract size, and pubescence. Plants of *S. pedunculatum* are distinguishable from other Mexican species by their caulescent habit, opposite leaves, obovate bracts, and relatively short capsules. The specimens from Colima differ from some of the more southerly collections by their shorter (1–3 cm long) stems. In other characters, however, they are identical with the latter.

Leonard (1942) noted the similarities between *S. pedunculatum* and *S. mandioccanum* Nees of southern South America, the distinguishing characters being the pubescent capsules and densely retrorse-pubescent stems of the latter species. Examination of several specimens of *S. mandioccanum* from Brazil and Argentina reveals that these characters will not distinguish the two species. Several specimens of *S. pedunculatum* have pubescent capsules and the plants of *S. mandioccanum* that I examined all had strongly antrorse cauline trichomes. In fact, my cursory examination suggests that specimens referred to *S. pedunculatum* and *S. mandioccanum* may be part of the same species. Based on the few specimens of *S. mandioccanum* available to me, the distinctions in the following couplet serve to separate the taxa:

a. Cauline trichomes uniform in length, antrorse; plants of southern South America .... *S. mandioccanum*
b. Cauline trichomes consisting of an understory of straight to retrorse trichomes and an overstory of longer, flexuous trichomes; plants of southern North America and northern Central America .... *S. pedunculatum*

Perhaps these differences are more reflective of varieties of one species than separate species. Until *S. mandioccanum* and its relatives in South America have been thoroughly studied, however, it seems prudent to maintain these taxa at their present status and avoid possible future nomenclatural reductions.

7. **Stenandrium subcordatum** Standley, J. Arnold Arbor. 11: 48. 1930. TYPE: Mexico. Yucatán: Chichen Itzá, 3 June 1929, *J. Bequaert 20* (holotype, GH!).

Acaulescent perennial herb to 1 dm tall. Leaves petiolate, the petioles 10–57 mm long, pubescent with flexuous trichomes, the blades ovate to elliptic, 19–56 mm long, 13–24 mm wide, 1.2–2.9 times longer than wide, truncate to cordate (often asymmetric) at base, the blade not decurrent on the petiole, rounded to acute at apex, the surfaces pubescent, the upper surface sometimes pale green to whitish along the major veins, the margin entire to irregularly undulate, ciliate. Inflorescence a pedunculate spike to 100 mm long, the peduncles (5–)20–65 mm long, pubescent with flexuous trichomes 0.2–1 mm long, the flowers alternate to subopposite along the rachis. Bracts lance-subulate, 4.5–7 mm long, 0.5–1.5 mm wide, pubescent on abaxial surface, the margin ciliate. Bractlets subulate, 2.5–4 mm long, 0.5–0.7 mm wide, pubescent like bracts. Calyx 4–6 mm long, the lobes subulate, 4–5.5 mm long, pubescent like bracts. Corolla pinkish purple, 14–17 mm long, the tube 8–9 mm long, the upper lip 3.5–5 mm long with lobes 3–4 mm long, the lower lip 5–8 mm long with lobes 5–7.5 mm long, the lower-central lobe sparsely pubescent to nearly glabrous on the abaxial surface. Stamens 1.5 mm long, the anthers 1.1 mm long. Capsule 5.5–8 mm long, pubescent (trichomes sometimes very sparse). Seeds 1.5–2 mm long, 1–1.5 mm wide, covered with hair-like papillae.

Distribution. Known only from the state of Yucatán in Mexico and the department of Petén in Guatemala (Fig. 1) where the plants grow in clearings, dense forests, and along dry arroyos (Mar.–July).

Additional specimens examined. MEXICO. YUCATÁN: Chichen Itzá, Valladolid rd., *Lundell & Lundell 7511* (LL, MICH); Chichen Itzá, *Steere 1451* (MICH); Tizimín, *Swallen 2530* (MICH). GUATEMALA. PETÉN: Uaxactum, *Bartlett 12283* (CAS, K, MICH, TEX).

This rarely collected species is readily distinguishable from other Mexican species of *Stenandrium* by its leaf blades which are truncate to subcordate at the base and not decurrent along the petiole. *Stenandrium subcordatum* also has a distinctly zygomorphic corolla, more suggestive of the corolla in species of *Holographis* than that of other species of *Stenandrium,* with the lobes of the upper lip only about one-half the size of those of the lower lip. Unlike the corolla in species of *Holographis,* however, the corolla of *S. subcordatum* has an upper lip divided nearly to its base with obovate lobes. The affinities of *S. subcordatum* are with *S. dulce* from which it can be distinguished by the above mentioned characters as well as its shorter and narrower bracts and shorter capsules.

Perhaps the closest morphological relative of this species is *S. lyonii* J. R. Johnston of Venezuela. Both species have ovate to elliptic, basally truncate leaf blades sometimes with a whitish or pale green coloration along the major veins on the adaxial surface. Although *S. lyonii* was originally described as acaulescent (Johnston, 1908), examination of the type reveals it to be subcaulescent with slight internodal elongation. Other specimens of *S. lyonii* examined from Venezuela are conspicuously caulescent. These species can be distinguished by the following couplet:

a. Plants subcaulescent to caulescent; bracts (6–) 7–10 mm long; bractlets 0.3–0.5 mm wide; corolla 8–13 mm long; capsule glabrous; plants of northern South America .... *S. lyonii*
b. Plants acaulescent; bracts 4.5–7 mm long; bractlets 0.5–0.7 mm wide; corolla 14–17 mm long; capsule pubescent (sometimes sparsely so); plants of the Yucatán Peninsula .... *S. subcordatum*

8. Stenandrium pilosulum (Blake) T. F. Daniel, comb. nov. *Gerardia pilosula* Blake, Contr. Gray Herb. 52: 101. 1917. TYPE: Mexico. Chihuahua: vicinity of Madera, 27 May–3 June 1908, *E. Palmer 317* (holotype, GH!; isotype, US!).

Acaulescent perennial herb to 7.5 cm tall from a woody rhizome, the rhizome bearing numerous fleshy roots along its length. Leaves (plants often leafless or nearly so at anthesis) ascendant, petiolate, the petioles to 15 mm long, the blades oblanceolate to narrowly elliptic to lanceolate (to ovate), 11–30 mm long, 3–7(–10) mm wide, 2.8–4.7 times longer than wide, attenuate to decurrent at base, acute to rounded at apex, the margin entire, eciliate, the surfaces glabrous (although the lower surface inconspicuously glandular along the basal portion) and punctate-pitted. Inflorescence consisting of pedunculate spikes to 30 mm long, the peduncles 5–35 mm long, nearly glabrous or pubescent with retrorse to erect trichomes 0.05–0.2 mm long, the flowers opposite to subopposite along spike axis, sessile. Bracts ovate to narrowly elliptic to obovate, 6–11 mm long, 1.5–4.5 mm wide, pubescent like peduncles although the trichomes more numerous and the margin inconspicuously ciliate with trichomes 0.05–0.3 mm long. Bractlets linear to linear-lanceolate, 6–10 mm long, 0.5–1 mm wide, pubescent like bracts. Calyx 7–14 mm long, the lobes linear-subulate to linear-lanceolate, subequal, 6.5–13.5 mm long, pubescent like bracts. Corolla purplish, 10–23 mm long, the tube 6–15 mm long, the upper lip 3–8 mm long, the lower lip 4–8.5 mm long, the lobes subequal, 3–7.5 mm long, the lobes and tube glabrous or sparsely pubescent on the abaxial surface, the lower-central lobe often densely pubescent. Stamens 2.5–3 mm long, the anthers 1.5 mm long. Capsule 9–12 mm long, pubescent over the entire surface. Seeds 3–4 mm long, 3–3.5 mm wide, densely pubescent with long, bristle-like trichomes bearing lateral barbs or branches.

Distribution. Sierra Madre Occidental of western Chihuahua and eastern Sonora (Fig. 3) on gravelly slopes in pine-oak associations at elevations from 1,720 to 2,250 meters (Mar.–May).

Additional specimens examined. MEXICO. CHIHUAHUA: 4 mi. S of Guerrero, *Correll & Johnston 21612* (ASU, LL, NY, US); 2 mi. E of Yepachic, *Spaulding 75-3-58* (ARIZ). SONORA: ca. 5 mi. W of Yécora, *Hubbell s.n.* (ARIZ); 7 mi. NW of Yécora, *Moran et al. 21965* (ENCB).

This little known species was described by Blake (1917) as *Gerardia pilosula* based on a single collection from Chihuahua. Recent collections have been either unidentified or misidentified. Plants of *S. pilosulum* are readily recognized by their diminutive stature and ascendant, glabrous (though inconspicuously glandular) leaves (which are often absent at anthesis). Although its affinities to other species were not noted in the protologue, it is morphologically similar to *S. dulce*, from which it can be distinguished by the following couplet:

a. Plants leafless at anthesis or leaves glabrous; bracts not conspicuously ciliate, the margin pubescent with trichomes 0.5–0.3 mm long; bractlets linear to linear-lanceolate, tapering to apex from above the middle if at all; capsule entirely pubescent; plants restricted to the northern Sierra Madre Occidental of Sonora and Chihuahua .... *S. pilosulum*

b. Plants leafy at anthesis, leaves pubescent; bracts conspicously ciliate, the trichomes (0.3–)0.5–2 mm long; bractlets subulate to lance-subulate, tapering to apex from at or below the middle; capsule glabrous or pubescent on upper half; plants occurring east and south of Sonora and Chihuahua .... *S. dulce*

9. Stenandrium dulce (Cav.) Nees in DC., Prodr. 11: 282. 1847. *Ruellia dulcis* Cav., Icon. Pl. 6: 62, t. 585, f. 2. 1801. TYPE: Chile. Concepción: near Talcahuano, Née herbar. (not seen). *Gerardia dulcis* (Cav.) Blake, Contr. Gray Herb. 52: 101. 1917.

Crossandra fascicularis Benth., Pl. Hartweg. 22. 1839. TYPE: Mexico. Jalisco: Lagos, 1837, *T. Hartweg 182* (holotype, K!; isotypes, GH!, K!). *Stenandrium fasciculare* (Benth.) Wasshausen, Phytologia 12: 427. 1965.

Stenandrium dulce (Cav.) Nees var. *floridanum* A. Gray, Syn. Fl. N. Amer. 2(1): 327. 1878. TYPE: United States. Florida: Indian River, 1894, *E. Palmer 350* (holotype, GH!). *Stenandrium floridanum* (A. Gray) Small, Fl. Southeast U.S. 1st edition. 1085. 1903. *Gerardia dulcis* (Cav.) Blake var. *floridana* (A. Gray) Blake, Contr. Gray Herb. 52: 101. 1917.

Stenandrium guatemalense Leonard, Publ. Carnegie Inst. Wash. 461: 212. 1936. TYPE: Guatemala. Alta Verapaz: Cubilguitz, 1892, *H. von Turckheim 3588* (holotype, US!; isotypes, GH!, K!).

Stenandrium mexicanum Leonard, Kew Bull. 1938: 62. 1938. TYPE: Mexico. México: Temascaltepec, San Lucas, 7 July 1933, *G. Hinton et al. 4292* (holotype, K!; isotypes, ARIZ!, GH!, MO!, US!).

Acaulescent perennial to 20 cm tall from stout rootstock or rhizome. Leaves (subsessile) petiolate, the petioles 5–65 mm long, the blades ovate to ovate-elliptic (to oblanceolate to strap-shaped), 13–100 mm long, 4–44 mm wide, 1.5–5.5(–18) times longer than wide, rounded to acute to attenuate (to decurrent along petiole) at base, acute to rounded (rarely emarginate) at apex, the surfaces pubescent (rarely glabrous), usually glandular-punctate, the margin entire, crenulate, or somewhat irregularly undulate, flat to slightly revolute, ciliate or eciliate. Inflorescence a subsessile or pedunculate, head-like or usually elongate spike to 85 mm long, the peduncles 5–200 mm long, the peduncle and rachis pubescent with trichomes 0.1–1.5 mm long or nearly glabrous, the flowers sessile, alternate or opposite along the rachis. Bracts lanceolate to elliptic (rarely oblanceolate, obovate, or strap-shaped), (6–)9–20 mm long, 2–7.5 mm wide, usually conspicuously 3-nerved, the outer surface densely pubescent or glabrous, the margin ciliate with trichomes (0.3–)0.5–2 mm long. Bractlets lance-subulate to subulate, 3–9 mm long, 0.3–1(–1.5) mm wide, ciliate or eciliate, sometimes inconspicuously glandular along the margin. Calyx 4–11 mm long, the lobes lance-subulate, 3.5–9 mm long, often ciliate at tips and usually inconspicuously glandular along the margin. Corolla pink to purple, marked with white within, (10–)16–20(–27) mm long, the tube (6–)9–16 mm long, the upper lip 3–11 mm long with lobes 2.5–10 mm long, the lower lip 4–14 mm long with lobes 3.5–11 mm long, the lower-central lobe usually pubescent on abaxial surface, the other lobes mostly glabrous. Stamens 1.5–2.5 mm long, the anthers 1.2–1.5 mm long. Capsule 6.5–12 mm long, glabrous or sparsely pubescent above the middle. Seeds 2.5–4 mm long, 2–3 mm wide, pubescent with long, appressed, bristle-like trichomes bearing flexuose or downward-pointing lateral barbs or branches.

Distribution. Southern United States (Florida and Texas), Mexico (Aguascalientes, Chihuahua, Coahuila, Durango, Hidalgo, Jalisco, México, Michoacán, Nayarit, Nuevo León, Oaxaca, Puebla, San Luis Potosí, Sinaloa, Tamaulipas, and Zacatecas), Guatemala, Colombia, Ecuador, Peru, Chile, Bolivia, and Argentina. Plants in Mexico and adjacent regions (Fig. 3) occur in arid associations (with *Opuntia, Larrea, Condalia, Berberis, Flourensia, Yucca,* and *Parthenium*), grasslands, deciduous thorn-forest, and pine-oak communities at elevations from 20 to 2,700 meters. In Florida, the species occurs in seasonally wet pinelands (Feb.–Oct.).

FIGURE 5. Illustration of *Stenandrium dulce* from A. J. Cavanilles's "Icones et Descriptiones Plantarum," published in 1791.

Representative specimens examined. UNITED STATES. FLORIDA: Citrus Co., just N of Homosassa Springs, *Eyles & Eyles 8260* (GH); Collier Co., Fla. 846, Seminole Indian Reservation, *Lakela 28987* (RSA); Dade Co., Biscayne Bay, *Curtiss 1945* (GH, K, US); Highlands Co., Rt. 18, 5 mi. W of Childs, *Brass 15363* (GH, US); Hillsborough Co., Old Memorial Highway, ca. 1.5 mi. from Rt. 580 NW of Tampa, *Lakela et al. 25084* (GH, RSA), *Lakela 25243* (GH); Lee Co., vic. of Fort Meyers, *Standley 71* (GH, US); County undetermined, locality unspecified, *Simpson s.n.* 1889 (DS, US). TEXAS: Hidalgo Co., Santa Ana Natl. Wildlife Refuge, *Fleetwood 7007* (TEX); Starr Co., Hwy. 4, E of Fort Ringgold, *Runyon 3256* (TEX); Webb Co., Rio Grande, Laredo, *Palmer 1005* (GH, K); Willacy Co., ca. 4 mi. NNW of headquarters, Sauz Ranch, *Johnston 53266.6* (TEX). MEXICO. AGUASCALIENTES: 30 km al W de Aguascalientes, *Rzedowski 14020* (ENCB). CHIHUAHUA: 14 mi. SE of Rancho La Gloria on rd. to Cerros Blancos, 27°15′40″N, 104°09′W, *Johnston et al. 9003* (LL, MEXU). COAHUILA: Sierra del Pino, *Johnston & Muller 393* (GH, LL); vic. of Saltillo, *Palmer 529* (US), *578* (US). DURANGO: San Juan del Alamo, *Robert 4024* (ENCB); ca. 12 mi. NW of Canatlán along Rt. 39, *Pinkava et al. 9373* (ASU). HIDALGO: N of Jacala de Ledesma, *Clark 7011* (MO). JALISCO: near rd. to León, Gto., 5 mi. SE of jct. at Lagos de Moreno, *McVaugh 17798* (MICH); near Guadalajara, *Pringle 11353* (GH). MÉXICO: Temascaltepec, Chorrera, *Hinton et al. 754* (ENCB, GH, K, LL, MO, NY, US), *8080* (K, LL, MICH, NY, US); Peñon, *Hinton et al. 6086* (F, GH, K, MO, NY, US). MICHOACÁN: Loma Santa Maria, vic. of Morelia, *Arsène 2756* (US). NAYARIT: 23 mi. NNW of Tepic along Hwy. 15, *Marcks & Marcks 1182* (LL); between Acaponeta and Pedro Paulo, *Rose 3316* (US); 1–3 km W of El Venado along rd. from Ruiz to Jésus Maria, *Breedlove & Almeda 45287* (CAS). NUEVO LEÓN: 1–2 mi. SW of Pablillo, *Correll & Johnston 19928* (LL, US). OAXACA: 28 km NW of La Ventosa along Trans-Isthmian Hwy., *King*

636 (MICH). PUEBLA: vic. of San Luis Tultitlanapa, near Oaxaca, *Purpus 3340* (F, MO, UC). SAN LUIS POTOSÍ: Bagre, Minas de San Rafael, *Purpus 5229* (F, MO, UC, US). SINALOA: between Concepción and Rosario, *Rose 1534* (US); between Rosario and Colomas, *Rose 3179* (US). TAMAULIPAS: 2 mi. S of Marcella, between Peña Nevada and Hermosa, *Stanford et al. 2522* (DS, US). ZACATECAS: 6.5 mi. from San Tiburcio on rd. to Concepción del Oro, *Johnston 2612* (TEX). STATE UNDETERMINED: locality unknown (probably Nayarit or Sinaloa), *Sessé et al. 2174* (MA). GUATEMALA. PETÉN: Chiche, Petén, *Lundell 3707* (F, MICH).

Stenandrium dulce (Fig. 5) is the most widely distributed species in the genus and the most morphologically variable. Plants from North and Central America show considerable variation in height, pubescence, leaf form, size of the corolla, bract shape, and density of flowers in the inflorescence. Several species have been described or proposed based on some of the diverse forms of *S. dulce.* Leonard (1936) described *S. guatemalense* and distinguished it from related Mexican species by its narrow, sharply acuminate, and pilose bracts. Later (Leonard, 1938), he described *S. mexicanum* and characterized it by broad leaf blades, obtuse or rounded bracts, and large purple flowers. He noted its close relationship to *S. dulce* from Chile. Gibson (1974) included *S. guatemalense* within *S. dulce* in her treatment of the Acanthaceae of Guatemala and *S. mexicanum* is here included in this common species. In 1932 Leonard labelled several diminutive, small-leaved specimens of *S. dulce* from north-central Mexico with a manuscript name at US. Several specimens from Michoacán and an unusual form from west-central Mexico were likewise given manuscript names. Leonard obviously believed *S. dulce* to be a South American species and the various morphological entities from North and Central America to be worthy of specific status. Examination of a large number of specimens from throughout America leads me to conclude that all of Leonard's entities are part of a single morphologically diverse species that lacks consistent gaps among the various forms. Species with large ranges and considerable morphological variability are well known in several other genera of American Acanthaceae (e.g., *Aphelandra aurantiaca* (Scheidweiler) Lindley, *Carlowrightia arizonica* A. Gray, *Elytraria imbricata* (Vahl) Pers., *Justica carthagenensis* Jacq., *Ruellia geminiflora* H.B.K., and *Tetramerium nervosum* Nees).

One of the entities "recognized" by Leonard is worthy of some discussion. Specimens from southern Sinaloa and northern Nayarit (*Breedlove & Almeda 45287*; *Marcks & Marcks 1182*; *Rose 1534, 3179, 3316*; *Sessé et al. 2174*) are rather distinctive by their long, narrow (3–18 times longer than wide), and strap-shaped or oblanceolate (rarely elliptic) leaves, long (100–200 mm) peduncles, and glabrous corollas. In addition, the bracts vary from emarginate to rounded to acute at the apex and the bractlets and calyces of these plants are frequently glabrous. In specimens of *S. dulce* from other regions the leaves are usually wide (1.5–3.5 times longer than wide) and ovate or ovate-elliptic; the peduncles are usually less than 100 mm long; the lower-central petal lobe is usually pubescent; the bracts are acute at the apex; and the bractlets and calyces are normally conspicuously pubescent. Further, most of the specimens from Sinaloa and Nayarit are from regions of deciduous thorn-forest (*Breedlove & Almeda 45287* is from a savanna) whereas all other collections of *S. dulce* from west-central Mexico are from grassland communities at relatively high elevations. This assemblage may eventually prove worthy of varietal or specific status because of the minor morphological tendencies and apparent ecological and geographical distinctness. The general overlap of all of the characters mentioned above between these plants and more typical specimens of *S. dulce* preclude formal taxonomic recognition of this assemblage until the variation from throughout the range of *S. dulce* has been considered. Indeed, some plants of *S. dulce* from Florida (e.g., *Simpson s.n.,* 1889) closely resemble the specimens from Sinaloa and Nayarit.

Asa Gray (1878) recognized *S. dulce* var. *floridanum* on the basis of glabrous plants with only the upper bracts and bractlets lightly hirsute-ciliate. Long (1970) noted the very similar appearance of *S. dulce* var. *floridanum* with *S. dulce* var. *dulce* and claimed the former differed by usually having the upper bracts and bractlets glabrous or sparingly hirsute-ciliate rather than hirsute. This distinction does not hold up when specimens from throughout the range of the species are examined. Long further noted the close relationship of this variety with *S. mexicanum* and the relationship between *S. faciculare* and *S. dulce.* Most of the variation encountered in *S. dulce* in the region covered by this revision can be seen among the diverse specimens from peninsular Florida.

The various forms comprising *S. dulce* are held together by a suite of characters including the acaulescent habit, usually conspicuously petiolate leaves lacking long (1–4 mm), white, shaggy trichomes, and lanceolate to elliptic (rarely obovate or strap-shaped) bracts. Several Mexican species, including *S. pilosulum* and *S. barbatum,* appear to be closely related to or even derived from *S. dulce.* These latter species are restricted to northern Mexico and adjacent regions of the United States, north and west of the range of *S. dulce.* The ranges of these three species are not known to overlap. The distinctions among them are summarized in the key and are further discussed elsewhere in the text.

EXCLUDED TAXA

Stenandrium pelorium Leonard, Wrightia 2: 83. 1960. = *Holographis peloria* (Leonard) T. F. Daniel, Madroño 31: 90. 1984.

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NOTE ADDED IN PROOF: After this revision went to press, a chromosome count of $n = 26$ was obtained for *S. barbatum.* Relationships among *Stenandrium, Holographis,* and *Aphelandra* are discussed further by Daniel et al. (Syst. Bot. 9: 346–355. 1984) based on known chromosome counts of species in these genera.

A BIBLIOGRAPHY OF NUMERICAL PHENETIC STUDIES IN SYSTEMATIC BOTANY

Bernard R. Baum,[1] Thomas Duncan,[2] and Raymond B. Phillips[3]

Introduction

The purpose of this paper is to supplement the bibliography in a review of numerical phenetics (Numerical phenetics: its uses in botanical systematics. 1981. T. Duncan & B. Baum, Annual Rev. Ecol. Syst. 12: 387–404). Due to space limitations, a listing of numerical phenetic applications in botany could not be included in that review. This compilation of applications in plant groups is provided below. Papers that deal with the development of methods with only incidental mention of plant groups have been excluded. These studies illustrating applications of numerical phenetics are listed according to the taxon covered by each author(s) (Table 1). Each study is listed using the lowest taxonomic rank to include all organisms examined. For studies involving two or more taxonomic groups of equal rank, the study is listed under each group mentioned. Genus is the lowest taxonomic rank used. We have included the references cited in Sneath and Sokal (1973) in order to provide a complete listing for botany arranged according to taxonomic group. Our literature search ends with 1982. The references included here complement the recent bibliography of cladistic studies of plant groups (A bibliography of botanical cladistics. I. 1981. V. Funk & W. H. Wagner, Jr. Brittonia 34: 118–124). These two bibliographies and the review cited above will serve as a basic guide to numerical taxonomic studies in botany. We would appreciate knowing of any additions, deletions, or other corrections to our list.

Table 1. Numerical phenetic applications in botany arranged according to plant group studied.

Taxonomic Group	Reference(s)
Abelmoschus	Chheda & Fatokun, 1982; Singh et al., 1980
Abronia	Pimentel, 1981
Acacia	Farrell & Ashton, 1978
Aegilops	Kaltsikes & Dedio, 1970a, 1970b; Tsuji & Tsunewaki, 1976; Tsunewaki et al., 1976
Aesculus	Wyatt & Lodwick, 1981
Allium	Jacobsen, 1979, 1980
Allium subg. *Molium*	Badr & Elkington, 1978
Allium subg. *Rhizirideum*	El-Gadi & Elkington, 1977
Alloplectus	Stearn, 1968, 1969
Alternaria	Joly, 1969
Andropogoneae (Poaceae)	Clayton, 1972a, 1972b
Anemia subg. *Coptophyllum*	Mickel, 1962
Anigozanthos	Hopper, 1977, 1978
Antennaria	Beals, 1968
Anthyllis	Gonnet, 1980
Apocynum	Balbach, 1965
Aquilegia	La Roche, 1980; Taylor & Campbell, 1969
Arachis	Brown et al., 1975; Stalker et al., 1979
Arceuthobium	Hawksworth et al., 1968
Archochaetiaceae	Gabany, 1979
Armoracia	Rhodes et al., 1969
Arundinelleae (Poaceae)	Clayton, 1970; Phipps, 1970, 1972a, 1972b, 1972c, 1972d
Asclepias	Gilmartin, 1980a
Asclepiadaceae	Gilmartin, 1974, 1980b, 1981
Atriplex	Kowal & Kuzniewski, 1959
Athyrium	Seong, 1972
Avena	Baum, 1970, 1974, 1975, 1977; Baum & Brach, 1975; Baum & Lefkovitch, 1972a, 1972b, 1973
Baptisia	Flake & Turner, 1968
Basidiomycetes	Kendrick & Weresub, 1966
Beta sect. *Vulgares*	Ford-Lloyd & Williams, 1975
Betula	Baranov & Basargin, 1979

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Ann. Missouri Bot. Gard. 71: 1044–1060. 1984.

TABLE 1. Continued.

Taxonomic Group	Reference(s)
Blue-green algae	Whitton, 1969
Blumea	Dakshini & Prithipalsingh, 1977
Boleum	Gomez-Campo, 1981
Brassica	Cole & Phelps, 1979; Dass & Nybom, 1967; Vaughan & Denford, 1968; Vaughan et al., 1970; Yamasishi & Takayanagi, 1982
Brassiceae (Brassicaceae)	Clemente Munoz & Hernandez Bermejo, 1978
Brassicinae (Brassicaceae)	Takahata & Hinata, 1980
Bromeliaceae	Gilmartin, 1969a, 1969b, 1974, 1981
Bulbostylis	Hall et al., 1976
Bulnesia	Comas et al., 1979; Crisci et al., 1979
Bupleurum	Cauwet-Marc et al., 1978
Bursera	Mooney & Emboden, 1968
Cakile	Rodman, 1980
Calypogeia	Bischler & Joly, 1970
Campanula	Hubac, 1964, 1967, 1969
Campanulaceae	Dunbar & Wallentinus, 1976
Candida	Kocková-Kratochvilová, 1970; Shechter, 1973; Shechter et al., 1972
Cannabis	Small et al., 1976
Capsicum	Eshbaugh, 1970; Pickersgill et al., 1979
Carex	Krzakowa et al., 1978
Carya	Stone et al., 1969
Cassia sect. *Apoucouita*	Irwin & Rogers, 1967
Caucalideae (Umbelliferae)	McNeill et al., 1969
Chamaesyce	Hassal, 1976
Chenopodiaceae	Williams & Ford-Lloyd, 1974
Chenopodium	Crawford, 1974; Crawford & Julian, 1976; Crawford & Reynolds, 1974; Kowal & Kuzniewski, 1959; Reynolds & Crawford, 1980
Chlorella	Cullimore, 1969
Chlorococcum	McGuire, 1969
Chlorodesmis	Ducker et al., 1965
Chrysobalanaceae	Prance et al., 1969
Chrysophyceae	Van Valkenburg et al., 1977
Chrysothamnus	McArthur et al., 1978
Cicer	Narayan & Macefield, 1976
Cirsium	Davidson, 1963
Citrus	Barrett & Rhodes, 1976
Clarkia	Bloom, 1976; Small et al., 1971
Clethra	Duncan, 1978
Coelorhachis	Clayton, 1969

TABLE 1. Continued.

Taxonomic Group	Reference(s)
Collomia	Wilken, 1978
Columnea	Stearn, 1968, 1969
Conidiobolus	King, 1976a, 1976b
Correa	Whiffin, 1977
Crotalaria	Bisby, 1970, 1973
Cucumerinae (Cucurbitaceae)	Dass et al., 1974
Cucurbita	Bemis et al., 1970; Rhodes et al., 1968
Cycadales	Petriella & Crisci, 1975
Cyrtathus	Ising & Fröst, 1969
Cyrtisus	Sneath, 1968
Dactylis	Cenci, 1982
Daucus	Small, 1978b
Debaryomyces	Kocková-Kratochvilová et al., 1978
Dermatophytes	Komenda et al., 1973; Landau et al., 1968; Shechter, 1973
Desmodium	Bhalla & Dakwale, 1977
Dichanthelium	Allred & Gould, 1978
Digitaria	Clayton, 1974
Dioscorea	Akoroda, 1982; Martin & Rhodes, 1977, 1978
Ectocarpaceae	Gabany & Russell, 1978
Elymus	Baum, 1979
Empetraceae	Moore et al., 1970
Epilobium	Bowman, 1980; Fitter, 1980
Eragrostis	Costanza et al., 1979
Erechtites	Drury & Randal, 1969
Ericaceae	Judd, 1979
Ericales	Watson et al., 1967
Eryngium	Hideux et al., 1978; Van der Pluym & Hideux, 1977a, 1977b
Eucalyptus	Banks & Hillis, 1969; Hopper et al., 1978; Kirkpatrick, 1974; Phillips & Reid, 1980; Whiffin, 1981
Eulophia	Hall, 1965
Euphorbieae	Hassal, 1976
Farinosae	Hamann, 1961
Festuca	Bidault, 1968; Bidault & Hubac, 1967; Parreaux, 1972
Fimbristylis	Hall et al., 1976
Flindersia	Whiffin, 1982a, 1982b
Fragaria	Jensen & Hancock, 1982
Fungi Imperfecti	Kendrick & Proctor, 1964
Fusarium	Whitney et al., 1968
Genisteae (Leguminosae)	Bisby & Nicholls, 1977
Gerronema	Machol & Singer, 1977
Gleasonia	Koek-Noorman, 1980
Gleicheniaceae	Duek et al., 1978
Glycine	Broich & Palmer, 1980; Edye et al., 1970

TABLE 1. Continued.

Taxonomic Group	Reference(s)
Glycine subg. *Glycine*	Newell & Hymowitz, 1978
Gossypium	Johnson & Thein, 1970
Haemanthus	Bjornstad & Friis, 1972
Hamamelidae	Barabe et al., 1981
Hansenula	Poncet, 1970
Haplopappus	Jackson & Crovello, 1971
Haplopappus Sect. *Blepharodon*	Ramon, 1968
Haptophyceae	Van Valkenburg et al., 1977
Helianthus	Schilling & Heiser, 1981
Helminthosporium	Ibrahim & Threlfall, 1966
Henriquezia	Koek-Noorman, 1980
Hesperomecon	Ernst, 1967
Hibiscus sect. *Furcaria*	Wilson, 1974
Holcus	Zandee & Glas, 1982
Hordeum	Baum, 1980; Booth & Richards, 1976; Kahler & Allard, 1981; Molina-Cano, 1976; Molina-Cano & Rossello, 1978; Nevo et al., 1979
Humulus	Small, 1978a, 1980
Hydrophyllum	Beckmann, 1979
Hydropus	Kiefer, 1979; Machol & Singer, 1977
Hyperthelia	Clayton, 1975
Hypoxylon	Whalley, 1976; Whalley & Greenhalgh, 1973a, 1973b, 1975a, 1975b
Jansenella	Phipps, 1972b
Juglans	Hills et al., 1974
Juniperus	Adams & Turner, 1970; R. P. Adams, 1977; Flake et al., 1969; Kelley & Adams, 1978
Klebsielleae	Barnett et al., 1975
Kluyveromyces	Poncet, 1973
Labiatae	Cheng, 1977; El-Gazzar & Watson, 1970
+*Laburnocytisus*	Sneath, 1968
Laburnum	Sneath, 1968
Laminaria	Chapman, 1973
Larrea	Yang et al., 1977
Leguminosae	Gilmartin, 1974
Leptographium	Kendrick & Proctor, 1964
Lesquerella	Curtis, 1975
Liliatae	Clifford & Williams, 1980
Limnanthaceae	Ornduff & Crovello, 1968; Parker, 1976
Limnanthes	Arroyo-Kalin, 1973
Lithophragma	Taylor, 1966
Lithospermum	Govoni, 1975
Lolium	Thomson, 1974

TABLE 1. Continued.

Taxonomic Group	Reference(s)
Lotus	Grant & Zandstra, 1968; Simon & Goodall, 1968
Loudetia	Lubke & Phipps, 1973
Lupinus	Riggins et al., 1977
Lychnis	McNeill, 1978
Lycoperdon	Demoulin & Schumacker, 1972
Lycopus	Webber & Ball, 1980
Lygodium	Duek et al., 1979
Magnoliatae	Young & Watson, 1970
Magnoliophyta	Dolph, 1976; Hill, 1980
Mangifera	Rhodes et al., 1970
Manihot	Rogers & Fleming, 1973
Meconella	Ernst, 1967
Medicago	Classen et al., 1982; Simon & Goodall, 1968; Yamada & Suzuki, 1974
Melandrium	McNeill, 1978
Melastomaceae	Gilmartin, 1981
Melilotus	Bukowiecki et al., 1976
Mentha	Olsson, 1967
Mentzelia	Hill, 1977
Menziesia	Hickman & Johnson, 1969
Micraira	Clifford, 1964
Mimulus	Wells, 1980
Montieae (Portulacaceae)	McNeill, 1974
Mosla	Cheng, 1980
Nanoplankton	Van Valkenburg et al., 1977
Nassauviinae (Compositae)	Crisci, 1974
Neottioideae (Orchidaceae)	Lavarack, 1976
Nocardia	Kurup & Schmitt, 1973
Nodulisporium	Van Valkenburg et al. 1977; Whalley & Greenhalgh, 1975a
Nymphaeaceae	Bukowiecki et al., 1972, 1974
Olea	Loukas & Krimbas, 1983
Oenothera	Rostanski, 1968, 1969
Oncidiinae (Orchidaceae)	Wirth et al., 1966
Ononis	Ivimey-Cook, 1968, 1969
Oplonia	Stearn, 1971
Orchidaceae	Clifford & Lavarack, 1974
Oryza	Janoria et al., 1976; Morishima, 1969; Morishima & Oka, 1960; Ng et al., 1981; Ogbe & Williams, 1978; Palanichamy & Siddiq, 1977; Shahi et al., 1969
Oryzopsis	Kam & Maze, 1974
Oxalis sect. *Ionoxalis*	Denton & Del Moral, 1976
Panicum	Lloyd & Thompson, 1978; Pernes et al., 1970

TABLE 1. Continued.

Taxonomic Group	Reference(s)
Parahebe	Garnock-Jones & Langer, 1980
Pennisetum sect. *Brevivalvula*	Brunken, 1979
Pennisetum	Beillard et al., 1980
Petunia	Natarella & Sink, 1974
Phaeophyta	Russell & Fletcher, 1975
Phaseolus	M. W. Adams, 1977; Sagar et al., 1976; Sahai & Rana, 1977
Phlox	Levin & Schaal, 1970; Levy & Levin, 1975
Phyllota	Jancey, 1966
Picea	Birks & Peglar, 1980; Gordon, 1976; La Roi & Dugle, 1968; Mitton & Andalora, 1981; Taylor & Patterson, 1980
Pichia	Poncet, 1967a, 1967b
Pieris	Judd, 1982
Pinophyta	Young & Watson, 1969
Pinus	Prus-Glowacki et al., 1978; Gambaryan, 1965; Jeffers & Black, 1963; Thielges, 1969
Piperaceae	Gilmartin, 1981
Plantago	Rahn, 1974; Warwick & McNeill, 1982
Platycarpum	Koek-Noorman, 1980
Platystemon	Ernst, 1967; Hannan, 1982
Pleurothallidinae (Orchidaceae)	Pridgeon, 1982
Poa	Williamson & Killick, 1978
Poaceae	Clayton & Cope, 1980; Clifford, 1965, 1969; Clifford & Goodall, 1967; Clifford et al., 1969; Hilu & Wright, 1982
Polygonum	McDonald, 1980
Pooideae (Poaceae)	MacFarlane & Watson, 1982
Populus	Pallardy & Kozlowsky, 1979
Portulaca	Gorske et al., 1979
Psilanthele	Stearn, 1971
Pteridophyta	Birks, 1976
Pyrola	Haber, 1983
Pyrus	Kajiura et al., 1979
Quercus	Hicks & Burch, 1977; Jensen, 1977a, 1977b; Jensen & Eshbaugh, 1976a, 1976b; Knops & Jensen, 1980; Olsson, 1975; Rushton, 1978, 1979
Ramalina	Sheard, 1978
Ranunculus	Duncan, 1980, 1981; Duncan & Estabrook, 1976
Raphanus	Lewis-Jones et al., 1982

TABLE 1. Continued.

Taxonomic Group	Reference(s)
Relbunium	Porto & Mariath, 1975
Rhizopus	Dabinett & Wellman, 1973
Rhododendron	King, 1977
Rhynchosia	Walraven, 1970
Rhytachne	Clayton, 1969
Rosa	Kuhns & Fretz, 1978
Rosa sect. *Pimpinellifoliae*	Roberts, 1977
Rubiaceae	Gilmartin, 1981; Hogeweg & Koek-Noorman, 1975
Sabatia	Bell & Lester, 1978
Saccharomyces	Kocková-Kratochvilová et al., 1969; Kocková-Kratochvilová, 1970
Saccharum	Gupta et al., 1978
Salix sect. *Sitchenses*	Crovello, 1968a, 1968b, 1968c, 1968d, 1969
Salvia	El-Gazzar et al., 1968; Johnson & Holm, 1968
Sarchina	Hubac, 1967
Sarcostemma	Johnson & Holm, 1968
Sarracenia	Schnell & Krider, 1976
Saxifraga	Jaworska & Nybom, 1967
Secale	Dedio et al., 1969a; Sencer & Hawkes, 1980
Sematophyllaceae	Seki, 1968
Setaria	Chikara & Gupta, 1980; Williams & Schreiber, 1976
Silene	Aeschimann et al., 1981; McNeill, 1978; Prentice, 1979
Sinapis	Vaughan & Denford, 1968
Solanum	Brown & Moss, 1976; Heiser, 1972; Heiser et al., 1965; Martin & Rhodes, 1979; Raeuber et al., 1978; Schilling, 1981; Schilling & Heiser, 1976; Soria & Heiser, 1961
Solanum sect. *Androceras*	Whalen, 1979
Solanum sect. *Solanum*	Edmonds, 1978
Solidago	Melville & Morton, 1982
Sorghum	Mendoza & Torregroza, 1978; De Wet & Huckabay, 1967; Gupta et al., 1978; Ivanyukovich & Malkina, 1978; Liang & Casady, 1966; Shechter, 1975
Spilanthes	Jansen, 1981
Spiranthes	Catling, 1981
Stellaria	Whitehead & Sinha, 1967
Stenotaphrum	Busey et al., 1982

TABLE 1. Continued.

Taxonomic Group	Reference(s)
Stipa	Barkworth, 1978; Barkworth et al., 1979
Stylidium	Coates, 1981
Stylosanthes	Burt et al., 1971; Mannetje, 1969
Suaeda	Ungar & Boucaud, 1974
Taphrina	Snider & Kramer, 1974a, 1974b
Thelypodieae (Brassicaceae)	Hauser & Crovello, 1982
Thuidiaceae	Gier, 1980
Tiarella	Taylor, 1971
Tithonia	La Duke, 1982
Trifolium	Mannetje, 1967; Parups et al., 1966
Trigonella	Simon & Goodall, 1968
Tripsacum	Stalker et al., 1977a, 1977b
Triticale	Dedio et al., 1969b; Kaltsikes, 1974
Triticeae (Poaceae)	Baum, 1977, 1978a, 1978b, 1978c, 1982; Baum et al., 1980; Baum & Tulloch, 1982; Tulloch et al., 1980
Triticum	Schulze-Motel, 1978; Syme & Thompson, 1981; Tsuji & Tsunewaki, 1976; Tsunewaki et al., 1976; Wrigley et al., 1981, 1982
Tsuga	Kessell, 1979
Ulmus	Jeffers & Richens, 1970; Melville, 1978
Umbelliferae	Gilmartin, 1980b; Hideux et al., 1978
Uredinales	Shipton & Fleischmann, 1969
Vaccinium	Smith, 1969; Van der Kloet, 1977b, 1978
Vaccinium sect. *Cyanococcus*	Van der Kloet, 1977a
Vella	Gomez-Campo, 1981
Verbena	Barber, 1982
Verbenaceae	El-Gazzar & Watson, 1970; El-Gazzar, 1974
Vernonia	Dakshini & Dadlani, 1976
Verticillium	Whitney et al., 1968
Vigna	Sahai & Rana, 1977
Viola	Gilmartin & Harvey, 1976
Vitis	Rogers & Rogers, 1978
Yeasts	Barnett et al., 1975; Jones, 1975
Zea	Camussi, 1979; Camussi et al., 1980; Casas et al., 1968; Doebley & Iltis, 1980; Fujino, 1980; Goodman, 1967, 1968; Goodman & Bird, 1977; Jancey, 1975; Bird & Goodman, 1977; Rhodes & Carmer, 1966; Tarcicio et al., 1978; Stalker et al., 1977a, 1977b
Zinnia subg. *Diplothrix*	Katz & Torres, 1965

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NOTES ON *SYMPHYTUM* (BORAGINACEAE) IN NORTH AMERICA

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ABSTRACT

In this paper I present the results of a morphological comparison of the North American material of *Symphytum* with herbarium material of European hybrid populations for which cytological data are available. In addition to *S. officinale* cytotypes and rarely *S. asperum,* also the hybrid *S.* × *uplandicum* Nym. is present in North America. A key to all taxa, *S. tuberosum* L., *S. asperum* Lepech., *S.* × *uplandicum* Nym. ($2n = 36$ and $2n = 40$), and the three cytotypes of *S. officinale* L. ($2n = 24$, 48, 40) is given.

Some species of the Old World genus *Symphytum* have escaped from cultivation (Ingram, 1961) and become naturalized in various habitats in North America. They usually grow on (damp) roadsides, in waste places and disturbed habitats, sometimes along ditches. Four species are dealt with in various floras:

Symphytum asperum Lepech. (Jepson, 1925; Fernald, 1950; Abrams, 1951; Munz & Keck, 1959; Hitchcock et al., 1959; Gleason, 1968; Rickett, 1966, 1971; Scoggan, 1979).
S. uliginosum Kern. (Fernald, 1950).
S. officinale L. (Fernald, 1950; Rydberg, 1954; Hitchcock et al., 1959; Steyermark, 1963; Rickett, 1966; Gleason, 1968; Scoggan, 1979).
S. tuberosum L. (Fernald, 1950; Rickett, 1966; Gleason, 1968).

Three species belong to subgenus *Symphytum* (= *Ramosa* Bucknall), one (*S. tuberosum*) to subgenus *Simplicia.* The subgenus *Symphytum* is characterized by branched stems and fusiform branched roots, subgenus *Simplicia* by simple stems and creeping tuberous roots. The representative of subgenus *Simplicia, S. tuberosum,* is readily identifiable by those features and will not be treated further in this paper. Moreover, this species seems to be rather local in North America (Rickett, 1966; Fernald, 1950). The three other species hybridize and form hybrid swarms consisting of F_1 and backcross hybrids (Gadella, 1972; Gadella & Kliphuis, 1973, 1978). *Symphytum officinale* is cytologically heterogeneous: $2n = 24$, $2n = 40$, $2n = 48$—cytotypes occur in various parts of Europe. *Symphytum asperum* ($2n = 32$) does not hybridize with the diploid ($2n = 24$) form of *S. officinale* in Europe but produces hybrids (and backcrosses) with the $2n = 40$ and $2n = 48$ cytotypes of *S. officinale.* The primary hybrids, with $2n = 36$, or $2n = 40$, are collectively known under the name *S.* × *uplandicum* Nyman. In Europe the parental species are largely allopatric with a very small zone of overlap in the northwest Caucasus (Kusnetsov, 1910). In the zone of overlap, hybridization does not occur because *S. officinale* and *S. asperum* grow at different altitudes. Apparently the hybrids arose outside the Causasus (Tutin, 1956; Wade, 1958). In many parts of western, northwestern, or central Europe the hybrid swarms are more common than the parental species. Because of the widespread use of *Symphytum officinale* and its hybrids in "green drinks,"[2] and as a fodder-plant (Farnsworth, 1979; Hills, 1976). Huizing et al. (1982) focused their attention on the presence or absence of the hepatotoxic pyrrolizidine alkaloids and on their possible use as chemotaxonomic markers. Lycopsamine, acetyllycopsamine, and symphytine or their isomers were found in the *S. officinale* cytotypes, echimidine and symphytine in *S. asperum.* The interspecific hybrids contained all alkaloids mentioned.

Consultation of many North American floras clearly showed that the hybrid *S.* × *uplandicum* is not reported from North America. Some years ago I received 38 herbarium sheets of *Symphytum* on loan from the U.S. National Museum (US) and 33 from Herbier Marie-Victorin, Botanical Institute of Montreal (MT). Identification of these plants made clear that *S.* × *uplandicum*

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[2] Green parts of comfrey are blended with water and the filtrate is used as a "green drink."

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was present in North America. For that reason I present in this paper the results of a morphological comparison of the North American material with herbarium material of European hybrid populations for which cytological and chemical data are available.

MATERIALS AND METHODS

Seventy-one herbarium sheets of North American plants of *Symphytum* were compared with collections of European plants and hybrids.

RESULTS

Of the 71 North American specimens, 57 plants were originally identified as *S. officinale*, but only 33 belong to that species. Although 45% of all plants (32 plants) belong to the interspecific hybrid *S.* × *uplandicum*, not a single plant of the herbarium collection from North America was referred to this taxon. Most plants that were referred to *S. asperum* appeared to belong to *S.* × *uplandicum* (nine sheets), some to *S. officinale* (four sheets), and only two plants proved to be correctly identified. Some plants were incorrectly assigned to *S. officinale* but appeared to belong to *S. asperum*. *Symphytum peregrinum* Ledeb. proved to be absent from North America—all sheets (three) under this name proved to belong to *S.* × *uplandicum*. At least two cytotypes of *S. officinale* occur in North America: $2n = 24$ or $2n = 48$ (these taxa are indistinguishable if the flower color of the latter is white; diploids are always white-flowered), and $2n = 40$. Twenty-nine sheets studied proved to belong to *S. officinale* (white-flowered plants: $2n = 24$ or $2n = 48$; purple-flowered plants: $2n = 48$). Plants with $2n = 40$ are usually purple-flowered and usually occur in very moist habitats. In the Netherlands the $2n = 40$ cytotype is very common in the low lying peat lands of Noord Holland, Utrecht, and Friesland. Populations with $2n = 40$ may have a much wider European distribution because some of the characters of this cytotype closely match those of plants from Hungary and southern Russia. These latter plants were referred to *S. uliginosum* Kern. by de Soo (1926) and to *S. tanaicense* Steven by Degen (1930). *Symphytum tanaicense* is the correct name. Four plants at US very closely match the $2n = 40$ cytotype of *S. officinale* in morphology. All other plants of *S. officinale* probably belong to the cytotype $2n = 48$ (or $2n = 24$). In this paper the plants with $2n = 40$ are assigned to *S. officinale* and not to *S. tanaicense* because the European plants with the same morphological characters have to be studied more carefully both morphologically and experimentally before we can arrive at more definite conclusions on the taxonomic status of *S. tanaicense*. In the following survey the species and hybrids will be described in more detail and a key to all species and hybrids will be given.

KEY TO THE NORTH AMERICAN SPECIES AND HYBRIDS

1a. Stems simple; roots tuberous, creeping .... *S. tuberosum* L.

1b. Stem branched; roots fusiform, branched 2

2a. Stem not winged; 90–200 cm long; leaves usually not decurrent (if so the decurrent wing on the stem not longer than 1 cm); corolla campanulate; connective not projecting beyond the thecae; fruits brown and dull, areolate-granulate 3

2b. Stem winged, 30–120 cm long; leaves always decurrent, usually along the entire internode; corolla urceolate, upper part of the corolla recurved; connective projecting beyond the thecae; fruits black and shining, not areolate-granulate but smooth 4

3a. Flowering stems very scabrid with curved subretrorse hairs, 90–200 cm long; calyx 3 mm long, divided to ¾ of its length; flower buds red, corolla sky blue, 9–14 mm long; corolla-scales lingulate, papillae of the margin of the corolla scales long and narrow .... *S. asperum* Lepech.

3b. Flowering stems scabrid or soft hairy, 90–140 cm long; calyx 5.5 mm long, divided to ⅔ of its length; flower buds purple or pink, corolla pink or blue-purple, 13–16 mm long; corolla scales triangular lanceolate; papillae of the margin of the corolla-scales short and broad 5

4a. Stems hispid, 30–120 cm long, soft to the touch; leaves without scabrous tubercular-based hairs, or, if present, the hairs not deciduous or prickly; marginal setae of calyx in an irregular pattern; calyx without tubercular-based scabrous hairs; corolla in bud white or purple; corolla white or purple, red (or intermediate between red and purple) at anthesis .... *S. officinale* L. ($2n = 24, 48$)

4b. Stems scabrous, 30–70 cm long; stems with prickly tubercular-based stiff and scabrous setae harsh to the touch; adaxial side of leaves with many scabrous tubercular-based (deciduous) hairs; marginal setae of calyx in a regular pattern; calyx with dorso-median and marginal row of hairs with tubercular base; flowers purple (rarely white), bud purple (rarely white) .... *S. officinale* L. ($2n = 40$)

5a. Indument of the stem harsh to the touch; prickly tuberculate based stiff scabrous hairs present; leaves not decurrent; indument of the adaxial side of the leaves as in 4b; indument of the calyx as in 4b; scale apex narrowly mucronate; corolla in bud purple, blue purple when in flower .... *S.* × *uplandicum* Nym. ($2n = 36$)

5b. Indument of the stem not harsh to the touch; prickly hairs absent; leaves sometimes decurrent to 1 cm; indument of adaxial side of leaves: many short appressed stiff setae, which are not deciduous; indument of calyx margin as in 4a; scale apex broad rotundate; corolla pink in bud and pink or pinkish blue in flower .... *S.* × *uplandicum* Nym. ($2n = 40$)

Symphytum officinale L. Sp. Pl. 136. 1753. TYPE: Herb. Linn. 185/1, photo.

S. bohemicum Schmidt, Fl. Boem. 3: 13. tab. 263. 1795.

S. tanaicense Steven, Bull. Soc. Imp. Naturalistes Moscou 24: 577. 1851.

S. uliginosum Kerner, Oesterr. Bot. Z. 13: 227. 1863.

Stem to 120 cm long, distinctly winged, hispid; the indument renders the stems soft to the touch; basal leaves lanceolate or ovate, to 60 cm long, acute at the apex, acuminate and attenuate at the base; lamina 10–40 cm long, 2–12 cm wide; petiole 2–20 cm long; middle and upper stem leaves of the same type, but much smaller; adaxial side of the leaves with many short and long hairs, which are never scabrid; sometimes these hairs have a tubercular base that is not deciduous; abaxial side of the leaves with long appressed hairs along the veins and many shorter hairs between the veins; the leaf base is decurrent from node to node; calyx to 8 mm long, divided to ¾ of its length, calyx lobes triangular lanceolate and acute, marginal stiff setae with an irregular distribution pattern; these marginal setae lack a tubercular base; corolla urceolate, 15–17 mm long, white or cream in diploids ($2n = 24$) and tetraploids ($2n = 48$), purple or red (or various intermediate colors between white and dark purple) in the tetraploids; stamens to 7 mm long, anthers longer than the filament and shorter than the corolla scales with which they alternate; connective projecting beyond the thecae; squamae of the corolla triangular-lanceolate, 7–7.5 mm long and 2 mm wide at the base; apex mucronate, papillae obtuse, papillae more densely crowded at the tip of the scale margin; fruit black and shiny, 4–5 mm long, 2–2.5 mm wide; reproduction: both cytotypes are obligate allogamous, they are strictly self-incompatible. The production of fruits (nutlets) varies considerably among different populations. Even plants with normal fertility have many flowers which produce only 3, 2, 1, or even 0 viable nutlets.

The diploid cytotype was assigned to *S. bohemicum* Schmidt by A. Murin and J. Majovsky (Acta Fac. Rerum Nat. Univ. Comenianae Bot. 29: 1982).

The exact status of *S. bohemicum, S. tanaicense* and *S. uliginosum* appears to require further investigation. The West European cytotype $2n = 40$ of *S. officinale* L. (q.v.) and *S. tanaicense* Steven are supposed to be very closely related or identical.

Specimens examined. CANADA. NOVA SCOTIA: Gran Pre Kings Co., 9 Aug. 1950, *Warren s.n.* (MT). ONTARIO: Comté de Prescott, 18 July 1935, *Rouleau 1132* (MT); Westport, 23 Sept. 1905, *Godfrey s.n.* (MT). QUEBEC: Abercorn, Co. de Brome, 23 June 1935, *Marie Victorin & Rolland-Germain 43251* (MT); Comté de Jacques Cartier, Pointe Claire, 18 July 1937, *Frère Cléonique 9297* (MT); Montreal, Mont Royal, 9 June 1944, *Rolland-Germain 70075* (MT); Montreal, Outremont, 14 June 1927, *Roy 63* (MT). U.S.A. GEORGIA: Tallapoosa, 1900, *Way s.n.* (US). MASSACHUSETTS: exact provenience unknown, 4 July 1906, *Knowlton s.n.* (US); exact provenience unknown, 12 Aug. 1888, *Sturtevant s.n.* (US). NORTH CAROLINA: Biltmore, 28 May 1897, *Anonymous 3429b* (US); Plainfield, 29 May 1879, *Tweedy s.n.* US); exact provenience unknown, 1880, *Hyams s.n.* (US). NEW JERSEY: Amsterdam Co., Amandale, 6 Oct. 1905, *Fisher s.n.* (US); Sussex Co., Stockholm, 18 July 1894, *Sickle s.n.* (US). NEW YORK: Hamburg, 4 July 1918, *Johnson 1158* (US); Syracuse, s.d., *Straub s.n.* (US); Warsaw, 21 June 1925, *Keeler s.n.* (US). VERMONT: Peacham, 30 June 1889, *Blanchard s.n.* (US); Peacham, 7 July 1892, *Stevens s.n.* (US). WASHINGTON: exact provenience unknown, 1915, *Seaman s.n.* (US). WISCONSIN: Manitowa, 1 July 1936, *Benke 5791* (US). WYOMING: Castile, 18 June 1916, *Killip s.n.* (US).

Symphytum officinale L. ($2n = 40$).

Stem to 70 cm long, distinctly winged, prickly and asperous, harsh to the touch; decurrence of the stem usually less pronounced than in the $2n = 24$ and $2n = 48$ cytotypes, at least in the upper leaves, but still distinctly present; shape of the leaf the same as in *S. officinale* ($2n = 24, 48$). Indument of the leaf on adaxial side of the lamina very scabrous with many short tubercular based prickly setae that are deciduous; between the hairs many short curved or uncinate hairs with or without a tubercular base; calyx to 9 mm long, divided to ¾ of its length: calyx lobes triangular-lanceolate with an acute tip; stiff marginal setae in a very regular distribution pattern; some of the marginal and dorso-median hairs with a tubercular base; corolla urceolate, 16–19 mm, usually dark or light purple, very occasionally white; stamens as in the 24/48 cytotype of *S. officinale,* but stamens somewhat longer than squamae; papillae of the corolla scales more densely crowded in the middle of the scale margin, otherwise the same as in *S. officinale* $2n = 24, 48$; fruit as in the $2n = 24/48$ cytotypes of *S. officinale*; reproduction obligate allogamous, plants strictly self-incompatible. Even plants with normal fertility may have flowers that produce only 3, 2, 1, or even (and not occasionally) 0 viable nutlets.

Specimens examined. U.S.A. NEW JERSEY: Communipaw Ferry, Hobokenville, 29 May 1880, *Brown s.n.* (US). NEW YORK: N of New York, 29 July 1929, *Parker Phelps 704* (US); Hermon, 11 Aug. 1915, *Parker Phelps 1716* (US). VIRGINIA: Roanche Girl Scout Camp, West Virginia, 10 Aug. 1946, *Wood 6588* (US).

Symphytum asperum Lepechin in Nova Acta Acad. Sci. Imp. Petrop. Hist. Acad. 14: 442. plate. 1850. TYPE: a specimen grown in the Botanical Garden of the Academy of Sciences in St. Petersburg (Leningrad). The seeds originated from the Caucasus (LE).

S. orientale L., Sp. Pl. 136. 1753, pro parte excl. typ.
S. asperrimum Donn ex Sims, in Bot. Mag. 24: t. 929. 1806.
S. echinatum Ledebour, Index Sem. Hort. Dorpat. Suppl. 5. 1811.
S. patens Fries, Novit. Fl. Suec. Mant. 2: 13. 1839, pro parte.
S. majus Guldenst. ex Ledebour, Fl. Ross. 3: 115. 1847.

Stem to 200 cm, never winged, very scabrid with aculeate curved subretrorse hairs; the hairs with a tubercular base; basal leaves ovate-elliptic, with an acuminate apex and a rounded cordate base; lamina 15–19 cm long, 7–12 cm wide; petiole to 10 cm long; stem leaves gradually smaller, 10–20 cm long, 4–10 cm wide, ovate or elliptic, acuminate at the apex and cuneate at the base; leaves not decurrent; adaxial side of the leaf very scabrid with short more or less appressed hairs with a small tubercular base and smaller shorter hairs without a tubercular base; abaxial side of the leaves with shorter uncinate hairs and with setae on the veins; calyx to 3 mm long, divided to ¾ of its length, calyx lobes linear oblong and obtuse in flower, becoming triangular in fruit; stiff marginal setae irregularly distributed; setae with a small tubercular base; corolla campanulate, 9–14 mm long, red in bud, sky-blue in flower; stamens 4–5 mm long; corolla scales shorter than the stamens; anther longer than filament, connective not projecting beyond the thecae; squamae of the corolla lingulate, 6 mm long, 1 mm wide, with a broad rotundate apex; marginal papillae fewer in number, longer and narrower than in all cytotypes of *S. officinale*; papillae acute, regularly distributed along the margin; fruit brown and dull, urceolate-granulate, 3–4 mm long and 3 mm wide at the base; reproduction strictly allogamous, plants self-incompatible. The production of ripe nutlets varies considerably in different plants, even fertile plants may have many flowers which produce only 1, 2 or 3 (and often 0) nutlets which are able to germinate.

Specimens examined. CANADA. QUEBEC: Cap Rouge, 10 Aug. 1931, *Michel 362* (MT). U.S.A. MASSACHUSETTS: Ashland, 6 July 1880, *Morong 365* (US); Sherborn, 9 June 1918, *Loomis 1853* (US).

Symphytum × uplandicum Nyman, Syll. Fl. Eur. 80. 1854–1855. TYPE: not seen.

S. patens Fries, Novit. Fl. Suec. Mant. 2: 13. 1839, pro parte.
S. orientale Fries non L., Novit. Fl. Suec. Mant. 3: 18. 1842.

S. × uplandicum Nyman ($2n = 36$).

Stem to 130 cm long, not decurrent, rough to the touch, provided with scabrous hairs that are deciduous in older stems; scabrous hairs with a tubercular base; basal leaves elliptic-lanceolate with an acuminate apex and a rounded more or less cordate base; lamina of basal leaves 15–30 cm long and to 6 cm wide, petiole to 12 cm long; stem leaves smaller, often with winged petiole, the uppermost ones nearly sessile with a cuneate base; indument of the adaxial side of the leaves sometimes as in *S. officinale* ($2n = 40$), sometimes as in *S. × uplandicum* ($2n = 40$), q.v.; abaxial side of the leaves with some tubercular based hairs along the veins and otherwise glabrous; length of the calyx up to 5.5 mm, calyx divided to ⅗ of its length, triangular-lanceolate and obtuse at the apex; calyx lobes with stiff marginal setae with a regular distribution pattern; setae usually without a tubercular base; corolla slightly campanulate 13–16 mm, purple in bud, blue-purple in flower; squamae of the corolla 7–7.5 mm long, 2 mm wide at the base, triangular-lanceolate, apex broad and rotundate; papillae acute and densely crowded at the middle of the scale margin; stamens 5–6 mm, shorter than the scales; anthers longer than the filaments, connective not projecting beyond the thecae; fruit brown and dull, areolate-granulate, 3–4 mm long and to 3 mm wide at the base; reproduction strictly allogamous, plants self-incompatible. Most plants show a reduced fertility, but some are as fertile as the parental species (q.v.).

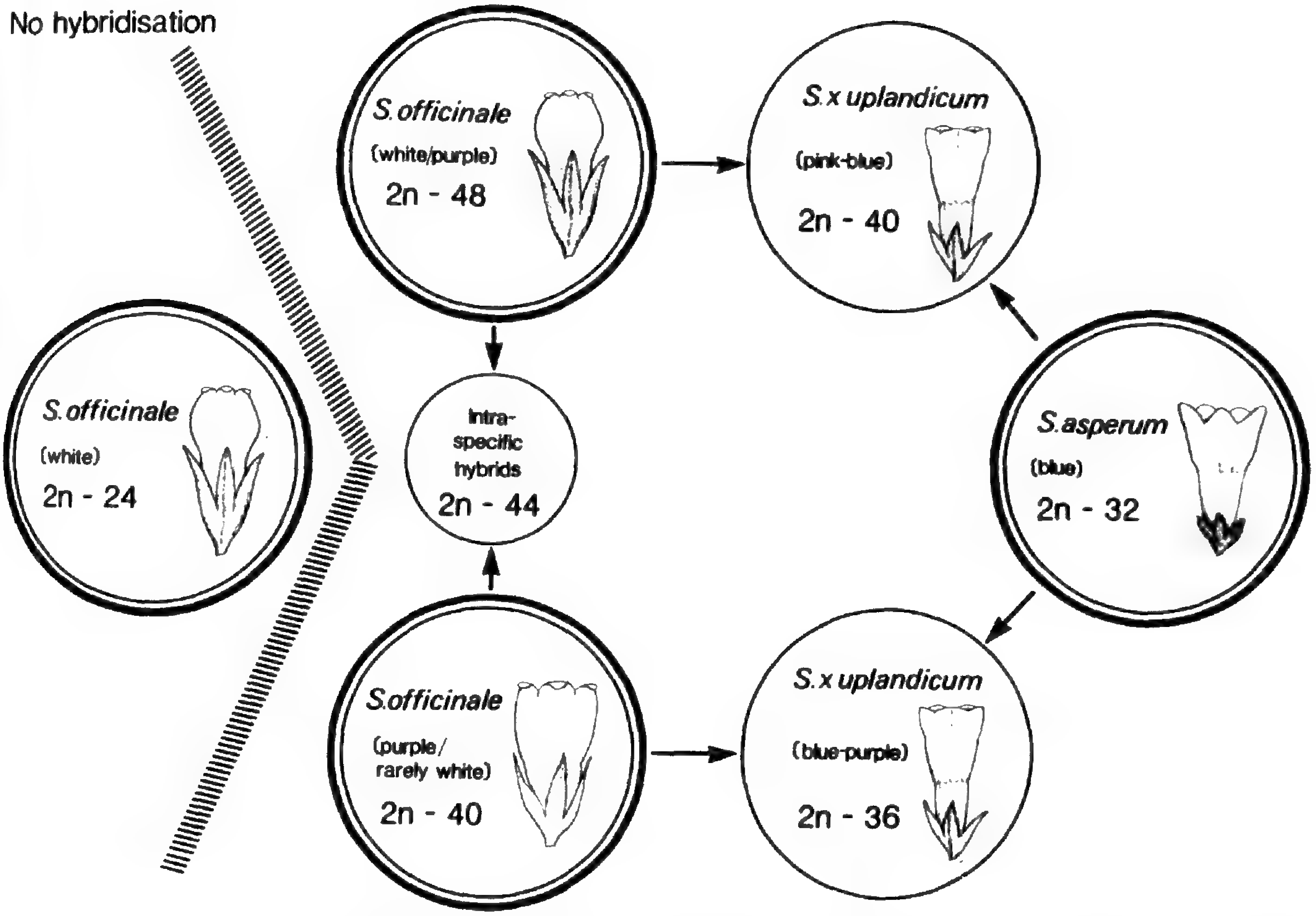

FIGURE 1. Crossing relationships in the *Symphytum officinale/S. asperum* complex. The shape of the corolla and calyx as well as the chromosome number of the three cytotypes of *S. officinale, S. asperum,* and the two *S.* × *uplandicum* hybrids are indicated.

Specimens examined. CANADA. BRITISH COLUMBIA: Ladner, 3 June 1960, *Beamish & Vrugtman s.n.* (MT, US). NOVA SCOTIA: Brook Glendyer, 2 Aug. 1951, *Smith 4794* (MT). ONTARIO: Meaford, Grey Co., 4 June 1942, *Mauger 9* (MT). PRINCE EDWARD ISLAND: Springvale, near Milton, 7 July 1952, *Erskine 1223* (MT). QUEBEC: Chemin St. Foy, s.d., *Desmarais 647* (MT); Laprairie, 24 July 1930, *Cléonique 12614* (MT); Montreal Sherbrooke, 18 June 1963, *Legault & Brisson 2122* (MT); St. Roch. des Aulnaies, Co. l'Islet, 3 June 1949, *Hamel 36* (MT). U.S.A. MICHIGAN: Douglas Lake, Cheboyan, 29 June 1934, *Ehlers 5570* (US). NEW YORK: Hobokenville, 11 Aug. 1895, *Maxon s.n.* (US). WASHINGTON: San Juan Islands, 25 June 1917, *Zeller & Zeller 1230* (US).

S. × uplandicum Nyman ($2n = 40$).

Stem to 140 cm long, soft to the touch, setae neither prickly, nor scabrid; if the setae have a tubercular base, this is always small and deciduous, never broad and conspicuous as in *S. officinale* ($2n = 40$); leaf decurrence sometimes present, but usually not longer than 1 cm along the internode; shape and size of leaves as in *S.* × *uplandicum* ($2n = 36$), q.v.; adaxial side of the leaves with many appressed setae, the majority of which have a small tubercular base; these setae are not deciduous; indumentum of the abaxial side of the leaf as in *S.* × *uplandicum* $2n = 36$ (q.v.); calyx to 4 mm long, divided to ⅗ of its length; calyx lobes triangular-lanceolate and sub--acute or acute; stiff marginal setae irregularly distributed; corolla 13–15 mm long, slightly campanulate, pink or pinkish blue in flower; squamae of the corolla with acute papillae, regularly distributed along the scale margin; stamens as in *S.* × *uplandicum* $2n = 36$ (q.v.); fruit as in *S.* × *uplandicum* $2n = 36$ (q.v.); reproduction strictly allogamous, plants self-incompatible; many plants show a reduced fertility and produce only a few nutlets; sometimes plants as fertile as the parental species (q.v.).

Specimens examined. CANADA. QUEBEC: Compte l'Assomption, 13 June 1936, *Bonin 36* (MT); Cap Blanc, 30 June 1933, *Marie Victorin, Rolland Germain & Meilleur 44372* (MT, US); Cap Rouge, 30 July 1927, *Adrien 1922* (MT); Montreal, 26 June 1932, *Robert 241* (MT); Montreal, Outremont, 10 June 1927, *Roy 532* (MT); Petit Saguenay, 30 June 1919, *Marie Victorin 9607* (US, MT); Pointe Preston, 21 July 1933, *Michel 2292* (MT); Montreal, Pointe-aux-Trembles, 21 June 1943, *Marie Victorin & Rolland-Germain s.n.* (MT, US). U.S.A. CONNECTICUT: Bridgepost, 3 Aug. 1893, *Eamesson s.n.* (US). MICHIGAN: Emmet and Cheboygan Counties, near Douglas Lake, 24 June 1917, *Ehlers 368* (US). NEW YORK: Mohawk Herkinen Co., 10 June 1919, *House 6196* (US). PENNSYLVANIA: Lehigh Co., 23 May 1964, *Schaeffer 70187* (US).

All North American plants of the genus *Symphytum* that I have seen can be identified with the aid of this key. The crossing relationships between *S. officinale* and *S. asperum* are illustrated in Figure 1.

DISCUSSION

Judging from this limited but probably representative sample of herbarium sheets, it appears that *S. officinale* and the two *S.* × *uplandicum* hybrids are the most common taxa in North America. The two cytotypes of *S.* × *uplandicum* ($2n = 36$ and $2n = 40$) are present in almost equal proportions. *Symphytum asperum* seems to be much rarer in North America. Macbride (1916), who checked up the determinations of the genus *Symphytum* in the Gray Herbarium, cited 14 specimens from Canada and U.S.A. Two specimens came from Vermont, Townshend (collected by Wheeler) and from Massachusetts, Sherborne (collected by Loomis), respectively. Both specimens were assigned by him to *S. asperum* Lepechin. I consulted two specimens, preserved in the herbaria of MT and US, from the same localities. The material collected in Vermont belongs to *S.* × *uplandicum* ($2n = 40$), the material from Massachusetts to *S. asperum*. This shows that confusion of *S. asperum*, and *S.* × *uplandicum*, even after a careful inspection, may occur. *Symphytum peregrinum* was not among the specimens I examined from North America. At least two cytotypes ($2n = 48$ and probably $2n = 24$; $2n = 40$) of *S. officinale* are present. The $2n = 40$ cytotype of *S. officinale* will not be assigned to *S. tanaicense* Steven in this paper because experimental studies that might permit definite conclusions in this respect are lacking. *Symphytum tanaicense* is the correct name for *S. uliginosum* Kern., a name which is used by Fernald (1950) in Gray's "Manual of Botany." The $2n = 40$ cytotype does occur in North America, but further conclusions on the status of this taxon can only be reached after experimental studies and a careful comparison of all the relevant material.

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TWO NEW SPECIES OF *PASSIFLORA* (PASSIFLORACEAE) FROM PANAMA, WITH COMMENTS ON THEIR NATURAL HISTORY[1]

SANDRA KNAPP[2] AND JAMES MALLET[3]

ABSTRACT

Passiflora macdougaliana and **P. eueidipabulum** are described from middle elevation wet habitats, bringing the number of species of Passifloraceae in Panama to 34. Both these species are of uncertain affinities in the genus *Passiflora.* One of the species is a new host plant record for the heliconiine butterfly *Eueides lineata,* and is also found in the peculiar low cloud forest on the Osa Peninsula in Costa Rica. The occurrence of new and unusual species in middle elevation Atlantic slope forests and the urgency of collecting in these forests are briefly discussed.

Passiflora macdougaliana S. Knapp & Mallet, sp. nov. TYPE: Panama. Colón: along the Río Guanche about 1 km from the Portobelo Highway, 0–50 m, 9°30′N, 79°40′W, 11 Apr. 1982, *Knapp, Mallet & Huft 4587* (holotype, MO; duplicates to be distributed). Figures 1 and 3a.

Frutex scandens. *Caulis* teres glaucus. *Stipulae* lineares falcatae caducae. *Folia* alterna ovata insuper nitida subter glauca, apicibus acutis retusis, basibus acutis. *Flores* ad nodos solitaria, bracteis triangularibus spadiceis. *Calycis* tubus conicus. *Sepala* anguste triangularia alba carnosa, apicibus obtusis, aestivatione quincunciali, marginibus expositis glandulosis. *Petala* anguste triangularia alba, apicibus obtusis. *Coronae filamenta* 10-seriata alba, 8 extimis filamentosis corrugatis, 2 intimis erectis rigidis brevibus. *Operculum* plicatum. *Ovarium* ellipticum glabrum nitide viride albo maculatum.

Huge woody canopy liana, young stems round and glabrous; new growth erect and glaucous; stipules linear, 1.5–2 mm long, falcate, very early deciduous. Leaves coriaceous with petioles ca. 25 mm long, biglandular just beyond the middle; the glands raised hemispheres ca. 2 mm wide; blades ovate, ca. 135 mm long, 80 mm wide, 5-veined from the base; apex acute with a tiny notch, base cuneate; upper leaf surface shining, lower surface glaucous with prominent green venation, laminar nectaries absent. Flowers solitary at each node, erect, sweetly fragrant; pedicel ca. 45 mm long, joint ca. 25 mm from the base; tendrils present on new growth, but early deciduous; floral bracts 3, scattered from the joint to 10 mm below the joint, deltoid, ca. 1 mm long, 1 mm wide at the base, pale brown; buds green, shining, coriaceous, aestivation quincuncial, with 5 lenticular glands evenly spaced about the bud ca. 5 mm from top of the calyx tube; calyx tube ca. 13 mm wide, 5 mm deep; sepals thick and fleshy, ca. 30 mm long, 10–15 mm wide, narrowly triangular, apex obtuse, white adaxially, green and shining abaxially; with 5 raised circular glands 1 mm diam. on sepal margins outermost in bud, 5 mm from sepal base (2 sepals with 2 glands, 1 with 1 gland, and 2 with no glands); petals ca. 35 mm long, 15 mm wide, narrowly triangular, apex obtuse, white; coronal rows 10, densely packed, grading into one another, all rows white fading to cream at base, the outer rows 1 mm diam. at base tapering to crumpled zigzag tips; the outermost 5 coronal rows ca. 35 mm long, filamentous; the next 2 rows ca. 7 mm long

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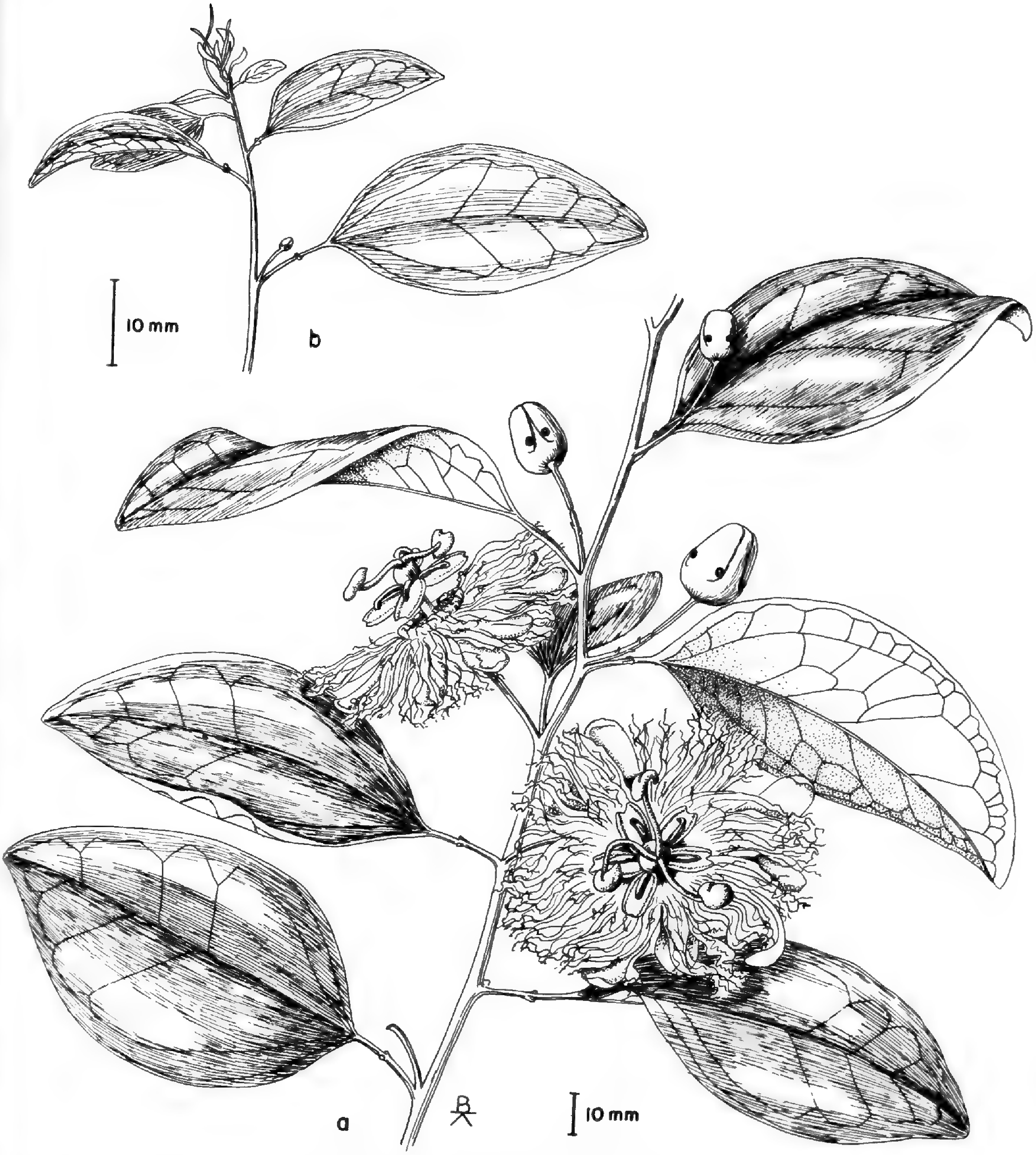

FIGURE 1. *Passiflora macdougaliana.*—a. Habit.—b. New growth (from *Knapp, Mallet & Huft 4587*).

followed by a filamentous row ca. 3 mm long; innermost 2 coronal rows 2 mm long, stiff and upright; operculum plicate, ca. 5 mm long, white, the upper surface incurved and covering the limen; floral nectary arising just inside the base of the operculum, nectar secreting area a trough ca. 4 mm deep, 2 mm wide, lined with a yellow pad; limen red, arising from inner edge of the trough, 1 mm high, covered by the tip of the operculum; androgynophore ca. 7 mm long from base to filament origin, white, from above slightly asymmetric; stamens 5, filaments ca. 7 mm long, green, anthers ca. 13 mm long, 6 mm wide, greenish yellow; style branches 3, ca. 15 mm long, 1 mm wide, white; stigmas discoid, revolute, ca. 7 mm wide, 5 mm long, creamy green; ovary ellipsoid, ca. 7 mm long, 6 mm diam., pale green with whitish specks, glabrous and shining. Fruit unknown.

Passiflora macdougaliana is a large canopy vine in mature forest. It appears to flower only when at the very tops of trees and therefore is very difficult to collect. This species is fairly common on Santa Rita Ridge, Colón province, judging from the number of individuals encountered as fallen leaves and flowers on the forest floor.

This species has unclear affinities; it possesses a hodgepodge of characters of a number of Killip's (1938) subgenera. The glands on the sepals suggest *P. variolata* Poepp. & Endl. in subgenus *Distephana* and *P. ernestii* Harms in subgenus *Adenosepala* (subgenera sensu Killip, 1938). In having a single flower at each node and a many ranked corona, *P. macdougaliana* is similar to many species in subgenus *Passiflora* (incl. *Granadilla*). The hemispherical petiolar glands suggest subgenus *Astrophea* or *Passiflora*. The plicate operculum is suggestive of subgenus *Plectostemma* or series *Kermesinae* of subgenus *Passiflora*. One peculiar group of Killip's subgenus *Plectostemma, P. obovata* Killip (section *Mayapathanthus*), is quite similar to *P. macdougaliana* in its leaf morphology, coriaceous buds, erect new growth, and scar-like petiolar glands, but differs in having the flowers paired at each node and in having fewer coronal rows.

The species is named in honor of John MacDougal of Duke University, a student of *Passiflora* systematics, who has been most kind and patient with our many queries about *Passiflora*, and who has stimulated our interest in this fascinating genus.

Additional specimens examined. PANAMA. COLÓN: Santa Rita Ridge, 20 km from the Transisthmian Highway, 300–500 m, 9°25'N, 79°37'W, 22 May 1982, *Knapp & Schmalzel 5278* (MO, duplicates to be distributed).

Passiflora eueidipabulum S. Knapp & Mallet, sp. nov. TYPE: Panama. Colón: Santa Rita Ridge Road 7 km from the Transisthmian Highway, 200 m, 9°22'N, 79°40'W, 21 May 1982, *Knapp & Schmalzel 5256* (holotype, MO; duplicates to be distributed). Figures 2 and 3b.

Scandens suffrutescens. *Caulis* teres glaucus. *Stipulae* minutae setaceae. *Folia* alterna peltata ovata subter glauca, apicibus acutis, basibus obtusis. *Pedunculi* irregulariter dichotomi cirrhiferi, bracteis caducis. *Calycis* tubus valde brevis. *Sepala* triangularia. *Petala* triangularia undulata. *Coronae filamenta* 3-seriata, extimis complanatis, intimis filiformibus inaequalibus. *Operculum* plicatum ad marginem irregulariter fimbriatum. *Ovarium* ellipticum molliter albopubescens. *Semina* ferruginea, foveolata, 4-alata.

Woody vine, about 2 cm thick at base, new growth recurved in a gentle acute angle, juvenile shoots softly pubescent with unicellular or uniseriate distally glandular trichomes ca. 0.1 mm long; stems round, smooth and waxy; stipules minute, setaceous; ca. 1 mm long, 0.25 mm wide at base, yellowish green or glaucous white. Leaves peltate, petiole 45–80 mm long, petiolar glands 4–6, in 2 or 3 subopposite pairs; blades ovate, 100–180 mm long, 50–125 mm wide, petiole inserted 12–20 mm from basal margin on the midrib; base rounded, sometimes slightly cordate, apex acute, apiculate; leaves prominently reticulate veined, glabrous above, papillose beneath, long white papillose on the veins, with a few scattered unicellular or uniseriate distally glandular trichomes on leaves of juvenile shoots, laminar nectaries present at junctions of some veins below, 10–15. Flowers borne in pairs on the tendrils, 15–30 (or more) mm from the base; pedicels ca. 52 mm long, joint 42 mm from base; floral bracts 3, scattered above and below the joint; if above larger, lanceolate, to 15 mm long and 5 mm wide, apex blunt; buds soft white puberulent; flowers sweetly fragrant; calyx tube ca. 15 mm wide, 2 mm deep, convex at point of pedicel insertion; sepals white with a green central stripe abaxially, ca. 25 mm long, 16 mm wide at base, broadly triangular, apex obtuse; petals white, very thin and delicate, ca. 25 mm long, 15 mm wide at base, broadly triangular, apex obtuse; margins of petals undulate and nearly transparent; coronal rows 3, outer row ca. 15 mm long, linear and laterally compressed, basal 5 mm mottled olive green and maroon, terminal 10 mm bright lemon yellow; second coronal row 4–5 mm long, grading into the third, mottled olive green and maroon, clavate, the clubs bristly; third (inner) coronal row 2–3 mm long, clavate, the clubs bristly, mottled olive green and maroon; operculum also mottled olive green and maroon, plicate, 5 mm long, round and covering the limen, semi-circular in cross section; margin of operculum irregularly fimbriate and bristly, olive green; floral nectary ca. 2 mm wide, 1 mm deep; limen deep maroon, recurved, 2 mm long, 1 mm wide at base; androgynophore ca. 12 mm from base to point of filament origin, pale glaucous green; stamens 5, filaments ca. 8 mm long, green, anthers ca. 6 mm long, 2 mm wide, pale green, pollen bright yellow; style branches 3, puberulent, ca. 8 mm long, stigmas green, discoid and revolute; ovary ellipsoidal, 5 mm long, pale green with soft white pubescence. Fruit ovoid, ca. 70

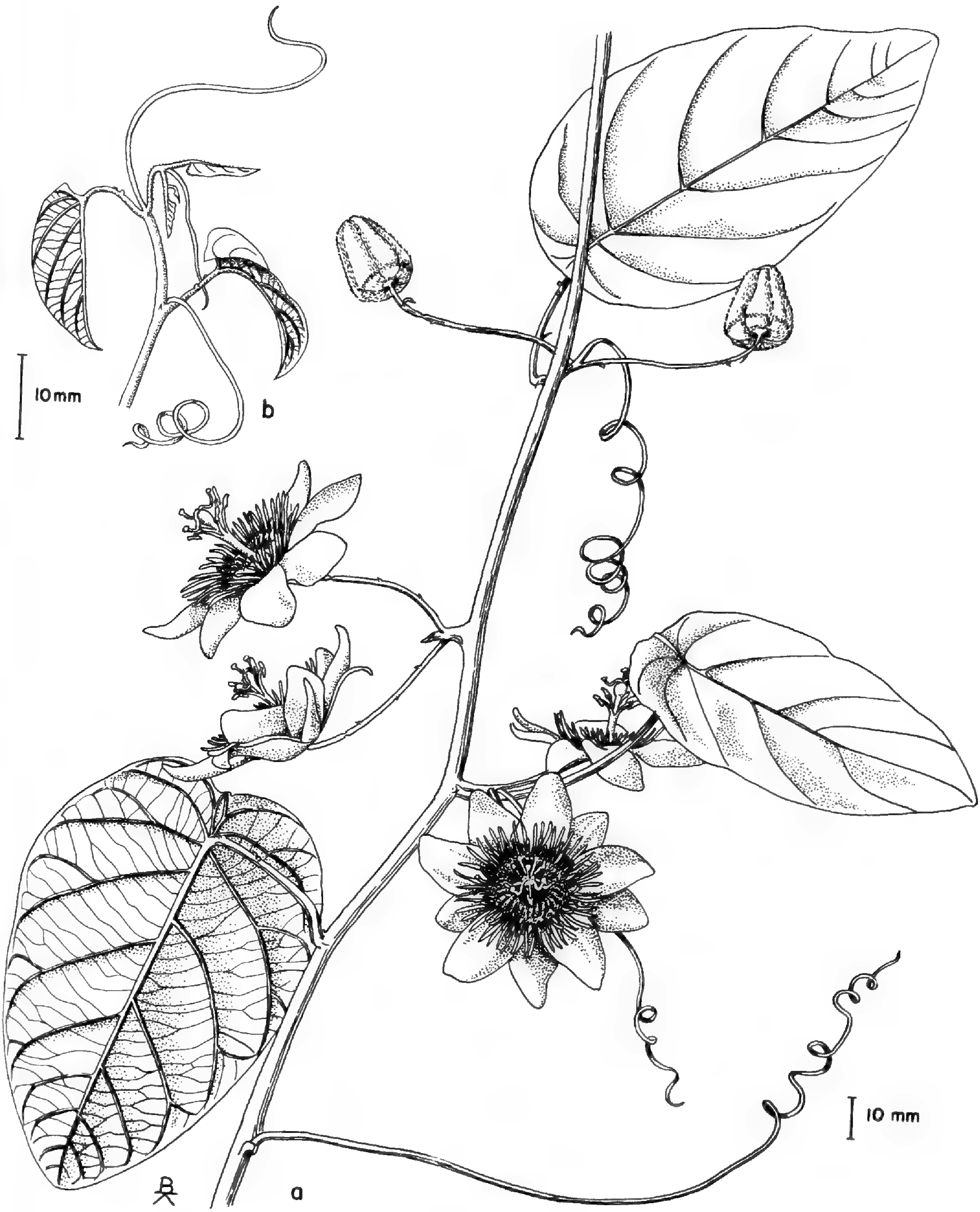

FIGURE 2. *Passiflora eueidipabulum.*—a. Habit.—b. New growth (from *Knapp & Schmalzel 5256*).

mm long, 50 mm wide, light yellow-green. Seeds rusty brown, narrowly elliptic lenticular, alate; body of seed ca. 10 mm long, 3.5 mm wide, minutely pitted; wings 4, a pair on each of the long axes, ca. 5 mm long, each pair ca. 2 mm apart on narrow edge of seed, striate, margins irregularly laciniate (fruit and seed description from *Antonio 1792*).

Passiflora eueidipabulum is vegetatively very distinctive. The large peltate leaves, minute stipules, and tendril-bearing peduncles make this

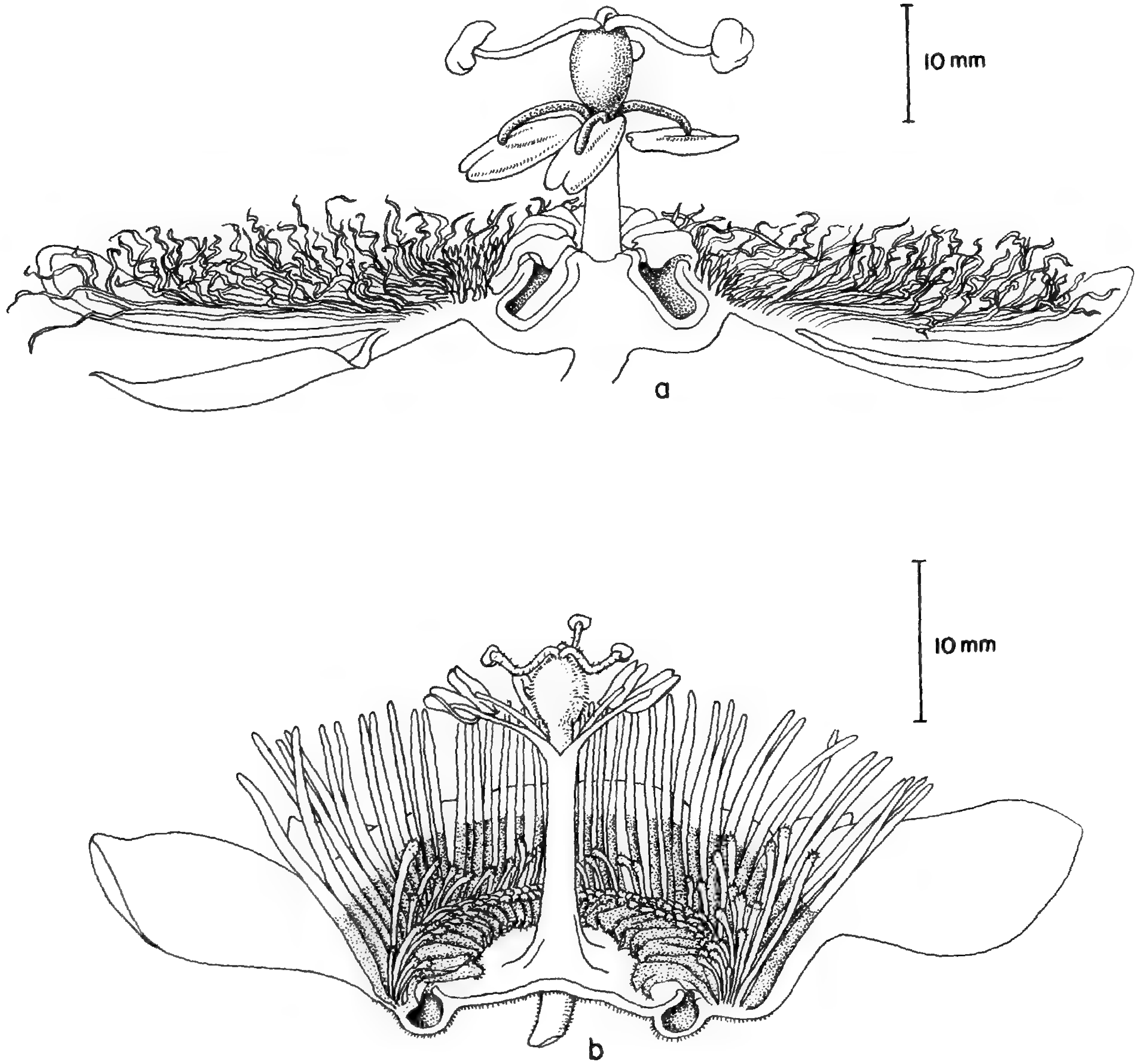

FIGURE 3.—a. Cross section of the flower of *Passiflora macdougaliana* (from *Knapp, Mallet & Huft 4587*).—b. Cross section of the flower of *Passiflora eueidipabulum* (from *Knapp & Schmalzel 5256*).

species immediately recognizable in the field. Only one other Panamanian *Passiflora* species, *P. gracillima* Killip (incorrectly equated with *P. tryphostemmatoides* Harms in Woodson & Schery, 1958), has flowers always borne on the tendrils. *Passiflora eueidipabulum* is easily distinguished from *P. gracillima* by its much larger flowers, larger peltate leaves, plicate operculum, and prominent petiolar glands. *Passiflora eueidipabulum* morphologically resembles *P. deidamioides* Harms, a rare species from southeastern Brazil. The two species both have plicate opercula and flowers borne on the tendrils, but their leaf morphologies are quite distinct (see Killip, 1938 for description). The relationships of *P. eueidipabulum* within the genus are unclear. We therefore hesitate to assign this species to one of Killip's subgenera until character combinations and relationships in the genus are carefully re-analyzed.

Passiflora eueidipabulum is very closely related to another new species from lowland forest in Veracruz province, Mexico (to be described by L. E. Gilbert of the University of Texas, Austin, in prep.). These two taxa are remarkably similar, but differ in certain key features. The leaves of the Mexican species are not peltate, and do not have the pronounced glaucous cast of those of *P. eueidipabulum*. The flower buds of the Mexican species are completely glabrous, while those of *P. eueidipabulum* are soft white puberulent. The flowers of *P. eueidipabulum* are shallower and more flattened in aspect, a feature not readily apparent on the herbarium sheet, but quite obvious in live specimens. The Mexican species has a peculiar juvenile morphology (Gilbert, in prep.), which is lacking in *P. eueidipabulum.* The winged seeds are an unusual and distinctive feature of both species.

Passiflora eueidipabulum is the species predicted by Mallet and Longino (1982) to occur in southern Central America. This prediction was made on the basis of the distribution of a butterfly species, *Eueides lineata* Salvin & Godman, whose host plant was found to be the above mentioned Mexican *Passiflora* (Mallet & Longino, 1982). In lower Central America, *E. lineata* was present in three of the five areas where *P. eueidipabulum* was seen: in the low cloud forest on the Osa Peninsula (Costa Rica), at Río Blanco del Norte (Coclé, Panama), and on the slopes of the Santa Rita Ridge (Colón, Panama). On the Osa Peninsula we found eggs of a *Eueides* species on the leaves, but were unable to rear these to adulthood. In Coclé province, all stages of *E. lineata* were found in abundance on the old and new growth of *P. eueidipabulum.* It is satisfying to report that the solution to a puzzle in butterfly biology has led to a botanical discovery.

This elusive species is named in honor of the butterfly, *Eueides lineata,* which led us to the plant. The larvae of *E. lineata* feed on the leaves of *P. eueidipabulum* (eueides—after the butterfly, meaning beautiful; and pabulum—fodder).

Two of the following additional specimens are both sterile, but we are certain they represent individuals of *P. eueidipabulum*; the leaf morphology is unmistakable. We have also seen, but not collected, sterile individuals of this species in another locality in Panama and in one locality in Costa Rica. The species was discovered in the peculiar low cloud forest on the Osa Peninsula of Costa Rica (8°30′N, 83°27′W) by Mr. J. Longino in 1980. *Passiflora eueidipabulum* also occurs along the Río Guanche (9°30′N, 79°40′W) in Colón province on the Atlantic coast of Panama. We have seen this *Passiflora* only in degraded forest and second growth. The large size of the type specimen is perhaps indicative of its canopy position in undisturbed forest.

Additional specimens examined. PANAMA. COCLÉ: sawmill above El Copé, 1,000 m, 8°40′N, 80°36′W, 13 Feb. 1982, *Knapp & Dressler 3440* (MO); near Caño Sucio, just W of Río Blanco del Norte, 500 m, 8°44′N, 81°40′W, 21 Feb. 1982, *Knapp & Dressler 3765* (MO). COLÓN: Cerro Santa Rita ca. 6 mi. from Transisthmian Highway, 800–900 ft., 13 Sept. 1979, *Antonio 1792* (MO) (in fruit).

Both of the new species described here owe their discovery to our specialized interest in *Passiflora* and its host specific herbivores, heliconiine butterflies (Gilbert, 1975; Benson et al., 1976). There are 34 described species of Passifloraceae from Panama (Woodson & Schery, 1958; Gentry, 1975), but we have found at least another eight species there. In some cases we have encountered only sterile plants, and in many cases the material may represent range extensions of South American species. Ecologists and zoologists working in the tropics should take special caution when identifying plants important to their work. Even in areas and countries well collected by general collectors (e.g., Panama), many species remain to be discovered. Those unfamiliar with plant identification may tend to force species to conform to what botanists have already described or recorded for the area. This can lead to gross misidentifications, as has been pointed out by Gilbert (1982). Sterile material in many groups such as the Passifloraceae is nearly as useful as flowering material, and is usually identifiable by someone familiar with the group in the study area. Regional or complete keys to sterile material would be of great use to ecologists or others who use systematic botany as a tool.

Both *P. macdougaliana* and *P. eueidipabulum* are found in very wet habitats and in low cloud forests, which generally occur on ridges below 1,000 m that are often covered in clouds and mist. In both Central and South America Gentry (1976, 1978, 1982) has shown that the wetter the region, the richer it is in both plant species and plant families. Extremely wet regions, such as the Chocó of Colombia, also appear to be rich in endemic and unusual species (Gentry, 1982). In Panama and Costa Rica wet forests are located all along the Atlantic slope, and in Costa Rica the isolated Pacific slope Osa Peninsula also receives high rainfall. The mid elevation ridges of these areas usually do not have a pronounced dry season and are similar to low cloud forest areas such as Santa Rita Ridge and Cerro Jefe. The endemic flora (Lewis, 1971) of low cloud forest areas in Panama is probably not restricted to any given summit or ridge, but is instead scattered throughout lower Central America in similar habitats. *Passiflora eueidipabulum* and *Passiflora macdougaliana* are both found in one such "endemic" area, Santa Rita Ridge, but also occur on the lower Atlantic slopes of this ridge. The isolated mountain ridges of the central Osa Peninsula merit distinction as a westward extension of the low cloud forest habitat. This area has been poorly collected (but see specimens of Knapp and Mallet at CR and BH), but we suspect it will have floristic affinities with the Atlantic slope of Panama. The forest is physiognomically similar to that on the Santa Rita Ridge. That new and unusual species are being found in these mid elevation wet forests emphasizes the importance of collecting in less accessible habitats. These interesting habitats should be visited repeatedly with an emphasis on the collection of unusual taxa, particularly seasonal bloomers and high canopy plants. *Passiflora macdougaliana,* for example, was found in an extremely popular collecting area in north central Panama. This more thorough collecting approach will undoubtedly result in range extensions of "endemic" taxa and additions to a rich and already relatively well known flora.

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NEW SPECIES AND COMBINATIONS IN APOCYNACEAE FROM PERU AND ADJACENT AMAZONIA[1]

ALWYN H. GENTRY[2]

ABSTRACT

Among recent collections from Peru and adjacent regions are the six new species of Apocynaceae described here. A new combination is also proposed for the widespread plant previously known as *Mandevilla velutina*. The genus *Pacouria* is reported for the first time from Peru and the very unusual fruits of *Allamanda weberbaueri* described for the first time.

Aspidosperma tambopatense A. Gentry, sp. nov. TYPE: Peru. Madre de Dios: Tambopata Reserve, 26 km S of Puerto Maldonado on E side of Río Tambopata, 12°49'S, 69°17'W, 280 m, subtropical moist forest life zone, 12 Nov. 1979, *G. Hartshorn 2421* (holotype, MO; isotypes, CR, F, USM).

Arbor grandis. Lamina folii elliptica vel anguste obovata, cuneata, obtusa, discoloria. Inflorescentia multum ramosa, ex parte glabriuscula, pedicellis rufescentibus, floribus albidis, calycis lobis ovatis, acutis, corolla tubulosa, sericea, ad tubi apicem constricta.

Canopy tree to 30 m tall, producing white latex, the branchlets irregularly angled, more or less whitish lenticellate when young, glabrous or glabrate. Leaves alternate, the blade elliptic to narrowly obovate, cuneate at base, obtuse to subacutish at apex, 5–16 cm long, 2–7 cm wide, chartaceous, glabrous or with a few scattered trichomes near base of midvein, discolorous with the densely and minutely glandular-papillate undersurface strikingly paler; petiole slender, dark-drying, 1–3 cm long. Inflorescence ebracteate, ramiflorous and leaf-opposed or subterminal on short axillary branches, openly branching and with well-developed peduncles, rather inconspicuously and glabrescently appressed puberulous, the trichomes more concentrated on the distinctly rufescent pedicels. Flowers whitish, the five calyx lobes ovate, acute, 1–1.5 mm long; corolla tubular, densely whitish sericeous, slightly constricted at apex of tube, the round lobes somewhat reflexed, 1 mm long, the tube 3–4 mm long, to 2 mm wide at broadest point; stamens inserted near middle of tube, the anther thecae slightly divergent, ca. 1 mm long, the connective acuminately extended; ovary conical, 1 mm long and wide, densely white puberulous; style ca. 1 mm long, the stigma minute. Fruits asymmetrically obovate in outline, compressed "pyriform," 6.5 cm by 4 cm, rather thick (ca. 2.5 cm) and woody valved, with a slightly raised median ridge, conspicuously whitish lenticellate.

Distribution. Moist forests on relatively good soils along the base of the Andes, 280–400 m altitude.

Additional collections examined. PERU. MADRE DE DIOS: Tambopata Reserve (type locality), 23 Apr. 1980, *P. Barbour 4985* (MO). SAN MARTIN: Mariscal Caceres, Ramal de Aspuzana, Uchiza, 390–400 m, 16 July 1973, *Schunke 6306* (F, MO, USM, to be distributed). LORETO: Cerros Campanquíz, R bank of Río Marañon opposite mouth of Río Santiago, 300–450 m, 2 Nov. 1962, *Wurdack 2525* (MO).

This species belongs to Woodson's (1951) series *Pyricolla* on account of its small corolla with a constricted tube apex and ebracteate inflorescence. It keys to *A. parvifolium* in Woodson's key because of its extremely short round corolla lobes less than one-quarter the tube length and the reddish inflorescence tomentum. *Aspidosperma parvifolium,* presumably the closest relative of *A. tambopatense,* is restricted to coastal Brazil (Bahia to São Paulo) and differs in having smaller obovate leaves that are usually pubescent beneath, a much denser and less appressed inflorescence tomentum, and especially a reddish tomentellous corolla tube, the latter very different from the whitish sericeous corolla tube of *A. tambopatense. Aspidosperma tambopatense* is also very similar to *A. vargasii,* the only member of series *Pyricolla* with which it is sympatric, and the Wurdack collection was identified as *A. var-*

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gasii by Woodson. It differs from *A. vargasii* in having a much more open inflorescence with a largely glabrescent tomentum (the inflorescence branches thus appearing blackish), mostly composed of reddish rather than grayish yellow trichomes. The calyces of *A. tambopatense* are relatively sparsely puberulous and brownish drying. The leaves of *A. vargasii* are much more concentrated near the branchlet tips than in *A. tambopatense.* The fruit described for *A. tambopatense* is a detached one picked up from the forest floor but comes from the type locality and is not referable to any other Peruvian *Aspidosperma*; this fruit is larger than that of *A. vargasii* (4–5 cm by 2.5–3 cm) and has much thicker valves although its general form is similar. Apparently *A. vargasii* occurs in drier habitats than does *A. tambopatense* and in Peru appears to bloom precociously whereas *A. tambopatense* blooms with the mature leaves.

Aspidosperma provides an excellent example of the inadequacy of the coverage of Amazonian plants in the "Flora of Peru." In Macbride's (1959) "Flora of Peru" treatment, only three species of *Aspidosperma* were reported to occur in Peru, although several other species that might be expected were also noted in the Flora. Twelve additional species of *Aspidosperma* are now known from Peru, quintupling the number of species reported in the Flora. Besides *A. tambopatense,* the additional Peruvian species are:

A. australe Muell.-Arg. [Cajamarca, Mandanguia (*Woytkowski 6817* (MO)).]

A. capitatum L. Wms. [Huanuco, Rupa-Rupa (*Gutierrez 95,* fide Fieldiana, Bot. 31: 249. 1967).]

A. cruentum Woods. [Loreto, Río Itaya (*Revilla 2367* (MO)); see Gentry, 1974, for correct use of this name.]

A. cylindrocarpon Muell.-Arg. [Huanuco, Pachitea, fide L. Williams, Fieldiana, Bot. 31: 18. 1964; Junin, Río Colorado, 500–600 m (*Gentry et al. 40109* (MO)).]

A. excelsum Benth. [San Martin, Tocache Nuevo (*Schunke 10019* (MO)); Loreto, Mishana (*Gentry & Aronson 25313* (MO), *Gentry et al. 31693* (MO)).]

A. macrocarpon Mart. [Loreto, Distrito Calleria, fide L. Williams, Fieldiana, Bot. 31: 18. 1964; San Martin, Tocache Nuevo (*Gentry et al. 25538* (MO); *Schunke 8673* (MO)).]

A. marcgravianum Woods. [Huanuco, Codo de Pozuzo, 450 m (*Foster 9274* (MO)); Madre de Dios, 20 km W of Puerto Maldonado (*Gentry et al. 19721* (MO)).]

A. megaphyllum Woods. [Madre de Dios, Manu Park (*Gentry et al. 26949* (MO)).]

A. nitidum Benth. [Loreto, Mishana (*Gentry et al. 25323, 25355, 25364, 36500* (all MO)), Laguna de Yarana, Río Nanay (*Diaz et al. 447* (MO)), Río Tacsha Curaray (*Croat 20413* (MO)); a common species of seasonally inundated tahuampa forests, occasionally also on upland white sand, especially in poorly drained areas. Some of this material has been identified as *A. marcgravianum* but the Loreto collections have the leaf-opposed, rather than terminal, inflorescences and larger less acuminate leaves of *A. nitidum* and are clearly not conspecific with the specimens cited above as *A. marcgravianum* despite the very similar small verrucose fruits.]

A. schultesii Woods. [Loreto, Mishana (*Gentry et al. 25312, 26169* (both MO)).]

A. cf. *verruculosum* Muell.-Arg. [Loreto, Mishana (*Gentry et al. 25219, 25272, 26084* (all MO)); sympatric with and very close to *A. schultesii* but has red latex.]

A. sp. nov. aff. *pichonianum* [Loreto, Mishana (*Gentry et al. 31682, Gentry & Aronson 25299* (both MO)). Although it is highly likely that this species is undescribed, it seems best to await the discovery of its flowers before describing it. The leaves are coriaceous, and narrowly oblong with a rounded or retuse acumen, asymmetrically cuneate revolute-margined base, and obscure secondary veins. This species is vegetatively most similar to *A. pichonianum* of the Guayana Highlands, an unlikely identification on phytogeographic grounds. The fruit of the Peruvian plant is flattened and suborbicular, ca. 10 cm by 8 cm, with a minutely roughened black-drying surface, very short stipe, and no raised midrib; the suborbicular seeds are ca. 8 cm diam. Another noteworthy feature is the abundant red latex in the younger branches.]

A. sp. [At least one additional species is represented by a sterile transect voucher that I have been unable to match in the herbarium.]

Pacouria boliviensis (Mgf.) A. Chev., Rev. Int. Bot. Appl. 28: 455. 1948. *Landolphia boliviensis* Mgf., Notizbl. Bot. Gart. Mus. Berlin

9: 1041. 1926. TYPE: Bolivia. *Steinbach 6537* (not seen).

The few American species generally attributed to the otherwise exclusively African genus *Landolphia* are a famous trans-Atlantic disjunction, complicated by the fact that the oldest name for any member of the group, *Pacouria* Aublet, has been rejected against *Landolphia. Pacouria guianensis,* described from French Guiana (Aublet, 1775), was not re-collected for well over a century, leading Bentham (1876) and others to suggest that Aublet's plant might have been introduced from Africa. Monachino (1945) summarized the convoluted taxonomic history of the rarely-collected American members of this group, accepting three species, of which he had seen only four collections.

At the time of Monachino's summary, the African species of this alliance were usually retained in a rather heterogeneous sensu lato *Landolphia.* However, for better or for worse, taxonomic custom has changed, and all African authors (e.g., "Flora of West Tropical Africa" and the various checklists of plants of northwest Gabon) now accept *Dictyophleba* and *Ancylobothrys,* with distinctive terminal inflorescences having curved lateral branches that apparently serve as "grappling hook" tendrils, as separate from *Landolphia,* which has short contracted, mostly axillary inflorescences. The American species are closest to either *Ancylobothrys* (Monachino, 1945: 309) or *Dictyophleba* (because of the non-keeled anthers and glabrous fruit, cf. Pichon, 1953: 39–40). While the American species are clearly not very different from either of these African genera, Pichon (1953) elected to treat them as generically distinct under a resurrected and narrowly defined *Pacouria,* a decision supported by several current students of the family (Zarucchi, pers. comm.; Leeuwenberg, pers. comm.). Nevertheless, as Pichon (1953) himself remarked, American *Pacouria* appears to be intermediate between the advanced African genera *Dictyophleba, Vahadenia,* and *Ancylobothrys* and the relatively unspecialized African genus *Landolphia*!

All of this becomes relevant to Peru because of the discovery of *Pacouria boliviensis* in Peru (*Ancuash 339* (MO), Amazonas Dept., Quebrada Huampi, determined as *Landolphia boliviensis* by Markgraf; *Gentry 43294, 43408* (both MO), Madre de Dios, Cocha Cashu Biological Station, Manu National Park).

Geissospermum, a small genus of three species plus the two additional ones described here, has not been reported previously from Peru. It differs from *Aspidosperma* in having dextrorse rather than sinistrorse corolla aestivation, in lacking slits in the corolla tube at the level of the anthers, and especially in having a non-compressed ellipsoid or ovoid fruit that contains small wingless, though rather flattened, seeds. The three known species are *G. laeve* (Vell.) Miers from coastal Brazil (*G. vellosoi* Allem. is a synonym), and two species from Central and lower Amazonia and the Guianas. *Geissospermum argenteum* Woods. occurs from the Guianas south through central and lower Amazonian Brazil (mostly north of the Río Amazonas except in the Xingu region). According to Markgraf (1978), *G. argenteum* is a synonym of *G. sericeum,* but it is his own *G. fuscum* Mgf. that is really conspecific with the type of *G. sericeum* (*Sagot 966* (P)). *Geissospermum sericeum* Benth. & Hook. occurs from the Río Negro region of Venezuela and Brazil north to Surinam and east to Amapá. One of the new species described here occurs in southern Amazonian Brazil from the Tocantins and Tapajos to the Bolivian border in Rondonia. The other is known only from an isolated patch of dry forest in Central Amazonian Peru.

KEY TO THE SPECIES OF *GEISSOSPERMUM*

1\. Corolla tube 9–10 mm long, the lobes 4–5 mm long; follicles acuminate; leaves less than 8 cm long and 3 cm wide; coastal Brazil .... *G. laeve*
1\. Corolla tube less than 6 mm long, the lobes less than 3 mm long; follicles obtuse to apiculate; some leaves usually more than 8 cm long and 3 cm wide; Amazonia.
  2. Leaves densely sericeous below with silvery or brownish trichomes, the tertiary venation hidden by the pubescence and hardly evident; northern and eastern Amazonia.
    3. Stem pubescence brown, not appressed; leaf pubescence brownish sericeous; corolla lobes 2–3 mm long .... *G. sericeum*
    3. Stem pubescence tan, appressed; leaf pubescence silvery sericeous; corolla lobes 1–2 mm long .... *G. argenteum*
  2. Leaves almost glabrescent below, the tertiary venation conspicuously prominulous; southern or western Amazonia.
    4. Corolla tube 5–6 mm long, enlarged at base and constricted at throat; inflorescence few-flowered; calyx lobes separate to base, obtuse .... *G. urceolatum*
    4. Corolla tube 3–4 mm long, uniformly tubular; inflorescence many-flowered; calyx lobes fused at base, acute .... *G. reticulatum*

Geissospermum reticulatum A. Gentry, sp. nov. TYPE: Peru. Huanuco: Pachitea, Carretera Miel de Abejas, 1 km arriba de Tournavista, Honoria, 300 m, Bosque Nacional de Iparia, bosque seco tropical, 29 Dec. 1966, *J. Schunke 1446* (holotype, MO; isotype, P; other duplicates distributed by F as *Aspidosperma* aff. *polyneuron*).

Arbor lactifer. Folia elliptica vel anguste ovata, cuneata, acuminata, infra sparsim puberula trichomatibus adpressis, nervatura intricate prominula. Inflorescentia lateralis, pedunculata, ramosa, dense puberula, floribus eburneis, calyce cupulato, 1.5 mm longo, acute 5-lobato, puberulo, corolla tubulosa, dense sericea. Fructus immaturus ovoideus, dense velutinus.

Tree 14 m tall, producing white latex; branchlets more or less terete, appressed puberulous, elenticellate. Leaves alternate, elliptic to narrowly ovate, long acuminate, cuneate at base, 8–11 cm long, 3–4.5 cm wide, chartaceous, minutely appressed-puberulous on midvein above and below and sparsely and inconspicuously over whole surface below, the venation intricately prominulous above and below; petiole 4–7 mm long. Inflorescence mostly scattered along the branches, sometimes opposite the leaves, each inflorescence with a well-developed peduncle, often ca. 1 cm long with several main bifurcations, densely appressed-puberulous with tannish trichomes; the ultimate flower clusters subtended by ca. 1 mm long appressed tannish-puberulous bracts. Flowers cream; the calyx cupular, ca. 1.5 mm long, the five acute lobes split ½ to ⅔ of way to base, densely appressed tannish puberulous; corolla tubular, the round thick lobes reflexed at anthesis, ca. 1 mm long, the tube 3–4 mm long, 1–1.5 mm wide, densely tannish sericeous; stamens inserted near top of tube, the parallel thecae completely fused, ca. 0.6 mm long, the prolonged connective acute; ovary ovoid, puberulous, sulcate. Very immature fruits (only 5 mm long) ovoid, densely tannish-velutinous.

Distribution. Known only from the strongly seasonal forest of the central Río Ucayali drainage south of Pucallpa.

Geissospermum reticulatum is most closely related to *G. argenteum,* from which it is differentiated especially by lack of a conspicuously sericeous leaf undersurface and the intricately prominulous network formed by the leaf venation. Although the type collection was identified as *Aspidosperma* aff. *polyneuron,* and *G. reticulatum* is superficially somewhat similar to that species and some other Aspidospermas, the prominulously intricately reticulate fine leaf venation of *G. reticulatum* is quite unlike the leaf venation of any *Aspidosperma* species at MO.

Geissospermum urceolatum A. Gentry, sp. nov. TYPE: Brazil. Pará: Belterra, 3 Nov. 1957, *Black 47-1909* [holotype, MO; isotype, P, MG (not seen)].

Arbor lactifer. Folia elliptica vel ovata, acuminata, ad basim obtusa, plerumque glabrata. Inflorescentia lateralis, pauciflora, floribus viridibus, calycis lobis separatis, lanceolatis, corolla tubulo-urceolata, tubi apice constricta, dense puberula. Fructus duobis folliculis ellipsoideis tomentosis compositus, seminibus complanatis, exalatis.

Tree to 10 or more m tall, producing white latex, the branchlets subterete, distinctly longitudinally striate-ridged, puberulous with short subappressed trichomes, elenticellate. Leaves alternate, the blade elliptic to ovate, acuminate to long acuminate, obtuse to broadly cuneate at base, 4.5–12 cm long, 1.5–5 cm wide, chartaceous, mostly glabrescent, minutely appressed-puberulous only on midvein and very sparsely over lower surface, the venation prominulous above and below; petiole 3–8 mm long. Inflorescence lateral, few-flowered, tannish puberulous with subappressed trichomes. Flowers greenish, the calyx of 5 separate lobes, the lobes lanceolate, obtuse, ca. 1.5 mm long, appressed puberulous; corolla tubular-urceolate, the base distinctly swollen, the neck constricted, the tube 5–6 mm long, almost 2 mm wide at base, densely tannish puberulous, the trichomes over basal swelling not appressed, the lobes 1–1.5 mm long. Fruits of 2 ellipsoid follicles, rather densely but glabrescently tannish tomentose, ca. 3 mm long, 1.5–2 cm wide; seeds flattened, wingless, rather angular, 6–9 mm long, ca. 10 mm wide.

Distribution. Amazonian Brazil south of the Amazon.

Additional collections examined. BRAZIL. PARA: Breu Branco, Estrada de Ferro Tocantins, terra firme highland forest, 29 Sept. 1948, *Froes 23576* (MO). RONDONIA: Guajará-Mirim, campina, 17 Dec. 1949, *N. Silva 338* (MO; two sheets, one with number changed to "438" with pencil).

This species resembles *G. laeve* (*G. vellosoi*) of coastal Brazil in its relatively large flowers and few-flowered inflorescences but differs strongly from that species in its much smaller corolla lobes and urceolate corolla tube. Its leaves are similar to those of *G. reticulatum* in lacking an obvious sericeous pubescence, but the corolla is larger and differently shaped, the inflorescences have fewer flowers, and the calyx is split to the base and has obtuse rather than acute lobes.

Mandevilla arcuata A. Gentry, sp. nov. TYPE: Peru. Amazonas: Valle del Río Santiago, 77°40′W, 3°50′S, Quebrada 2–3 km atras de la comunidad de Caterpiza, 200 m, 29 Jan. 1980, *S. Tunqui 674* (holotype, MO; isotype, USM).

Herba glabra scandens. Folia anguste obovato-elliptica, acuminata, basi truncata, margine ciliato excepto glabra. Inflorescentia racemosa, axillaris, fere glabra, floribus eburneis, calyce 2 mm longo, lobis subulato-acuminatis, corolla ad apicem tubulo-campanulata, ad basim anguste tubulosa, curvata, gibbosa. Fructus duobis folliculis lineariis inter semina constrictis compositus, seminibus ad apicem plumosis.

Vine, stems terete, slender, glabrous or with a few scattered minute inconspicuous trichomes. Leaves opposite, narrowly obovate-elliptic, acuminate, the base narrowly truncate, not at all cordate, 5–7 cm long, 1.5–2.5 cm wide, membranaceous, glabrous except the minutely subciliate margin and a few minute scattered trichomes, some leaves with obvious glands on the midrib above; petiole 0.5–0.8 cm long. Inflorescence racemose, axillary, virtually glabrous, not at all 1-sided, the pedicels 7–8 mm long. Flowers cream, the calyx 2 mm long, 5-lobed, the subulate-acuminate lobes with a few short trichomes along margins; corolla narrowly tubular-campanulate above a narrow strongly curved gibbous basal tube, glabrous outside, the throat (in bud) 1 cm long and 5 mm wide, the basal tube ca. 1.5 cm long, less than 1 mm wide except toward base. Fruit apocarpous, the 2 follicles linear, strongly constricted between seeds, glabrous, 18–20 cm long, ca. 3 mm wide at thickest points; seed body narrow, conspicuously longitudinally grooved, 1 cm long, with a dense apical tuft of 1.2–2 cm long brownish trichomes.

Distribution. Known only from the Ecuador-Peru border region of northeastern Amazonas Department.

This species belongs in subgenus *Exothostemon* because of its strongly arcuate gibbous corolla tube. It is most closely related to *M. polyantha* K. Schum. ex Woods. based on the unusual corolla shape. Although the cream flower color would key it out with *M. polyantha,* it does not have the secund inflorescence used to distinguish *M. polyantha* in Woodson's (1933) key. Nevertheless, a secund inflorescence, which in any event may be partially a pressing artifact, is not universal in *M. polyantha* and that feature thus is not a major differentiating character between *M. arcuata* and *M. polyantha.* One of the most obvious differences between these two species is that *M. arcuata* is essentially glabrous almost throughout—only a few minute and inconspicuous trichomes are scattered over its stems, inflorescences, and leaves (especially the subciliate margins)—whereas *M. polyantha* is conspicuously puberulous on stems, leaf undersurfaces, petioles, and inflorescence. *Mandevilla arcuata* has smaller leaves that taper to a narrow, abruptly truncate base whereas the leaf of *M. polyantha* narrows to a distinctly cordate base. The flower of *M. arcuata* is apparently somewhat smaller than that of *M. polyantha. Mandevilla polyantha* is endemic to the lower Huallaga Valley around Yurimaguas but *M. arcuata* occurs further northwest in the Río Santiago Valley near the Ecuador border.

Mandevilla is a large and taxonomically difficult genus and it is with some hesitation that I propose a new species in it, even such a distinctive one. Thirty-five new species of *Mandevilla* have been published since Woodson's monograph. I have seen no material of a number of these but have checked the descriptions of all species proposed from Central and western South America. None of these species is even remotely similar to *M. arcuata* or *M. polyantha.*

Mandevilla pohliana (Stadelm.) A. Gentry, comb. nov. *Echites pohliana* Stadelm., Flora 24(1): Beibl. 73. 1841. TYPE: Brazil. Minas Geraes, *Pohl s.n.* (not seen).

Dipladenia gentianoides Muell.-Arg. var. *glabra* Muell.-Arg. in Mart., Fl. Bras. 6(1): 124, pl. 37, fig. 2. 1860. *Mandevilla velutina* (Mart.) Woods. var. *glabra* (Muell.-Arg.) Woods. Ann. Missouri Bot. Gard. 20: 732. 1933. (9 additional synonyms are cited under var. *glabra* by Woodson.) SYNTYPES: Brazil. São Paulo, *Lund 889, Sellow s.n., Pohl 474*; Minas Geraes, *Weddell s.n.* (not seen).

Mandevilla pohliana (Stadelm.) A. Gentry var. **velutina** (Mart. ex Stadelm.) A. Gentry, comb. nov. *Echites velutina* Mart. ex Stadelm., Flora 24(1): Beibl. 72. 1841. *Dipladenia velutina* (Mart. ex Stadelm.) DC., Prodr. 8: 483. 1844. *Dipladenia gentianoides* Muell.-Arg. var. *velutina* (Mart. ex Stadelm.) Muell.-Arg. in Mart., Fl. Bras. 6(1): 124. 1860. *Mandevilla velutina* (Mart. ex Stadelm.) Woods. var. *typica* Woods., Ann. Missouri Bot. Gard. 20: 732. 1933. TYPE: Brazil. São Paulo, *Martius 503* (not seen).

The plant generally known as *Mandevilla velutina* is one of the commonest and best known species of the genus, occurring through most of southeastern Brazil, Paraguay, and into Bolivia [*Cardenas 5500* (MO) from between San Ignacio and San Miguel, Santa Cruz Department, is apparently a first report for Bolivia]. While not yet reported from Peru, this is the kind of distribution pattern that might be expected of the plants that will be found in the botanically unexplored Pampas de Heath on the Bolivian border.

When Woodson (1933) proposed his new combination for this species, he apparently failed to realize that the epithet "velutina" was already preoccupied in *Mandevilla* by *M. velutina* K. Schum. (in Engler & Prantl, Nat. Pflanzenfam. 4(2): 171. 1895), a Costa Rican plant previously placed by Woodson in synonymy under *Fernaldia pandurata* (DC.) Woods. Resurrection of the next available name for the plant usually known as *M. velutina* is unavoidable. This plant must thus be known as *M. pohliana,* based on *Echites pohliana,* published concurrently with *E. velutina* by Stadelmeyer. However, there are two distinctive variants of this plant, a glabrous-leaved and a pubescent-leaved form, the latter including the type of *Echites velutina* and designated *M. velutina* var. *typica* by Woodson. The type of *Echites pohliana* belongs to the glabrescent-leaved form, usually referred to as variety *glabra,* which thus becomes var. *pohliana.* Luckily an epithet older than Woodson's "typica" is available at varietal rank for the pubescent-leaved plant that Mueller-Argoviensis (1860) reduced to varietal status as *Dipladenia gentianoides* var. *velutina* long before Woodson proposed his variety *typica.* Thus the pubescent taxon becomes *M. pohliana* var. *velutina* (Mart. ex Stadelm.) A. Gentry.

Odontadenia macrostoma A. Gentry, sp. nov. TYPE: Peru. Amazonas: Valle del Río Santiago, 77°40′W, 3°50′S, Quebrada Caterpiza, 2–3 km atras de la comunidad de Caterpiza, 200 m, 14 Jan. 1980, *S. Tunqui 602* (holotype, MO; isotype, USM).

Frutex scandens. Folia elliptica, acuminata, basi obtusa, infra secus nervos minute puberula. Inflorescentia corymboso-paniculata, terminalis, floribunda, minute puberula, floribus luteis, calycis lobis ovatis, obtusis, 5–6 mm longis, puberulis, corolla late infundibuliformi-campanulata supra tubi partem basalem, dense puberula, antheris in tubi parte basali inclusis. Fructus ignotus.

Liana; stems reddish brown, with conspicuous small raised blackish lenticels. Leaves opposite, elliptic, acuminate at apex, broadly cuneate to obtuse at base, very minutely and sparsely puberulous along main veins below and base of midvein above, otherwise glabrous, 9–12 cm long, 3–4.5 cm wide, chartaceous; petiole 0.8–1 cm long; stipules not seen, early caducous, leaving an interpetiolar scar. Inflorescence corymbose-paniculate, terminal, many-flowered, the branches and pedicels minutely puberulous. Flowers with the calyx lobes ovate, obtuse, uniformly 5–6 mm long, not at all or barely unequal, densely minutely puberulous outside, the squamellae thin and inconspicuous; corolla yellow, broadly infundibuliform-campanulate above the narrow basal tube, the basal tube 1–1.5 cm long, 2–3 mm across at basal bulge, 1–2 mm across above bulge, the upper tube (throat) ca. 2 cm long, 1.5–2 cm broad at mouth, minutely papillose-puberulous outside, especially conspicuously so in bud, the anthers included in basal tube, linear, 5 mm long, with acuminate connective and acuminate basal tails; ovary ovoid, densely minutely puberulous, 1.5 mm long, ca. 1 mm wide, surrounded by the annularly accrescent nectaries. Fruit unknown.

It is surprising that not a single new species of *Odontadenia* has been described since Woodson's (1935) monograph (although an apparently unpublished name suggested by Markgraf is represented in the MO herbarium). *Odontadenia macrostoma* is closest to *O. cognata* (Stadelm.) Woods., a widespread and variable species, and keys out to that species both in the "Flora of Peru" and in Woodson's (1935) monograph because of its prominent lenticels, thyrsiform-subcorymbose terminal inflorescence, infundibuliform puberulous corolla, stamens inserted in basal part of the tube, acute-based leaves, and 5–6 mm long calyx lobes. However, I do not think that the broadly infundibuliform campanulate corolla (1.5–2 cm broad at mouth) of *O. macrostoma* can possibly fit into the range of variation of *O. cognata,* the maximum orifice diameter of which is 1 cm according to Woodson and in the material examined by me. The character of "corolla throat about 5.5 cm across" given in Macbride's (1959: 438) key is erroneous and presumably a typographical error for 0.55 cm. The shape of the *O. cognata* corolla is also very different, with the upper part of the tube (throat) much more uniformly tubular as well as narrower and broadening much more gradually from the narrow basal tube. In Peru *O. cognata* has red or red-orange, presumably hummingbird-pollinated flowers, whereas *O. macrostoma* has yellow flowers. Although flower color is too variable in this group to be very useful taxonomically—*O. cognata* has uniformly yellow flowers in Panama, coastal Colombia, and lower Amazonian Brazil—the difference in flower color, shape, and size between *O. macrostoma* and *O. cognata* strongly suggest that differentiation of the two taxa involved an evolutionary shift between hummingbird and bee pollination in Peru.

Allamanda weberbaueri Mgf., Notizbl. Bot. Gart. Berlin 9: 77. 1924.

The fruits of this species, endemic to the Balsas region of the Marañon Valley, have never been described. A recent collection (*Dillon & Turner 1710* (F, MO, USM)) is the first to include the distinctive fruits of this plant. Contrary to Macbride's suggestion that *A. weberbaueri* might be no more than a variant of widespread *A. cathartica* L., its fruits are so different from those of *A. cathartica* or any other species of *Allamanda* as to suggest that generic separation might even be warranted. *Allamanda weberbaueri* has smooth elliptic fruits 2–2.5 cm long and 1.2–1.5 cm wide. All but one other *Allamanda* species have spiny echinate fruits; the single smooth-fruited species is *A. laevis* Mgf. of Minas Geraes, Brazil which otherwise shares the much larger orbicular fruit of typical *Allamanda*. The thin, brownish-winged seeds of *A. weberbaueri*, 4–5 mm long and 4–6 mm wide, are generally similar to those of other species of *Allamanda*. The Peruvian plant is reported as being an erect shrub or tree to 5 m tall whereas most *Allamanda* species are scandent. The leaves of *A. weberbaueri* are sometimes whorled as in other species of *Allamanda* but on some branches of the Dillon and Turner collection the leaf whorls are very irregular or even lacking, the leaves becoming irregularly apically clustered. The flowers of the new collection are much smaller than those of the two previous ones but of the same general form; their reported white corolla color is probably erroneous (Dillon, pers. comm.). On balance, the evidence suggests that *A. weberbaueri* is best considered a highly atypical species of *Allamanda*.

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NEW SPECIES OF *GALAXIA* (IRIDACEAE) AND NOTES ON CYTOLOGY AND EVOLUTION IN THE GENUS[1]

PETER GOLDBLATT[2]

ABSTRACT

Galaxia kamiesmontana and **G. parva** are new species, both of subgenus *Eurystigma. Galaxia kamiesmontana* is restricted to the Kamiesberg in Namaqualand, where it grows in shallow soils overlying rock, while *G. parva* is known only from the Mierkraal flats near Bredasdorp in the southern Cape. Chromosome number is $n = 9$ in *G. kamiesmontana* and $n = 6$ in *G. parva.* Both numbers are new for the subgenus, in which $n = 8$, 7, and 17 have been recorded. The chromosome number in *G. kamiesmontana* links subgenus *Eurystigma* to the more specialized subgenus *Galaxia* in which $x = 9$ is basic. Chromosome evolution in *Galaxia,* reviewed in the paper, is seen as having proceeded from a base of $x = 9$ by aneuploid reduction to $n = 8$, 7 and ultimately 6 by unequal translocation and centric loss. *Galaxia kamiesmontana* is evidently a primitive relict species retaining the ancestral basic karyotype, while *G. parva,* an inbreeding, autogamous species with a highly derived karyotype is one of the most specialized.

Galaxia is a small genus of Iridaceae subfamily Iridoideae restricted to the winter rainfall area of the southwestern coast and interior of southern Africa. All species of *Galaxia* are small corm bearing plants with a basal rosette of short bifacial leaves and *Crocus*-like flowers with an underground ovary and a perianth tube that raises the flower well above the ground. The flowers are fugaceous, lasting for 3–6 hours, and this, together with their small size, makes the plants very inconspicuous. As a result, the genus is relatively poorly collected. In the recent revision of the genus (Goldblatt, 1979a) I recognized 12 species in two subgenera. The two species described here were discovered subsequent to the publication of the 1979 revision, *G. kamiesmontana* in 1980 and *G. parva* in 1981. Both are clearly very local endemics and in view of the high level of knowledge of the Cape Flora, it seems unlikely that they occur elsewhere.

RELATIONSHIPS

The two new species belong to subgenus *Eurystigma,* in which the stigma lobes are entire, the filaments typically united below and free for some distance above, and the flowers usually variously colored. In contrast, in the more specialized subgenus *Galaxia,* the stigma lobes are irregularly fringed, the filaments typically entirely united and the flowers yellow or, rarely, yellow and white. Basic chromosome number for the genus is probably $x = 9$ (Goldblatt, 1979a, 1979b), and $x = 9$ is the basic number for subgenus *Galaxia,* in which only multiples of this base occur (Table 1). Until now numbers of $x =$ 8 and 7 only, had been recorded in subgenus *Eruystigma* (Table 1), although I postulated that $x = 9$ probably occurred in the ancestral type of this, the less specialized subgenus. Chromosome number has been determined for both new species, *G. kamiesmontana* having $2n = 18$ and *G. parva,* $2n = 12$. Both numbers are thus new for the subgenus and substantially expand the impression of *Galaxia* as a cytologically variable genus. My prediction that $x = 9$ was basic for subgenus *Eurystigma* seems to have been fulfilled with the discovery of this number in *G. kamiesmontana.* The karyotypes of the new species and the cytological evolution of the genus is dealt with in more detail below.

CYTOLOGY

Chromosome numbers were established for *Galaxia kamiesmontana* and *G. parva* using a squash technique described previously (Goldblatt, 1979b). In both species the type collections serve as the voucher specimens for the chromosome counts.

The karyotype of *Galaxia kamiesmontana,* with $2n = 18$, comprises five pairs of larger chro-

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TABLE 1. Chromosome numbers in *Galaxia*. Voucher information for original counts is provided in a footnote to this table. The other counts were previously reviewed by Goldblatt (1979b).

Species	Diploid Number	Mean Length Haploid Chromosome Set μm
Subgenus *Eurystigma*		
G. kamiesmontana Goldbl.	18[a]	39.0
G. citrina Lewis	16, 14, 34	39.3
G. barnardii Goldbl.	16, 16[a]	38.3
G. versicolor Salisb. ex Klatt	16, 14	40.0
G. variabilis Lewis	14	38.9
G. parva Goldbl.	12[a]	42.0
Subgenus *Galaxia*		
G. grandiflora Goldbl.	18	—
G. ciliata Persoon	18	—
G. luteo-alba Goldbl.	18, 27	—
G. ovata Thunb.	18, 36, 54[a]	40.9
G. stagnalis Goldbl.	36	—
G. fugacissima (L. f.) Druce	18, 36	—
G. alata Goldbl.	18, 27	—
G. albiflora Lewis	18	—

[a] Voucher data:

G. kamiesmontana—Cape Province, Rooiberg, Kamiesberg, *Goldblatt 5560* (MO).

G. barnardii—Cape Province, Caledon, at the western end of town, *Goldblatt 6174* (MO).

G. parva—Cape Province, Mierkraal flats, SSW of Bredasdorp, *Goldblatt 6181A* (MO).

G. ovata—Cape Province, Mierkraal flats, SSW of Bredasdorp, *Goldblatt 6928* (MO).

mosomes, 4–6 μm long, and four smaller pairs, ca. 3 μm long, all strongly acrocentric or nearly telocentric (Fig. 1B). This karyotype corresponds closely to that of *G. fugacissima* (Fig. 1A), a representative species of subgenus *Galaxia*, with a karyotype characteristic of that group.

The karyotype of *Galaxia parva*, with $2n = 12$, is structurally heterozygous. It comprises the following: a long pair of metacentrics, ca. 10 μm long; a mismatched pair ca. 9 μm long, one acrocentric and one metacentric; another mismatched pair 7–8 μm long, also metacentric and acrocentric; a fourth pair of acrocentrics ca. 6.5 μm long; an apparently mismatched fifth pair, one ca. 5.5 and the other ca. 4 μm long; and a very small acrocentric pair ca. 3 μm long. This karyotype has been confirmed for the five individuals of the species so far examined.

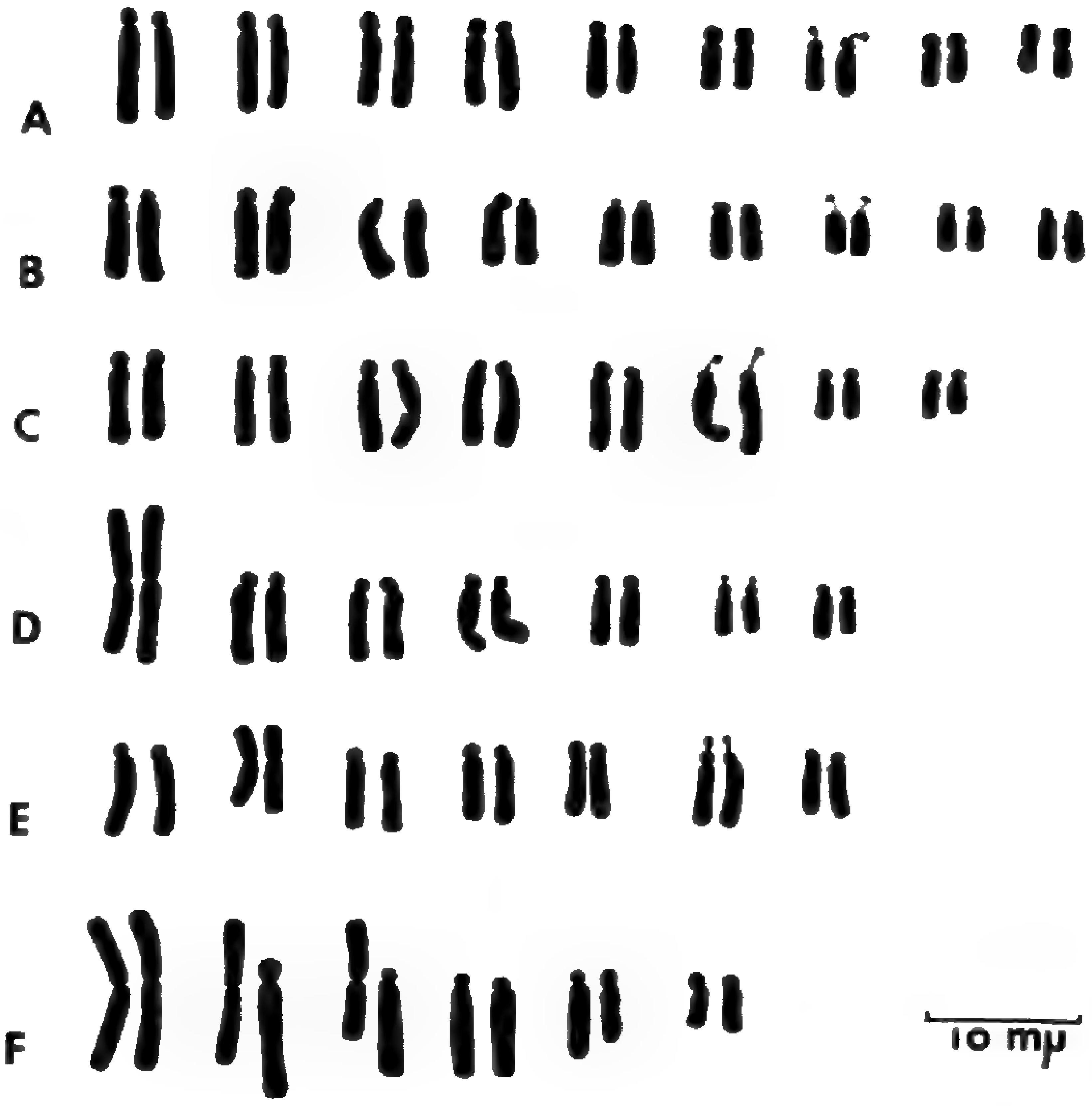

FIGURE 1. Karyotypes of species of *Galaxia*.—A. *G. fugacissima* ($2n = 18$) (subgenus *Galaxia*).—B. *G. kamiesmontana* ($2n = 18$).—C. *G. citrina* ($2n = 16$).—D. *G. versicolor* ($2n = 14$).—E. *G. variabilis* ($2n = 14$).—F. *G. parva* ($2n = 12$) (species B–F all subgenus *Eurystigma*).

Structural heterozygosity has also been recorded in Iridaceae in three species of the allied southern African genus *Homeria* (Goldblatt, 1980), where it is associated with autogamy. These species of *Homeria* were found to form chains or rings of chromosomes at meiosis, and thus constituted complex heterozygotes. The possibility that such a situation prevails in *G. parva*, which is also autogamous, seems likely, but meiotic studies are very difficult to make in *Galaxia* and this remains to be established.

In my review of cytology and karyotype change in *Galaxia* (Goldblatt, 1979b), I proposed the hypothesis that karyotypic evolution had proceeded by decreasing aneuploidy from a basic and relatively symmetric acrocentric complement with $n = 9$ to $n = 8$ and subsequently to $n = 7$. The reduction in chromosome number has been achieved by karyotypic reorganization with minimal loss of chromosome material (Table 1), the overall amount of which is very similar in all diploid species. This reduction is seen as having been achieved in two basic ways: either by unequal but symmetric translocation (Robertsonian fusion); or by unequal asymmetric translocation. In the former, the product is a large metacentric and a small centric fragment, while in the latter a long acrocentric and centric fragment result.

Both processes appear to have taken place in the course of evolution of *Galaxia* subgenus *Eurystigma.* In *G. citrina,* with $n = 8$ (Fig. 1C), as well as in *G. barnardii* and the $n = 8$ form of *G. versicolor,* there is a large acrocentric in place of two small acrocentrics in the basic *Galaxia* karyotype (Fig. 1A). The formation of the karyotype in the $n = 7$ form of *G. versicolor* (Fig. 1D) seems to have involved the fusion of two large acrocentrics to yield the very long metacentric pair in this karyotype. In *G. variabilis,* the same process may have taken place, but involving the fusion of two small acrocentrics to form the pair of long metacentrics found in this karyotype (Fig. 1E). Further unequal reciprocal translocation must have occurred in the evolution of the unusual karyotype of *G. parva.* It seems simplest to postulate that the species evolved from an ancestor with a karyotype like that found in the $n = 7$ form of *G. versicolor* (if not from *G. versicolor* itself), but not only has at least one unequal reciprocal translocation event taken place in the reduction of base number from $n = 7$ to 6, but a certain amount of structural rearrangement presumably occurred subsequently to result in the heterozygous karyotype of this species.

BIOLOGY AND REPRODUCTION

The biology of both *Galaxia kamiesmontana* and *G. parva* exhibits aspects that are unusual in the genus. *Galaxia kamiesmontana* is the earliest flowering species of *Galaxia,* blooming early in the winter, in May or June, typically three weeks after the first soaking winter rainfall. It grows in the rock shelf habitat characteristic for several other species of *Galaxia.* In these rocky sites, the thin covering of soil rapidly becomes waterlogged and because drainage is prevented by the underlying rocky pavement, water remains available to the plants for several weeks even without further rain. *Galaxia kamiesmontana* completes its flowering by the end of June but ripening of the capsules is delayed until late spring or until the soil dries out. Then the stem elongates, pushing the cluster of leaves and ripe fruits well above the ground, before it breaks and the fruit cluster is dispersed by the wind.

Galaxia parva is more typical of the genus in its flowering and fruiting cycle. It grows in the clay soil that is also favored by its allies, *G. versicolor* and *G. variabilis,* and flowers in the early spring. The small, pale flowers open in the late morning and fade at about 3:30 P.M. The species is self-compatible and, at least in the greenhouse, autogamous, and this breeding system is unique in its subgenus, but is curiously paralleled in subgenus *Galaxia* by *G. albiflora,* a species also having very small, and white, short lasting flowers. Autogamy is known in at least two other species of subgenus *Galaxia, G. stagnalis* and the southern populations of *G. fugacissima,* where it seems to have evolved independently.

SYSTEMATIC TREATMENT

Galaxia kamiesmontana Goldbl. sp. nov. TYPE: South Africa. Cape: Kamiesberg, Namaqualand, on Rooiberg, above 4,000 ft. in shallow soil on rock shelves, *Goldblatt 5560* (holotype, MO; isotypes, K, NBG, PRE, S, WAG). Figure 2.

Planta minuta, ad 2 cm alta, tunicis cormi pallido-brunneis, fibris reticulatis costis verticalibus, folia 2–5 falcatis, ad 3 cm longis 1 mm latis, floribus campanulatis pallido-purpureis, infra luteis, tubo perianthii 5–10 mm longo, tepalis 10–12 mm longis unguiculatis, unguibus ascendentibus, limbis horizontalibus 4–5 mm latis, filamentis connatis in columnam ca. 5 mm longam, supra liberis, antheris minus 2 mm longis, ramis styli brevibus ad apices antherae extensis, marginibus stigmatum integribus.

Plants tiny, to 2 cm high when in bloom. *Corm* ovoid, 3–5 mm diam., tunics light brown, fibers reticulate, with a few prominent vertical ribs. *Leaves* 2–5, falcate, lightly channelled or flat, to 3 cm long and 1 mm wide, acute, with broad transparent sheathing bases below the ground, margins smooth. *Stem* underground, reaching to 10 mm above ground as the capsules ripen. *Flowers* campanulate, light purple with yellow nectar guides at the base of the limbs, claws yellow; *perianth tube* 5–10 mm long, cylindric; *tepals* 10–12 mm long, distinctly unguiculate, claws ascending, forming a narrow cup enclosing the filament column, limbs extended horizontally, the outer to 5 mm wide, inner to 4 mm wide. *Filaments* ca. 5 mm long, united below in a cylindrical column, free in the upper 0.5–1 mm and curving outwards, yellow; *anthers* just under 2 mm long, diverging, yellow. *Style* diverging into three branches at mid anther level, *stigmas* with the lobes shorter than or barely overtopping the anthers, margins entire, minutely ciliate, incurving opposite the anther, radial margins slightly raised. *Capsules* 6–7 mm long; seeds angular, less than 0.5 mm diam. *Chromosome number* $2n = 18$ (*Goldblatt 5560*).

Flowering time. May–June.

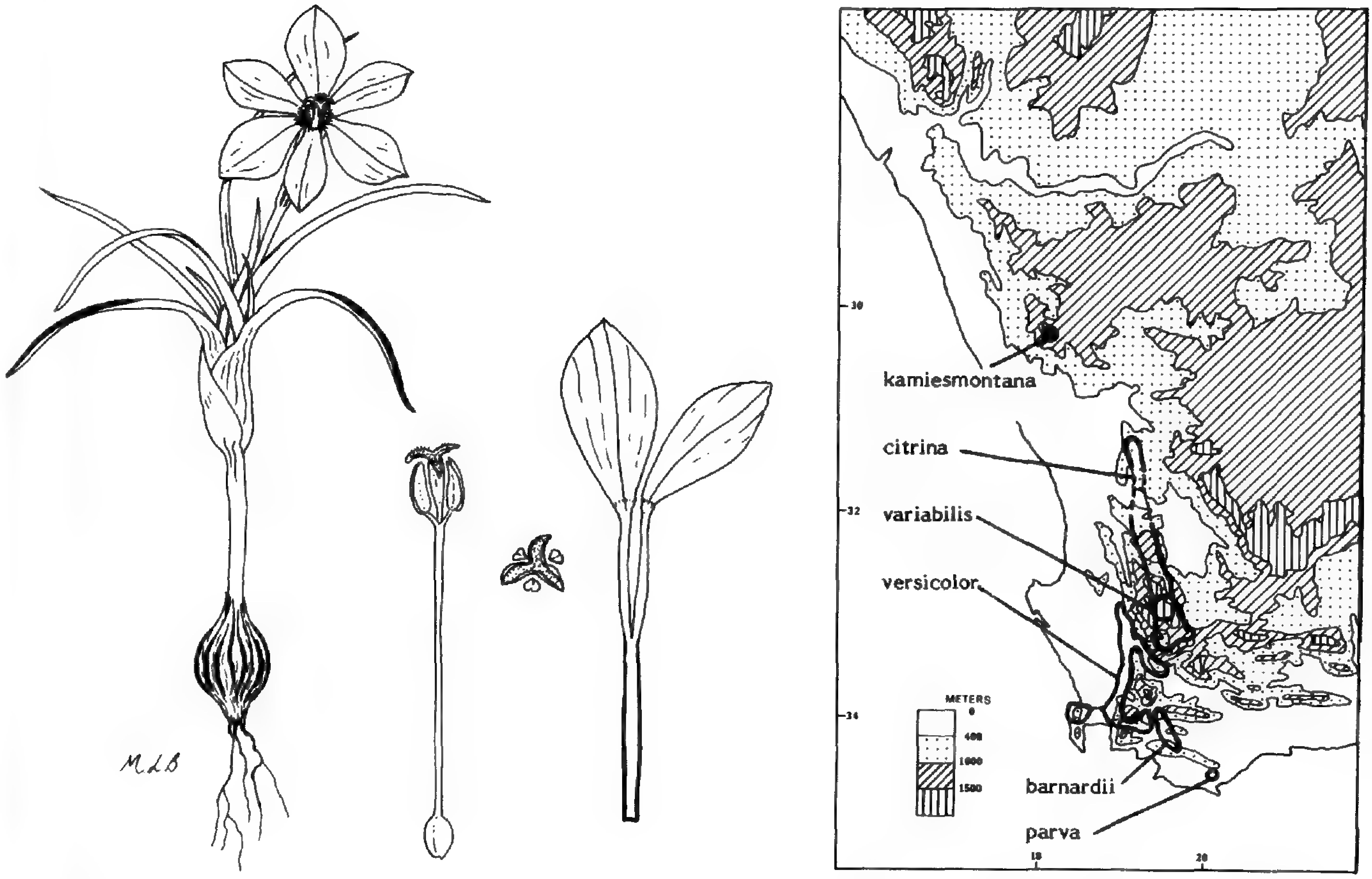

FIGURE 2. Morphology of *Galaxia kamiesmontana* with the distribution of all species of subgenus *Eurystigma*: whole plant and single flower ×1; section of the flower and top view of the stigma lobes much enlarged.

Distribution. Kamiesberg in central Namaqualand, on the Rooiberg above 4,000 ft., in shallow, seasonally waterlogged soil on rock shelves. Figure 2.

Galaxia kamiesmontana is an unusual species, and quite distinct in subgenus *Eurystigma* not only in its small size but in the structure of its flowers. In the other species of *Galaxia* the flowers are campanulate with flaccid, widely cupped tepals, or in *G. barnardii* the flower is hypocrateriform. In either case, there is little distinction between the limb and claw of the tepals. In *G. kamiesmontana,* however, the tepals are clearly clawed. The ascending claws form a narrow cup that encloses the filaments (Fig. 2), and the limbs are sharply flexed at right angles to the tube and extend horizontally.

The rock shelf habitat of *Galaxia kamiesmontana* is typical for the genus, several species of which are restricted to such situations. *Galaxia kamiesmontana* is the most northerly occurring species of subgenus *Eurystigma,* the other five species of which are found in the western part of the Cape Flora Region between Bredasdorp in the south and Nieuwoudtville in the north (Fig. 2).

The karyotype, with a diploid number of $2n = 18$, is unique for subgenus *Eurystigma,* and as described in detail above, the other species of the alliance have numbers of $2n = 16$, 14, and 12. The karyotype matches exactly that found in subgenus *Galaxia* and is probably the basic one for the genus. *Galaxia kamiesmontana* appears to be a primitive relict species, surviving in a specialized, seasonally moist habitat in the high mountains of semi-arid Namaqualand.

Specimens examined. SOUTH AFRICA. CAPE: 30.18 (Kamiesberg) Rooiberg, E slopes near Welkom (AC), *Goldblatt 5560* (K, MO, NBG, PRE, S, WAG), *5768A* (MO); Rooiberg, E slopes of ridge N of the main peak, *Goldblatt & Snijman 5588* (MO, NBG, PRE, US).

Galaxia parva Goldbl. sp. nov. TYPE: South Africa. Cape: Mierkraal flats, SSW of Bredasdorp, *Goldblatt 6181A* (holotype, MO; isotypes, K, NBG, PRE). Figure 3.

Planta parva, 2–3 cm alta, tunicis cormi brunneis, fibris costis verticalibus, foliis plus minusve planis vel canaliculatis, prostratis acutis 15–35 mm longis ad 8 mm latis, floribus campanulatis albis infra luteis cyaneis notatis, tubo perianthii 7–10 mm longo, tepalis 9–12 mm longis, filamentis connatis in columnam ca. 3 mm longam, supra liberis, antheris 1.5–2 mm longis,

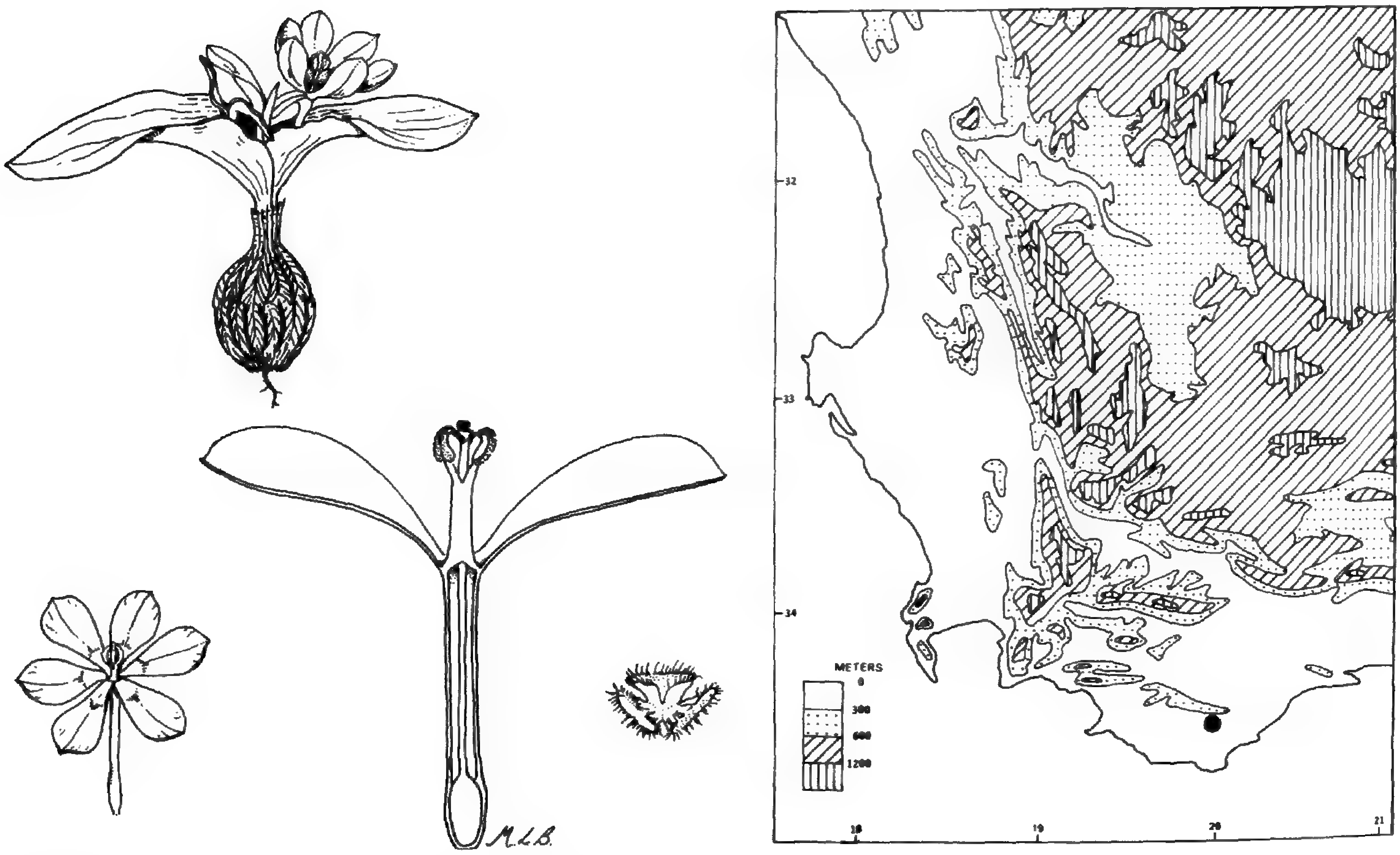

FIGURE 3. Morphology and distribution of *Galaxia parva*: whole plant ×1; dissected flower parts much enlarged.

ramis styli brevibus ad partem mediam antherae extensis, marginibus stigmatum integribus.

Plants solitary, small, 2–3 cm high. *Corm* tunics brown, with prominent woody vertical ribs. *Leaves* 3–4, bifacial, more or less flat or weakly channelled, the outer almost prostrate, acute and acuminate, undulate, 15–35 mm long, to 8 mm wide, margins hyaline, smooth. *Stem* underground, extending 2–4 cm above the ground in fruit. *Flowers* campanulate, white, with turquoise nectar guides and yellow in the center; *perianth tube* 7–10 mm long, cylindric; *tepals* 9–12 mm long, 5–6 mm at the widest point. *Filaments* 3–4 mm long, united in a cylindrical column below, free in the upper 0.6–1.5 mm and diverging, yellow; *anthers* 1.5–2 mm long, yellow. *Style* diverging near the base of the anthers, and reaching to about the middle of the anthers; *stigma lobes* with entire, minutely ciliate margins, the lobes distinct or more or less continuous at the edges with the adjacent lobes, radial margins slightly raised. *Capsules* not known. *Chromosome number* $2n = 12$ (*Goldblatt 6181A*).

Flowering time. Late July to early September.

Distribution. Known only from the flats at Mierkraal, SSW of Bredasdorp, on light clay in coastal renosterbos veld. Figure 3.

Galaxia parva has the smallest flowers in subgenus *Eurystigma* but it is in other respects a typical member of the alliance. The species seems most closely related to *G. versicolor*, the pink and purple flowers of which are similar in general shape and proportion, but *G. parva* differs significantly in having a short style so that the stigma lobes reach only to the middle part of the anthers. The pollen is thus in direct contact with the stigmas, and in fact *G. parva* is self-compatible, and at least under greenhouse conditions, autogamous. It is the only species in the subgenus that is not self-incompatible. The small white flower of this species is very similar to that of *G. albiflora* (subgenus *Galaxia*), which is also autogamous and has the smallest flowers in its subgenus. There seems no doubt that the two species are unrelated, and that the small white and yellow flower evolved independently, together with autogamy, in each subgenus.

Galaxia parva has the most easterly distribution of the subgenus, occurring some 50 km from the nearest populations of *G. barnardii*, its closest neighbor in the alliance. It occurs south of the east–west trending Bredasdorp Mts. which isolate it from suitable clay soils that are common to the north and west of the range. It seems likely that *G. parva* evolved from *G. versicolor* or its immediate ancestors, on a geographically isolated pocket of clay in an area of predominantly sandy or limestone soils to which it is not suited. The evolution of the species has been accompanied by an aneuploid reduction in chromosome number. The base number for the subgenus is $x = 9$, and it has the derived diploid number of $2n = 12$, the lowest number in the genus. The related *G. versicolor* has diploid numbers of $2n = 16$ and 14 (Goldblatt, 1979b). The karyotype, described in detail in the preceding pages, is structurally heterozygous (Fig. 3E) and because the species produces ample seed, its embryology will undoubtedly prove to be of unusual interest.

Specimens examined. SOUTH AFRICA. CAPE: 34.19 (Caledon) flats at Mierkraal, SSW of Bredasdorp (DB), *Goldblatt 6181A* (K, MO, NBG, PRE).

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THE PHYTOGEOGRAPHIC SIGNIFICANCE OF SOME EXTINCT GONDWANA POLLEN TYPES FROM THE TERTIARY OF THE SOUTHWESTERN CAPE (SOUTH AFRICA)[1]

J. A. COETZEE[2] AND J. MULLER†

ABSTRACT

Pollen assemblages of lower Miocene age from sediments in the southwestern Cape contain ancient Gondwana microfloras of considerable phytogeographic interest. The parent taxa, which are not represented in Africa today, indicate the existence of subtropical rain forest in these regions during the Tertiary. This microfossil record supports the hypothesis that a common South American–Antarctic–African–Madagascar flora existed in the Gondwana fragments during the Cretaceous. The final extermination of these elements in the southwestern Cape at the close of the Tertiary was probably related to the wide ranging effects of the glaciation of Antarctica. Sclerophyllous macchia has since become dominant and adapted to the present Mediterranean climate.

The unique flora of the southwestern Cape is very well known for its species richness and high degree of endemism. This vegetation, which belongs to the phytochorion Capensis (Taylor, 1978; Werger, 1978), occurs in the present summer-dry/winter-wet climate of the region. It does, however, extend eastward to the vicinity of Port Elizabeth, which receives precipitation all year. Interesting outliers of this sclerophyllous vegetation also occur at increasing altitudes to the north in the mountains of the Karoo and Namaqualand and along the eastern mountain chain as far as Ethiopia (Axelrod & Raven, 1978; Taylor, 1978). With regard to its history and phytogeography, the dominant sclerophyllous macchia (fynbos) of Capensis has been the focus of interest for a long time. Only in recent years have palynological investigations shown that this vegetation type, adapted to a Mediterranean climate, is not as old as previously thought (Coetzee, 1978, 1983). Pollen assemblages of Tertiary age from boreholes at Noordhoek on the Cape Peninsula and in the Saldanha region, both on the Atlantic margin, now indicate that entirely different vegetation and climates compared with the present had existed in the southwestern Cape.

Some of the fossil pollen types belong to ancient parent taxa that are extinct in Africa today (Coetzee, 1981; Coetzee & Praglowski, 1984). In this connection the pollen assemblages from Noordhoek on the Cape Peninsula are of particular interest and will be mainly referred to in this discussion (Figs. 1–7). Further investigation of the pollen spectra has provided additional evidence of other extinct types and, because these records are of considerable phytogeographic interest, they will be discussed in relation to their past distribution and paleoecology.

Two pollen assemblages have been distinguished. The older assemblage contains seven extinct pollen types, some of which are significant for the explanation of present disjunct distribution patterns of genera in the Southern Hemisphere. The younger assemblage does not contain these extinct microfossils but is characterized by the pollen of macchia (fynbos) vegetation of a type dominant in the region today.

LITHOLOGY AND AGE OF THE NOORDHOEK SEDIMENTS

A pocket of sediments containing pollen-bearing peaty clay horizons occurs within 2 km of the present coastline in a fault-controlled valley flanked by mountains, between Noordhoek and Kommetjie (34°09′S and 18°20′E) on the Cape

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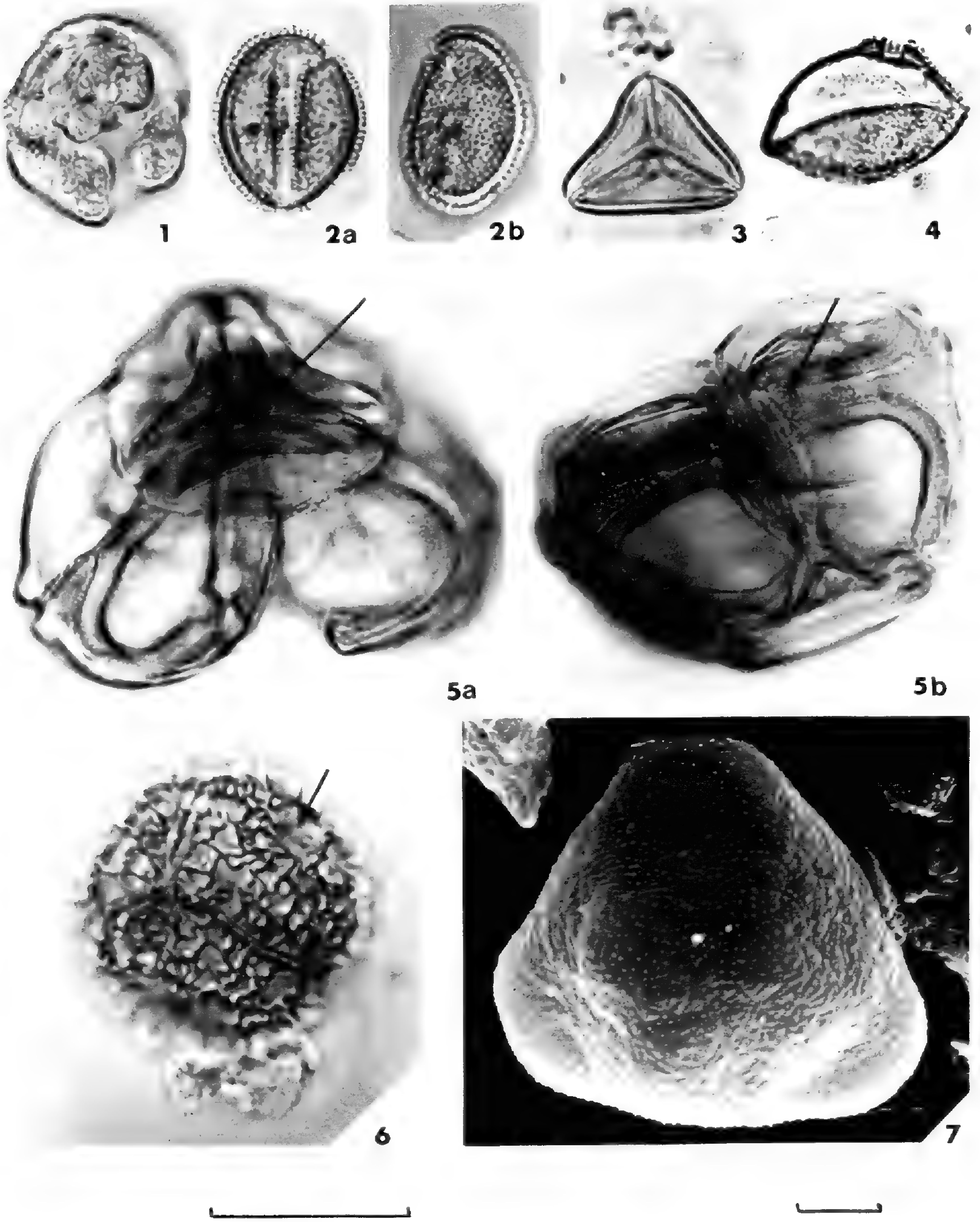

FIGURES 1–7. Extinct pollen types.—1. *Microcachrys* (Coniferae), Noordhoek 5836 no. 27, high focus. 2. *Ascarina*-type (Chloranthaceae).—2a. (cf. *A. rubricaulis*-type), Noordhoek 5836 no. 25, holotype, optical section.—2b. (cf. *A. phillipensis*-type), Noordhoek 5836 no. 36, holotype, Nomarski interference contrast, lateral view.—3. *Cupaniopsis*-type (Cupanieae, Sapindaceae), Saldanha, S1 7115 (co-ord. 7.6, 68.4).—4. *Sparganiaceaepollenites barungensis* Harris, Noordhoek 5836 (co-ord. 16.2, 72.6), median focus showing annulate pore. 5. *Xyloolaena*-type (Sarcolaenaceae), Noordhoek 7269.—5a. no. 9, holotype, tetrad at high focus level showing triangular island (arrow) enclosed by 3 ridges.—5b. no. 10, paratype, view of tetrad with common aperture (arrow) between 2 grains.—6. Winteraceae (*Bubbia*-type), Noordhoek 5836, no. 8, tetrad at high focus showing pore (arrow), Nomarski interference contrast.—7. Casuarinaceae, Noordhoek 7241, SEM micrograph showing spinules on linear ridges. Scale bar = 25 μm (nos. 1–6) and 10 μm (no. 7).

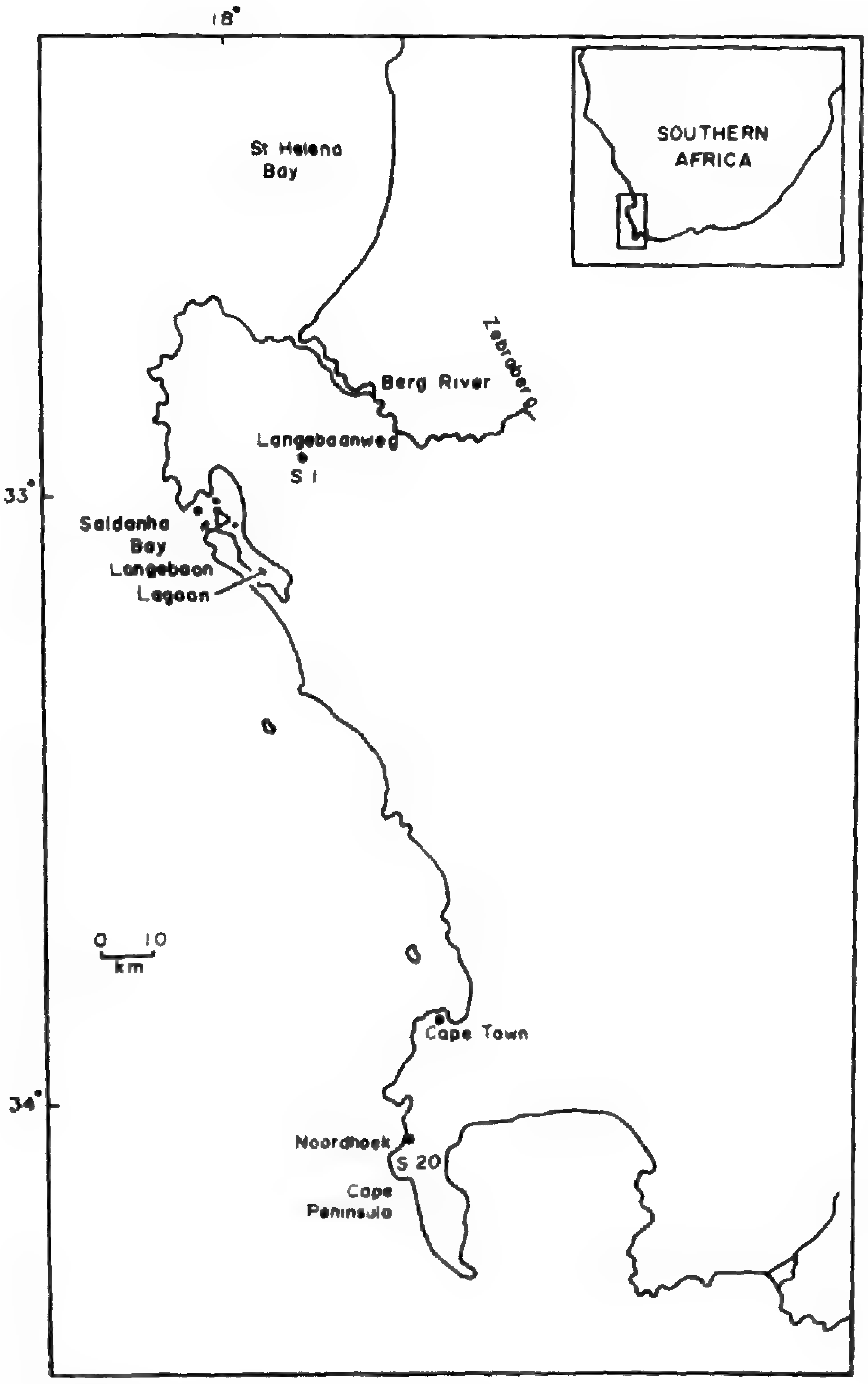

FIGURE 8. Locality map.

Peninsula (Fig. 8). These sediments, which lie below sea-level, have been subdivided into the following two Formations according to the sedimentological profile (Rogers, 1980): Bredasdorp Formation (Noordhoek member, −21 to 0 m) and Elandsfontyn Formation (−21 to −50 m). The Elandsfontyn Formation, characterized by coarse angular quartz sand, contains the bulk of the organic matter in the succession and shows no marine components. It is in this Formation that the older Tertiary pollen assemblage mainly occurs, while the younger assemblage falls mainly within the Noordhoek member of the Bredasdorp Formation. Here at −10 m rare sponge spicules are the only marine components. Further detailed parallel palynological and lithological investigations on these sediments are to be carried out in connection with paleoenvironmental assessments.

In the absence of present possibilities for firm age control the palynological assemblages of the Elandsfontyn Formation at Noordhoek previously had been assigned a relative Late Oligocene/Early Miocene age (Coetzee, 1978, 1983). This derivation had been made by comparison of the pollen types with apparently younger palynological assemblages in the Elandsfontyn Formation belonging to sediments further north in the Saldanha region. Here in Borehole S1 (33°58.20′S and 18°6.97′E) this Formation fits as follows into the succession that contains the paleontologically dated Early Pliocene Varswater Formation (Coetzee & Rogers, 1982):

Varswater Formation, Early Pliocene (vertebrate fauna) (Hendey, 1981a, 1981b).

"Saldanha" Formation (gravel member), Late Miocene (Tankard, 1975; Hendey, 1981a, 1981b) (now considered to be younger).

Elandsfontyn Formation, Early to Middle Miocene (Coetzee, 1980) (now considered to be younger).

Further palynological considerations by the present authors now confirm a Miocene age for the Noordhoek pollen assemblages and suggest an early rather than late Miocene age. Comparison is hardly possible with the well dated tropical Tertiary microfloral succession of Gabon (Salard-Cheboldaeff, 1979), Nigeria (Germeraad et al., 1968), and Senegal (Médus, 1975) because of the subtropical aspect of the Noordhoek microfloras. Only a few fossil pollen types are common to all these regions. A more direct comparison is, however, possible with the ecologically similar assemblages from the Ninetyeast Ridge and Australia. The time of the extinction of taxa obviously can not be used for age-comparisons. However, the first occurrence of widespread types is more significant and in this connection the pollen of Compositae is of paramount importance. The earliest records of the Tubiflora type are from the Oligocene of North America, Europe, and Ninetyeast Ridge, where they always occur in very low frequencies. They become more common worldwide in the Miocene (Muller, 1981). The fairly regular but sparse occurrence of Compositae pollen grains of the Tubiflora type with very low diversity in the older assemblage of Noordhoek suggests a Lower Miocene age for these pollen-bearing horizons. Unfortunately a section between the older and younger assemblages contains no pollen and probably indicates a hiatus in deposition that is difficult to explain until the detailed correlation of the lithology and palynology has been completed. This may be confirmed by the initial sharp increase and high diversity of Compositae in the younger assemblage. Such high numbers of Compositae pollen are characteristic of Upper Miocene and Pliocene or even Quaternary sediments.

GENERAL COMPOSITION AND FORMER DISTRIBUTION OF THE MICROFLORA

THE OLDER ASSEMBLAGE

Pollen of Podocarpaceae, *Widdringtonia*, Combretaceae (or *Dissotis* (Melastomataceae)), and Restionaceae are abundant at various periods whereas mostly low numbers of *Calodendrum* and Myrtaceae occur throughout the sequence. Pollen of Compositae and Gramineae are also very sparsely represented. These microfossils indicate the presence of elements of a temperate evergreen forest reminiscent of the present Afromontane forest enclaves in the Cape Province extending from east of Knysna, the Knysna forests, and the relict forest patches in valleys or "kloofs" of the Capensis phytochorion (Axelrod & Raven, 1978; Taylor, 1978; White, 1978). In addition abundant pollen was recorded of Palmae that are extinct in these regions today. These pollen types are different from those of the present South African palms, the southernmost of which, viz. *Phoenix* occurs near Bathurst in the eastern Cape. These microfossils together with pollen types such as *Croton*, Cupanieae, and others indicate the presence of subtropical floral elements. It is in this mixed type of vegetation that pollen of the following seven extinct taxa, already alluded to, has been recorded: *Microcachrys*, Winteraceae, Casuarinaceae, *Ascarina*-type, Sarcolaenaceae, *Cupaniopsis*-type, and *Sparganiaceaepollenites barungensis*. Further discussions will center around these taxa.

THE YOUNGER ASSEMBLAGE

The dominant microfossils in this assemblage belong to the Proteaceae, Ericaceae, *Cliffortia*, Compositae, Chenopodiaceae, Gramineae, Cyperaceae, and Restionaceae with some Thymelaeaceae and occasional *Casuarina/Myrica* types. The contrast with the preceding assemblage is thus considerable.

THE EXTINCT POLLEN TYPES (FIGS. 1–7)

Microcachrys (Coniferae). The relatively rare but highly characteristic trisaccate *Microcachrys* pollen (Fig. 1) is often associated in its occurrences with maxima of *Casuarina* pollen. At present the genus is restricted to Tasmania, where it occurs in the montane vegetation above 1,000 m. Its past distribution was much more extensive, and it has been reported from the Jurassic and Cretaceous of India, the Lower Cretaceous of Madagascar, the Jurassic, Cretaceous and Tertiary of Australia, the Lower Cretaceous–Tertiary of New Zealand, the Lower Cretaceous of Argentina, the Tertiary of Kerguelen, and the Paleocene and Oligocene of Ninetyeast Ridge (Archangelsky & Gamerro, 1967; Couper, 1960; Herngreen et al., 1982; Kemp & Harris, 1977; Venkatachala et al., 1972). Scott (1976) reported this pollen from the Lower Cretaceous of the Algoa Basin on the southeastern coast of South Africa, and more recently McLachlan and Pieterse (1978) recorded it from Lower and Upper Cretaceous sediments of the DSDP drilling site 361, 180 miles southwest of Cape Town.

Winteraceae. Tetrads of this family are also highly characteristic of the older pollen assemblage but occur scattered throughout the whole section. Two slightly different types appear to have been present. Comparison with the pollen morphological monograph of the family by Praglowski (1979) and a joint study with him of his reference material indicate that the larger type has most likely been derived from *Drimys* section *Tasmannia*. This plant group is at present confined to Malesia, Australia, and Tasmania, where it occurs in tropical forest, subtropical to temperate rain forest, and subalpine shrub vegetation (Fig. 9). Its closest affinity lies with the pollen of *Drimys piperita*. The smaller type (Fig. 6), however, closely resembles the pollen of *Bubbia isoneura*, a New Caledonian species. The genus *Bubbia* occurs at present from sea-level to montane habitats in New Caledonia, New Guinea, and the Moluccas but is found in Australia only in Queensland and thus appears less well adapted to colder climates (W. Vink, oral comm.). The oldest record of Winteraceae is from the Aptian/Albian of Israel (Walker et al., 1983) and it is of special interest that this is the only other extant angiosperm family besides the Chloranthaceae which, so far known, has a Lower Cretaceous occurrence.

It is of interest to note that the South African fossil pollen types appear to be more related to Old World representatives of the family than to the New World group of *Drimys* section *Drimys*. They also differ from *Takhtajania perrieri* (*Bub-

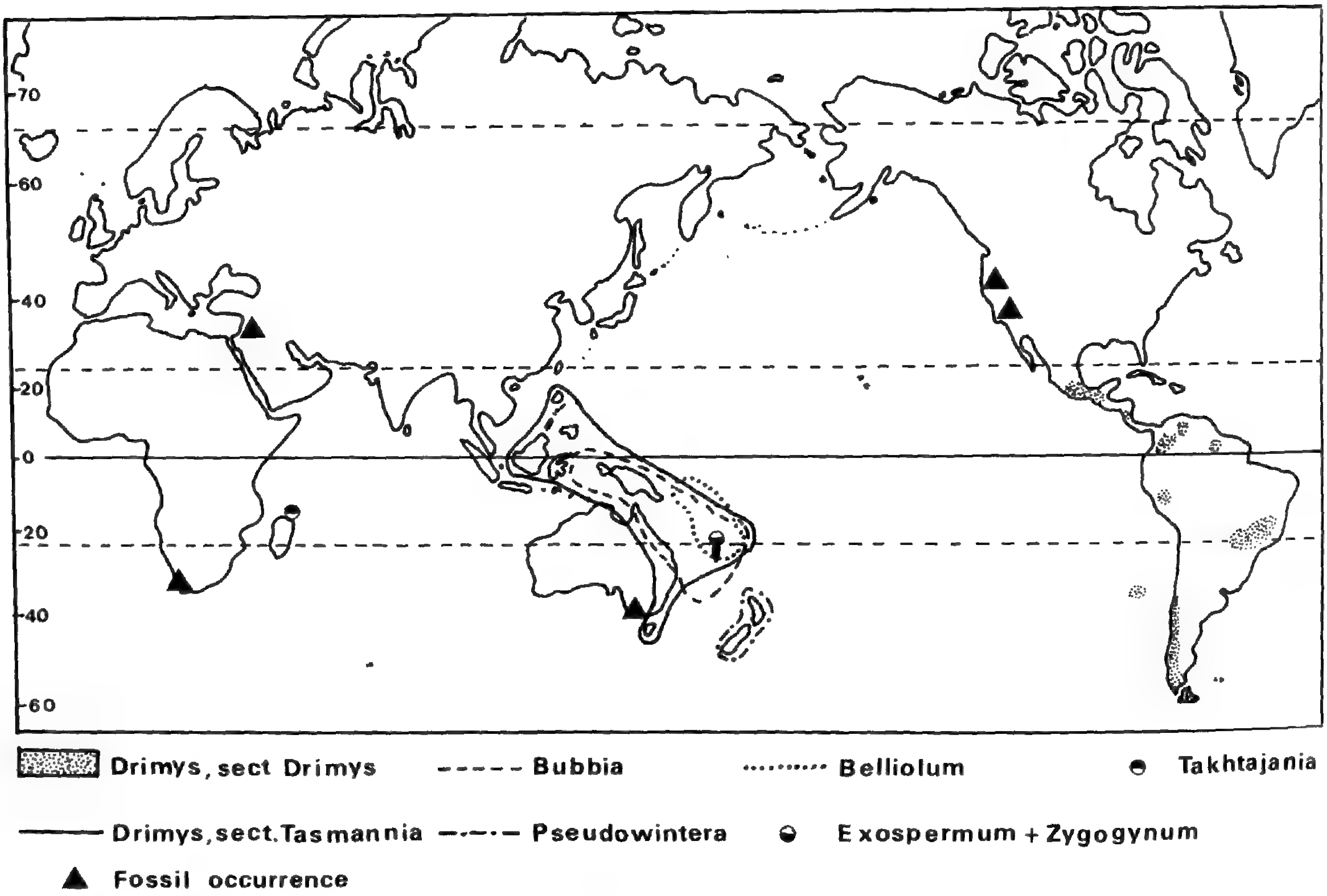

FIGURE 9. Distribution map of recent and fossil Winteraceae.

bia perrieri), the only representative of the family in Madagascar.

Fossil pollen of Winteraceae has been described from the Maestrichtian of South Australia and New Zealand as *Gephyrapollenites* by Stover and Partridge (1973), who recognized three species without indicating affinities with recent pollen types of the family. Martin (1978), however, pointed out that its closest relationship is with *Drimys* section *Tasmannia*. Mildenhall and Crosbie (1979) considered *Gephyrapollenites* a junior synonym of *Pseudowinterapollis*. They are of the opinion that this genus is similar to the recent endemic genus *Pseudowintera* of New Zealand. The specimens from South Africa do not fall within the circumspection of *Pseudowinterapollis* as previously thought by Coetzee (1981).

Casuarinaceae. The pollen type of this family (Fig. 7) is very common throughout the older assemblage and shows marked changes in abundance. The possibility that many of these forms could belong to this family has already been alluded to (Coetzee, 1983) and it has now been proved beyond doubt at the SEM and TEM levels by Praglowski (Coetzee & Praglowski, 1984) that Casuarinaceae existed in South Africa in the Tertiary. The pollen can easily be confused at the light microscope level with that of *Myrica*, which also occurs in the assemblage (cf. also Muller, 1981).

Unfortunately it is not possible to differentiate between the pollen of the inland representatives of the family and that of the widespread *Casuarina equisetifolia*, which is a pioneer of tropical sandy beaches.

Casuarinaceae are adapted to a subtropical-tropical climate and are found today in a wide range of rainfall conditions. The main development of the family is undoubtedly centered in Australia with radiation into the Pacific and Southeast Asia, the range of *C. equisetifolia* being much wider. The probable native range of the family is indicated in Figure 10.

Fossil pollen has been found in abundance in Tertiary sediments of New Zealand, Australia, the Ninetyeast Ridge, and Borneo, and recorded as *Haloragacidites* (= *Triorites*) *harrisii* or as *Casuarinidites cainozoicus*. Macrofossils have been found in the Paleocene of Argentina, and the occurrences at Noordhoek fit in well with a formerly much wider range of the family.

Ascarina-type (Chloranthaceae). This pollen type (Fig. 2) is especially frequent in the lower

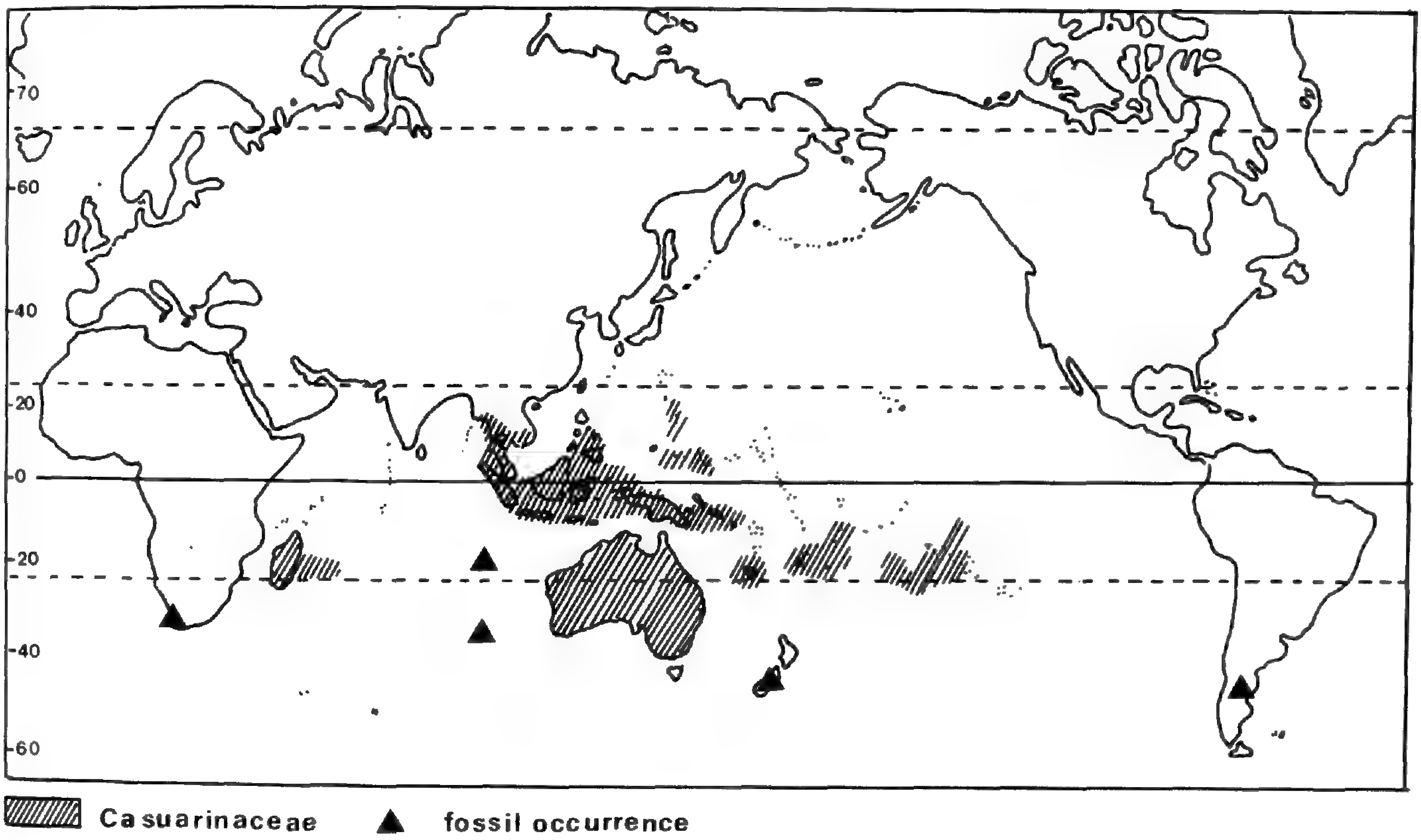

FIGURE 10. Distribution map of recent and fossil Casuarinaceae.

part of the section, where it alternates with maxima of *Casuarina, Microcachrys, Podocarpus, Widdringtonia,* Combretaceae/Melastomataceae, and Proteaceae pollen. More than one subtype comparable to *Ascarina rubricaulis* (Fig. 2a), *A. philippinensis* (Fig. 2b), and *Ascarinopsis coursii* appears to be present. The last species, often included in *Ascarina,* is a rare endemic found in humid montane forests at an altitude of 1,700–1,800 m in the northeast of Madagascar. The seven species of *Ascarina* occur in East Malesia and New Guinea in montane rain forest from 1,010–3,300 m and in the west Pacific in New Zealand also in a humid climate, but from sea-level to 1,500 m (Fig. 11).

In this case also, the fossil occurrence of *Ascarina* in the Miocene of South Africa fits in well with its formerly much more widespread range, which in the Palaeogene covered Australia and the Ninetyeast Ridge (Fig. 11). In the Cretaceous this pollen type (as *Clavatipollenites*) was even much more widespread, being found in central Africa, North and South America, and Europe (Muller, 1981) while it has been reported for the Lower Cretaceous by Scott (1976) from boreholes along the southeastern African coast, and by McLachlan and Pieterse (1978) from the DSDP site 361, 180 miles SW of Cape Town in the Upper Cretaceous sediments.

Xyloolaena-type (Sarcolaenaceae). The very characteristic pollen tetrads of this type (Fig. 5) are restricted to the genera *Leptolaena, Rhodolaena, Sarcolaena,* and *Xyloolaena* of the family Sarcolaenaceae, which is endemic to Madagascar. These tetrads occur scattered in the lower part of the older assemblage and appear to resemble most closely the tetrads of *Xyloolaena* (Carlquist, 1964; Straka, 1964).

Sarcolaenaceae are shrubs or small trees, rarely large trees, which occur mainly as rare elements in the humid forests of the eastern region of the island. Here they prefer the drier localities on sandy or rocky soil over a wide range of altitudes but are found also on coastal dunes (*Sarcolaena*) or, rarely, in the dry eastern region (*Leptolaena arenaria*) (Cavaco, 1952; Perrier de la Bâthie, 1920).

Cupaniopsis-type (Sapindaceae). This pollen type (Fig. 3), which is equivalent to the fossil genus *Cupanieidites,* is at present restricted to part of the tribe Cupanieae from America, Madagascar, and Australasia while it is conspicuously missing in genera occurring in Africa (Muller & Leenhouts, 1976; Muller, 1981). The pollen occurs in comparatively low frequencies in the older assemblage and is not correlated with maxima of other pollen taxa.

The fossil pollen genus *Cupanieidites* was abundant in the Upper Cretaceous both of central Africa, becoming extinct here in the early

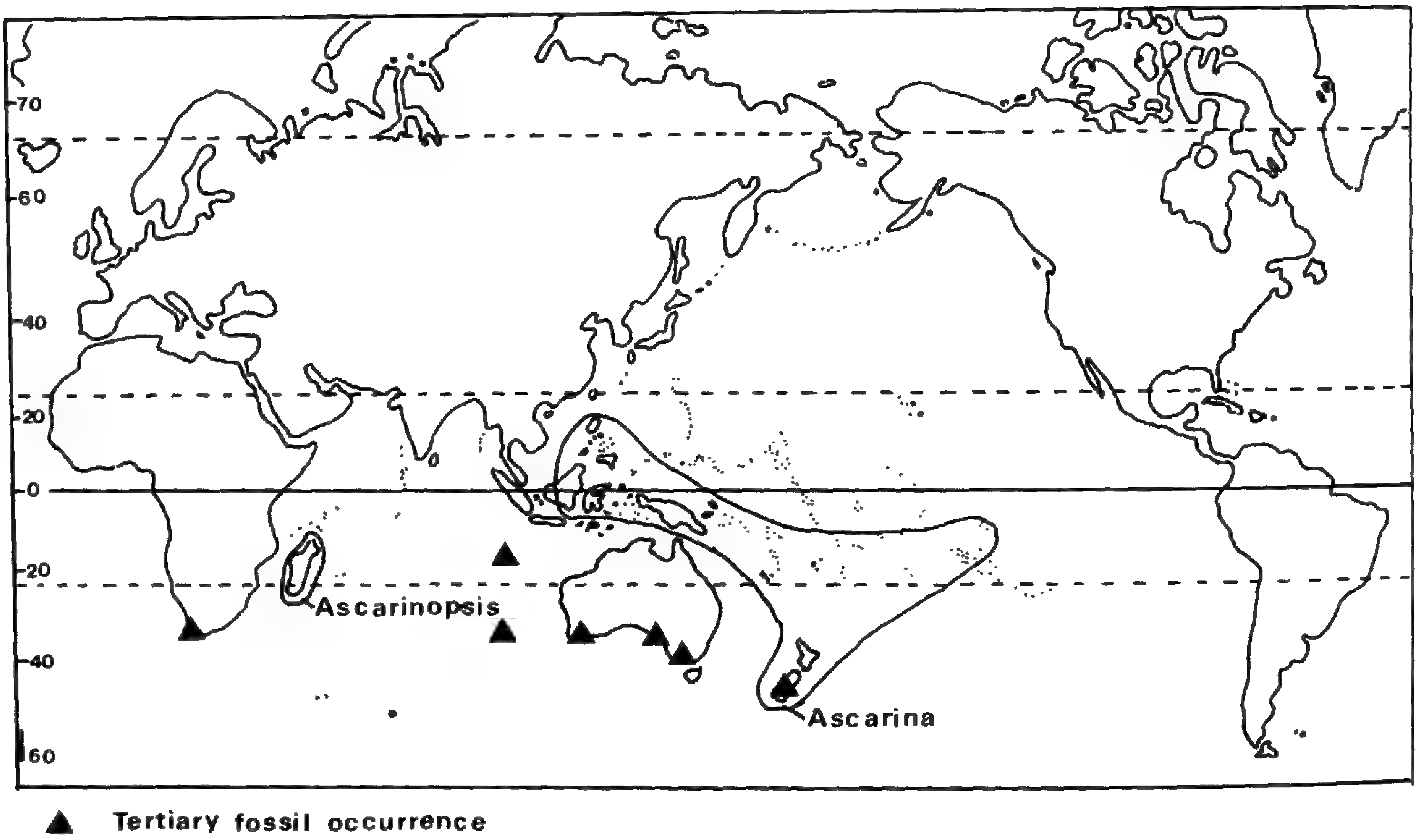

FIGURE 11. Distribution map of *Ascarina* and *Ascarinopsis* (Chloranthaceae) and Tertiary occurrences of fossil *Ascarina*-type pollen.

Tertiary (Muller & Leenhouts, 1976), and of South Africa from where it was reported from the Upper Cretaceous sediments from DSDP site 361 (McLachlan & Pieterse, 1978). *Cupanieidites* has an Upper Cretaceous record in Brazil and the earliest record for Australia is from the Palaeocene (Muller, 1981). The genera of Cupanieae with this pollen type occur at present in a wide range of humid tropical to subtropical environments (Fig. 12).

Sparganiaceaepollenites barungenis Harris (Typhales) (Aglaoreidia qualumis Partridge). This pollen type (Fig. 4) probably has been derived from a taxon related to Typhaceae or Sparganiaceae but cannot be identified with a living species, although Martin (1973) suggested that the pollen of the living *Sparganium antipodum* is rather similar.

In the older assemblage it is common and fluctuates greatly in abundance as does the pollen of Restionaceae. Both pollen types probably are derived from marsh vegetation around fresh water inland lakes.

The fossil pollen type was first described from the Eocene–Miocene of Australia and New Zealand (Harris, 1972; Mildenhall & Crosbie, 1979). *Sparganiaceaepollenites* has also been recorded from the Palaeocene of Argentina (Archangelsky, 1973).

DISCUSSION

In general the Miocene pollen flora of the southwestern Cape, the composition of which has been broadly discussed by Coetzee (1978, 1983), appears to represent lowland and montane subtropical rain forest in which palms were prominent. This vegetation type does not occur in the area at present although the Knysna forest to the southeast possibly could be considered an impoverished remnant of it. This flora clearly antedates the development of a Mediterranean climate in the Cape region, possibly in the Pliocene (Hendey, 1981b) or Late Pleistocene (Axelrod & Raven, 1978), as discussed by Coetzee (1983). The humid forest in Madagascar that at present contains taxa similar to those of the Miocene rain forest of the Cape (*Ascarinopsis*, Cupanieae, Winteraceae, and Sarcolaenaceae) is also a modified descendant from this ancient vegetation type, which was postulated by Axelrod and Raven (1978, Fig. 6) to have been present in the Late Miocene in both regions.

It is obvious from the pollen assemblages that links existed with the ancient floras of Gondwanaland (Raven & Axelrod, 1974). These floras may have dispersed almost directly among the closely situated Gondwana fragments, possibly from the mid-Cretaceous to the Palaeogene.

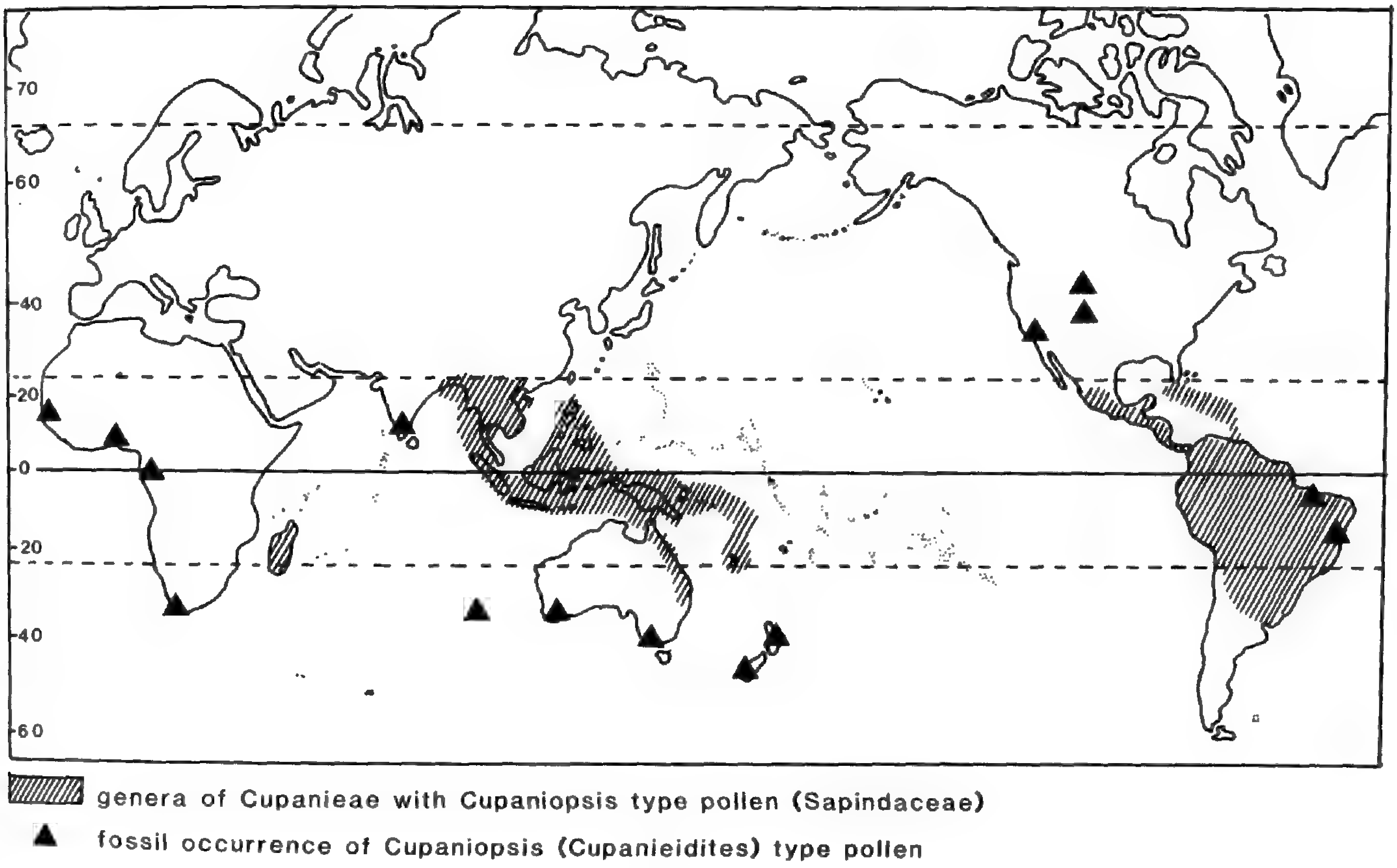

FIGURE 12. Distribution map of genera of Cupanieae with *Cupaniopsis*-type pollen and fossil occurrences.

In these latter periods the dispersal routes were either tropical or subtropical or more temperate with Antarctica in both cases in the central position (Raven & Axelrod, 1974).

With regard to the common Africa-Madagascar floral elements, recent geophysical evidence (Rabinowitz et al., 1983) indicates that the motion of Madagascar relative to Africa was from the north and probably started in the mid-Jurassic (165 million years ago) or somewhat later depending on the postulated spreading rates. Separation from the continental margin of Kenya and Somalia must have been effective at least from the Cenomanian (95 million years ago) onward. This is confirmed by the presence, in the Albian of Madagascar, of a microflora indicative of the Gondwana province of Herngreen and Chlonova (1981; Herngreen et al., 1982), suggesting southern contacts rather than east African ones at that time. Raven and Axelrod (1974) and Axelrod and Raven (1978) visualized these connections, via the now largely submerged Mascarene plateau, with India and Antarctica and lasting till the late Cretaceous. This connection then could have provided a route for the Cretaceous dinosaurs as well as for the rich angiosperm floras of Madagascar and the Seychelles.

Microcachrys. This is undoubtedly the most prominent ancient Gondwana element with a probable continuous range in the Cape region from the Lower Cretaceous into the Miocene. The records of the former distribution of *Microcachrys,* as discussed earlier, are all from ancient fragments of Gondwanaland. This former range is in sharp contrast with the present day relict occurrence in Tasmania. The genus may have originated in the Jurassic or earlier and dispersed widely in the Jurassic–Lower Cretaceous, after which it became variably extinct. It is of special interest that *Microcachrys* survived much longer in South Africa than in India, which, during its northward drift, passed through totally different climatic zones. It is interesting that another Mesozoic gymnosperm genus, *Araucaria* (*Araucariacites*), the pollen of which occurs concomitantly with *Microcachrys* in the Cretaceous of South Africa (McLachlan & Pieterse, 1978; Scott, 1976), did not survive as long as *Microcachrys* in the Cape.

Winteraceae. Like the other ancient angiosperms represented in the Tertiary pollen assemblages, this family forms a specific link with the austral floras, especially with the subtropical-temperate types. Of importance is the evidence in the Miocene of the Cape of representatives of the Australasian group of Winteraceae. That this family was formerly more widespread was already suggested by the discovery of fossil wood in the Upper Cretaceous of North America (Page, 1981). The nature of the wood has suggested a relationship with the Old World Winteraceae but the anatomical features are now thought to be correlated with climate rather than with taxonomy (P. Baas, oral comm.).

The primitive characters of the Winteraceae are well in accord with at least an early Cretaceous origin as indicated by the presence of fossil pollen attributed to this family (Walker et al., 1983) in Israel, which formed part of the ASA floral province at that time. According to Herngreen and Chlonova (1981) this province covered the tropical-subtropical zone of a joint South American–African–Arabian continent including Israel, and overland dispersal in Gondwanaland was clearly possible in the early Cretaceous. The survival of the related genus *Takhtajania* in Madagascar indicates local evolution also from an ancient Gondwana matrix. To reach Madagascar the dispersal to this island must, according to Axelrod and Raven (1978), have occurred before 80 million years ago. In view of its early separation from Africa, dispersal was probably from the south. Raven and Axelrod (1974: 616) inferred that the ancestors of the Winteraceae reached Australia in mid-Cretaceous time along a tropical or subtropical route.

The present day American representatives of the Winteraceae grouped in *Drimys* section *Drimys* may be a later development from West Gondwana ancestors, separate from development in Australia.

The records for *Casuarina, Ascarina,* and Cupanieae, which will be discussed next, refer to elements that are less clearly restricted to temperate, subtropical, or montane tropical climates.

Casuarinaceae. This family is found in tropical lowland, montane, and subtropical climates. Fossil and present day distributions point to a wide range in the past covering the Pacific, Southeast Asia, Australia, Madagascar, and the southern parts of Africa and America (Fig. 10). Raven and Axelrod (1974: 616) suggested that the ancestors of Casuarinaceae may have reached Australia in mid-Cretaceous times by a subtropical to tropical route from Africa. The oldest-known fossil pollen dates from the Palaeocene of New Zealand (Muller, 1981). Evidently the contraction of its range was related to the effects of cooling during the maximum glaciation of Antarctica in the Terminal Miocene.

Ascarina-type. The relationship of *Ascarina* with the Lower Cretaceous *Clavatipollenites* group (cf. Muller, 1981), which may even have originated in Central Africa (Doyle et al., 1977), most likely refutes the postulation of Raven and Axelrod (1974) that this genus reached Madagascar from the east. Its abundant presence still in the Miocene of South Africa strongly suggests that a chloranthaceous matrix developed somewhere on the African mainland and its descendants could easily have reached Madagascar while spreading out over Antarctica and other Gondwana fragments. The marked contraction of its range is probably connected with competition with younger angiosperm groups as well as with climatic change. Its survival in Madagascar (as *Ascarinopsis*) is evidently due to the isolation of this island and the continued equable climate at these latitudes. The climatic requirements may have been more subtropical to tropical-montane than was the case with *Casuarina.*

Cupanieae. Cupanieae have also had a long history on the African continent as is shown by the abundance of *Cupaniopsis*-type pollen in the Upper Cretaceous of West Central Africa and the Miocene of South Africa. They presumably reached Madagascar in mid-Cretaceous time after it separated from East Africa.

The range contraction of those genera of Cupanieae that were characterized by *Cupaniopsis*-type pollen was completed much earlier in tropical central Africa than in the subtropical southern region where some taxa still survived in the Miocene. The explanation for the extinction of part of the Cupanieae in Africa is at present obscure. In Madagascar the genera *Molinaea* and *Tina* of this group have survived until the present day and are widespread from sea-level up to more than 2,000 m. In Australasia and America the genera of this group are still widespread today and range from tropical to subtropical temperate climates (Fig. 12).

Xyloolaena-type. For Sarcolaenaceae a similar development may be postulated, although a comparable fossil record is lacking. The occurrence in South Africa of the highly developed *Xyloolaena*-type in the Miocene of the Southwestern Cape is the first fossil record of the family but certainly does not represent the oldest occurrence of the Sarcolaenaceae. It is not clear whether we are dealing here with an endemic African family that migrated to Madagascar and later become restricted to the island, as was inferred by Raven and Axelrod (1974). Its ecology, although slightly more specialized than that of *Ascarina* and Cupanieae, still fits into a humid subtropical to tropical-montane pattern. These three groups probably occurred together in the same forest type that they inhabit today in the humid forest of Madagascar. The history of Sarcolaenaceae and *Ascarina* appears to be comparable and the contraction of their ranges may have been due to similar climatic causes.

Sparganiaceaepollenites barungensis-pollen type. This is less indicative of former connections with other continents or of specific climates. The occurrence of this Australian Tertiary pollen type indicates former connections of Africa with South America and Australia. It also fits into the general pattern of an austral Gondwana connection indicated by *Microcachrys,* Winteraceae, and *Casuarina.* Dispersal routes may have been via South America–Antarctica to Australia or via the islands of the Indian Ocean. The possibility of bird dispersal must be taken into account here. The relatively young Tertiary age of this pollen type suggests either wider dispersal capabilities for the parent plant or an earlier unrecognized occurrence of the ancestral complex. The fossil record of Typhales, however, goes back only to the Palaeocene (cf. Muller, 1981). The extinction of the parent taxon of this pollen type at the end of the Tertiary in South Africa, Australia, and New Zealand is difficult to explain.

CONCLUDING REMARKS

The evidence discussed here not only throws light upon the relationship between Africa and Madagascar floras, but also on the contacts between Madagascar and South America as discussed by Raven and Axelrod (1974: 612). The data presented support the hypothesis that a common South American–Antarctic–African–Madagascar flora, which existed in the Cretaceous, became fragmented due to plate movements and that taxa common to Madagascar and South America today had their origin in the West Gondwana–Antarctic section of Gondwanaland. The evidence does not support the postulation of long-distance dispersal of some of these ancient taxa from Australia to Madagascar.

Long distance dispersal around the Indian Ocean before the Pliocene desertification in the Middle East, however, may have been responsible for the distribution of such taxa as *Adansonia, Hibbertia,* and *Nepenthes.*

The final problem on which the evidence discussed has considerable bearing is that of the impoverishment of the African flora in the course of the Tertiary. This phenomenon has been discussed by many authors, notably Moore (1973) for the palms and by Raven and Axelrod (1974). It would appear now that the hypothesis of local extinction, to explain the absence in Africa of many angiosperm taxa that are still present in South America, Madagascar, and SE Asia, finds support in the fossil record. A good example is the disappearance of the *Nypa* palm from tropical Africa at the end of the Eocene (Germeraad et al., 1968). For Cupanieae the disappearance from the microfossil record of the taxa characterized by the *Cupaniopsis* pollen type in the Palaeogene is documented by Jan du Chêne et al. (1978) and Salard-Cheboldaeff (1979). Their survival in South Africa well into the Miocene was presumably due to more stable and humid climatic conditions. *Ascarina* had become extinct over large areas much earlier (Muller, 1981).

It is thus evident that extinction may not have been a single event. It must have varied locally according to the severity of environmental changes associated with the maximum glaciation of Antarctica at the end of the Tertiary. Macchia must have spread during the Pliocene and Pleistocene when there were fluctuations of warm and cold water offshore (Axelrod & Raven, 1978; Tankard & Rogers, 1978). Some of these elements were already present in the summer rainfall climate of the Miocene and earlier and became adapted to summer droughts during periods of cold water currents. Axelrod and Raven (1978) considered the present mediterranean climate, in which the hardiest macchia taxa have survived and profoundly speciated, to have originated in the Late Pleistocene. The older periods (not earlier than 5 million years ago) of this type of climate were less intense (D. I. Axelrod, pers. comm.). On the basis of paleontological data, however, Hendey (1981b) postulated that the transition to the mediterranean type of climate could have occurred in the early Pliocene (5 million years ago). By that time the last relict occurrences of some warm temperate to subtropical taxa discussed here could have disappeared from the southwestern Cape (Coetzee & Rogers, 1982).

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MAIZE INTROGRESSION INTO TEOSINTE—A REAPPRAISAL[1]

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ABSTRACT

Maize (*Zea mays* L. subsp. *mays*) and its wild relatives, the teosintes (*Zea* spp.) have been considered by many authors to be undergoing substantial reciprocal introgression. While there is evidence that some maize populations contain teosinte germplasm, the evidence for maize introgression into teosinte has been largely circumstantial. A re-consideration of the evidence for maize introgression into teosinte proved it wanting. Red sheath color, large grain size, triangular fruitcase shape, and the presence of internal chromosome knobs, all characters attributed to maize introgression into teosinte, appear rather to reflect the adaptation of particular teosinte populations to the exigencies of specific habitats. Apparently, the taxa of teosinte have remained relatively free of long-lasting maize contamination at least in respect to those characters that affect the survival of teosinte in the wild. Low-level introgression from maize to teosinte, although possible, remains undocumented.

Introgressive hybridization, or more simply, introgression, is the incorporation of genes from one population into another with a different adaptive norm (Anderson & Hubricht, 1938). This process is of obvious importance to taxonomists and evolutionists because, along with mutation, gene drift, and recombination, it is a potential source of evolutionary variation within and among species. Introgression is of particular interest to scientists studying cultigens and their wild ancestors because these plants generally lack barriers to hybridization and they often grow sympatrically. For these reasons, one would expect introgression between crop species and their ancestors to occur with some frequency.

The cultigen maize (*Zea mays* L. subsp. *mays*) and its wild relatives, the teosintes, have been considered model examples of reciprocal introgression (de Wet & Harlan, 1972; Heiser, 1973; Wilkes, 1977). The evidence for teosinte introgression into maize seems good. Where farmers in Mexico encourage the hybridization of teosinte and maize in an effort to "improve" their maize strains, the resultant maize populations have many teosintoid characteristics (Wilkes, 1970, 1977). The reverse introgression of maize germplasm into teosinte seems less likely to occur because maize has many characteristics that prevent it and its hybrids with teosinte from surviving in nature. Nevertheless, the frequency of maize-teosinte hybrids in the wild in Mexico and Guatemala (10% or more of the teosinte plants in a field may actually be hybrids), coupled with the fact that maize and teosinte show parallel variation over much of their range, has led some authors to conclude that many teosinte populations have been substantially altered by maize introgression. In this paper, I will review and reinterpret the evidence for maize introgression into teosinte and articulate the viewpoint that the teosintes have not been substantially altered by maize introgression.

A critical problem in the study of introgression is to distinguish natural evolutionary variation from that produced by introgressive hybridization (Anderson, 1953). This generally proves a difficult task because within any taxon there exists a certain amount of natural variation, some of which will inevitably be in the direction of other closely related taxa. For example, within many plant genera, one finds some natural variability for seed and fruit size. This being the situation, claims that those populations with intermediate-sized organs represent hybrids of the large and small organed forms should be viewed askance (cf. Weatherwax, 1918). Further, even if

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a particular taxon demonstrates intermediacy for a number of morphological or genetic characters, thereby appearing to be of hybrid origin, this does not preclude the possibility that this taxon represents an evolutionary intermediate (cf. Mangelsdorf & Reeves, 1939: 207).

The introgression problem in *Zea* is particularly perplexing. Not only does cultivated maize commonly occur in the proximity of its wild relatives, but it has been observed to hybridize in the wild with all of them (Wilkes, 1967; Collins, 1921a; Iltis et al., 1979). In addition, there exists considerable variation in the shape and size of organs among the teosintes, which easily lends itself to the hypothesis that maize germplasm is introgressing into teosinte. The case for maize introgression into teosinte seems difficult to repudiate. Yet, one may interpret the variation in teosinte as natural evolutionary variation, and, as will be shown below, such an interpretation coincides well with known ecological and evolutionary principles.

In the following discussion, it is important that the reader have a basic knowledge of the taxonomic relationships in *Zea*. The genus is divided into two sections. Section *Luxuriantes* contains three species: (1) *Z. diploperennis* Iltis, Doebley & Guzman, a diploid perennial from Jalisco, Mexico; (2) *Z. perennis* (Hitchc.) Reeves & Mangelsdorf, a tetraploid perennial from Jalisco, Mexico; and (3) *Z. luxurians* (Durieu & Ascherson) Bird, an annual from southeastern Guatemala and Honduras. Section *Zea* contains a single species with three subspecies: (1) *Z. mays* subsp. *mays,* the cultigen; (2) *Z. mays* subsp. *mexicana* (Schrader) Iltis, a large spikeleted annual from high elevation of central and northern Mexico, including races Chalco, Nobogame, and Central Plateau; (3a) *Z. mays* subsp. *parviglumis* Iltis & Doebley var. *parviglumis* (Balsas teosinte), a small spikeleted annual from low or middle elevations in southwestern Mexico; and (3b) *Z. mays* subsp. *parviglumis* var. *huehuetenangensis* Iltis & Doebley, a genetically distinct form of this subspecies from western Guatemala (Iltis & Doebley, 1980; Doebley & Iltis, 1980; Doebley, 1983). As this taxonomy suggests, the teosintes of section *Luxuriantes* are not particularly closely related to the cultigen, whereas those of section *Zea* are so close as to be regarded as conspecific. Finally, in this discussion, I will, at times, mention the genus *Tripsacum* which, along with *Zea* forms the subtribe Tripsacinae of the tribe Andropogoneae of the family Gramineae.

HISTORICAL BACKGROUND

Since the time when Ascherson, Beadle, Collins, Kempton, Longley, and others first began to document the extent of variability among teosinte populations, researchers have demonstrated a bias in favor of maize introgression to explain this variability. Thus, Collins (1921a: 340, 345), who noticed that both maize and teosinte of the Valley of Mexico have dark red, densely pilose sheaths, speculated that teosinte acquired these characters from maize via introgression. Part of Collins's reason for proposing this explanation was that he had never before seen "pure teosinte" with these characters. Later, Mangelsdorf (1947: 165) and then Wilkes (1977) reiterated this idea.

Collins also (1921a: 350) theorized that perennial teosinte (*Zea perennis*) had hybridized with maize to produce annual teosinte. However, he offered no evidence to support this idea other than his observation that maize and teosinte show parallel variation wherever they co-occur. Collins apparently failed to recognize that such parallel variation could easily result from either teosinte introgression into maize or simply convergent evolution. A few years later, Collins (1925: 378, 1930: 201) modified his thesis somewhat by suggesting that either *Z. luxurians* (Florida type) or *Z. perennis* might have hybridized with maize to produce the Mexican annual teosintes (*Z. mays* subsp. *mexicana* and subsp. *parviglumis*). As evidence in support of this hypothesis, he reported that ". . . forms resembling the Mexican type [*Zea mays* subsp. *mexicana*] always appear in hybrids between Florida teosinte [*Zea luxurians*] and maize" (Collins, 1925: 378).

Kempton and Popenoe (1937: 216–217) discussed "the assumption of other workers" that the triangular shape of the fruitcase of Mexican annual teosinte represents the by-product of maize introgression into *Zea luxurians,* which has trapezoidal fruitcases. However, Kempton and Popenoe questioned the validity of this hypothesis based on their observation that the triangular "fruited" Huehuetenango teosinte occurs in "almost pure stands," and thus, is free of maize introgression. Ultimately, they decline to conclude, one way or the other, whether Mexican annual teosinte represents a good species or a hybrid of "pure teosinte" with maize (Kempton & Popenoe, 1937: 217).

Longley (1937, 1941a) proposed that the internal chromosome knobs (heterochromatic regions) of Mexican annual teosinte resulted from the contamination of "pure teosinte" (*Zea luxurians*), which has many terminal knobs, with maize, which is characterized by many internal knobs. However, he declined to rule out the possibility that the Mexican annual teosintes acquired their internal chromosome knobs via mutation, with *Z. luxurians* being their more primitive ancestor.

Mangelsdorf and Reeves (1938, 1939) went one step further than Collins, Kempton, and Longley and advanced their hypothesis that teosinte "... appears to be nothing more than *Zea* [the hypothetical wild maize] with a slight infection of *Tripsacum* germplasm" (1939: 209). This idea actually originated with Edgar Anderson (cf. Mangelsdorf & Reeves, 1939: 212; Anderson, 1969; Mangelsdorf, 1974: ix). Under the viewpoint of this hypothesis any variability in teosinte manifests nothing more than differences in the relative proportions of "wild maize" and *Tripsacum* germplasm (Mangelsdorf & Reeves, 1939: 215).

This view of variability in teosinte has influenced others as well. Thus, in his study of the genetic mechanisms controlling inheritance of inflorescence characters in maize-teosinte hybrids, Rogers (1950), a student of Mangelsdorf, found evidence that, in his view, called the purity of the Mexican annual teosintes into question. He reported that hybrids with Nobogame (*Zea mays* subsp. *mexicana*) produced the most maize-like inflorescences and those with southern Guatemalan teosinte (*Zea luxurians*) the least maize-like ones. Durango (*Z. mays* subsp. *mexicana*) and "northern" (western) Guatemalan (*Z. mays* var. *huehuetenangensis*) teosintes were intermediate in this regard. To Rogers, these results indicated that Nobogame teosinte is highly contaminated with maize, the other Mexican teosintes are somewhat less so, and southern Guatemalan teosinte is the least contaminated of all. He concluded that his evidence supports "... the hypothesis that the more maize-like teosintes represent the original teosinte with a substitution of maize germplasm on various chromosomes" (Rogers, 1950: 555).

Wilkes (1967), another of Mangelsdorf's students, considered the teosinte populations of Mexico and Guatemala to express various degrees of maize admixture. He believed teosinte in the Chalco region to be highly introgressed "as evidenced" by its dark red, hairy leaf sheaths, which are similar to those of the maize of this region (Wilkes, 1972: 1067–1077, 1977: 384–385). Wilkes (1967: 81), ostensibly disagreeing with Rogers (see above), found little evidence of maize introgression into teosinte in the Nobogame area. Wilkes (1967: 72) considered the principal direction of gene exchange in the Balsas river valley to be from teosinte to maize and not vice versa. Wilkes (1967: 82) reported hybrids to be rare in southeastern Guatemala, and thus, introgression unimportant. Wilkes (1967: 82) also concluded that teosinte in the Huehuetenango region of Guatemala was little introgressed by maize, though he found many hybrids of this teosinte and maize in the wild. Wilkes (1967: 80–81) considered the teosinte of the Mexican Central Plateau to show signs of maize admixture in its pistillate spike, including paired spikelets and a nonbrittle rachis. In addition, he regarded the large grain size and triangular fruitcase of some Central Plateau populations and of Chalco teosinte as evidence of maize introgression (Wilkes, 1977: 278). More recently, Wilkes (1979) proposed that all the racial varieties of annual teosinte resulted from the hybridization of maize with *Zea diploperennis*, coming full circle back to Collins's (1921a) similar suggestion involving *Zea perennis*.

Bird (1978: 362) also considered maize introgression to have played an important role in the morphology of extant teosinte populations. He regarded tall plants with large leaves, few tillers, a great number of and large fruitcases, and large caryopses as heavily introgressed by maize. Further, he hypothesized that Huehuetenango teosinte is a hybrid of maize and *Zea luxurians*.

Many authors have reiterated these contentions concerning the introgression of maize germplasm into teosinte (Heiser, 1973; Galinat, 1975; de Wet et al., 1978; de Wet & Harlan, 1972). However, a few authors have adjured this line of reasoning, and taken either the viewpoint that teosinte is not significantly introgressed by maize or that the evidence for such introgression is wanting (Melhus et al., 1949; Kato, 1976; Iltis & Doebley, 1980).

For many of the authors discussed above, their views on maize-teosinte introgression formed part of their models on the origin of corn because an understanding of teosinte is prerequisite to understanding the evolution of maize. As stated by Collins (1921b: 505) "... the many resemblances between maize and teosinte, together with the fact that the two forms interbreed with perfect freedom, make it certain that whatever the origin of maize it must be intimately associated with teosinte." Thus, in the early part of this century, when very little was known of teosinte, hybridization and introgression theories seemed to solve the dilemma of teosinte being genetically the same species as maize but morphologically too dissimilar from maize to be its ancestor.

RECONSIDERING VARIABILITY IN TEOSINTE

Five trends in teosinte variation lend themselves to easy interpretation as examples of maize introgression into teosinte. (1) *Grain size.* Because some teosinte populations produce larger grains than others, various authors (Wilkes, 1977; Bird, 1978) have either hypothesized or stated quite unequivocally that the large-grained forms show the effects of introgression from the relatively giant-grained maize. (2) *Fruitcase shape.* The fruitcases of the teosintes vary from trapezoidal through triangular but blunt on the axial side to triangular and pointed or "pinched" on the axial side. The pointed triangular forms, it has been argued, are the most introgressed and the trapezoidal the least (Kempton & Popenoe, 1937; Mangelsdorf & Reeves, 1939; Reeves, 1953; Wilkes, 1977). (3) *Sheath characters.* Teosinte in the Valley of Mexico, like the native maize of this area, possesses densely pilose and dark red leaf sheaths. Teosinte is said to have obtained these characters from maize through introgression (Collins, 1921a; Mangelsdorf, 1947; Wilkes, 1967, 1972, 1977). (4) *Disease resistance.* Teosinte from southeastern Guatemala expresses resistance to a common maize virus. According to one author it could have obtained this resistance from local races of maize, which are themselves resistant to the same disease (Brewbaker, 1979). (5) *Internal chromosome knobs.* Annual teosinte from southeastern Guatemala possesses only terminal chromosome knobs whereas the annuals of Mexico, as well as cultivated maize, have many internal knobs. As discussed above, Longley (1937, 1941a, 1941b) and others have suggested that the Mexican annual teosintes obtained their internal knobs from maize.

Despite the facility with which these assertions often have been made, there are other explanations that do not necessitate introgression. Phylogeny and ecology of teosinte populations furnish the basis for a more parsimonious explanation for variability in teosinte than admixture with maize. In the following discussion each of the aforementioned five trends is reconsidered in the light of this viewpoint.

Grain size. "The seed is one of the least plastic organs on a plant; plants respond to stress phenotypically by varying almost every other component of yield before seed size is affected" (Harper, 1977: 664). Seed size results from a delicate compromise between a great number of conflicting exigencies including available moisture, temperature, amount of competition, length of growing season, and many other factors (Harper et al., 1970; Stebbins, 1972; Harper, 1977). Once a species has optimally adapted its grain or seed size to local environmental conditions, it will vary the *numbers* produced 100-fold before varying *size* one-fold (Harper, 1977). Thus, one would expect natural selection against incorporation of maize germplasm in teosinte plants, which would upset the fragile adaptive balance they have obtained in relation to grain size. This ecological principle impels us to conclude that grain size is one of the least likely features of the teosinte plant to be altered by maize introgression.

In addition to the above theoretical reason for expecting little alteration in grain size because of maize introgression, there exists some empirical evidence to support such a view. This evidence lies in the mean cupulate fruitcase weights (including caryopsis) for the different taxa of teosinte. Quite simply, if maize introgression accounts for the variability in grain weight (size), then one would predict those taxa genetically closest to maize and crossing most frequently with it to have the largest fruitcases. The data, however, fail to meet this expectation in several ways. First, despite their greater genetic-evolutionary distance from maize, some species of *Tripsacum,* the perennial teosintes, and *Zea luxurians,* all produce much heavier fruitcases than *Zea mays* subsp. *parviglumis,* which is genetically more closely related to maize and crosses more frequently with it (Table 1) (Wilkes, 1977; Iltis & Doebley, 1980). Second, *Zea luxurians,* long recognized as one of the least maize-like teosintes and crossing but rarely with maize in its native habitat, produces grains often heavier than those of the supposedly greatly contaminated Chalco teosinte (*Z. mays* subsp. *mexicana*).

If not maize introgression, what then explains the observed variability in the grain or fruitcase size among the teosintes? There are several fac-

TABLE 1. Average weight (mg) of teosinte cupulate fruitcases with caryopsis (N = number weighed).

Species Population	Collection	Wt.	N
Tripsacum dactyloides, cult.			
Ft. Meade, Maryland		118	50
Zea diploperennis			
Manantlan, Jalisco	*Iltis et al. 1375*	75	100
La Ventana, Jalisco	*Guzman 777*	72	100
Las Joyas, Jalisco	*Iltis et al. 1250*	68	100
$\bar{x}$		72	
Zea perennis			
Los Depositos, Jalisco	*Iltis et al. 1050*	83	100
Zea luxurians			
Honduras	*Galinat 76-2076-B*	90	20
Ipala, Chiquimula	*Iltis G-42*	99	100
Agua Blanca, Jutiapa	*Iltis G-38*	86	100
El Progreso, Jutiapa	*Iltis G-5*	84	100
El Progreso, Jutiapa	*Iltis G-36*	76	100
$\bar{x}$		87	
Zea mays subsp. *mexicana*			
Churintzio, Michoacan	CIMMYT K69-3	62	100
Quinceo, Michoacan	*Iltis & Cochrane 276*	95	100
Los Reyes, Mexico	*Iltis & Lasseigne 769*	86	50
$\bar{x}$		87	
Nobogame, Chihuahua	*Gentry 17973*	58	30
Nobogame, Chihuahua	*Wilkes* (1967)	62	–
Zea mays subsp. *parviglumis*			
Balsas drainge:			
Huetamo, Michoacan	CIMMYT K67-15	50	50
Valle de Bravo, Mexico	CIMMYT K67-21	56	100
Tzitzio, Michoacan	*Iltis & Cochrane 308*	43	100
Palo Blanco, Guerrero	USDA 343237	31	100
SW Jalisco:			
La Huertita	*Guzman s.n.*	79	100
El Palmar	*Puga 11065*	73	100
Guatemala:			
San Antonio Huista	*Iltis & Lind G-120*	51	100
$\bar{x}$		53	

tors that seem to influence seed size in plants. First, the amount of *competition* that a species normally encounters influences the size of seeds produced. Species whose seedlings face intense competition require larger seeds than those of open habitats (Harper et al., 1970; Abrahamson & Gadgil, 1973; Carlquist, 1974; Werner & Platt, 1976). *Plant habit* also affects seed size, with perennials producing fewer and larger seeds than annuals (Salisbury, 1942; Hart, 1977; Primack, 1979). This results partly from the general occurrence of perennials in later seres (greater competition). *Length of growing season* influences seed size, with larger seeds being more easily formed in regions with long growing seasons (Baker, 1972). If other factors place a premium on small seed size in a region with a long growing season, then the plant will take advantage of the long growing season to produce a greater number of seeds rather than larger ones. *Available moisture* plays an important role in determining seed size, with small seeds common in wet areas and large seeds frequent in dry areas. Seedlings in drier habitats more frequently encounter drought

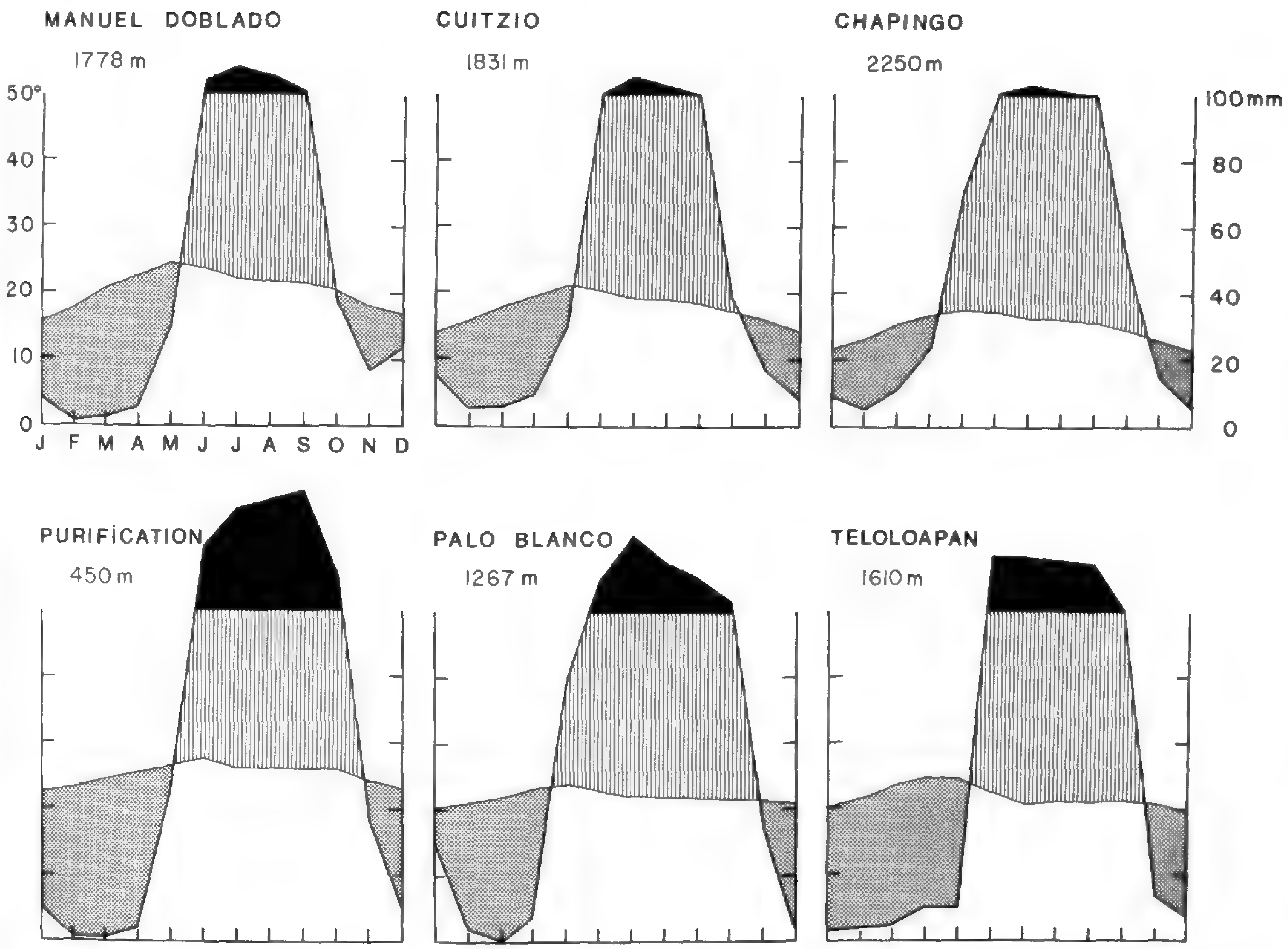
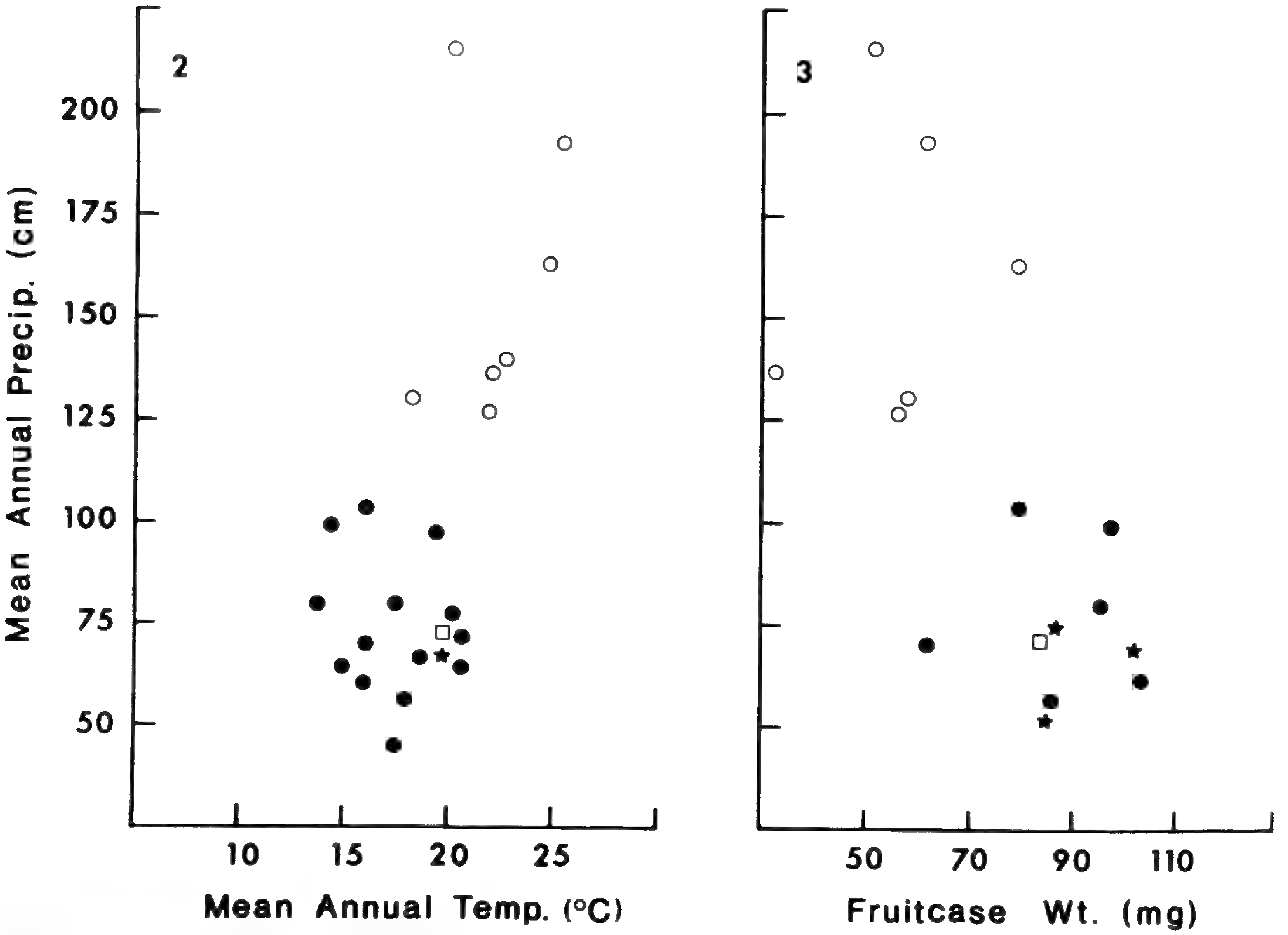


FIGURE 1. Climatic diagrams for some Mexican annual teosinte stations. The upper three diagrams represent sites of *Zea mays* subsp. *mexicana* and the lower three diagrams of subsp. *parviglumis*. On the diagrams the two curves represent mean monthly temperature (°C) and mean monthly precipitation (mm). Where precipitation exceeds 100 mm, curve is drawn at truncated scale (1 : 10) and the portion above 100 mm is black. Where rainfall curve exceeds temperature curve, space between curves is filled by vertical lines (or black, if rainfall exceeds 100 mm) whereas if rainfall curve falls below temperature curve, that space is filled by small dots. At top left of each diagram are name of station and altitude. These diagrams are patterned after those from the *Klimadiagramm-Weltatlas* (Walter et al., 1967) using data from Garcia (1974).

stress during the early stages of growth (Baker, 1972; Werner & Platt, 1976). Large seeds allow plants to establish themselves rapidly, and thus, reduce the likelihood of severe drought stress during early life. Further, larger seeds may germinate deeper in the soil where the moisture supply is more reliable (Schimpf, 1977).

Evidently, the ecological determination of seed size is immensely complex. Nevertheless, it is clear that seed size is an important aspect of the adaptive strategies of plants. Further, with so many factors influencing seed size and number, and with these factors often in competition with one another, it would be unreasonable to expect easy explanations for all the known variability in grain size among the teosintes. However, upon examining the fruitcase (including caryopsis) weights of these taxa (Table 1) the correspondence of this information to environmental parameters seems good.

First, the perennial taxa produce relatively few large fruitcases as predicted. Both perennial taxa have fruitcases considerably larger than *Zea mays* subsp. *parviglumis,* and nearly as large as those of *Z. mays* subsp. *mexicana.* The large fruitcases of *Zea luxurians* could be explained by the relatively dry conditions under which this species grows with only 500–1,000 mm of rainfall annually, an environment similar in many ways to the Mexican Central Plateau. The difference between the small "seeded" populations of the Balsas river drainage (*Z. mays* subsp. *parviglumis*) and the larger "seeded" ones of the Central Plateau and the Valley of Mexico (*Z. mays* subsp. *mexicana*) appears to be closely related to available moisture. As shown by the climatic dia-



FIGURES 2–3.—2. A graph of mean annual temperature (°C) versus mean annual precipitation (cm) for various teosinte populations: *Zea perennis* (hollow square), *Zea luxurians* (stars), *Zea mays* subsp. *mexicana* (solid circles), and subsp. *parviglumis* (hollow circles). Data for Mexico from Garcia (1974) and that for Guatemala from Urrutia (1964).—3. Graph of mean annual precipitation against fruitcase weight demonstrating the negative correlation between these two variables; large fruitcases in dry areas and small ones in wet areas. Symbols as in Figure 2.

grams (Fig. 1), the Balsas sites receive a much greater amount of rain during the growing season than the Central Plateau and Valley of Mexico sites. The difference between the climates in the regions of *Zea mays* subsp. *mexicana* and subsp. *parviglumis* is dramatically portrayed in Figure 2, in which mean annual temperature is graphed against mean annual precipitation, while the relationship between fruitcase weight and precipitation is graphically displayed in Figure 3. The Huehuetenango population of *Z. mays* subsp. *parviglumis*, which occurs in a very wet area with 2,000–3,000 mm rainfall annually although with a longer growing season than Balsas teosinte, produces small fruitcases as well. Another point of interest in regard to the differentiation between the small and many-grained *Z. mays* subsp. *parviglumis* and the larger and fewer-grained *Z. mays* subsp. *mexicana* was noted by Wilkes (1967), namely that the grains of the later can successfully germinate deep (6 in.) in the soil while the former must germinate near the surface. This coincides well with Schimpf's (1977) observation that species from dry habitats produce large seeds capable of successfully germinating deep in the soil where the moisture supply is more reliable. Finally, that Nobogame teosinte produces grains of intermediate size despite its dry climate seems surprising but can be explained by the shortness of the growing season of this most northern of all teosintes, and by its adaptation to grow in thickets along streams (a locally and seasonally wet environment) (Wilkes, 1967, 1977).

In summary, an examination of the evidence suggests that for grain size and number the teosinte populations are highly variable, with each population adapted to the demands of its particular habitat and seasonal growth form.

Fruitcase shape. The fruitcase in teosinte is composed of the female spikelet and its attached rachis segment. Its shape ranges from trapezoidal and *Tripsacum*-like through triangular though blunt on the axial side, and ultimately to triangular and sharply pointed, or "pinched," on the axial side. Many authors have considered that the sharply pointed forms display the effects of *condensation* produced via maize introgression (Kempton & Popenoe, 1937; Reeves, 1953; Wilkes, 1977). According to this view, those teosinte populations with trapezoidal fruitcases are free of maize germplasm, whereas those with "pinched" triangular fruitcases show a high degree of maize contamination.

Using measurements from both male tassels and female spikes, the hypothesis that the triangularity of the teosinte cupulate fruitcase results from condensation acquired via maize introgression can be tested. If genes for condensation obtained through maize introgression account for the transformation of the trapezoidal fruitcases into triangular ones, then one would expect the procession from trapezoidal to triangular female rachis segments to be correlated with a gradual shortening (condensation) of the internodes of the central spike and branches of the teosinte male tassel. This expectation emerges from the demonstrated homology of the male and female inflorescences in *Zea mays* subsp. *mays* (Kellerman, 1895; Montgomery, 1906; Iltis, 1911; Anderson, 1944). From Table 2, one can readily see that no such correlation exists. Instead, those teosinte populations with trapezoidal fruitcases (sect. *Luxuriantes*) possess the shortest male internodes on both the central and lateral spikes, and those with triangular fruitcases (sect. *Zea*), the longest. Indeed, the triangular "fruited" teosintes do not have tassel internodes intermediate in length between those of the trapezoidal types and maize, but rather they have the longest tassel internodes (i.e., the least condensed) in all of *Zea*. These facts cast doubt on the claim that maize introgression into a teosinte with trapezoidal fruitcases gave rise to the teosintes with triangular fruitcases.

If maize introgression fails to explain the variation in teosinte fruitcase shape, what then can explain the diversity of observed forms? The answer might be quite simply that the triangular shape of the fruitcases of sect. *Zea* represents an evolutionary advancement over the more primitive trapezoidal shape found in sect. *Luxuriantes* and the genus *Tripsacum*. The triangular shape might allow more efficient packing of the rachis segments in the individual spikes or easier dispersal. If triangularity allows more efficient packing, then one might expect the ratio of the weight of the cupulate fruitcase to that of the caryopsis to be lower for the triangular type. Measurements made on the fruitcases show this to be generally the case with a progression from large to small ratios from *Tripsacum* > *Zea diploperennis* > *Z. perennis* > *Z. luxurians* > *Z. mays* subsp. *mexicana* > *Z. mays* subsp. *parviglumis* (Table 3). However, there is considerable overlap between *Z. luxurians* and *Z. mays* subspp. *mexicana* and *parviglumis*.

TABLE 2. A comparison of internode length (mm) for the male and female inflorescences of *Zea*.

Species	Male Internode Length		Female Fruitcase Length
	Central Spike	Lateral Branch	
Sect. *Luxuriantes*			
Zea diploperennis	3.16	3.06	7.30
Zea perennis	3.76	3.68	7.20
Zea luxurians	4.39	4.48	8.33
Sect. *Zea*			
Zea mays subsp. *mexicana*	5.13	5.65	6.92
Zea mays subsp. *parviglumis*	5.54	5.96	6.05

In summary, the observations (1) that there is no clear-cut correlation between condensation in the male and female teosinte inflorescences to support the maize introgression hypothesis, and (2) that fruitcase shape may reflect different degrees of divergence from the primitive trapezoidal *Tripsacum*-like condition to a more efficient triangular shape, undermine the interpretation that variation in fruitcase shape is evidence for maize introgression into teosinte.

Sheath color and pilosity. Introgression has also been enlisted to explain the co-occurrence of dark red coloration and extreme pilosity on the leaf sheaths of maize and teosinte in the Valley of Mexico (Collins, 1921a; Mangelsdorf, 1947; Wilkes, 1967, 1972). Wilkes hypothesized that these teosintes are maize mimics (which evolved as a result of inadvertent selection) that copy the coloration of the native maize of the region and thus are able to escape the eye and sickle of the *campesinos* weeding their corn fields. Wilkes (1972, 1977) like his predecessors, Collins and Mangelsdorf, evoked maize introgression as the mechanism by which the teosintes of the Valley of Mexico acquired the genes for this "protective" coloration, although he did not dismiss convergence as an alternative hypothesis. Initially, one might ask, could not introgression have

TABLE 3. Mean weight of the total fruitcase and caryopsis, and the ratio of these two values for some teosintes and *Tripsacum* (N = number weighed).

Species Population	Collection	Total Fruitcase Wt. (mg)	Caryopsis Wt. (mg)	Ratio	N
Tripsacum dactyloides					
Ft. Meade, Maryland		122	35	3.69	10
Zea diploperennis					
Las Joyas	*Iltis et al. 1250*	75	25	2.98	10
Manantlan	*Iltis et al. 1375*	75	25	2.97	10
$\bar{x}$				2.98	
Zea perennis					
Los Depositos	*Iltis et al. 550*	106	36	2.92	10
Zea luxurians					
Agua Blanca	*Iltis G-38*	87	31	2.78	10
Ipala	*Iltis G-42*	125	38	3.05	12
Progreso	*Iltis G-36*	87	37	2.35	16
Progreso	*Iltis G-5*	90	37	2.40	12
$\bar{x}$				2.65	
Zea mays subsp. *mexicana*					
Quinceo	*Iltis & Cochrane 276*	109	44	2.48	12
Los Reyes	*Iltis & Lasseigne 769*	85	36	2.36	10
Amecameca	*Iltis & Cochrane 176*	97	44	2.18	10
Chalco	*Iltis & Cochrane 175*	103	43	2.38	10
$\bar{x}$				2.35	
Zea mays subsp. *parviglumis*					
Tzitzio	*Iltis & Cochrane 308*	45	23	2.04	10
San Antonio Huista	*Iltis & Lind G-120*	54	23	2.45	15
La Huertita	*Guzman s.n.*, cult.	82	38	2.17	10
$\bar{x}$				2.22	

proceeded in the opposite direction from teosinte into maize? Unfortunately, this possibility has received little consideration.

In order to explore other potential explanations for the occurrence of dark red pilose sheaths in teosinte and maize from the Valley of Mexico, I will first review the functions these traits might fulfill in maize and teosinte. Red tissue coloration results from the presence of anthocyanins, which fulfill many different functions for the species which produce them (McClure, 1975; Harborne, 1976). One particular function, cold resistance, has been attributed to anthocyanins that occur as a more or less permanent part of leaf tissues. Speculation that anthocyanins help adapt plants to cold environments first emerged when botanists began to notice that species of the cold high altitudes are often more deeply red pigmented than similar species at warmer lower elevations (Kerner, 1891; Bonnier, 1895; Clausen et al., 1940). Researchers have also noted that plants develop greater red coloration when artificially grown in cold environments. This is true for *Hydrocharis* (Overton, 1899), *Impatiens* (Alston, 1959), *Pyrus* (Creasy, 1968), *Chrysanthemum* (Rutland, 1968), and *Euphorbia* (Marousky, 1968). More recently Ganders et al. (1979) noted that in populations of *Collinsia, Mimulus,* and *Trifolium*, phenotypes with dark red spotted leaves are more frequent in colder microhabitats. These latter authors hypothesized that the dark red pigmentation in the leaves of these species functions to absorb radiant energy, and thus, warm the plant. Galinat (1967) proposed this same hypothesis, viz. that red pigmentation acts to absorb radiant energy, thereby warming the plant, to explain the predominance of red plant color among high altitude varieties of maize in Latin America. Galinat noted the lack of experimental verification for this hypothesis. Since that

TABLE 4. Sheath pubescence[a] and color,[b] altitude (m)[c] and mean annual temperature (°C)[c] for some teosinte populations.

Species Population	Collection	Sheath Pubescence	Sheath Color	Mean Annual Temp.	Alt.
Zea mays subsp. *mexicana*					
Valley of Mexico:					
Amecameca	USDA 343246	3	2	14.4	2,425
Chalco	*Iltis & Doebley 401*	3	2	15.9	2,250
Los Reyes	*Iltis & Lasseigne 769*	3	2	16.0	2,180
Central Plateau:					
Patambicho	*G. Prior s.n.*	2	2	16.4	2,132
Quinceo	*Iltis & Cochrane 276*	2	2	17.6	1,940
Churintzio	CIMMYT K 69-3	1	1.5	—	1,900
Nobogame	ex G. Beadle	1	1.5	—	1,850
Degollado	*Puga 11066*	1	1	—	1,625
Zea mays subsp. *parviglumis*					
Balsas drainage:					
Valle de Bravo	CIMMYT K 67-21	0	1	18.3	1,350
Teloloapan	CIMMYT W 71-3	0	1	21.9	1,610
Palo Blanco	USDA 343237	0	0	22.0	1,267
Jalisco:					
El Palmar	*Puga 11065*	0	0	—	980
La Huertita	*Guzman s.n.*	0	0	—	1,100
Jirosto	*Iltis & Nee 1480*	0	0	—	500
Purificacion	*Iltis & Nee 1471*	—	—	25.4	450
Guatemala:					
San Antonio Huista	*Iltis & Lind G-120*	0	0	20.0	1,300

[a] 0 = essentially glabrous; 1 = hairy along upper sheath margins; 2 = pubescent throughout; 3 = densely pubescent throughout.

[b] 0 = green or slightly red; 1 = red; 2 = dark red.

[c] This information from Garcia (1974) and Urrutia (1964).

time, however, two studies have shown that varieties of maize with dark red sheaths stay warmer than similar dilute red types (Greenblatt, 1968; Chong & Brawn, 1969).

If anthocyanins do aid in warming the teosinte plant as experimentation shows they do in maize, then one would predict that those teosinte populations growing in the coldest environments would be the most heavily pigmented and those in the warmest areas the least pigmented. While looking for characters to distinguish various teosinte populations, I took some notes on the degree of coloration of the sheaths among 14 populations I had growing in Florida. Each population was grown in two different randomly assigned rows. Without knowing the origin of the plants in a row, I subjectively categorized the sheaths of the plants in it as either green or slightly red (0), red (1), or dark red (2) (see Table 4). A two-sided Tau-test (a non-parametric test of association) shows significant correlations of both mean annual temperature ($P < 0.02$) and altitude ($P < 0.01$) (which in Mexico is closely related to temperature) to sheath color (Table 4). This suggests that teosinte populations display varying degrees of red coloration not as the result of fortuitous hybridizations with maize or even as an attempt to mimic maize (though red coloration might certainly function in that capacity and thus be reinforced), but rather as an adaptation to a local environmental condition—temperature.

The situation with sheath pubescences is similar to that with anthocyanins. Again, naturalists and ecologists have often noted that dense pubescence functions to preserve the warmth within plants in cold environments (Daubenmire, 1947: 186; Carlquist, 1974: 563–565). Dense pubescence increases the boundary layer surrounding the organ it bedecks, thus causing temperature fluctuations in the plant to lag behind those of the environment. In this way the plants may escape injury during short periods of extreme temperature (Daubenmire, 1947: 172). Various naturalists have commented on the correlation between the density of pubescence and temperature in *Potentilla* (Clausen et al., 1940: 141–142) and *Senecio* (Carlquist, 1974: 563–565).

Returning to Table 4, it is clear that there exists in teosinte a correlation between temperature and density of pubescence, with the most hirsute populations found in the highest coldest habitats and the glabrous ones in the lower warmer sites. A two-sided Tau-test of association shows significant correlations of both mean annual temperature ($P < 0.01$) and altitude ($P < 0.01$) to the density of sheath pubescence. As with sheath coloration these data suggest that pubescence in teosinte results not from haphazard hybridizations with maize, but from each individual population adapting to the exigencies of its particular habitat.

Although coloration and pubescence in teosinte have their adaptive functions, this does not *preclude* the possibility that teosinte obtained these characters from maize. However, teosinte is a natural wild plant that has undoubtedly persisted in the diverse climatic regions of Meso-America for tens-of-thousands of years. There can be little doubt that it achieved its present adaptation long before man and maize arrived on the scene.

A final curious fact worthy of comment concerns the manner in which both maize and teosinte of the Valley of Mexico carefully restrict the intense expression of dark red pigmentation and dense pilosity to the leaf sheath, thus leaving the photosynthetic leaf blade essentially free of all hairs and red color. This, too, bespeaks the adaptive importance of the traits. The function of the leaf sheath is primarily protective rather than photosynthetic, its salient role being to shield the stem from both insects and desiccation. In this same manner, the red color and hairiness of the sheaths of certain teosintes might act to maintain the temperature of the stem at a slightly higher temperature than otherwise possible especially late in the growing season when nights are cool.

In summary, given (1) that one likely role of anthocyanaceous pigmentation and dense pubescence is to protect plants in cold environments, (2) that maize and teosinte are C-4 plants, and thus, thermophiles, and (3) that there is a close correlation between both degree of red coloration and pubescence on the one hand, and mean annual temperature on the other, it is highly unlikely that teosinte acquired these characters by sporadic hybridization with maize. Further, there is no better reason for presuming that dark red coloration and dense pubescence would have introgressed from maize to teosinte than there is for expecting the reverse introgression from teosinte to maize. In fact, given that teosinte is a highly successful wild species and that maize is not, the latter seems much more probable.

Disease resistance. Brewbaker (1979) suggested that *Zea luxurians* obtained resistance to Maize Mosaic Virus and the rust, *Puccinia sorghi*, when genes for resistance to these diseases were transferred to it from local Caribbean maizes. However, introgression, if it occurred at all, probably moved in the opposite direction—from teosinte into maize. The reasons for this are quite simple. First, *Zea luxurians* is the most primitive annual species in *Zea*, and thus, closely related to the perennials *Z. perennis* and *Z. diploperennis* (Doebley & Iltis, 1980). These, and most perennials, of necessity, maintain high disease and insect resistance because their sedentary and long-lived life-style renders them easily locatable by pests, which they tend to accumulate (Nault & Delong, 1980; Nault et al., 1980). Annuals, however, which do not accumulate pests or disease because of their annual habit, generally show less resistance to disease and predation (Feeny, 1976). Thus, it appears likely that *Zea luxurians*, which resembles the perennials morphologically, cytologically, and genetically (cf. Doebley & Iltis, 1980), retains, as a legacy of its phyletic affiliation with the primitive perennial taxa of *Zea*, a low susceptibility to disease.

Chromosome knobs. Longley and others have argued that the internal chromosome knobs of the teosintes in Mexico came from maize, and that the original "pure teosinte" (*Zea luxurians*) possessed only terminal knobs. On the surface of it, this suggestion seems fairly improbable, for if the Mexican teosintes are merely *Zea luxurians* with a "slight infection" of maize germplasm, then one would expect them to have chromosome knob patterns more closely resembling the pattern of *Zea luxurians* than they do. Rather, the Mexican teosintes have knob patterns essentially identical to maize (i.e., they have many internal knobs). The similarity between the Mexican teosintes and maize would seem best explained not by introgression, but by considering these teosintes as ancestral to maize (Kato, 1976).

Other available evidence also lends little credence to the thesis that knobs introgress from maize into teosinte. Kato and Galinat (1975), in a study of the occurrence of chromosome knobs among sympatric populations of maize and teosinte in the Chalco and Balsas regions, found no clear-cut documentation for introgression in either direction. And, as Kato (1976) demonstrated, the annual teosintes of Mexico possess some knob positions that are found neither in maize nor in *Zea luxurians.* The hypothesis that the Mexican annual teosintes are a mixture of maize and *Z. luxurians* does not account for the presence of these knob positions unique to the Mexican annual teosintes. If these Mexican annuals, like other teosintes, are the products of gradual evolutionary development from a common ancestor, however, then the unique knob positions of these teosintes, like their distinguishing morphological features, would have had sufficient time to arise in response to varying environments (Kato, 1976).

CONCLUSION

References to maize introgression into teosinte are numerous in the literature on teosinte. As shown above, the evidence for such introgression is largely circumstantial, and this evidence may be more plausibly interpreted as the result of adaptive radiation. Why then have researchers displayed such a bias in favor of the introgression hypothesis? There is one primary reason. Authors who believed that maize evolved from an unknown wild maize sought an explanation for teosinte that could remove it as a possible ancestor of maize. Thus, they interpreted the various forms of teosinte as nothing more than *Tripsacum* or a primeval teosinte with varying degrees of maize germplasm.

All things considered, there appears to be little or no clear-cut evidence to support the idea that the teosintes have been greatly altered by maize introgression. Whether one considers grain size, fruitcase shape, sheath color and pilosity, chromosome knob positions, or disease resistance, the patterns of variation among the populations of teosinte can best be explained on the basis of ecology and phylogeny. Seen from the viewpoint of the ecologist and evolutionist, *Zea* is not a helter-skelter conglomeration of maize-*Tripsacum* or maize-*Zea luxurians* hybrids, but rather an orderly product of allopatric variation among local populations that strikingly displays the effects of natural selection and geographic speciation.

Finally, the goal here has not been to take the undoubtedly indefensible position that never in the history of maize-teosinte sympatry has a single gene crossed the bridge from maize to teosinte, but rather that at present, only circumstantial evidence of such crossings can be found, and further, that such introgression holds little hope of permanently affecting characters essential to the survival of the teosinte plant in the wild. For these reasons, I believe that the morphology and general character of the teosinte populations as we perceive them today are in all likelihood not substantially altered from the condition in which they existed prior to the domestication and dispersal of maize.

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RECONSIDERATION OF *OENOTHERA* SUBG. *GAUROPSIS* (ONAGRACEAE)[1]

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ABSTRACT

Oenothera havardii and *O. dissecta,* primarily of northern Mexico, and a third species, *O. canescens,* of the High Plains of the U.S., previously were placed together in subg. *Gauropsis* by P. A. Munz. New data on morphology, cytology, and seed anatomy were gathered to evaluate the relationships of these species to one another and to the remainder of the genus. *Oenothera canescens* is diploid, $n = 7$; *O. dissecta* tetraploid, $n = 14$; and *O. havardii* has both diploid and tetraploid populations. Morphological and anatomical data clearly demonstrate that *Oenothera havardii* is not closely allied with the other species placed in subg. *Gauropsis.* Further, *O. havardii* is not closely related to any other species in the genus, and therefore, it is placed in a new monotypic section, sect. *Paradoxus.* The remaining two species are not closely related, but they do appear to be more closely related to each other than either is to any other species. For this reason, they are here retained in sect. *Gauropsis.* Sect. *Gauropsis* is related to sect. *Hartmannia,* and especially to the white-flowered species, *Oenothera tetraptera* and *O. kunthiana.* The phylogenetic relationships of *O. havardii* are obscure, at best, but it appears to represent a lineage that diverged relatively early in the evolution of the genus. It may have shared a common ancestor with species of sects. *Anogra, Gauropsis, Hartmannia, Kneiffia, Lavauxia,* and *Xylopleurum.*

Oenothera subg. *Gauropsis* has been studied relatively little. Only Munz (1932, 1965) has published taxonomic studies of these plants during the past 50 years. Munz included three species, *Oenothera canescens, O. dissecta,* and *O. havardii,* which had been placed in various segregate genera in the past: *O. canescens* in the monotypic genus *Gaurella* (Small, 1896); *O. canescens* and *O. dissecta* as members of the genus *Megapterium* (Britton, 1894; Small, 1896); and *O. dissecta* and *O. havardii* in the genus *Hartmannia* by Rose (1905). These species were apparently an enigma to Munz, one that was heightened because his study was based on very few specimens, especially of *O. havardii* and *O. dissecta.* He grouped them together in subg. *Gauropsis* partly because they did not fit conveniently into any other of his subgenera. He stated that they shared several features such as bushy habit, ovoid capsules with angled or keeled valves, and seeds in several rows per locule.

These three species do share a bushy to sprawling habit, but it is difficult to ascertain whether this suggests a relationship between them or merely superficial similarity. Ovoid capsules not only occur in these species, but also in several other sections of the genus, some of which differ greatly in other respects. The disposition of the seeds in several irregular rows per locule occurs in *O. canescens* and *O. dissecta,* but not in *O. havardii,* which has seeds in one or two rows per locule. On the other hand, there are numerous

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differences between these three species in characters such as flower color, habit, and capsule morphology, and there appear to be few if any characters that clearly link them. For these reasons, it is difficult to maintain subg. *Gauropsis* in its present form.

Recently, a series of modern systematic studies of *Oenothera* have been initiated, typically involving an investigation of crossing relationships, cytology, and examination of variation within and between populations in the field (Dietrich, 1977; Straley, 1977; Raven et al., 1979; Dietrich et al., 1985; Wagner, unpubl. data; Wagner et al., 1985). In 1978 I began study of the species Munz included in subg. *Gauropsis* at the Missouri Botanical Garden. The basic thrust of the study was to gain a better understanding of the relationships of these three distinctive species to one another and to the remainder of the genus, and to provide an expanded taxonomic treatment of them based on extensive field and herbarium study. Munz saw only limited herbarium material and apparently observed only *Oenothera canescens* in the field. This treatment is based on the study of over 500 pressed collections, observations of populations of each species throughout its range, and study of several cultivated strains of each species grown together. Evidence from a genus-wide study of the anatomy and morphology of seeds (Tobe et al., unpubl. data; Wagner, unpubl. data) is also considered here along with the other information.

The information available was considered in the light of three alternative hypotheses: 1) all three species should be placed in monotypic sections, 2) *Oenothera canescens* and *O. dissecta* should be kept in sect. *Gauropsis* with *O. havardii* removed to its own monotypic section, or 3) one or more of these species should be placed with related species in sect. *Hartmannia* sensu lato. These possibilities were evaluated in relation to the narrow sectional concepts of Lewis and Lewis (1955).

CYTOLOGY

Cytological observations to determine chromosome number, and in certain strains the meiotic configuration, were made on root-tips or buds from field collections or from greenhouse-grown progeny from field-collected seed. Buds for meiotic chromosome studies were fixed and stored in 1 : 3 acetic acid : absolute ethanol under refrigeration. Prior to staining in 1% acetocarmine buds were hydrolyzed in a mixture of concentrated HCl and 95% ethanol for 20 minutes. Fresh root-tips were prepared for examination with a four hour treatment in 8-hydroxyquinoline and fixed for at least one hour in 1 : 3 acetic acid : absolute ethanol. The root-tips were then hydrolyzed for ca. six minutes in 10% HCl and stained in 2% propionic-carmine.

A total of 11 strains representing all three species have been examined (Table 1), including three unpublished reports provided by Peter Raven and Wilfried Stubbe. The one strain of *Oenothera canescens* examined was diploid, $n = 7$. In contrast, the majority of the counts made for *O. dissecta* and *O. havardii* were tetraploid. *Oenothera dissecta,* sampled throughout its range, appears to be entirely tetraploid, whereas *O. havardii,* also sampled throughout its range, is tetraploid in Arizona and Mexico, but diploid in western Texas. Quadrivalents occur frequently in meiosis in the tetraploids of both *O. dissecta* and *O. havardii,* indicating that the two diploid sets of chromosomes in each of these species would pair at meiotic metaphase I, and suggesting that they might literally be autotetraploids. This fact, in conjunction with the occurrence of diploid plants of *O. havardii* in Texas, suggests that polyploidy has occurred independently in both species. The addition of these two species brings the total number of polyploid or partly polyploid species in *Oenothera* to ten (ca. 8% of the genus), distributed in eight sections. Half of these, like *O. havardii,* include both diploid and tetraploid populations.

GREENHOUSE STUDY

The experimental study of *Oenothera canescens, O. dissecta,* and *O. havardii* at the Missouri Botanical Garden has been difficult. Most strains reproduced almost entirely vegetatively by adventitious shoots from lateral roots, especially during stress periods, and all three species were particularly susceptible to fungus in the hot, humid climate of St. Louis. *Oenothera havardii* and *O. canescens* flowered sparsely when grown outside, and *O. dissecta* produced only four flowers during three years of cultivation. The following results must be viewed with these limitations in mind. Strains studied are listed in Table 2. A majority of the flowers produced in all three species were used to test for self-incompatibility by self-pollination. Plants grown from strain (a) of *O. dissecta* were self-compatible, as were those

TABLE 1. Chromosome observations of plants in sects. *Gauropsis* and *Paradoxus*. All specimens deposited at MO.

Species	Locality	Collection	Source or Investigator[a]	Chromosome Observations[b]
sect. *Paradoxus*				
Oenothera havardii				
	Mexico			
	Chihuahua	*Wagner & Brown 3922*	W	$2n = 28$
	Durango	*Wagner & Brown 3935*	W	$5_{IV} + 4_{II}$
	U.S.A.			
	Arizona			
	Cochise Co.	*Wagner 3813*	W	$2n = 28 + 2\text{–}5$ b's
	Texas			
	Brewster Co.	*Powell 3901*	W	$2n = 14$; 3 plants
	Presidio Co.	*Powell s.n. in 1982*	W	$2n = 14$
		Powell 2195	P. Raven	$2n = 14$
			W. Stubbe	$2n = 14$
sect. *Gauropsis*				
Oenothera dissecta	Mexico			
	Jalisco	*McVaugh 16984*	P. Raven	$5_{IV} + 4_{II}$
	Zacatecas	*Wagner & Solomon 4224*	W	$2n = 28$
		Wagner & Solomon 4237	W	$2n = 28$
		Wagner & Solomon 4251	W	$2n = 28$; 2 plants
Oenothera canescens	U.S.A.			
	Texas			
	Lubbock Co.	*Raven 19293*	P. Raven	$5_{II} + \odot 4$

[a] Literature source or investigator who made the determination; W = Warren L. Wagner.
[b] $\odot$ = ring at meiotic metaphase I or diakinesis; II = bivalent; IV = quadrivalent.

of strains (a) and (b) of *O. canescens*; in contrast, plants of all four strains of *O. havardii* were self-incompatible. Attempts at interspecific hybridization among the species listed in Table 2 uniformly failed.

MORPHOLOGY AND ANATOMY

In this section the characters that are useful in delimiting *Oenothera canescens*, *O. dissecta*, and *O. havardii* and those that are critical in the evaluation of relationships will be discussed. Careful comparison of a wide array of characters is essential in any attempt to evaluate the relationships of these isolated species to each other and to the rest of the genus.

Habit. All three species begin growth as a rosette, as typical in *Oenothera*. The rosette leaves are normally quickly lost, but in *O. canescens* they are somewhat persistent. Plants of all three species form clumps of sprawling or decumbent stems. In *O. havardii*, and to some extent also in *O. dissecta*, the stems often twine among other grasses and herbs. Plants of *O. canescens* tend to form clumps up to 50 cm across from adventitious shoots from lateral roots. Both *O. havardii* and *O. dissecta* also have the ability to form adventitious shoots, but the above-ground leafy portion dies back during the dry season. When the rains return, numerous new shoots sprout from the roots. Consequently, they do not form clumps. In fact, this is the principal means of reproduction in these two species; both produce few capsules.

Leaves. The three species have rather similar leaves (Figs. 1–7), ranging from lanceolate to linear. In general, the rosette leaves in all three species (e.g., Fig. 7) are larger and have fewer and more shallow teeth than the cauline leaves. The principal differences between the species are in leaf size and margins. *Oenothera havardii* (Figs. 5, 6) has pinnately lobed to sinuate-dentate leaves 1–5 cm long, whereas *O. dissecta* has mostly irregularly pinnatifid leaves with linear-oblong to linear lobes, the blades 2–8 cm long (Fig. 3) or the lower ones sometimes irregularly pinnately lobed (Fig. 4). *Oenothera canescens* (Figs. 1, 2) has sinuate-denticulate to subentire or rarely serrate margins and blades mostly 0.6–1.5 cm long.

Pubescence. These three species typically have only one hair type, rather than two or three as is common in many other species of *Oenothera.* The terminology here follows that established for *Oenothera* in Wagner et al. (1985). All three species are predominantly strigillose, and the hairs are typically 0.1–0.3 mm long. In *Oenothera dissecta,* the hairs are rarely to 0.4 mm, whereas in *O. canescens* they typically are 0.4–0.6 mm long, or rarely to 0.8 mm. *Oenothera dissecta* also is occasionally sparingly hirsute only on the margins and veins of the leaves. The hairs of this pubescence type are mostly straight with slightly broadened bases and are 0.6–1.5 mm long. Both the strigillose and hirsute types are similar in morphology and length to those same types in many other sections of the genus.

Buds. The buds of all three species are erect. *Oenothera havardii* and *O. canescens* both lack free sepal tips, while in *O. canescens* they may occasionally be present and are 0.2–0.3 mm long. In contrast, *O. dissecta* has conspicuous free sepal tips 1–6 mm long.

The buds of all three species split along one suture and are reflexed to one side as a unit, although those of *O. canescens* occasionally split along two sutures and the sepals are reflexed in pairs. Similar patterns of anthesis are common in several sections of the genus. The buds of *O. havardii* are unique in that they are often somewhat twisted.

Flowers. Both *Oenothera havardii* and *O. dissecta* have one to occasionally several flowers opening per day near sunset, the common flowering pattern for the genus, especially for the hawkmoth-pollinated species. *Oenothera havardii* is pollinated by *Hyles lineata* (Fabricius) according to Gregory (1963, 1964). *Oenothera dissecta* is also visited by hawkmoths, based on observations of an unidentified hawkmoth visiting flowers of this species in Zacatecas, Mexico (*Wagner & Solomon 4217*).

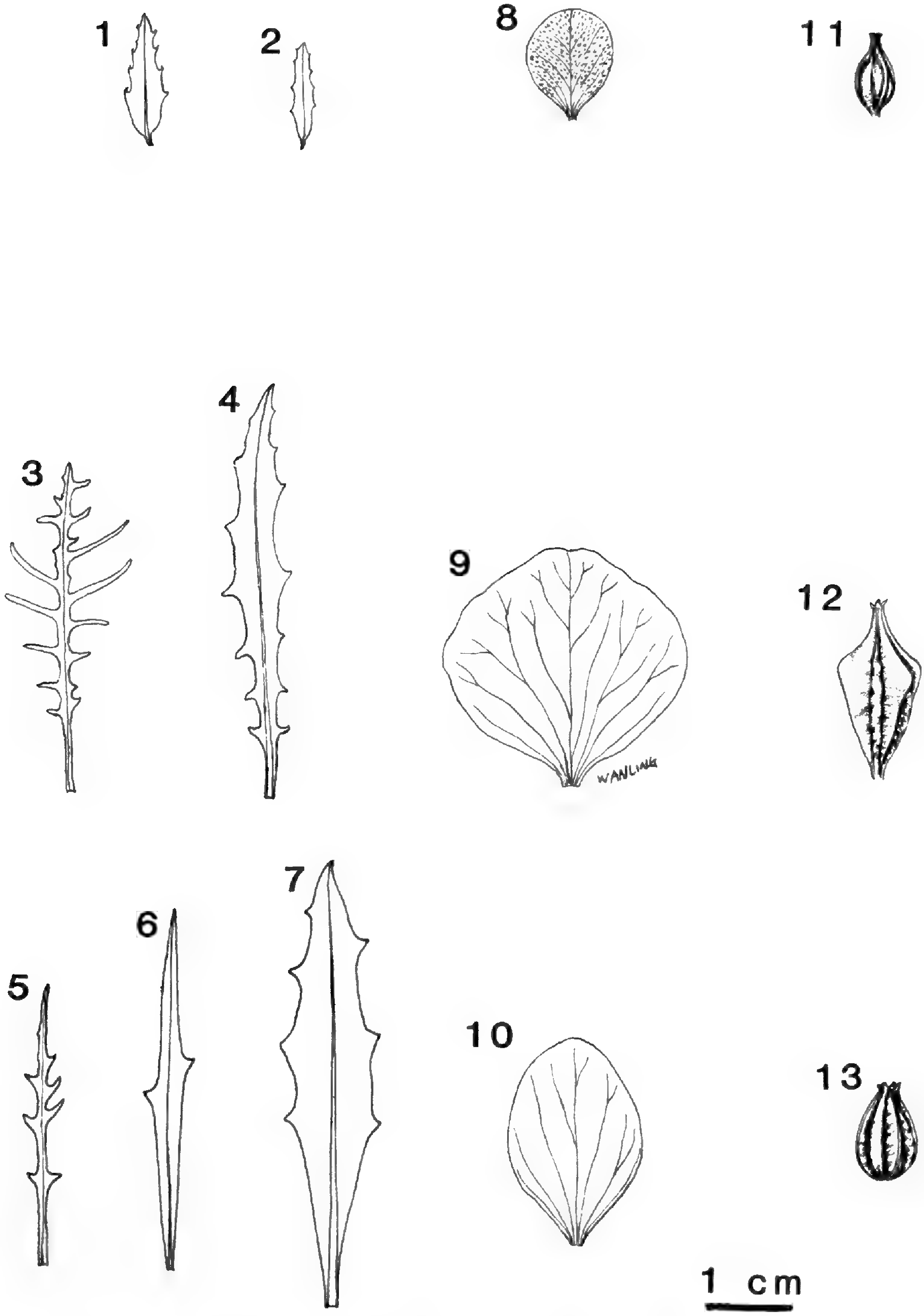
TABLE 2. Voucher information for strains of *Oenothera* used in experimental greenhouse study. Numbers following collector numbers refer to garden planting numbers, used also on herbarium vouchers. All vouchers are deposited at the Missouri Botanical Garden (MO), unless otherwise indicated.

O. canescens:	a) U.S.A., TX, Lubbock Co., *Raven 19293* (seeds from *W. Stubbe 65-135*); *M1209.* b) U.S.A., CO, Cheyenne Co., *Wagner 3691*; CO-3.
O. deserticola:	Mex., Durango, *Breedlove 44134*; *M2088.*
O. dissecta:	a) Mex., Zacatecas, *Wagner & Brown 3980*; MEX-5. b) Mex., Zacatecas, *Wagner & Solomon 4224*; MEX-7A. c) Mex., Zacatecas, *Wagner & Solomon 4237*; MEX-8. d) Mex., Zacatecas, *Wagner & Solomon 4251*; MEX-9.
O. havardii:	a) Mex., Chihuahua, *Wagner & Brown 3922*; MEX-1. b) Mex., Durango, *Wagner & Brown 3935*; MEX-2. c) U.S.A., AZ, Cochise Co., *Wagner 3813*; AZ-3. d) U.S.A., TX, Brewster Co., seeds from *Stubbe 67-381* originally from *Powell 2195*; M1208.
O. kunthiana:	Mex., Zacatecas, *Wagner & Solomon 4226*; MEX-7b.

In contrast to this widespread pattern, *Oenothera canescens* typically has many flowers opening per day at sunset. This specialization is perhaps related to a shift to pollination by noctuid moths (Raven, pers. comm.), which visit these flowers in greater abundance than hawkmoth pollinators.

Floral tube length is somewhat variable as is typical for many species of *Oenothera.* Those of *O. havardii* and *O. dissecta* fall into the typical range for species pollinated by short-tongued hawkmoths such as *Hyles*; those of *O. havardii* are (3.7–)4.5–6(–6.5) cm long; whereas those of *O. dissecta* are somewhat shorter, (2.6–)3.5–4.2 cm long. The floral tubes of *O. canescens* are considerably shorter, (0.8–)1–1.5(–1.7) cm long, which presumably is related to visitation by the shorter-tongued noctuid moths.

Each of the three species has petals of a different color. *Oenothera havardii* has lemon yellow petals, which is the presumed ancestral color for the genus. In contrast, *O. dissecta* has white



FIGURES 1–13. Leaves, petals and capsules of *Oenothera canescens, O. dissecta,* and *O. havardii.* 1–7. Leaves.—1, 2, *O. canescens,* Sedgwick Co., Kansas, *Stephens 55690* (KANU).—3, 4. *O. dissecta,* Mexico, *Schumann 531* (GH).—5–7. Two cauline leaves and one basal (7) of *O. havardii,* Chihuahua, Mexico, *Wagner & Brown 3922* (MO). 8–10. Petals.—8. *O. canescens, Stephens 55690.*—9. *O. dissecta, Schumann 531.*—10. *O. havardii, Wagner & Brown 3922.* 11–13. Capsules.—11. *O. canescens,* Cheyenne Co., Colorado, *Wagner 3691* (MO).—12. *O. dissecta,* San Luis Potosí, Mexico, *Parry & Palmer 249* (BM).—13. *O. havardii,* Chihuahua, Mexico, *Pringle 1146* (VT).

petals, similar to those of the presumably related species, *O. tetraptera* and *O. kunthiana* (sect. *Hartmannia*). Apparently white petals have also evolved independently in the common ancestor of sect. *Pachylophus* (five species), in *O. muelleri* Munz and *O. tubifera* Sér. of an undescribed related section, in both species of sect. *Kleinia,* and in *O. centauriifolia* Spach and *O. acaulis* Cav. of sect. *Lavauxia. Oenothera canescens* is unique in having petals that are pink or white and streaked or flecked with red, a pattern possibly related to the shift in pollinators in this species. The petals of both *O. dissecta* and *O. canescens* are obovate, although those of *O. dissecta* are broadly so, sometimes nearly orbicular. Those of *O. dissecta* are rather typical in size for the genus, (1.5–)2–4 cm long, whereas those of *O. canescens* are rather smaller, (0.8–)1–1.7 cm long. In contrast, the petals of *O. havardii* are elliptic to occasionally oblanceolate, a shape shared only with several species of sect. *Oenothera* subsect. *Raimannia.* This shape appears to have evolved independently in these two groups. The petals of *O. havardii* are (1.8–)2.1–3(–3.2) cm long.

The red anthers of *Oenothera havardii* are unique in the genus. It should be noted, however, that those of *O. canescens* often have a red longitudinal stripe. With these exceptions, no other species of *Oenothera* is known to have any red in its anthers.

Capsules. Capsules in this group, as is typical for the genus, provide good diagnostic characters for identification and analysis of relationships. Within sections there is usually a high degree of similarity in the capsule features among the species. However, the capsules of these three species differ in texture, shape, ornamentation of the margins of the valves, apex, and degree of dehiscence.

Both *Oenothera havardii* and *O. dissecta* produce relatively few capsules, and seem to reproduce primarily by vegetative means. Although *O. canescens* also reproduces well vegetatively, it also produces large numbers of capsules.

The capsule features of *Oenothera canescens* and *O. havardii* are clearly specialized and unique in the genus. The capsules of *O. havardii* are extremely hard and woody in texture at maturity, and have a prominent median ridge on each valve. They are oblong-ovoid to ovoid, 8–13(–16) mm long, have short, blunt sterile beaks 2–3 mm long, and sharply angled valves. At maturity they are tardily dehiscent for about ⅓ the length of the capsule. *Oenothera canescens* produces capsules that are also very hard at maturity, ovoid, (7–)9–12(–14) mm long, and abruptly constricted to a conspicuous sterile beak mostly (2–)3–4.5 mm long. The margins of the valves have narrow wings 0.8–1.5 mm wide running the entire length of the capsule. At maturity they are indehiscent, a feature that is unique in the genus and is most closely approached by *O. havardii.*

In contrast, the capsules of *Oenothera dissecta* are hard and leathery rather than woody. They are ovoid to narrowly ovoid, (9–)13–20 mm long, and abruptly constricted to a sterile beak 2–6 mm long. The valves have a median ridge, although it is not as conspicuous as that in *O. havardii,* and the margins of the valves have triangular wings 2–2.5 mm wide that extend the length of the capsule. These capsule features of *O. dissecta* are rather similar to those of the capsules of *O. tetraptera* and *O. kunthiana* in sect. *Hartmannia. Oenothera dissecta* further shares with the species of sects. *Hartmannia* and *Kneiffia* capsules that dehisce ca. ⅓ their length and have a sterile, basal portion that is pedicel-like. This stipe is 1–4 mm long in *O. dissecta,* whereas it is much longer in species of sects. *Hartmannia* and *Kneiffia.*

Seeds. Seed features have long been employed as a principal consideration in the delimitation of infrageneric groupings in *Oenothera* (Spach, 1835a, 1835b; Raimann, 1893; Munz, 1965). In his summary work on the Onagraceae for "North American Flora," Munz (1965) distinguished his subgenera of *Oenothera* largely on seed and capsule features. Therefore, it was critical to examine in depth the external and internal features of the seeds of *Oenothera havardii, O. dissecta,* and *O. canescens* in order to evaluate their proper placement and relationship to one another. Comparison of the gross features of the seeds of these species is summarized in Table 3. *Oenothera havardii* clearly is the most distinctive of the three species based on its seed characters. Both seed shape and the nonpersistence of the seeds on the placenta at maturity, however, are shared with *O. canescens.* In all other features the seeds of *O. dissecta* and *O. canescens* are essentially identical. Moreover, most of these characters are shared not only between these two species but also with the species of sects. *Hartmannia* and *Kneiffia.*

Table 4 summarizes anatomical features of the testa of these species based on a recent genus-wide study of the anatomical features of seeds (Tobe et al., unpubl. data). As with the external seed characters, the anatomical features of *Oenothera havardii* are clearly distinctive. Likewise, *O. dissecta* and *O. canescens* are virtually identical in their structure of the testa. They only differ in that the exotesta is much thicker in *O. canescens.* In fact, the exotestal cell thickness of *O. canescens* is the greatest in the genus. In summary, comparison of the seed features of these species clearly demonstrates that *Oenothera havardii* is different than the other two species and

TABLE 3. Comparison of seed features of *O. havardii, O. dissecta,* and *O. canescens.*

Seeds	*O. havardii*	*O. dissecta*	*O. canescens*
# rows/locule	1–2	indefinite rows, reduced to one at maturity	2–4
#/capsule	30–60	100–130?	50–100
Shape	asymmetrically cuneiform to rhombic, angled	ovoid, obscurely angled	asymmetrically cuneiform, angled
Color	yellowish green with purple spots to purplish brown	light brown	light brown to brown, dark spot at distal end and micropyle
Size (mm)	2–2.5(–3.3) by 1.2–1.5	1.5 by 0.6–0.8	1.2–1.5 by 0.4–0.5
Surface	distal wing, raised ridge, beaded	smooth and glossy, obscurely reticulate	smooth and glossy, obscurely reticulate
Attachment to placenta	readily detaches	persistent	readily detaches

that *O. dissecta* and *O. canescens* share nearly all features, differing only modally in others.

DISCUSSION

The morphological and anatomical data gathered in this study clearly demonstrate that *Oenothera havardii* is not closely allied with either *O. dissecta* or *O. canescens,* and that it should not be included in the same section with them. In fact, it is not closely related to any other species in the genus, and therefore it is placed here in a new monotypic section, sect. *Paradoxus,* described below. *Oenothera havardii* possesses a number of unique derived characters including red anthers, twisted buds, and distinctively angled capsules, each valve with a prominent median ridge. Closely related groups of species in *Oenothera* (i.e., species of a single section) generally share similar capsule characters, and the fact that *O. havardii* has capsules unique for the genus argues for giving it sectional status. In further support of this, *O. havardii* possesses certain characters that in combination set it apart from other species of the genus, and especially from *O. canescens* and *O. dissecta.* These characters include the elliptic to oblanceolate yellow petals; seeds in 1–2 rows per locule; seed shape, size, and color; and mesotesta 2–5 cells thick, with sclerotic pitted walls and the seed surface with a beaded appearance. Retained primitive features of *O. havardii* include yellow petals; hawkmoth pollination; seeds that readily detach from the placenta; mesotesta 2–5 cell layers in thickness, the cells sclerotic and pitted; and capsules that dehisce ca. ⅓ their length.

TABLE 4. Anatomical features of the testa of *O. havardii, O. dissecta,* and *O. canescens.*

	O. havardii	*O. dissecta*	*O. canescens*
Endotesta			
Thickness (μm)	10.6–12.7	5.3–6.3	4.2–5.3
Cell shape	radially flattened	radially flattened	radially flattened
Cell-wall thickenings	inner wall	inner wall	inner wall
Mesotesta			
Thickness (cell-layers)	2–5	0	0
Cell type	sclerotic, pitted	crushed	crushed
Exotesta			
Thickness (μm)	67.6–99.3	46.5–59.2	74–152
Cell shape	radially elongated, papilla-like	radially elongated, pillar-like	radially elongated, pillar-like

Certain characters that *Oenothera havardii* shares with other species of the genus appear to represent convergent evolution. The leaf size and lobing pattern of *O. havardii* is very similar to that of *O. dissecta*. Many species in the genus, however, have the same basic oblanceolate leaf shape, coupled with toothed or irregularly pinnatifid leaves. The overall similarities of these two species, including the reduction of leaf size, could merely be the result of convergence related to their occurrence in xeric desert habitats. Elliptic to oblanceolate petals, another derived feature, is also shared with several species of sect. *Oenothera* subsect. *Raimannia*, such as *O. rhombipetala* Nutt. ex Torrey & A. Gray. It appears very likely that this shape has evolved independently in both groups, since they have little else in common.

The seeds of *Oenothera havardii* are similar in a number of ways to those of species of sect. *Lavauxia*. The cuneiform seeds of *O. havardii* with a raised ridge, small distal wing, and beaded surface are strikingly similar to the seeds of species of sect. *Lavauxia*, especially the North American members. Seed size is also similar. Moreover, both *O. havardii* and species of sect. *Lavauxia* share similar exotesta cell shape and have thickenings only on the inner wall of the endotesta (Tobe et al., unpubl. data). This type of endotestal cell-wall thickening, however, is found in a large number of species in the genus distributed in several sections. The unique similarities between the seeds of *O. havardii* and those of sect. *Lavauxia* thus are restricted to their size and external morphology. Because of their exposure to the environment, external features of seeds are presumably much more subject to adaptive change than are the internal ones. Therefore, it is difficult to suggest any close relationship between sect. *Lavauxia* and *O. havardii* since they differ in most respects except in the seed features listed above. On the other hand, the anatomical seed features of *O. havardii*, including thin endotesta, the cells radially flattened, with only the inner walls thickened, and greatly enlarged exotestal cells, clearly ally it with that part of the genus including sects. *Anogra, Gauropsis, Hartmannia, Kneiffia, Lavauxia,* and *Xylopleurum* (Tobe et al., unpubl. data).

The remaining two species, *Oenothera canescens* and *O. dissecta*, are not particularly closely related, yet they appear to be more closely related to each other than either is to any other species. They are related to the same group of sections listed above for *Oenothera havardii*, although they are more closely related to them than *O. havardii*. Furthermore, they are most closely related to sects. *Hartmannia, Kneiffia,* and *Xylopleurum*, based on a number of common characters including winged capsules, seeds clustered in each locule, and similar seed size. *Oenothera dissecta* shares even more characters with these sections, including seeds persistent on the placenta, similar capsule shape and capsule wings, and a sterile, basal part of the capsule only 1–4 mm long, which is typically much longer in the other sections. *Oenothera dissecta* further shares white petals with *O. tetraptera* Cav. and *O. kunthiana* (Spach) Munz of sect. *Hartmannia*. It also has suborbicular to elliptic, glabrous cotyledons that are very similar to those of *O. kunthiana* and *O. rosea* L'Hér. ex Ait. of the same section. The full distribution of this cotyledon type, however, is not presently known. These characters appear to be derived ones and suggest a shared common ancestor between sects. *Gauropsis, Hartmannia, Kneiffia,* and *Xylopleurum*. Sect. *Gauropsis* probably is related most closely to *O. tetraptera* and *O. kunthiana*. This relationship has been suggested in the past when Rose (1905) included *O. dissecta* in sect. *Hartmannia*.

Although they are related to species of sect. *Hartmannia, Oenothera dissecta* and *O. canescens* are clearly specialized and therefore should be placed in an adjacent section. To include them in sect. *Hartmannia* would make this section much more heterogeneous than it is at present and more so than many other sections of the genus. The principal unique derived features of *O. dissecta* and *O. canescens* are the specialized sprawling habit and seeds with pillar-like exotestal cells. Vegetative reproduction by adventitious shoots from lateral roots also distinguishes these two species from sect. *Hartmannia*, although it is probably a retained primitive feature. Both species are individually specialized in a number of ways that set them apart from other members of the genus, but especially from sect. *Hartmannia*. *Oenothera dissecta* appears to be entirely tetraploid and makes only fleeting appearances above ground, spending most of the dry parts of the year underground as rootstocks. This latter specialization is also shared to some degree with *O. havardii*, but appears to have been independently derived in each. Related to this extensive vegetative growth is the very low seed production in *Oenothera dissecta*. *Oenothera canescens* is even more specialized. Its nut-like, indehiscent capsules are unique in the genus. It also has made a major shift in its breeding system to pollination by noctuid moths. Presumably related to this pollinator shift was the increase in the number of flowers, petal color change, and great reduction in floral tube length. In summary, *O. dissecta* and *O. canescens* do not fit well into any other section of the genus because they have certain shared and unique specializations as well as similar retained primitive features. They are retained together here in sect. *Gauropsis,* which appears to be most closely allied to sect. *Hartmannia.* This is most evident in the similarity of *O. dissecta* to *O. tetraptera* and *O. kunthiana.*

SYSTEMATIC TREATMENT

KEY TO THE SECTIONS OF *GAUROPSIS* AND *PARADOXUS*

1. Petals yellow, elliptic to oblanceolate; anthers entirely red; capsules angled, never winged, each valve with a prominent median ridge; seed surface beaded, dull; self-incompatible ________ I. sect. *Paradoxus*

1'. Petals pink, flecked with red, or completely white, obovate to broadly obovate or nearly orbicular; anthers yellow or sometimes with a red stripe; capsules narrowly winged, the wings 1–2.5 mm wide, each valve with a low median ridge or ridge absent; seed surface obscurely reticulate, appearing finely granular, glossy; self-compatible ________ II. sect. *Gauropsis*

I. Oenothera L. sect. **Paradoxus** W. L. Wagner, sect. nov. TYPE: *O. havardii* S. Wats.

Oenothera subg. *Gauropsis* sensu Munz, Amer. J. Bot. 19: 766. 1932, pro parte. N. Amer. Fl., Ser. 2, 5: 93. 1965, pro parte.

Herbae foliosae compactae ad decumbentes, propagatione asexuali per surculos adventitiae e radicibus effusis, caulibus aliquando ad nodos radicantibus. Gemmae saepe tortae, apicibus sepalorum cohaerentibus. Petala citrina, elliptica vel oblanceolata. Antherae rubrae. Capsula durissima, quadrangularia, valvula quoque crista mediana prominente. Semina grosse papillosa, in loculo quoque uni- vel biseriata, seriebus seminorum superpositis.

Leafy, compact to sprawling perennial herbs spreading by adventitious shoots from lateral roots, stems branched or simple, weakly erect becoming decumbent, often twining among vegetation, sometimes rooting at the nodes. Leaves irregularly pinnately lobed to sinuate-toothed or dentate. Buds erect, the apex long-acuminate, often twisted, sepal tips coherent. Petals lemon yellow, fading orangish red, drying reddish purple, elliptic to oblanceolate. Sepals splitting along one suture and reflexed as a unit to one side. Anthers red. Capsules few, very hard, 8–15 mm long, 4-angled and with a prominent median ridge on each valve, tardily dehiscent for ca. ⅓ capsule length. Seeds in 1 row or 2 overlapping rows in each locule, irregularly angled, the surface beaded. Self-incompatible, $n = 7, 14$.

The sectional name, *Paradoxus,* refers to the obscure relationship of *Oenothera havardii* to the other species of the genus.

1. **Oenothera havardii** S. Wats., Proc. Amer. Acad. Arts 20: 366. 1885. TYPE: Texas. Presidio Co.: Prairies near Marfa, 1,430 m, July 1883, *Havard 122* (lectotype, GH, photo MO; isolectotypes, CU, US; Munz, Amer. J. Bot. 19: 768. 1932). *Hartmannia havardii* (S. Wats.) Rose, Contr. U.S. Natl. Herb. 8: 328. 1905.

Hartmannia palmeri Rose, Contr. U.S. Natl. Herb. 8: 329. 1905. TYPE: Mexico. Durango: near Santiago Papasquiaro [25°03'N, 105°25'W, 1,900 m], Apr. and Aug. 1896, *Palmer 45* (holotype, US-304795, photo MO; isotypes, GH, UC).

Leafy, compact to sprawling perennial herbs, often producing adventitious shoots from spreading lateral roots, stems 5–25(–70) cm long, usually many-branched, sometimes simple, weakly erect becoming decumbent, often twining among vegetation, sometimes rooting at the nodes, canescent-strigillose, the hairs 0.1–0.3 mm long. Stem leaves linear-lanceolate to linear, 1–5 cm long, 2–8 mm wide, pinnately-lobed to sinuate-dentate, the lobes widely spaced, strigillose, sometimes more densely so along the margins, occasionally subglabrous; rosette leaves oblanceolate, few toothed, generally quickly deciduous, 2–5 cm long, 5–15 mm wide; petioles on both types 0–6 mm long. Buds erect, oblong, the apex long-acuminate, often twisted, sepal tips coherent. Flowers 1–few opening per day near sunset. Ovary canescent-strigillose, (7–)9–13 mm long, sessile. Floral tube (3.7–)4.5–6(–6.5) cm long, flaring to 3.6–4.1 mm at the mouth, densely strigillose, glabrous within. Sepals splitting along one suture and reflexed to one side as a unit at anthesis, (1.6–)1.8–2.6(–3) cm long, 1.5–2.3 mm wide, canescent-strigillose, the margins with a conspicuous reddish purple stripe. Petals lemon yellow, fading orangish red, drying reddish purple, elliptic to occasionally oblanceolate, (1.8–)2.1–3(–3.2) cm long, (0.9–)1.2–1.5(–1.8) cm wide. Staminal filaments yellow, 15–18(–22) mm

FIGURE 14. Distributions of *Oenothera canescens* (stars), *O. dissecta* (dots), and *O. havardii* (open triangles).

long. Anthers red, 6–13 mm long. Style (5.5–) 6.5–8.6(–9.4) cm long; stigma lobes red, (2–)3.5–5 mm long, well elevated above the anthers at anthesis. Capsules few, very hard at maturity, oblong-ovoid to ovoid, 8–13(–16) mm long, 3–4 mm diam. tapering to a short sterile beak 2–3 mm long, with free tips 1–2 mm long, the base truncate and slightly asymmetrical, the valves with a prominent broad median ridge, the margins of the valves sharply angled, tardily dehiscent about ⅓ the capsule length. Seeds ca. 30–60 per capsule arranged in 1 or 2 partially overlapping rows per locule, asymmetrically cuneiform to rhombic, often rather irregular (due to compression from packing arrangement), irregularly angled, yellowish green with scattered purple spots to sometimes purplish brown, 2–2.5 (–3.3) mm long, 1.2–1.5 mm wide, sometimes with a small wing at the distal end or a raised ridge along one longitudinal margin, the surface minutely beaded. Self-incompatible. Gametic chromosome number, $n = 7$, 14.

Distribution. Locally common in depressions, seasonally wet flats, stream banks or margins of irrigated fields, sandy or clay soils, often growing among tufted grasses like *Sporobolus wrightii* Scribn., primarily in the Chihuahuan desert from Marfa (Presidio Co.) and Alpine (Brewster Co.), Texas, Cochise Co., Arizona, south to F. I. Madero, southeastern Durango, Mexico and Juan Aldana, Zacatecas, Mexico, 1,300–2,000 m. Flowering from April to October. Figure 14.

Additional specimens examined. MEXICO. CHIHUAHUA: 5 mi. S of [Rancho los] Gallegos along Hwy. 45, *Breedlove 15732* (DS); 10 mi. S of Montezuma on Hwy. 45, *Dwyer 14157* (MO); 5 mi. E of Allende turnoff on Hwy. 159 from Parral to Camargo, *Freytag & Baxter M64* (MO); 21.2 mi. SW of El Morrion, *Lehto & Broome L22870* (ASU, MO); S of cd. Guerrero, ca. 28°33′N, 107°30′W, *McGill et al. 8363* (ASU); Basuchil, 28°30′N, 107°24′W, *Mexia 2544* (F, GH, MICH, MO, NY, PH, POM, UC, US); vic. of Aldama, 28°30′N, 106°34′W, *Palmer 252* (GH, NY, US); Valle del Rosario, 27°19′N, 106°18′W, *Pennington 367* (TEX); Chihuahua, 28°38′N, 106°05′W, 1887, *Pringle s.n.* (MEXU); near Chihuahua, near 28°38′N, 106°05′W, *Pringle 1146* (GH, VT); 15 km S of Escobillas, near 28°49′N, 104°06′W, *Stewart 2360* (GH); 5 mi. E of cd. Jiménez, near 27°08′N, 104°54′W, *Wagner & Brown 3922* (MO), *White 2137* (MICH). DURANGO: on rd. to Juan Aldama, near 24°19′N, 103°21′W, *Moldenke 1591* (DS); Tepehuanes, 25°21′N, 105°44′W, *Palmer 301* (F, GH, MO, NY, UC, US); 5.2 mi. N of Guadalupe Victoria along Hwy. 40, near 24°27′N, 104°07′W, *Wagner & Brown 3935* (MO); 1.7 mi. NE of F. I. Madero, 24°23′N, 104°19′W, *Wagner & Solomon 4318,* pro parte (MO), vic. of cd. [Guadalupe] Victoria, 34–38 mi. NE of Durango, 24°27′N, 104°07′W, *Waterfall & Wallis 13348* (ISC, OKL, RSA, SMU). SONORA: 0.5 mi. S of Agua Prieta, rd. to Franteras, ca. 31°18′N, 109°34′W, *White 3856* (MICH). UNITED STATES. ARIZONA: Cochise Co., along U.S. Hwy. 80 ca. 3.5 mi. NE of Apache, 1962, *Hespenheide s.n.* (DUKE), *Wagner 3813* (MO); Elfrida, near Douglas, 1957, *Jones s.n.* (RSA). TEXAS: Brewster Co., Alpine, golf course, *Sperry T1332* (TAES, US); Presidio Co., Marfa, 1936, *Hinckley s.n.* (SRSC), *Hinckley 657* (BH, F, GH, NY, SMU), *Hinckley 707* (ARIZ, F, NY), *Hinckley 3472* (BH, CS, NY, RM, RSA, SMU, SRSC 2 sheets, US), *Hinckley 3477* (NY), *Hinckley 3504* (SRSC), 1926, *Orcutt s.n.* (POM, US), *Warnock 14152* (SRSC); Pecos Co., near Leon Spring, near Fort Stockton, 1851, *Wright s.n.* (GH); without further locality, *Smith s.n.* (NY).

Oenothera havardii sometimes occurs in habitats similar to those of *O. dissecta,* and at the southern end of its range, northeast of F. I. Madero, Durango, Mexico (*Wagner & Solomon 4318*), it grows together with it. They coexist here without any signs of hybridization.

II. **Oenothera** L. sect. **Gauropsis** (Torrey & Frém.) W. L. Wagner, comb. & stat. nov. *Oenothera* L. sect. *Euoenothera* (Torrey & A. Gray) Torrey & Frém. subsect. *Gauropsis* Torrey & Frém. in Frém., Rep. Exped. Rocky Mts. 315. 1845. TYPE: *O. canescens* Torrey & Frém. *Gauropsis* (Torrey & Frém.) Cockerell, Bot. Gaz. (Crawfordsville) 30: 351. 1900, non Presl, Epimel. Bot. 219. 1851 [1849].

Gaurella Small, Bull. Torrey Bot. Club 23: 183. 1896. TYPE: *G. guttulata* (Geyer ex Hook.) Small, nom. illeg. = *Oenothera canescens* Torrey & Frém.

Leafy, bushy to sprawling or compact perennial herbs, spreading by adventitious shoots from lateral roots, stems simple to branched, decumbent to ascending. Leaves lanceolate to linear-lanceolate in outline, strigillose, rarely also sparsely hirsute, basal leaves often oblanceolate, petioles 0–1.5 cm long. Buds erect, with or without free sepal tips. Petals pink and streaked or flecked with red, to white, fading purple to pink, drying purple. Capsules ovoid, constricted to a sterile beak, the valves with narrow wings 1–2.5 mm wide. Seeds in 2–4 irregular rows (or in *O. dissecta* 1 row at maturity by abortion), asymmetrically cuneiform to ovoid or oblanceoloid, angled, glossy, obscurely reticulate, appearing finely granular. Self-compatible. Gametic chromosome numbers, $n = 7$, 14.

KEY TO THE SPECIES OF SECT. *GAUROPSIS*

1\. Petals white, fading pink, drying purple, (15–)20–40 mm long; leaves 20–80 mm long, irregularly pinnatifid, the basal ones sometimes merely dentate; capsules (9–)13–20 mm long, dehiscing ca. ⅓ the capsule length; capsule wings 2–2.5 mm wide; Mexico ________ 2. *O. dissecta*

1′. Petals pink flecked with red, fading and drying bright purple, (8–)10–17 mm long; leaves (3–)6–15(–25) mm long, sinuate-denticulate to subentire; capsules (7–)9–12(–14) mm long, indehiscent; capsule wings 0.8–1.5 mm wide; High Plains, U.S.A. ________ 3. *O. canescens*

2\. **Oenothera dissecta** A. Gray ex S. Wats., Proc. Amer. Acad. Arts 17: 357. 1882. TYPE: Mexico. San Luis Potosí: sandy localities near San Luis Potosí [1,850 m], 1876, *Schaffner 168* (lectotype, GH, photo MO; isolectotype, PH; Munz, Amer. J. Bot. 19: 767.

1932). *Megapterium dissectum* (A. Gray ex S. Wats.) Small, Bull. Torrey Bot. Club 23: 184. 1896. *Hartmannia dissecta* (A. Gray ex S. Wats.) Rose, Contr. U.S. Natl. Herb. 8: 328. 1905.

Leafy, compact to sprawling perennial herbs, producing adventitious shoots from spreading lateral roots, stems simple to branched, 0.2–30 (–80) cm long, weakly erect becoming decumbent, older stems woody, strigillose, the hairs 0.1–0.3(–0.4) mm long. Stem leaves lanceolate, 2–8 cm long, 0.7–1.5 cm wide, irregularly pinnatifid, the lobes linear-oblong to linear, sparsely to densely strigillose, the hairs evenly distributed, rarely more dense along veins and margins, sometimes also sparsely hirsute, these hairs 0.6–1.5 mm long and confined to veins and margins; rosette leaves oblanceolate, 2–6 mm long, 1–1.5 cm wide, less divided than the stem leaves, dentate, or pinnately lobed or with oblong lobes, usually deciduous before flowering; petioles on all leaves 0–1.5 cm long. Buds erect, oblong-lanceolate, with free sepal tips 1–6 mm long. Flowers one rarely more per stem opening per day near sunset. Ovary 11–16(–18) mm long, densely strigillose, sessile. Floral tube (2.6–)3.5–4.2 cm long, flaring to 3–6 mm at the mouth, densely strigillose, glabrous within. Sepals splitting along one suture and reflexed to one side as a unit at anthesis, 1.8–3.5 cm long, 2–3 mm wide, strigillose, the margins with a conspicuous purple stripe often flecked with purple spots. Petals white, fading pink, drying purple, broadly obovate to nearly orbicular, (1.5–)2–4 cm long, (1.4–)1.7–3.6 cm wide. Staminal filaments 10–17 mm long. Anthers yellow, (6–)8–11 mm long. Style (4.4–)4.7–7 cm long; stigma lobes (3–)5–6 mm long, well elevated above the anthers at anthesis. Capsules few, hard and leathery at maturity, ovoid to narrowly ovoid, (9–)13–20 mm long, 3–5 mm diam. (excluding wings), the base cuneate, sometimes somewhat twisted, abruptly constricted to a sterile beak 2–6 mm long, with free tips ca. 0.5 mm long, the valves with a median ridge, the margins of the valves with a wing 2–2.5 mm wide extending the length of the capsule, usually widest above the middle, tapering to a pedicel-like, sterile basal portion 1–4 mm long, dehiscing ca. ⅓ the capsule length. Seeds ca. 100–130(?) per capsule, clustered in several indefinite rows (apparently reduced to one row in mature capsules), narrowly ovoid, obscurely angled, light brown, ca. 1.5 mm long, ca. 0.6–0.8 mm wide, the surface glossy, obscurely reticulate, appearing finely granular, rather persistent on the placenta. Self-compatible, but outcrossing. Mitotic chromosome number, $2n = 28$.

Distribution. Locally common in clay or sandy soils of arroyo banks or sometimes open flats, *Acacia* and *Opuntia* grasslands, *Larrea* scrub, in the Chihuahuan Desert from the vicinity of F. I. Madero, southeastern Durango to Zacatecas as far north as Concepción del Oro, southwest San Luis Potosí and vicinity of Ojuelos, northern Jalisco, 1,800–2,400 m. Flowering from May to September. Figure 14.

Additional specimens examined. MEXICO. DURANGO: vic. of Durango, 24°02′N, 104°40′W, *Palmer 966* (US); 1.7 mi. NE of Francisco I. Madero on Rt. 40, NE of Durango, 24°23′N, 104°19′W, *Wagner & Solomon 4318*, pro parte (MO). JALISCO: High Plains, Km 18, SW of Ojuelos on rd. to Aguascalientes, *McVaugh 16984* (MEXU, RSA, US). SAN LUIS POTOSÍ: San Luis Potosí, 22°09′N, 100°59′W, *Barroeta s.n.* (US), *Parry & Palmer 249* (BH, BM, E, F, G, GH, MO, NY, PH, US, VT), *Rzedowski 6157* (ENCB), *Schaffner 446* (BM, G, NY, P, US); 8 km NE de Laguna Seca, near 22°17′N, 100°52′W, *Rzedowski 6325* (ENCB, MEXU, RSA); 22 mi. NE of San Luis Potosí, *Straw & Forman 1430* (GH, MEXU, RSA); without further locality, 1891, *Nirlen s.n.* (P). ZACATECAS: 23 mi. S of Concepción del Oro along Hwy. 54, *Henrickson 6243* (MO), *Wagner & Brown 3980* (MO); 6 mi. WSW of Sierra Vieja, *Taylor 5867* (NY); 0.9 mi. E of jct. Rt. 54 on Rt. 45, E of Zacatecas, *Wagner & Solomon 4217* (MO); 7.4 mi. E of Guadalupe on Rt. 45–49, *Wagner & Solomon 4224* (MO); 7.5 mi. N of jct. Hwy. 45–49 on Hwy. 45, *Wagner & Solomon 4237* (MO); 8 mi. W of rd. to Sambrerete on Hwy. 45, *Wagner & Solomon 4251* (MO); without further locality, *Schueé s.n.* (RSA); Faral, *Schumann 531* (BM, F, GH, US).

3. Oenothera canescens Torrey & Frém. in Frém., Rep. Exped. Rocky Mts. 315. 1845. TYPE: Probably Colorado. Weld Co. or Wyoming, Morgan Co., along the South Platte River, "Upper waters of the Platte," 1–4 July 1843, *Fremont s.n.* (holotype, NY, photo MO; isotype, GH). Locality and date reconstructed with aid of McKelvey (1955: 845, 848). *Megapterium canescens* (Torrey & Frém.) Britton, Mem. Torrey Bot. Club 5: 235. 1894. *Gauropsis canescens* (Torrey & Frém.) Cockerell, Bot. Gaz. (Crawfordsville) 30: 351. 1900, nom. illeg. *Gaurella canescens* (Torrey & Frém.) A. Nels., Bot. Gaz. (Crawfordsville) 47: 437. 19 June 1909; in Coult. & A. Nels., New Man. Bot. Cent. Rocky Mts. 341. 22 Dec. 1909.

Oenothera guttulata Geyer ex Hook., London J. Bot. 6: 222. 1847. TYPE: Western Nebraska or southeastern Wyoming, perhaps Goshen Co.: (the only Wyoming county where *O. canescens* has been collected), "Plains of the upper Platte River," June 1843, *Geyer 178* (holotype, K not seen; isotypes, BM, photo MO, G). Locality reconstructed with aid of McKelvey (1955: 777). *Gaurella guttulata* (Geyer ex Hook.) Small, Bull. Torrey Bot. Club 23: 183. 1896, nom. illeg. *Gauropsis guttulata* (Geyer ex Hook.) Cockerell, Bot. Gaz. (Crawfordsville) 30: 351. 1900, nom. illeg.

Low, bushy perennial herbs with a subterranean to superficial caudex, forming clumps 10–50 cm across by adventitious shoots from lateral roots, densely strigillose throughout, the hairs (0.1–)0.4–0.6(–0.8) mm long, the stems many-branched from the base, decumbent to ascending, (10–)15–25(–38) cm long. Leaves canescent, lanceolate to linear, especially the smaller leaves, (3–)6–15(–25) mm long, (0.5–)1.5–4(–6) mm wide, sinuate-denticulate to subentire, acute at the apex, cuneate at the base in the broader leaves, subsessile. Buds erect, lance-elliptic to lanceolate in outline, the apex long-acuminate, without free tips or rarely with free tips 0.2–0.3 mm long. Flowers many opening per day near sunset. Ovary canescent, 5–10 mm long, sessile. Floral tube (8–)10–15(–17) mm long, flaring to ca. 2 mm at the mouth, glabrous within. Sepals splitting along one suture and reflexed to one side as a unit at anthesis, sometimes reflexed in pairs, (7–)8–12 mm long, (1.3–)1.5–2.2 mm wide, canescent, the margins with a reddish purple stripe, sometimes flecked with reddish purple splotches especially toward the base. Petals pink, rarely white, streaked or flecked with red, fading bright purple, obovate, (6.8–)1–1.7 cm long, (0.5–)0.6–1(–1.2) cm wide. Staminal filaments pale yellow, 6–8 mm long. Anthers yellow, often with a red longitudinal stripe, 3–6 mm long. Style (16–)22–27 mm long; stigma lobes 1.5–3(–4) mm long, well elevated above the anthers at anthesis. Capsule ovoid, (7–)9–12(–14) mm long, 2–4 mm diam. (excluding wings), the base cuneate to truncate and slightly asymmetrical, abruptly constricted to a conspicuous sterile beak (2–)3–4.5 mm long, becoming very hard at maturity, the margins of the valves with a narrow wing 0.8–1.5 mm wide, indehiscent. Seeds ca. 50–100 per capsule arranged in 2–4 irregular rows per locule, asymmetrically cuneiform or oblanceoloid (probably resulting from compression from adjacent seeds during development), angled, light brown to brown with dark spots at the distal end and at the micropyle, 1.2–1.5 mm long, 0.4–0.5 mm wide, the surface glossy, obscurely reticulate, appearing finely granular. Self-compatible, but outcrossing. Gametic chromosome number, $n = 7$.

Distribution. Locally common in prairie depressions, playas, margins of ditches, and other places with temporary water in the High Plains region from Goshen Co., Wyoming, southeast to Hayes Co., Nebraska, south through eastern Colorado, the eastern tier of counties in New Mexico, western Kansas, and to Garza and Dawson Cos. in the Texas Panhandle; also disjunct populations from Stafford, Sedgwick, and Chautauqua Cos., Kansas, (430–)750–1,700 m. Flowering from May to July, then sporadically through September. Figure 14.

Representative specimens examined. UNITED STATES. COLORADO: Cheyenne Co., 1 mi. E of Kit Carson on Hwy. 40, *Wagner 3691* (MO); Elbert Co., 15 mi. SW of Limon, *Ownbey 1303* (COLO, DS, GH, MO, MONT, NY, RM, UC, UTC, WS); Kiowa Co., 0.75 mi. W of Brandom, *Stephens & Brooks 22705* (DS, KANU); Kit Carson Co., Burlington, *Lemaire 1950* (NEB); Logan Co., 0.5 mi. E of Fleming, *Stephens 55793* (KANU); Lincoln Co., 10 mi. S of Arriba, *Christ 1436* (COLO, CS); Sedgwick Co., 17 mi. S & 3 mi. W of Julesburg, *Stephens 55690* (KANU); Washington Co., 4 mi. N & 15 mi. E of Elba, *Stephens 56128* (KANU, NY); Weld Co., 10 mi. SE of Grover, *Dodds 2125* (COLO, RM). KANSAS: Chautauqua Co., without further locality, 1897, *Hitchcock s.n.* (KSC); Cheyenne Co., 1.5 mi. S of Wheeler, *Stephens 86423* (KANU); Clark Co., 13 mi. W, 4 mi. N & 1 mi. E of Ashland, SW corner of Little Basin, *Stephens 84344* (KANU); Ellis Co., without further locality, *Smyth 2598* (KSC); Finney Co., Buffalo Wallows, *Hitchcock 162* (KSC, MO, NMC, NY, P, RM, US, YU); Gray Co., 2.5 mi. NE of Montezuma, *Stephens 54122* (KANU, NDA, NY); Greely Co., Tribune, 1892, *Reed s.n.* (KSC, UC); Hamilton Co., Syracuse, *Thompson 143* (KSC, MO, US); Kearney Co., near Lakin, 1928, *Howe s.n.* (NEB); Lane Co., 0.5 mi. W & 2.5 mi. S of Amy, *Stephens 55002* (KANU); Lincoln Co., without further locality, 1902, *Bergman s.n.* (NDA); Meade Co., 5 mi. E of Meade, *Horr 3375* (KANU); Norton Co., without further locality, 1892, *Smyth s.n.* (KSC); Scott Co., Scott City, 1900, *Granger s.n.* (NY); Sedgwick Co., Wichita, 1912, *Agrelius & Agrelius s.n.* (KANU); Seward Co., Liberal, 1892, *Carleton s.n.* (ILL, KSC); Sheridan Co., without further locality, 1931, *Weber s.n.* (KSC); Sherman Co., Goodland, 1892, *Smyth s.n.* (KSC, NY, UMO); Stafford Co., without further locality, 1885, *Kellerman s.n.* (F, MICH, MIN, MO, NY, OS, UMO, US); Stevens Co., golf course at Hugoton, *Shildneck C-4109* (ILLS); Wichita Co., 11.5 mi. S of Leoti, *Stephens 54946* (KANU). NEBRASKA: Banner Co., 20 mi. N of Kimball, *Porter & Porter 8751* (DS, GH, MIN, MSC, RM, RSA, TEX, UC); Chase Co., near Lamar, *Tolstead 411253* (ISC, MO, NEB); Cheyenne Co., Cheyenne, 1904, *Fawcett s.n.* (NEB); Deuel Co., 13 mi. E of Chappell, *Stephens 45578* (KANU, NCU); Hayes Co., 20 mi. W of Hayes Center, *Tolstead 411254* (ISC, MO, NEB, UC); Kimball Co., 9 mi. S of Kimball, *Stephens 44043* (KANU, NDA); Perkins Co., near Grant, *Tolstead 411255* (NEB). NEW MEXICO: Curry Co., Clovis, *Reynolds 252* (NEB); Quay Co., Bard, 1942, *Bradford s.n.* (NMC); Roosevelt Co., 10.5 mi. E of Elida, *Stephens 80144* (KANU); San Miguel Co., M. E. O'Connor Trust Ranch, Comic Strip Pasture, 1.8 mi. S of Rt. 104, 15 mi. E of Las Vegas, *Hill & Levandoski 12365* (MARY, MO); Union Co., 4 mi. NE of Folsom, 1951, *Clark s.n.* (UNM). OKLAHOMA: Beaver Co., 12.5 mi. W of Forgan, *Stratton 1338* (OKL, OKLA); Texas Co., Hitchland Playa near Hitchland, 1949, *Penfound s.n.* (OKLA). TEXAS: Armstrong Co., 8.75 mi. N of Paloduro, *Cory 13464* (ARIZ, POM); Bailey Co., 8 mi. NW of Baileyboro, *Rosson 844* (SAT, TTC, WTS); Briscoe Co., 1.2 mi. E of Silverton, *Whitehouse 9991* (SMU); Carson Co., 5 mi. N of Panhandle, *Shinners 8109* (SMU); Castro Co., lake S of Dimmitt, *York & Rodgers 425* (OKLA, SMU, TEX); Cochran Co., 22 mi. S of Muleshoe, Muleshoe Wildlife Refuge, *Stephens 80202* (KANU); Crosby Co., jct. of farm rds. 40 & 651, 7 mi. S of Crosbyton, 1968, *Morris s.n.* (NY); Dawson Co., on U.S. Hwy. 180, ca. 10.5 mi. E of Lamesa, *Lundell & Lundell 16972* (LL); Deaf Smith Co., 15 mi. N & 15 mi. W of Hereford, *Waller 964* (SMU, TTC); Dickens Co., 2 mi. S of McAdoo, 1965, *Rowell s.n.* (GH, KSC, OKLA, TTC, UC); Floyd Co., 1 mi. N of South Plains, *Spence 39* (DS); Garza Co., 11.1 air mi. NW of Post, *Hutchins 679* (OKLA, SMU, TTC); Gray Co., 16 mi. S of Pampa, *Stephens 76343* (KANU, NCU); Hale Co., SW of Kress, 6.6 mi. S on Hwy. 87 & 4.1 mi. W, *Whitehouse 9932* (MICH, NY, SMU, UC, US); Hall Co., 1 mi. W of Turkey, *Stephens 72179* (KANU, NY); Hansford Co., just S of Hitchland, Oklahoma, *Goodman 5288* (GH, NY, OKL, TEX); Hartley Co., 8 mi. E of Hartley, *Stephens 82120* (KANU); Hockley Co., Levelland, *Blassiugame 3932* (SAT); Hutchinson Co., 18 mi. NE of Stinnett, *Stephens 81921* (KANU); Lamb Co., 0.5 mi. S of Amherst, *Stephens 75973* (KANU, MASS, NCU); Lubbock Co., 5 mi. N of Slaton, *Rowell 8573* (GH, OKL, OKLA); Lipscomb Co., Booker on Hwy. 117, *Wallis 5048* (ARIZ, GH, OKLA, SMU); Lynn Co., Tahoka, *Tharp 4442* (TEX, US); Moore Co., 1.5 mi. W of Sunray, *Stephens 82015* (KANU); Ochiltree Co., 6.5 mi. SE of Perryton on U.S. Hwy. 83, *Wallis 4751* (GH, OKLA, SMU); Parmer Co., W edge of Hub, *Rowell 8634* (GH, OKLA, UC); Potter Co., Amarillo, *Reverchon 3840* (CAS, F, GH, LL, MIN, MO, NY, POM, US); Randall Co., ca. 1 mi. N of Canyon, *Higgins 4356* (ASU, BRY, MICH, NY, WTS); Sherman Co., 14 mi. E, 12 mi. S & 4.5 mi. E of Stratford, *Stephens 82387* (KANU). WYOMING: Goshen Co., S of Springer Reservoir, *Luce 94* (RM).

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SYSTEMATICS OF *OSMORHIZA* RAF. (APIACEAE: APIOIDEAE)[1]

PORTER P. LOWRY II[2] AND ALMUT G. JONES[3]

ABSTRACT

The genus *Osmorhiza* comprises ten species and two subspecies of woodland umbellifers native to temperate Asia and the Americas. Quantitative evaluation of nine morphological characters supports the recognition of two distinct subgenera: *Glycosma,* with a single species, *O. occidentalis,* and *Osmorhiza,* with the remaining nine species. The typical subgenus is further divided into three sections, each with three species. A complete synonymy and detailed description is provided for each taxon, along with an analytical key to the subgenera, sections, species, and subspecies. Phytogeographic data indicate that western North America is the center of distribution and diversity, and possibly the center of origin for *Osmorhiza,* although members of the genus are found in eastern North America as well as Asia and Central and South America. The amphitropical disjunctions between North and South America observed in the ranges of *O. chilensis* and *O. depauperata* (both sect. *Nudae*) are most likely the result of long-distance dispersal by migratory birds. By contrast, the disjunct populations of these taxa that occur in the Great Lakes region and eastern North America probably represent remnants of a more widespread, pre-Pleistocene distribution. The three species comprising *Osmorhiza* sect. *Osmorhiza* (the North American *O. claytonii* and *O. longistylis,* and the Asian *O. aristata*) provide an example of the classical eastern North American–eastern Asian pattern of disjunction. Although these taxa are very similar morphologically, the populations probably represent members of a relatively stable floristic assemblage that has persisted in these areas for a long period; the possibility that there has been any recent contact between these disjunct taxa through Beringia seems remote. The members of *Osmorhiza* sect. *Mexicanae* (*O. brachypoda, O. mexicana,* and *O. glabrata*) exhibit a somewhat broken distribution from northern California to central Argentina, and possibly represent derivatives of a common ancestral taxon that migrated southward along a chain of mountain tops with suitable temperate climatic conditions at some time during the Pliocene or Pleistocene. Ethnobotanical evidence indicates that at least five species of *Osmorhiza* were used for medicinal purposes by native Indian peoples of North America. The roots and greens of two species were also consumed as food by both North and South American Indians.

TAXONOMIC HISTORY

Osmorhiza (Apiaceae: Apioideae) is a small genus of perennial woodland herbs with representatives in temperate Asia and the Americas. Members of the genus typically flower in the spring, setting fruit by mid-summer. These fruits (schizocarps), which are armed with retrorse bristles in all but one species, are well adapted for epizoochory. Plants of *Osmorhiza,* commonly known as Sweet Cicely, may be quite abundant in some areas, but they rarely form uninterrupted stands, even under the most favorable of conditions.

Osmorhiza was first recognized as a distinct genus by Rafinesque in 1818, but it was not until the following year (Rafinesque, 1819a) that this

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name was validly published. Prior to that, specimens of *Osmorhiza* had been referred to three other genera: *Chaerophyllum* L. (Thunberg, 1784; Persoon, 1805), *Myrrhis* Miller (Michaux, 1803; Sprengel, 1813), and *Scandix* L. (Muhlenberg, 1813). During the next 80 years many new species were described in the genus. However, it was not until 1888, when Coulter and Rose published their "Revision of North American Umbelliferae," that an attempt was made to clarify the taxonomy of *Osmorhiza*. Twelve years later Coulter and Rose (1900) revised their previous treatment of the North American members of the genus, recognizing 12 taxa, including three new species. Mathias and Constance (1944), in their review of the Umbelliferae for the "North American Flora," listed eight species and two varieties of *Osmorhiza.*

Osmorhiza was treated for the first time on a world-wide basis by Constance and Shan (1948), who recognized the conspecificity of the North and South American populations now included in *O. chilensis* and *O. depauperata*. These authors included all the Asian populations of the genus under *O. aristata,* and described one new species, *O. bipatriata*. However, they acknowledged that "newer techniques" (i.e., biosystematic techniques) were not used in their study; they based their conclusions entirely on the examination and comparison of herbarium specimens.

Work on the current study was begun in 1974, at which time only two eastern North American species, *O. claytonii* and *O. longistylis,* were considered. Later, the scope of our work was expanded to a systematic investigation of the entire genus. Toward this end several approaches have been used, including (1) quantitative evaluation of nine morphological characters, (2) mapping of each species, (3) comparative examination of available type material, and (4) a broad survey of the literature on the genus. In addition, an analysis of electrophoretic banding patterns of water soluble seed proteins for most *Osmorhiza* species was conducted (Lowry & Young, 1979; Lowry, 1980).

In addition to the nearly 400 collections of *Osmorhiza* on deposit in ILL, approximately 8,500 specimens from 48 herbaria were studied. Photographs of type specimens unavailable for loan were received from LE and SGO. Voucher specimens for the more than 200 collections made by the first author are deposited in ILL, along with photographs of all type material examined.

The quantitative morphological data presented here support a revised taxonomy for *Osmorhiza* in which ten species and one subspecies are recognized. Two well delimited subgenera are distinguished, one of which is further divided into three sections. These conclusions are further supported by seed protein data (Lowry & Young, 1979; Lowry, 1980). Phytogeographic evidence indicates that western North America is the center of distribution and diversity, and possibly the center of origin for *Osmorhiza,* although members of the genus have migrated to and survived in eastern North America as well as in Asia and in Central and South America. Nomenclatural problems within the genus are dealt with, and a brief discussion of the ethnobotany is given.

NOMENCLATURE

Generic names. Species of *Osmorhiza* were originally placed in three other genera: *Chaerophyllum* L., *Myrrhis* Miller, and *Scandix* L. In 1818 Rafinesque published three alternative generic names for these taxa: *Washingtonia, Osmorhiza,* and *Gonatherus*. These were, however, invalidly published under Art. 34.1(a) of the "International Code of Botanical Nomenclature" (Voss et al., 1983), because they were not accepted by the author in the original publication. They may also be nomina nuda because they appear not to meet the requirements of Art. 41.2 of the "Code" (cf. Lowry & Jones, 1978; Lowry, 1985). In the same year Nuttall (1818) validly published the name *Uraspermum* for this taxon. Rafinesque (1819a), however, rejected *Uraspermum* Nutt., considering it too similar to (i.e., an incorrectly spelled later homonym of) *Urospermum* Scopoli, a genus of Asteraceae, and validated the name *Osmorhiza* with a reference to the description of *Uraspermum* Nutt. (Lowry & Jones, 1977, 1978). This interpretation has been followed by nearly all subsequent authors, although most have incorrectly considered Rafinesque (1819b) as the first place of valid publication for the name *Osmorhiza. Uraspermum* Nutt., however, cannot be treated as a later homonym since it is not spelled exactly like *Urospermum* Scopoli (cf. Art. 64.1 of the "Code"). Strict application of the rules of nomenclature would thus appear to require accepting the name *Uraspermum* Nutt. for the taxa currently recognized in *Osmorhiza*. In order to avoid this clearly undesirable change and to maintain nomenclatural stability, a proposal has been made to conserve the generic name *Osmorhiza* against *Uraspermum* (Lowry, 1985).

Subgeneric names. Two subgenera are recognized within *Osmorhiza*, one with nine species, including the type for the genus (i.e., the type of *O. claytonii*), and one with a single species, *O. occidentalis*. When *O. occidentalis* was first described it was placed in a new, monotypic genus, *Glycosma*, by Nuttall (in Torrey & Gray, 1840), who provided both generic and specific descriptions. Drude (in Engler & Prantl, 1897), following Torrey (1859), judged this species to be an *Osmorhiza*, but placed it in a separate subgenus, citing Nuttall's generic name *Glycosma* as the basionym; the correct name for this subgenus is: *Osmorhiza* subg. *Glycosma* (Nutt.) Drude in Engl. & Prantl.

Sectional names. Three sections are recognized within *Osmorhiza* subg. *Osmorhiza* (Lowry & Jones, 1979b; Lowry, 1980). Constance and Shan (1948) published names for all three of these: (1) *Aristatae*, (2) *Mexicanae*, and (3) *Nudae*, although not validly, because none of them was accompanied by a Latin description or diagnosis or a reference to a previously and effectively published Latin description or diagnosis of the same taxon (cf. Arts. 32.1 and 36.1 of the "Code"). Because the section *Aristatae* includes the type of the genus, its epithet is a synonym for *Osmorhiza* sect. *Osmorhiza*. Constance and Shan's sectional names *Mexicanae* and *Nudae* are validated herein.

Specific epithets. Rafinesque (1830: 249) published three new species: *Osmorhiza dulcis*, *O. vilosa* [sic], and *O. cordata*. This publication reads as follows: "*Osmorhiza dulcis*, Raf. 1817 (*Myrrhis claytoni* Mx?) Sweet Sisily [sic]. Root fusiform, with a sweet smell and taste, near aniseed [sic], edible, carminative, expectorant, demulcent, useful for coughs with *Malva*, for flatulent bowels with *Heracleum*, Eq. to *Angelica*. Children are fond of this root, may be poisoned by mistaking for it, two sp. of the same genus or *Myrrhis* Auct. called *Poison* or *Bastard Sisily* [sic], distinctive by the roots less aromatic, foliage the same, but in *O. dulcis* base of the folioles acute, in my *O. vilosa* [sic] or *M. longistylis* obtuse, in *O. cordata* Raf. cordate. These last produce, when eaten, effects similar to those of the virulent Umbellate . . . ." Traditionally, placement of these names in synonymy has been based solely on this reference; *O. dulcis* under *O. claytonii*, and *O. vilosa* and *O. cordata* under *O. longistylis*. The type specimen of *O. dulcis* (PH!) is, however, clearly a plant of *O. longistylis*, not *O. claytonii* as suggested by Rafinesque; *O. dulcis* is therefore a synonym of *O. longistylis*. The correct placement of the names *O. vilosa* and *O. cordata* may be inferred from Rafinesque's reference itself. *Osmorhiza dulcis* is said to have more aromatic roots than *O. vilosa* and *O. cordata*; the roots of *O. longistylis* are more aromatic than those of *O. claytonii* (Lowry & Jones, 1979a). Since *O. vilosa* is a synonym for *O. longistylis*, by inference *O. vilosa* and *O. cordata* belong in synonymy under *O. claytonii*. Rafinesque probably confused *O. claytonii* and *O. longistylis* when suggesting the synonymy for his new names.

Rydberg (1894) validly published the combination *Osmorhiza aristata* (Thunb.) Rydb. Nearly all subsequent authors have incorrectly attributed this combination to Makino and Yabe (in Makino, 1903), however; the only apparent exceptions are Constance (1972), Lowry and Jones (1979a), and Lowry (1980).

Accurate determination of the holotype of *Osmorhiza mexicana* Griseb. was possible only with the kind assistance of Professor Dr. G. Wagenitz (GOET). According to Wagenitz (pers. comm.), Grisebach usually marked voucher specimens he considered new by placing an "*m*" (for *mihi*), after the new name, while other vouchers were marked with "Gr." Examination of the authentic material from the Grisebach Herbarium at GOET shows that *Schaffner 37* is marked "*Osmorhiza mexicana m*" in Grisebach's hand, while two other specimens (*Mandon 594* and *Lorentz & Hieronymus 668*) are marked "*Osmorhiza mexicana* Gr." Thus, the Schaffner collection has been annotated as the holotype, whereas the other specimens are paratypes.

Lectotypes are designated here for four specific epithets: *O. brevistylis* DC., *O. depauperata* Philippi, *O. laxa* Royle, and *Myrrhis renjifoana* Philippi. There are several syntypes for each of these names, and extensive search in the literature has not revealed previous lectotypification for any of them.

The name *Myrrhis longistylis* Torrey (1824: 310) was published with the following type information: "In wet meadows near Albany, New York. *Tracy*. Near Geneva, N. Y. *Paine*. June. Near Hudson, N. Y. *Alsop*, & c." These specimens would by syntypes, although none of them has been located. An authentic collection by Paine marked "*Myrrhis* n. sp." in Torrey's hand (at

NY) is therefore designated as the neotype for *Myrrhis longistylis* Torrey.

ETHNOBOTANY

Species of *Osmorhiza* were used in a variety of ways by native peoples in many parts of North America, and by at least one tribe in South America. Available information indicates that *O. brachypoda, O. chilensis, O. claytonii, O. longistylis,* and *O. occidentalis* were used for medicinal purposes, while *O. chilensis* and probably *O. depauperata* were also consumed as food. Many uses of *Osmorhiza* by Indians of North America were reviewed by French (1971).

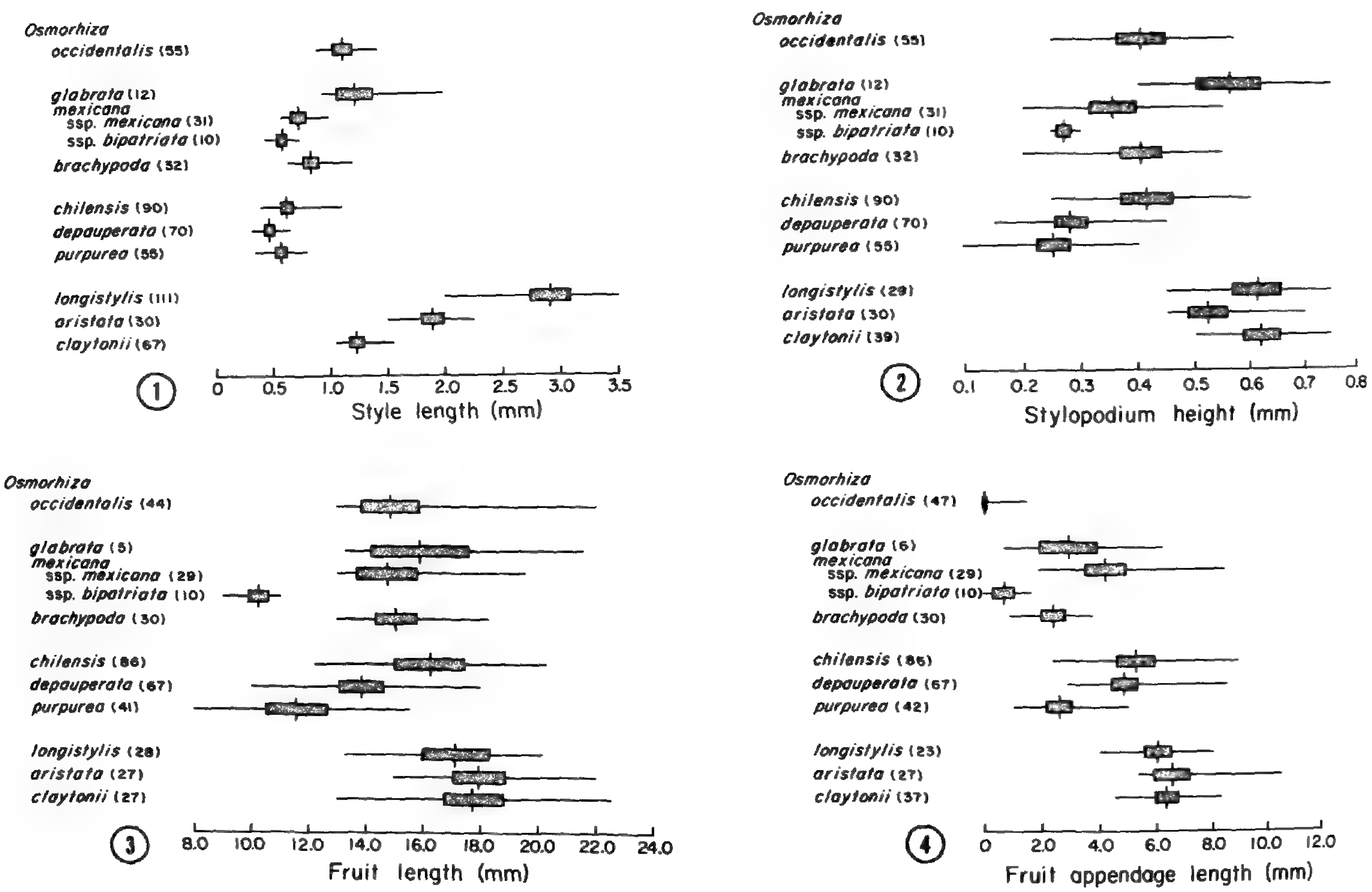
Perhaps the most widely used species was *Osmorhiza chilensis.* In their review of the ethnobotany of the Karok and other Indians of northern California, Schenck and Gifford (1952: 386–387) reported: "The root of this plant is one of the most important medicines. It can be dried and kept in the house. The medicine requires a formula (charm) always, but it is used for almost everything. The house is smoked with it, if there has been illness in the house. The root is thrown on the fire at dances. If put under the pillow at night, it keeps sickness away. For headache, a little piece of the root is chewed. If a person is grieving over a lost relative, medicine is made from the root (with formula) and the mourner is bathed with the medicine. A piece of the root is carried as protection against the 'devil.' In the spring the young tops are eaten as greens. It is very good luck to find it growing in a place where it has never been seen before. Georgia Orcutt [a local Indian woman] says this is the only herb that is dried and kept on hand in the house. It is good for 'everything'." Gunther (1945) reported that the Swinomish Indians of northwestern Washington chewed the roots of *Osmorhiza brevipes* (= *O. chilensis*) as a powerful love charm. She also noted that the Lummi and Skagit tribes of the same area did not seem to use *Osmorhiza.* Schneider (1906) indicated that the seeds of "*O. longistylis*" (certainly *O. chilensis*) were used by California Indians (probably the Paiutes) for medicinal purposes, primarily as a cough remedy. According to Steedman (1930: 480), the Thompson Indians of interior British Columbia ate the roots of *Osmorhiza chilensis*; she stated that "they are known for their delicate flavor and are especially appetizing because of their aromatic character."

Other species of *Osmorhiza* were used by Indians of western North America as cough remedies. The Paiutes prepared a decoction from the roots of *O. brachypoda* (Schneider, 1906), and several tribes from both Canada and the U.S. also used *O. occidentalis* for this purpose (Uphof, 1968).

Osmorhiza longistylis was used by many peoples of the midwestern U.S. According to Smith (1928: 249), the Meskwaki (i.e., Fox) Indians used this species for a variety of medicinal purposes: "It is chiefly used as an eye remedy. It is horse medicine, too, and the root is grated and mixed with salt for distemper. When hunting, they fed a pony with the root and he was thus enabled to catch the buffalo. Specimen *5154* of the Dr. Jones collection is the leaves of *Osmorhiza longistylis* and the bark of *Gleditsia triacanthos* mixed to make a tea which is drunk to regain flesh and strength." Gilmore (1919: 107) wrote: "The Omaha and Ponca say that horses were so fond of the roots of *Washingtonia* [*longistylis*] that if one whistled to them, while holding out the bag of roots, the horses came trotting up to get a taste, and so could easily be caught. An Omaha said that the roots were pounded up to make poultices to apply to boils. A Winnebago medicine-man reported the same treatment for wounds. A Pawnee said that a decoction of the roots was taken for weakness and general debility."

Smith (1932: 391) indicated that the Ojibwe (i.e., Ojibwa) Indians apparently did not distinguish between *Osmorhiza longistylis* and the closely related *O. claytonii.* He stated: "A tea for making parturition easier is prepared from the roots. The licorice flavor of the tea is said to be good for a sore throat." *Osmorhiza claytonii* was used by the Menomini Indians of northern Wisconsin to gain weight (Smith, 1923).

Osmorhiza was also used by Indians in southern South America. According to Mrs. Natalie Goodall of Harberton, Argentina (in a letter to Mrs. Helen Sharsmith, dated May 12, 1965, a copy of which was obtained from Dr. Lincoln Constance), *Osmorhiza* "was one of the three plants eaten by the [Yahgan] Indians besides fungi. . . . The owwunim [a Yahgan name] was eaten raw—leaves, stems, and roots, or the roots were baked in the fire . . . . My mother-in-law says that she often saw the Indians eating it as a child. Now it is hard to say, as there are only about four Yahgans left, two of them work in Harberton, but have forgotten their language." It is likely that the Yahgans did not distinguish between



FIGURES 1–4. Mean, standard deviation, range of variation, and sample size of quantitative morphological characters in *Osmorhiza* spp.—1. Style length (mm).—2. Stylopodium height (mm).—3. Fruit length (mm).—4. Fruit appendage length (mm).

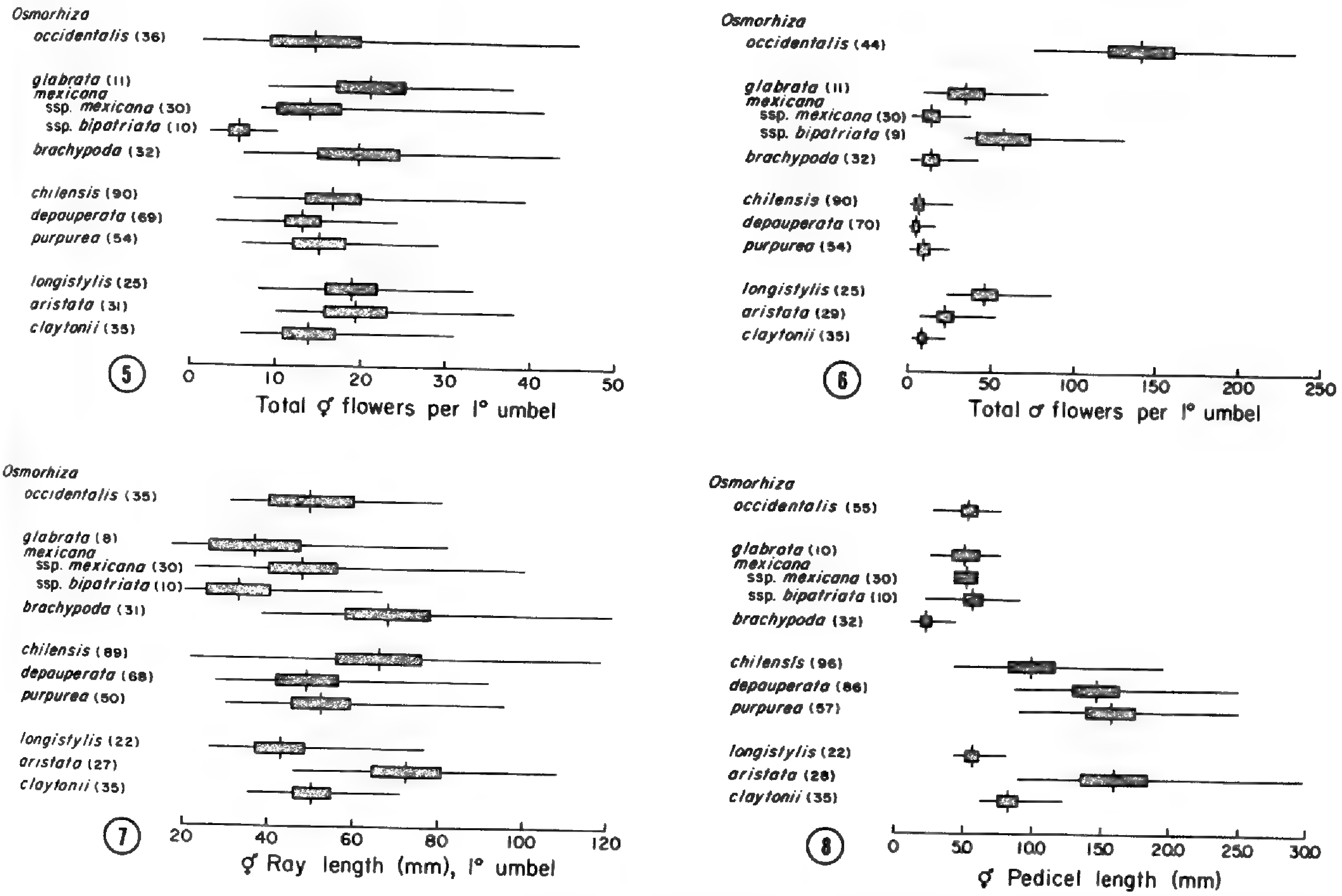
Osmorhiza depauperata and *O. chilensis*, both of which grow throughout southern South America, often together. If they did, however, Mrs. Goodall's comments probably apply to *O. depauperata*, a specimen of which (*Y. Mexia 7925*), collected in Tierra del Fuego, Argentina, has written on its label "Awanim (Yeagan)."

The widespread use of these plants by native North and South Americans would suggest that other Indian groups, whose ethnobotany has not been studied, also used species of *Osmorhiza*. It is even possible that *O. aristata* was used by the people of Asia, although no record of this has been found.

MORPHOLOGY

Nine morphological characters, selected for their potential diagnostic value, were evaluated for all 11 taxa of *Osmorhiza*. Representative specimens were selected for study from across the geographic range of each taxon. The quantitative value for each character was obtained by taking the average of four measurements per specimen (occasionally two or three). Statistical significance of the data was determined using contingency table analysis solved by chi square. We tested the null hypothesis that departures from random expectation are attributable to chance alone (Woolf, 1968). Mean, standard deviation, and range of variation of quantitative characters are presented in Figures 1–8. Sample sizes are given in parentheses. Comparison of values from the geographically disjunct areas of *Osmorhiza chilensis*, *O. depauperata*, and *O. aristata* is given in Tables 2–4, respectively.

1. *Style length.* This is a diagnostic character for the members of *Osmorhiza* sect. *Osmorhiza* (*O. longistylis*, *O. aristata*, and *O. claytonii*) but is of little taxonomic value for the other species (Figs. 1, 9a–c). Statistical analysis of style length values for members of section *Osmorhiza* yielded a chi square significant far beyond the 0.0005 probability level. The members of this section can readily be separated when this character is used in conjunction with geographic distribution. *Osmorhiza aristata*, with intermediate style length values, occurs only in Asia, whereas *O. longistylis* and *O. claytonii*, both of which are found in eastern North America, show no overlap in their ranges of values (Lowry, 1976; Lowry & Jones, 1979a; Ostertag & Jensen, 1980). Sev-



FIGURES 5–8. Mean, standard deviation, range of variation, and sample size of quantitative morphological characters in *Osmorhiza* spp.—5. Total hermaphrodite flowers per 1° umbel.—6. Total staminate flowers per 1° umbel.—7. Hermaphrodite ray length from 1° umbels (mm).—8. Pedicel length of hermaphrodite flowers (mm).

eral authors have relied entirely on style length to distinguish *O. longistylis* from *O. claytonii* (e.g., Deam, 1940; Steyermark, 1963).

2. *Stylopodium height.* The high-conic stylopodia of *Osmorhiza chilensis* are distinctive, and separate it from the other members of the section *Nudae,* which have low-conic to depressed stylopodia (Figs. 2, 9i–k). Statistical analysis of this character for the members of *O.* sect. *Nudae* resulted in a highly significant chi square. Furthermore, *O. glabrata* is distinguishable from the other members of the section *Mexicanae* by its fairly high, conic stylopodia (Fig. 2).

3. *Fruit length.* This character is diagnostic for the taxa included in *Osmorhiza* sect. *Nudae* (Figs. 3, 9i–k). These species are, in fact, distinguishable almost exclusively on the basis of fruit characters, including length and shape of the schizocarps, and size and shape of the stylopodium. Statistical analysis of fruit length measurements for the members of *O.* sect. *Nudae* yielded a highly significant chi square ($P \ll 0.0005$).

4. *Fruit appendage length.* The two subgenera of *Osmorhiza* are separable on the basis of presence or absence of caudate appendages on the base of the mericarps. All ten taxa comprising the typical subgenus have appendages of varying lengths, while they are lacking entirely from the fruits of *O. occidentalis* (*O.* subg. *Glycosma*), with a few rare exceptions (Figs. 4, 9). Within the typical subgenus, *O. purpurea* is distinct from the other members of the section *Nudae* by having short appendages. Similarly, *O. mexicana* subsp. *bipatriata* has shorter appendages than the other taxa in *O.* sect. *Mexicanae.*

Constance and Shan (1948) pointed out that the caudate appendages, along with the retrorse bristles on the fruits of most species, play an important role in dispersal. It is interesting to note that *O. chilensis* and *O. depauperata,* both of which have wide disjunctions in their ranges, have conspicuously armed fruits. By contrast, *O. occidentalis,* which lacks both appendages and bristles, has a continuous and somewhat restricted range in western North America. Similarly, *O. mexicana* subsp. *bipatriata,* with essentially

TABLE 1. Comparison of percentage of hermaphrodite flowers per 1° and 2° umbels in *Osmorhiza* species.

	1° Umbel			2° Umbel			
	Total ⚥ Fls./ Umbel	Total ♂ Fls./ Umbel	% ⚥ Fls.	Total ⚥ Fls./ Umbel	Total ♂ Fls./ Umbel	% ⚥ Fls.	Direction of Change
O. occidentalis	14.05	137.61	9.3	21.73	84.37	20.5	+
O. aristata	19.32	22.24	46.5	11.84	19.24	38.1	−
O. claytonii	13.94	8.20	63.0	10.68	10.32	50.9	−
O. longistylis	18.80	4.92	79.3	15.52	36.39	29.9	−
O. glabrata	20.73	32.50	39.9	11.60	21.40	35.2	−
O. mexicana subsp. *mexicana*	13.35	11.47	54.1	12.08	14.46	45.5	−
O. mexicana subsp. *bipatriata*	5.40	55.00	8.9	5.50	39.78	12.1	+
O. brachypoda	19.38	11.97	61.8	13.72	11.44	54.5	−
O. chilensis	16.49	5.10	76.4	11.39	7.84	59.2	−
O. purpurea	14.96	6.46	69.8	9.75	4.71	67.0	−
O. depauperata	13.20	3.04	81.3	9.98	2.67	79.0	−

glabrous fruits and very short appendages, has a very narrow range in Texas and northern Mexico.

5. *Total hermaphrodite flowers per 1° umbel.* Species of *Osmorhiza* are andromonoecious, a feature common to many genera of Apiaceae; their inflorescences contain both hermaphrodite and functionally staminate flowers. The staminate flowers have well-developed stylopodia that secrete nectar, but lack styles and functional ovaries, and consequently do not develop fruit (Lowry & Jones, 1979a; Lowry, 1980; see also Bell, 1971). The total number of hermaphrodite flowers produced in the primary umbels is quite uniform among *Osmorhiza* species (Fig. 5). Plants of each species produce similar numbers of fruits in their primary umbels (see below for the significance of this character).

6. *Total staminate flowers per 1° umbel.* This character is diagnostic in several ways. The two subgenera of *Osmorhiza* may be separated on the basis of this character; plants of *O. occidentalis* (*O.* subg. *Glycosma*) produce, on the average, more than twice as many staminate flowers per umbel as those of any taxon in *Osmorhiza* subg. *Osmorhiza* (Fig. 6). Furthermore, the members of *O.* sect. *Osmorhiza* are easily distinguishable from each other on the basis of this character. Values for the Asian *O. aristata* are intermediate between those for the North American *O. claytonii* and *O. longistylis* (Fig. 6). Statistical analysis of data for these three taxa yielded a very large chi square ($P \ll 0.0005$).

7. *Percentage of hermaphrodite flowers per 1° and 2° umbels.* The ratio of hermaphrodite to staminate flowers differs between the primary and secondary umbels in *Osmorhiza* species (Table 1). In members of the typical subgenus, the primary umbel has a higher percentage of hermaphrodite flowers than does the secondary umbel. Therefore, the primary umbels of these plants contribute relatively more to the gene pool of the next generation through their ovules than do the secondary umbels. The only exception to this pattern in *O.* subg. *Osmorhiza* is *O. mexicana* subsp. *bipatriata,* for which there is a slight increase in the percentage of hermaphrodite flowers from primary to secondary umbel. This may be the result of the remarkably low number of hermaphrodite flowers in its primary umbels. This pattern of increasing "maleness" (or decreasing "femaleness") with successively later flowering umbels is correlated with protandry in the hermaphrodite flowers of many apiaceous taxa, including *Ligusticum canadense* (L.) Britt. and *Daucus carota* L. (Bell, 1971), and *Osmorhiza longistylis* (Torrey) DC. (Robertson, 1888), as well as the other species of *Osmorhiza* subg. *Osmorhiza.*

By contrast, *O. occidentalis* (subg. *Glycosma*) shows a strong trend toward increasing "femaleness" from primary to later-flowering umbels (Table 1). In these populations, the percentage of hermaphrodite flowers is more than twice as high in the secondary as compared to the primary umbel. Schlessman (1978, 1982) has shown that a similar increasing percentage of hermaphrodite flowers (expressed as a decreasing percentage of

TABLE 2. Morphological comparison of populations from the four major areas of distribution for *Osmorhiza chilensis*—mean, standard deviation, and sample size.

	Western North America			Great Lakes Region			Northeastern North America			Southern South America		
Character	$\bar{x}$	s.d.	N	$\bar{x}$	s.d.	N	$\bar{x}$	s.d.	N	$\bar{x}$	s.d.	N
Style length (mm)	0.61	0.08	38	0.57	0.06	6	0.64	0.06	9	0.69	0.14	24
Stylopodium ht. (mm)	0.42	0.09	38	0.38	0.04	6	0.43	0.07	9	0.37	0.08	24
Fruit length (mm)	16.66	2.71	36	16.42	0.93	6	18.74	1.47	9	14.97	1.72	22
Fruit appendage length (mm)	5.45	1.37	36	5.02	0.83	6	6.38	1.01	9	4.92	1.17	22
Total ☿ fls. per 1° umbel	17.58	6.02	38	13.00	6.60	6	15.44	6.33	9	16.50	7.53	24
Total ♂ fls. per 1° umbel	3.97	4.33	38	4.00	3.69	6	3.11	3.06	9	9.37	6.58	24
☿ ray length (mm) in 1° umbels	61.78	20.01	38	58.67	17.90	6	79.78	24.76	9	65.11	19.19	23
☿ pedicel length (mm)	9.65	3.26	38	11.39	3.39	6	10.78	3.83	9	9.00	3.51	29

staminate flowers) occurs in the protogynous species of tuberous lomatiums. Thus, although no observations have been made for *O. occidentalis,* circumstantial evidence suggests that it may be protogynous.

8. *Hermaphrodite ray length in 1° umbels.* Two types of rays are typically produced in the umbels of *Osmorhiza* species, those whose umbellets contain both hermaphrodite and staminate flowers (hermaphrodite rays), and those with umbellets composed entirely of staminate flowers (staminate rays). Hermaphrodite rays are generally rather stiff when the fruits reach maturity, ranging from 20 to 120 mm long, while staminate rays wither after flowering, and rarely exceed 10 mm. Hermaphrodite ray length is a useful diagnostic feature for distinguishing *O. aristata* from *O. longistylis* and *O. claytonii* (Fig. 7). This character is also useful for separating *O. brachypoda* from the other members of *O.* sect. *Mexicanae* (Fig. 7).

9. *Pedicel length of hermaphrodite flowers.* This is an excellent character for separating *O. aristata* from its North American relatives (Fig. 8). The pedicels in this species are, on the average, more than twice as long ($P \ll 0.0005$) as in plants of *O. longistylis* and *O. claytonii.*

10. *Comparison of disjunct populations of Osmorhiza species.* Comparison of values for morphological characters from the four geographically disjunct areas of *O. chilensis* (western North America, the Great Lakes region, northeastern North America, and southern South America) shows a remarkable similarity among the populations (Table 2). While a number of populations in the Great Lakes area, the northeast, and South America appear to have undergone some divergence, there is no doubt as to their conspecificity with populations from western North America, where the species possibly originated.

Similarly, populations of *O. depauperata* from these same disjunct areas are morphologically very similar to one another (Table 3). While some divergence has occurred in South America, the specimens examined from this area are clearly within the range of variation found within the species in western North America.

Constance and Shan (1948) recognized two varieties of *Osmorhiza aristata,* the variety *laxa,* from southwestern China and the Himalayan region, and the typical variety from the Altai region and eastern Asia. These varieties were distinguished on the basis of leaf characters; plants from Sachalin and Siberia show a maximum of leaf dissection, those from Japan are intermediate, and those from the Himalayas have leaves that are much less divided. Although this variation in leaf dissection is indeed recognizable, there is no apparent correlation with other morphological characters. Quantitative values for these characters for populations from eastern Asia and the Himalayan region are quite similar, and do not support the recognition of infraspecific taxa within *O. aristata* (Table 4).

PHYTOGEOGRAPHY

Nearly 8,000 herbarium specimens were examined to determine the limits of geographic

TABLE 3. Morphological comparison of populations from the four major areas of distribution for *Osmorhiza depauperata*—mean, standard deviation, and sample size.

	Western North America			Great Lakes Region			Northeastern North America			Southern South America		
Character	$\bar{x}$	s.d.	N	$\bar{x}$	s.d.	N	$\bar{x}$	s.d.	N	$\bar{x}$	s.d.	N
Style length (mm)	0.46	0.07	33	0.46	0.10	7	0.46	0.09	7	0.55	0.08	9
Stylopodium ht. (mm)	0.27	0.06	33	0.31	0.08	7	0.27	0.06	7	0.29	0.06	9
Fruit length (mm)	13.74	1.56	32	14.11	0.83	7	14.79	0.86	7	12.28	1.68	8
Fruit appendage length (mm)	4.98	0.93	32	4.75	0.47	7	5.21	0.56	7	4.00	0.76	8
Total ☿ fls. per 1° umbel	13.21	4.21	33	11.33	1.75	6	13.86	2.41	7	12.22	3.46	9
Total ♂ fls. per 1° umbel	3.09	3.30	33	0.05	1.23	6	2.57	1.40	7	4.22	5.02	9
☿ ray length (mm) in 1° umbels	49.17	15.69	32	42.50	10.07	6	50.50	20.19	7	55.33	10.79	9
☿ pedicel length (mm)	14.34	3.56	33	14.50	3.36	7	16.74	4.32	7	15.05	2.72	10

distribution for *Osmorhiza* species. Distribution was mapped for each taxon by placing dots on a base map; one dot (or occasionally two) for counties in the U.S., and one dot per locality for other areas. A number of important collections reported by Hultén (1947), Constance and Shan (1948), Shishkin (1950), and Liu (1977) not available for study were mapped as circles. In general, the ranges obtained are in agreement with those given by other authors, notably Hultén (1947), Constance and Shan (1948), Constance (1963), Wood (1972), and Marquis and Voss (1981).

OSMORHIZA SECT. OSMORHIZA. Two species, *O. claytonii* and *O. longistylis*, are widely distributed in eastern North America and are sympatric over much of their ranges (Lowry, 1976; Lowry & Jones, 1979a). Both occur on the Gaspé Peninsula, in Nova Scotia, and in southern Quebec and Ontario, and reach their eastern limits south along the Atlantic Coast. In the south, *O. claytonii* ranges from the southern Appalachian Mountains of North Carolina and Tennessee to the Ozark Plateau, approximately along the 35th parallel. In the west, this species reaches its limits along a line close to the 100th meridian, with extensions into north-central Nebraska and southwestern Manitoba (Fig. 10).

The range of *O. longistylis* extends farther to the south, reaching from the Piedmont Upland of central Georgia and South Carolina to Arkansas, eastern Oklahoma, and adjacent Texas. In the west, this species is found throughout the upper Great Plains, and has its limits along the base of the Rocky Mountains in Colorado, Wyoming, Montana, and Alberta (Fig. 11).

The third member of this section, *O. aristata*, occurs only in Asia, ranging from Sachalin and the lower Amur basin, through Japan, Korea, Taiwan, central and southern China, to the Hi-

TABLE 4. Morphological comparison of populations of *Osmorhiza aristata* from eastern Asia and the Himalayan Region—mean, standard deviation, and sample size.

	Eastern Asia			Himalayan Region		
Character	$\bar{x}$	s.d.	N	$\bar{x}$	s.d.	N
Style length (mm)	1.91	0.18	25	1.78	0.22	5
Stylopodium height (mm)	0.52	0.07	25	0.51	0.09	5
Fruit length (mm)	17.59	1.61	23	20.00	1.68	4
Fruit appendage length (mm)	6.27	0.99	23	7.91	1.82	4
Total ☿ fls. per 1° umbel	19.30	6.42	26	19.60	11.26	5
Total ♂ fls. per 1° umbel	23.04	9.73	25	17.25	7.23	4
☿ ray length (mm) in 1° umbels	71.09	14.17	23	80.29	26.18	4
☿ pedicel length (mm)	14.63	3.45	24	23.92	4.84	4

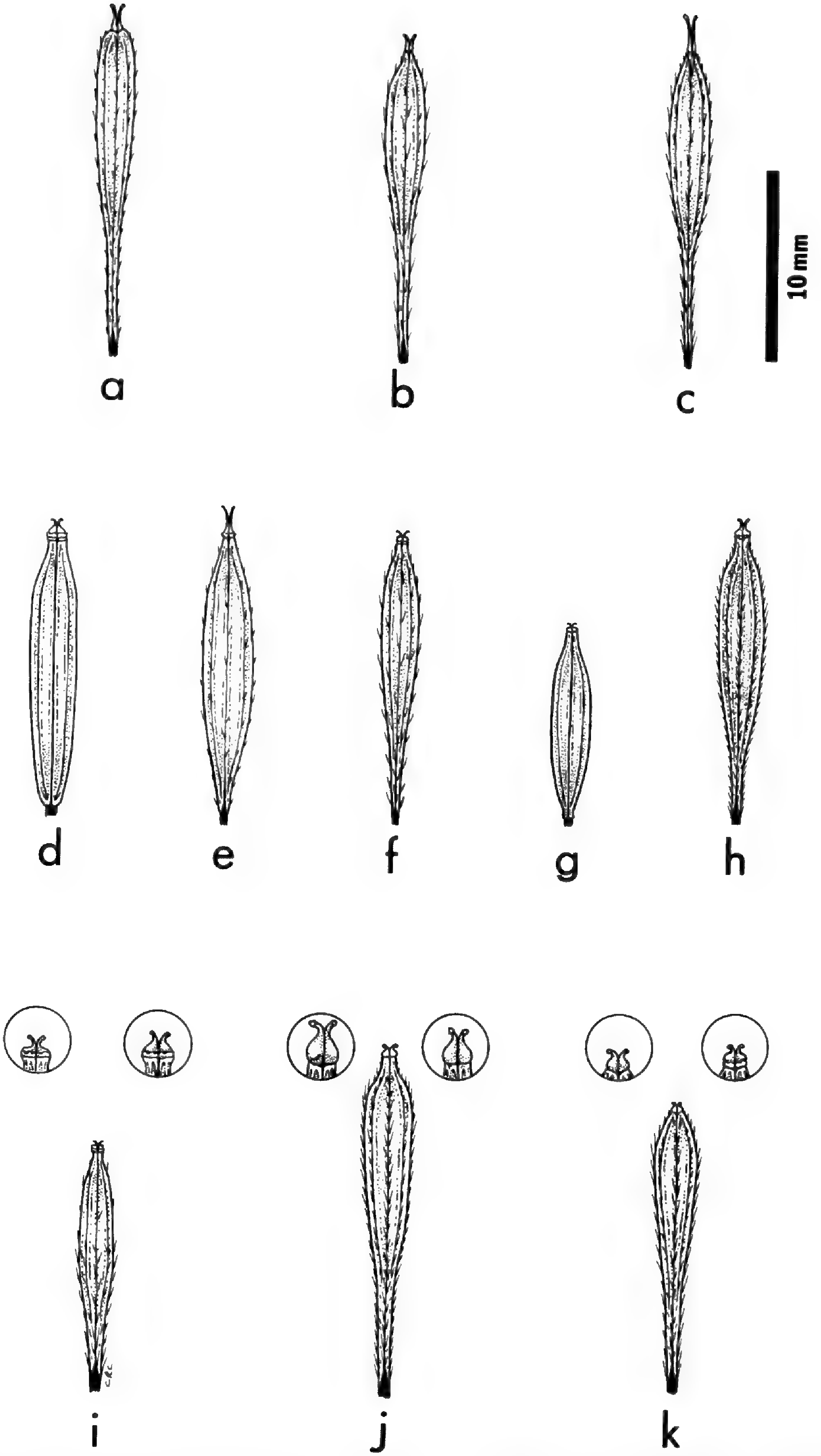


FIGURE 9. Drawings of the fruit of *Osmorhiza* species.—a. *O. aristata.*—b. *O. claytonii.*—c. *O. longistylis.*—d. *O. occidentalis.*—e. *O. glabrata.*—f. *O. mexicana* subsp. *mexicana.*—g. *O. mexicana* subsp. *bipatriata.*—h. *O. brachypoda.*—i. *O. purpurea.*—j. *O. chilensis.*—k. *O. depauperata.*

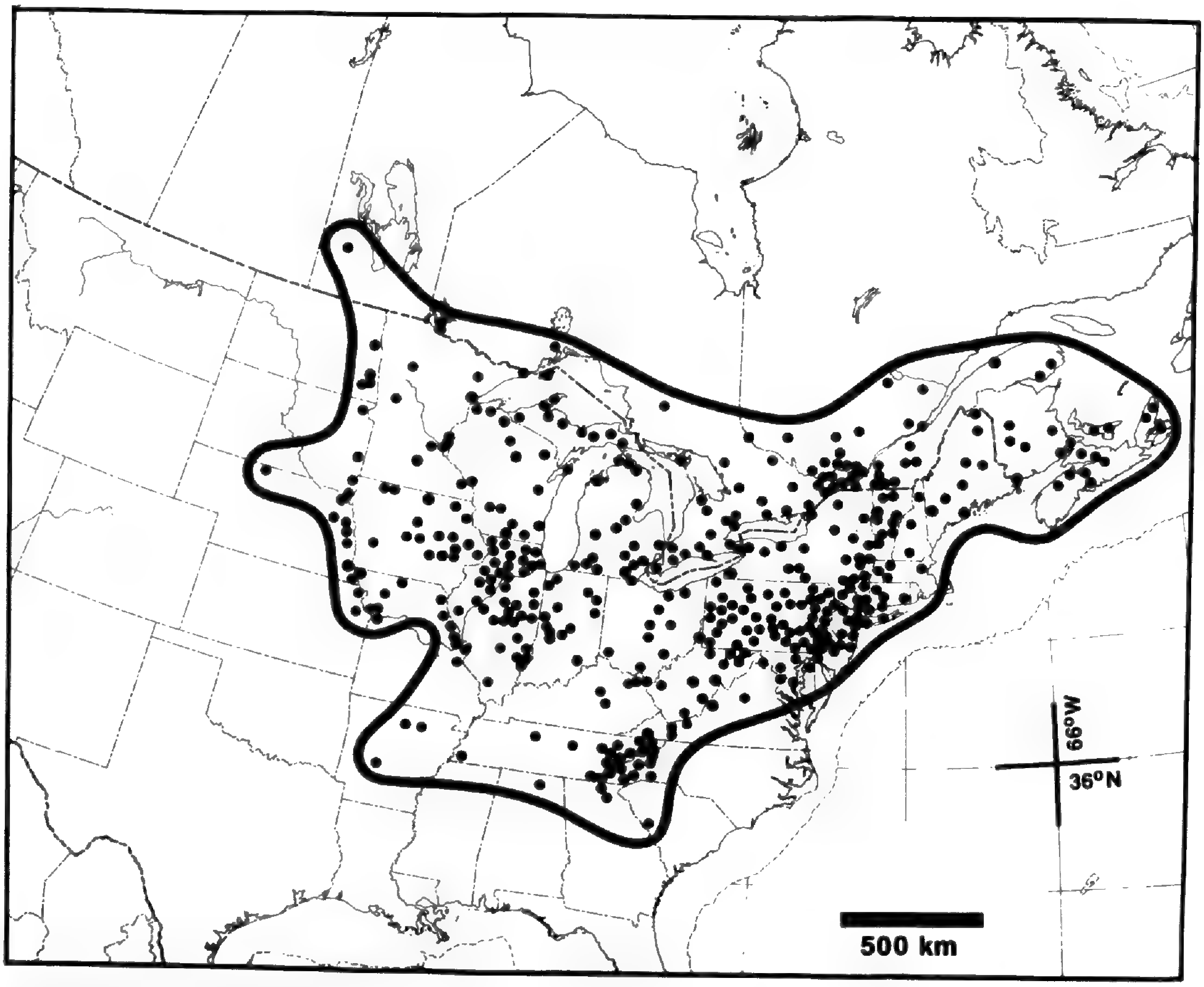


FIGURE 10. Geographic distribution of *Osmorhiza claytonii*.

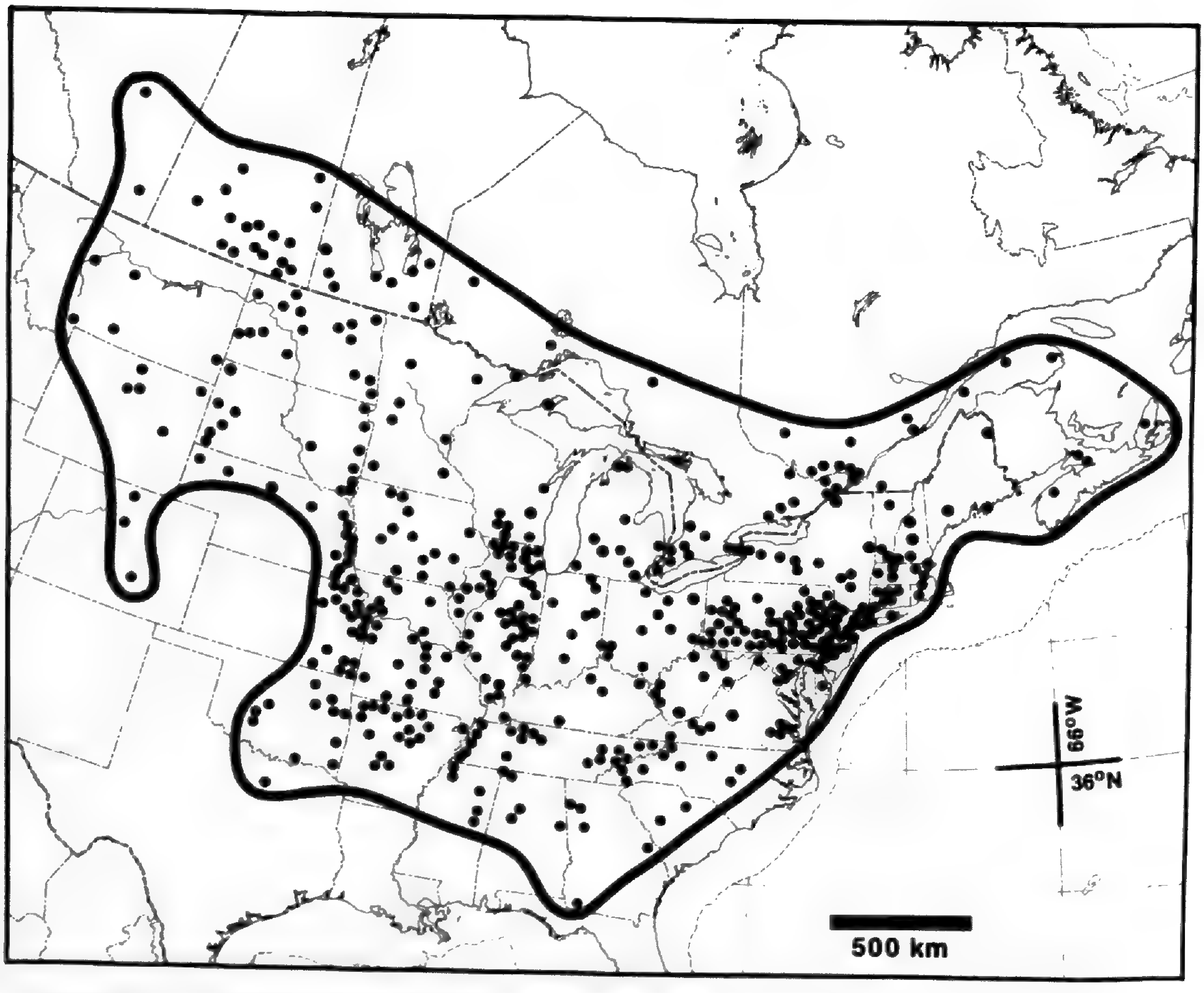


FIGURE 11. Geographic distribution of *Osmorhiza longistylis*.

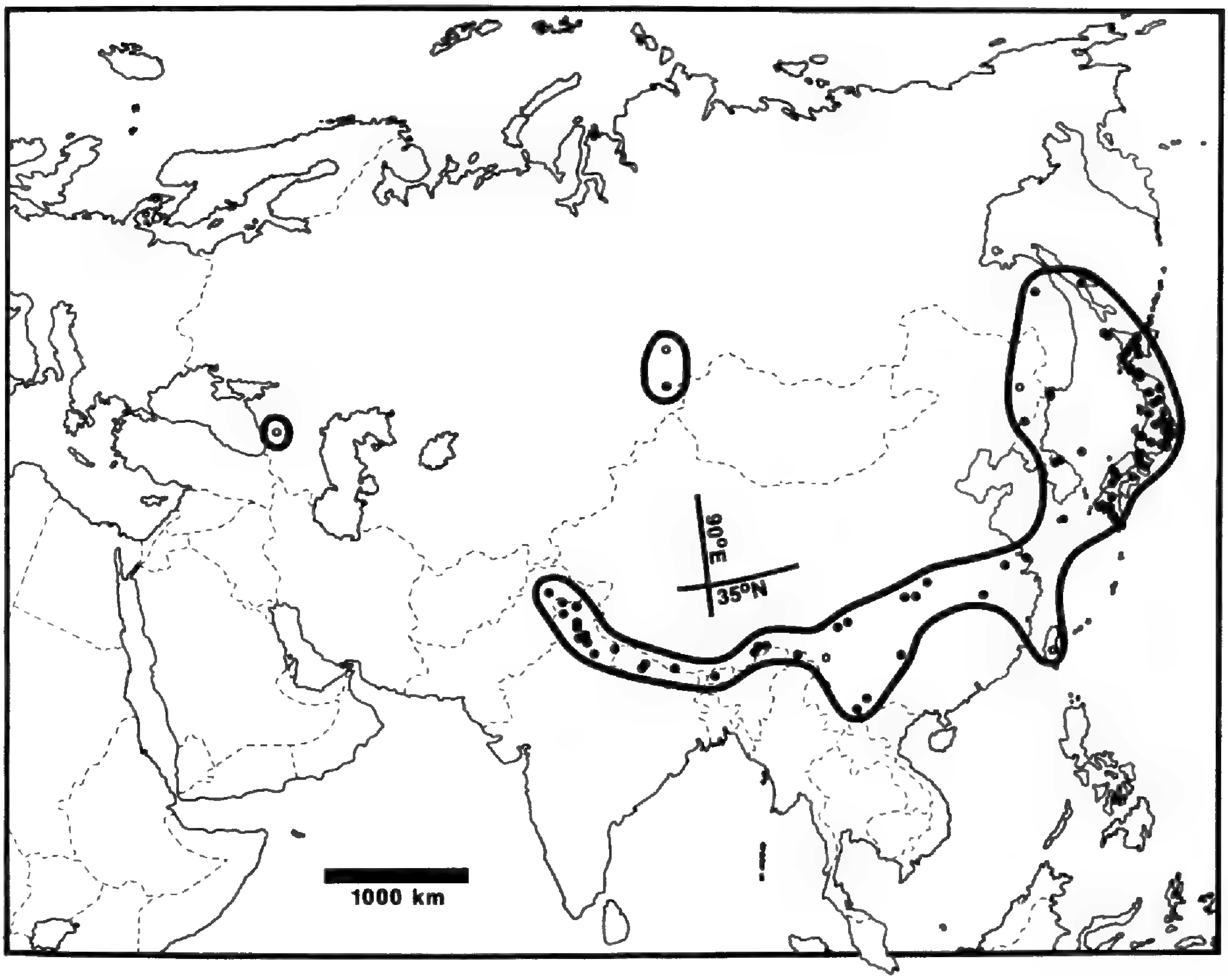


FIGURE 12. Geographic distribution of *Osmorhiza aristata.*

malayas of Bhutan, Nepal, India, and Pakistan. Disjunct populations occur in the Altai region of central U.S.S.R. and have been reported by Shishkin (1950) from the Caucasus Mountains of southeastern U.S.S.R. (Fig. 12).

The species of *Osmorhiza* sect. *Osmorhiza* provide an excellent example of the well known eastern North American–eastern Asian pattern of disjunction, which is shared by many members of the temperate deciduous forests of the two regions (Hara, 1952, 1956, 1972; Li, 1952, 1972; Constance, 1972; Wood, 1972; Ablaev et al., 1974). This pattern has long been recognized, e.g., by Linnaeus (1750; cf. Graham, 1966) and Thunberg (1784), but Asa Gray (1859) was the first botanist to examine it in detail. Gray indicated that many plants (including *Osmorhiza*) from eastern North America and Japan appear to be conspecific, and he also pointed out their conspicuous absence from western North America. To explain this phenomenon, he developed a hypothesis involving migration and exchange of species between North America and Asia across the Bering Strait, followed by their elimination from western North America and northeastern Asia during the Pleistocene.

Paleobotanical evidence confirms the widespread occurrence throughout much of North America and Eurasia of a number of genera, particularly woody ones, now restricted to the eastern parts of both continents. Wolfe (1969) indicated that certain members of the Tertiary flora of the Pacific Northwest survived changing climatic conditions, especially the shift from wet to dry summers, in relict habitats, particularly the mountains of southern Oregon and northern California. Wood (1972: 112) suggested that many plants occupying other regions of the Northern Hemisphere survived in a similar manner. He then stated: "The largest, and ecologically most complex, of the relict areas are eastern Asia and eastern North America; those of western North America and Europe-Asia Minor are smaller, and many genera that formerly occurred in them have disappeared." Wood concluded that the pattern of formerly widespread genera being restricted in distribution to eastern Asia and eastern North America by "orogenic movements, gradual climatic cooling, volcanism, and the Pleistocene glaciations seems to be well established."

The three species of *Osmorhiza* sect. *Osmorhiza* exhibit remarkable morphological similar-

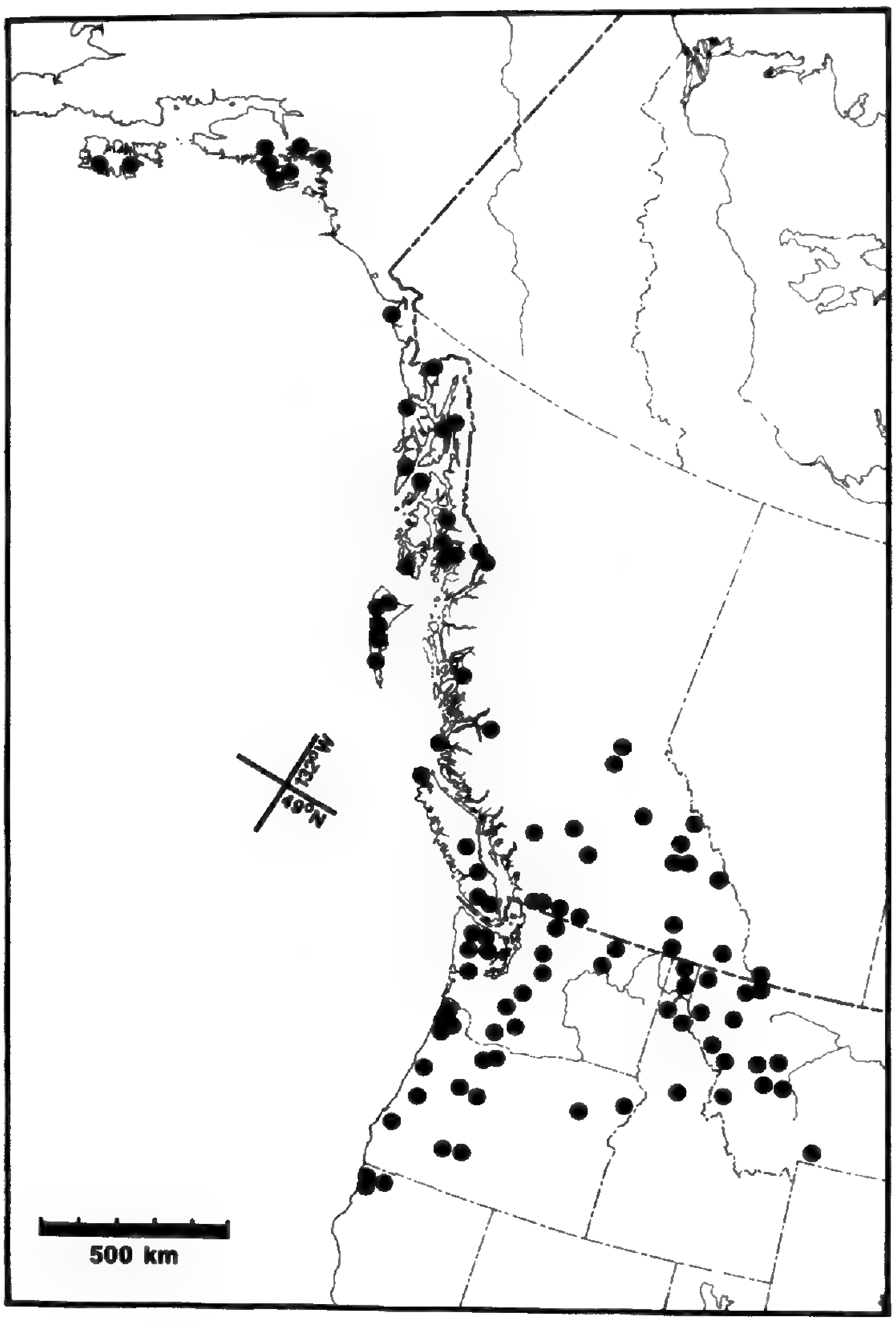


FIGURE 13. Geographic distribution of *Osmorhiza purpurea.*

ity and have been regarded as conspecific by a number of authors (e.g., Gray, 1859; Clarke, 1879; Kuntze, 1891; Boivin, 1968). Constance and Shan (1948) suggested that this similarity may be ascribed to one of two factors: either there has been a relatively recent contact between the Asian and North American populations through Beringia, or these species have differentiated from a once widespread common ancestral population at a very slow rate. While Wood's reasoning, as outlined above, tends to support the latter, Li (1972) took a different view, arguing that the observed morphological similarities between populations of eastern Asia and eastern North America may be the result of geographic and ecological similarities between these areas. He pointed out that the two areas lie at roughly the same latitude, are situated in the same relative position on their respective continents, are tempered by ocean currents from the south, and share features of their topography, soil, temperature ranges, precipitation distributions, etc. Li believed that these morphological similarities were probably the result of parallel evolution, and may not always accurately reflect an underlying phylogenetic relationship.

If, however, one regards eastern Asia and eastern North America as more or less stable, mesic refugia, it is possible that the species occupying these areas may have remained relatively unchanged both morphologically and genetically over long periods. Species of *Osmorhiza* appear to be stable taxa, with little or no indication of natural hybridization, and no "rapidly evolving" species. Rather than postulating the unlikely event of gene exchange in the recent past between the disjunct populations of this section, it seems more plausible to us to consider them parts of a relatively stable floristic assemblage that has persisted in eastern Asia and eastern North America over a rather long period.

OSMORHIZA SECT. *NUDAE.* All three species of this section occur in northwestern North America, and two of them, *O. chilensis* and *O. depauperata,* have disjunct populations in the Great Lakes area, northeastern North America, and southern South America.

Osmorhiza purpurea has a more restricted range, occurring more or less continuously along the Pacific Coast, from the redwood forests of northwestern California to Kodiak Island in southwestern Alaska. Inland, populations are found through the Cascade Mountains of Oregon and Washington eastward to the Rocky Mountains of Idaho, northwestern Montana, and extreme southwestern Alberta, and in much of southern British Columbia (Fig. 13).

Osmorhiza depauperata occurs sporadically in western North America, from the Warner Mountains of northeastern California, through Oregon, Washington, and central British Columbia, to the northern "pan-handle" and the Kenai Peninsula in Alaska. This species is much more commonly represented in the Rocky Mountains, where it ranges from southern Arizona and New Mexico northward to British Columbia, Alberta, and the extreme southwestern part of the Mackenzie District. Disjunct populations of *O. depauperata* are recorded from the Black Hills of South Dakota and the Cypress Hills in Alberta and Saskatchewan, and scattered populations are found across the Prairie Provinces of Canada in central Alberta, eastern Saskatchewan, and in Riding Mountain National Park, Manitoba. In the Great Lakes region, populations occur along the northern shore of Lake Superior, on Manitou Island in Lake Michigan, near Lake Nipigon in Ontario, and on Charlton Island in the James

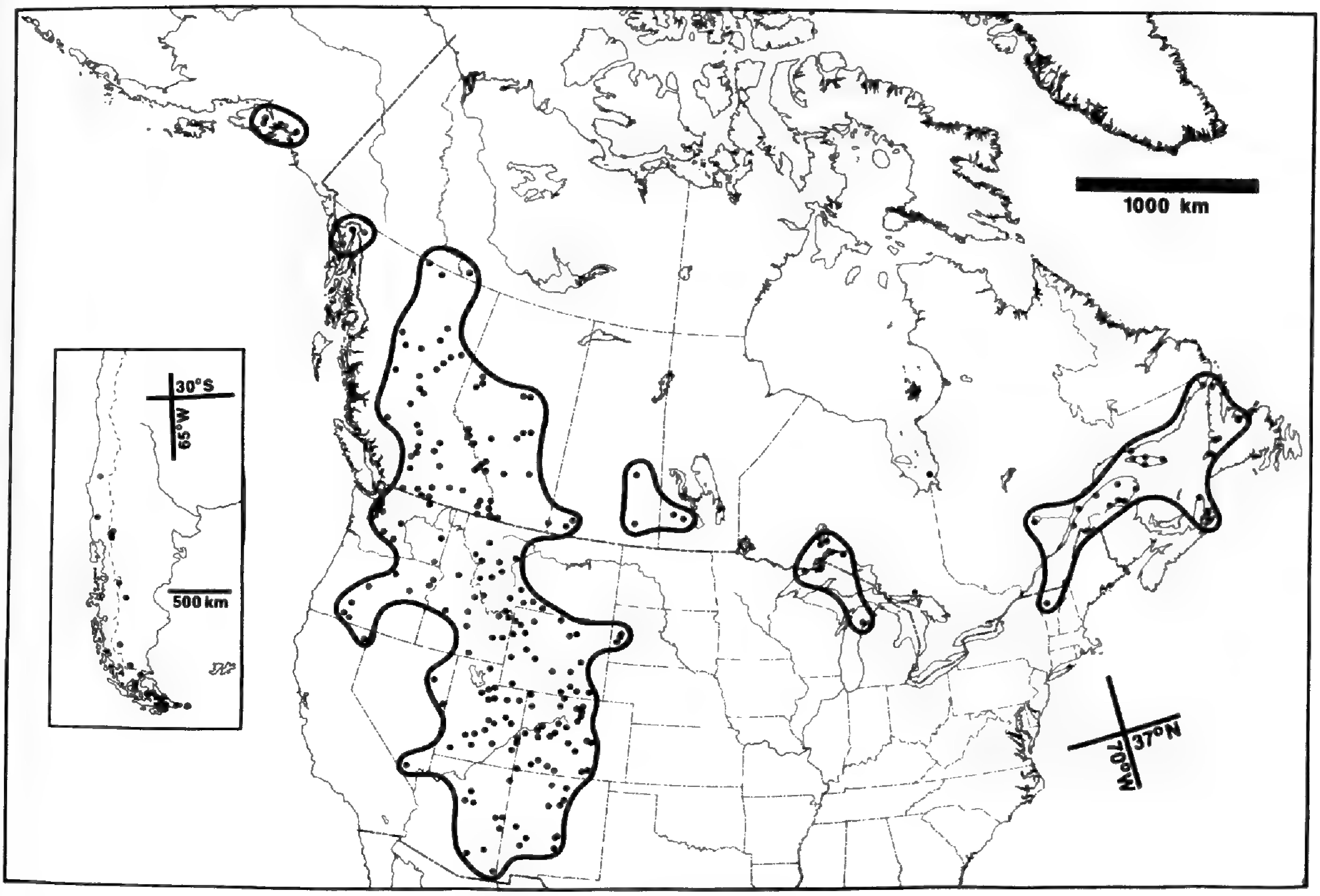


FIGURE 14. Geographic distribution of *Osmorhiza depauperata.*

Bay Region (over 600 km to the northeast). In the east, *O. depauperata* ranges from Vermont and Lake Saint John in Québec, through the Gaspé Peninsula, Anticosti and Mingan Islands, to eastern Nova Scotia, Newfoundland, and southeastern Labrador. This species is also represented in South America, where it extends from Tierra del Fuego northward through the Andes of southern Argentina, reaching its northern limit at Termas de Chillán in Prov. Ñuble, Chile (Fig. 14).

Osmorhiza chilensis shows a similar overall pattern of distribution, and is sympatric with *O. depauperata* throughout much of its range, although it is much less common in the southern Rocky Mountains, particularly in Arizona and New Mexico. By contrast, populations of *O. chilensis* are common along the west coast, ranging from southern California, through Oregon and Washington, to Vancouver Island, the Queen Charlotte Islands, and southeastern Alaska. Occurrence of this species has also been reported from the coast of southwestern Alaska, with its range extending as far west as Unalaska Island in the Aleutian Chain (Hultén, 1947). With the exception of two populations in south-central Alberta, *O. chilensis* appears to be absent from the Prairie Provinces of southern Canada. In the Great Lakes area, it is widely distributed along the western and southern shores of Lake Superior, eastward to Lake Huron and the Georgian Bay; in eastern North America the range extends from northern New Hampshire and Maine, through the Gaspé Peninsula, New Brunswick, and Nova Scotia, to Newfoundland. South American populations occur from the Tierra del Fuego through the Andes and along the central Chilean coast northward to Prov. Aconcagua, Chile (Fig. 15).

Two well known types of disjunction are exemplified by *O. chilensis* and *O. depauperata*; amphitropical disjunctions between North and South America, and disjunctions between western and eastern North America.

Similarities between the floras of temperate western North America and southern South America were recognized over 100 years ago by Gray and Hooker (1880). Since then, many botanists have dealt with this subject (e.g., Engler, 1882; Reiche, 1907; DuRietz, 1940; Campbell, 1944; Constance, 1963; Raven, 1963; and Moore, 1972). Constance (1963) suggested that *Osmo-*

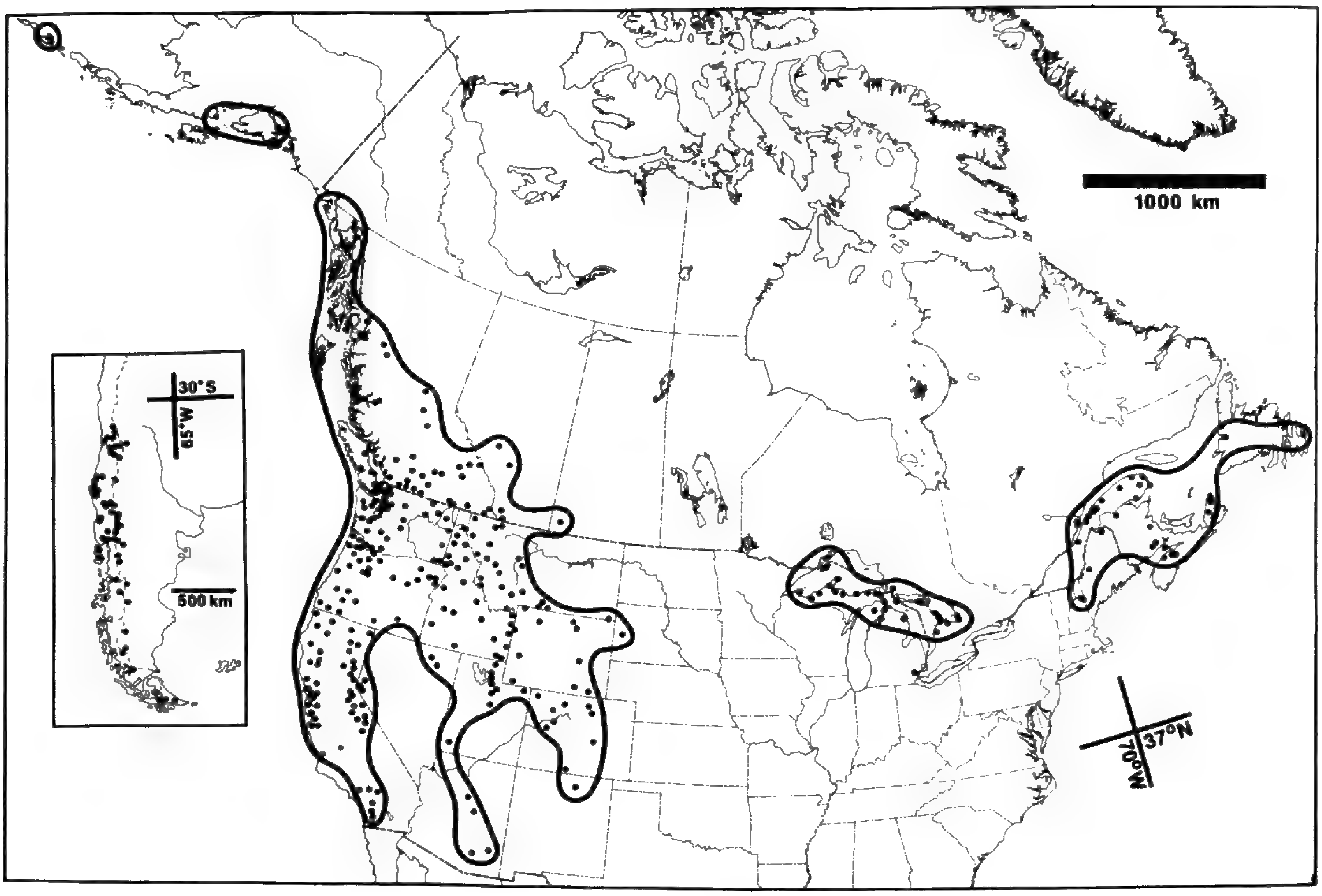


FIGURE 15. Geographic distribution of *Osmorhiza chilensis.*

rhiza chilensis and *O. depauperata* may have reached South America by a step-wise migration through the tropics along a route now marked by the members of the section *Mexicanae.* Raven listed about 130 species or species-pairs, including *O. chilensis* and *O. depauperata,* that exhibit patterns of disjunction between temperate North and South America. He also discussed the important factors concerning this pattern, which he summarized as follows: "(1) North and South American populations are closely related; (2) the plants are almost without exception self-compatible and often autogamous; (3) they constitute an unbalanced assemblage entirely unrepresentative of the floras of the two extratropical areas; (4) they grow almost exclusively in open communities, not in woodland or scrub associations; (5) there are no corresponding cases among terrestrial vertebrates and very few among the insects; and (6) the floras of the two areas have been distinct since at least the middle Cretaceous and are still very distinct at present." Raven (1963: 166) concluded that the only reasonable explanation to account for these facts is that "at least the great majority of the plants reached their disjunct areas by long-distance dispersal relatively recently." He noted further that, for temperate species, the Pliocene or Pleistocene were the most likely times for this kind of dispersal, and that the majority of species involved migrated from north to south. The distribution patterns of *O. chilensis* and *O. depauperata* fit very well into this overall syndrome. There is no doubt that the North and South American populations of each of these species are very closely related. Although a few South American populations of both taxa seem to have undergone some morphological divergence, the majority of them appear to be virtually identical to their North American counterparts. Conversely, a number of morphological variants of both species that occur in North America seem to be absent from South America.

Observations made as part of this study suggest that *Osmorhiza* species are facultatively autogamous, a condition that would permit even a single propagule to establish a new population. Both *O. chilensis* and *O. depauperata* produce fruit armed with caudate appendages and numerous retrorse bristles, making them well adapted for epizoochory. Furthermore, the amphitropical pattern of disjunction for these taxa corresponds closely to the migration routes of a number of bird species (Raven, 1963). Although many populations of both *O. chilensis* and *O. depauperata* occur in forest communities, these plants are also quite common in more open situations, making them accessible to a variety of potential dispersers. When taken together, these facts strongly suggest that the North American–South American disjunction found in *O. chilensis* and *O. depauperata* has resulted from long-distance dispersal by migratory birds, and that the direction of migration has been from north to south.

The western North America–eastern North America pattern of disjunction observed in *O. chilensis* and *O. depauperata* is somewhat less striking (Figs. 14, 15). Nevertheless, this type of disjunction has received considerable attention since Fernald (1924, 1925, 1926, 1933, 1935) developed his "nunatak" hypothesis to explain it (see also Marquis & Voss, 1981). Fernald believed that primarily arctic and western Cordilleran taxa were able to survive in eastern North America during the Pleistocene in unglaciated areas (nunataks) located around Lake Superior, on the Gaspé Peninsula, in the Long Range of Newfoundland, and in the Torngat Mountains of Labrador. Applying Willis's (1922) "age and area" hypothesis, Fernald (1925: 243) interpreted the failure of these eastern disjuncts to extend their ranges following the glaciations as evidence of their "antiquity," stating that "at the close of the Pleistocene they were already too old and conservative to pioneer, although they were able to linger as localized relicts in their special undisturbed crannies and pockets."

Many of Fernald's arguments have not withstood the test of time. All of his nunataks were in fact glaciated (Wood, 1972), and there is no reason why the plants involved could not have migrated to their present sites following the Pleistocene (Schofield, 1969, and references therein). Furthermore, the concept of senescence of species is no longer tenable (cf. Wood, 1972).

An alternative explanation for this pattern of disjunction is given by Stebbins (1935), who argued that each species involved migrated eastward at the end of the Pleistocene along the front of the receding ice sheet, becoming progressively more rare to the east. However, this hypothesis does not, by itself, explain the restriction of the majority of these taxa to the Great Lakes area and the northeast.

Schofield (1969: 200) adopted a somewhat modified version of Fernald's nunatak hypothesis, which he summarized as follows: "The most plausible explanation of their disjunctions is that the eastern representatives are remnants of a more widespread flora of the past, possibly of pre-Pleistocene arctic-alpine distribution in North America. The Pleistocene glaciations can be assumed to have eliminated the northcentral portion of the range, but since habitats were available in northeastern and western North America the species survived, probably south of the glacial boundary, but possibly in nunataks or coastal refuges, moving to their present sites following retreat of the ice sheet but being eliminated from their Pleistocene refugium by the encroaching vegetation and by a succession toward a more mesophytic temperate vegetation." To this we would add the observation that these disjunct taxa are most likely restricted to their present localities by a variety of ecological factors: they tend to occur in areas where there is reduced competition from the dominant eastern boreal taxa (Rune, 1954), and where climatic conditions, particularly snowfall and moisture availability during the spring, are more similar to those of western North America.

Schofield's hypothesis, as modified above, seems to be the most plausible to explain the western North American–eastern North American pattern of disjunction observed in *Osmorhiza chilensis* and *O. depauperata*. Nowhere in the literature have we found any suggestion that long-distance dispersal may have played a role in producing this type of disjunction; at least in the case of *Osmorhiza*, this type of dispersal would seem unlikely because the distribution of these plants does not seem to be correlated with the migration routes of any birds. Movement over shorter distances, however (e.g., from the Rocky Mountains into Saskatchewan and Manitoba), may be the result of epizoochory following the Pleistocene glaciations.

OSMORHIZA SECT. *MEXICANAE.* The representatives of this section form a "three-link chain" extending from the southwestern United States to central Argentina and Chile. The northernmost link is represented by *Osmorhiza brachypoda*, which has a relatively restricted distribution, ranging from the mountains of southwestern California northward through the Coast Range to Mount Diablo in Alameda County, and through the Sierra Nevada to Nevada and Sierra Counties, California. Disjunct populations occur in the Mazatzal Mountains of central Arizona

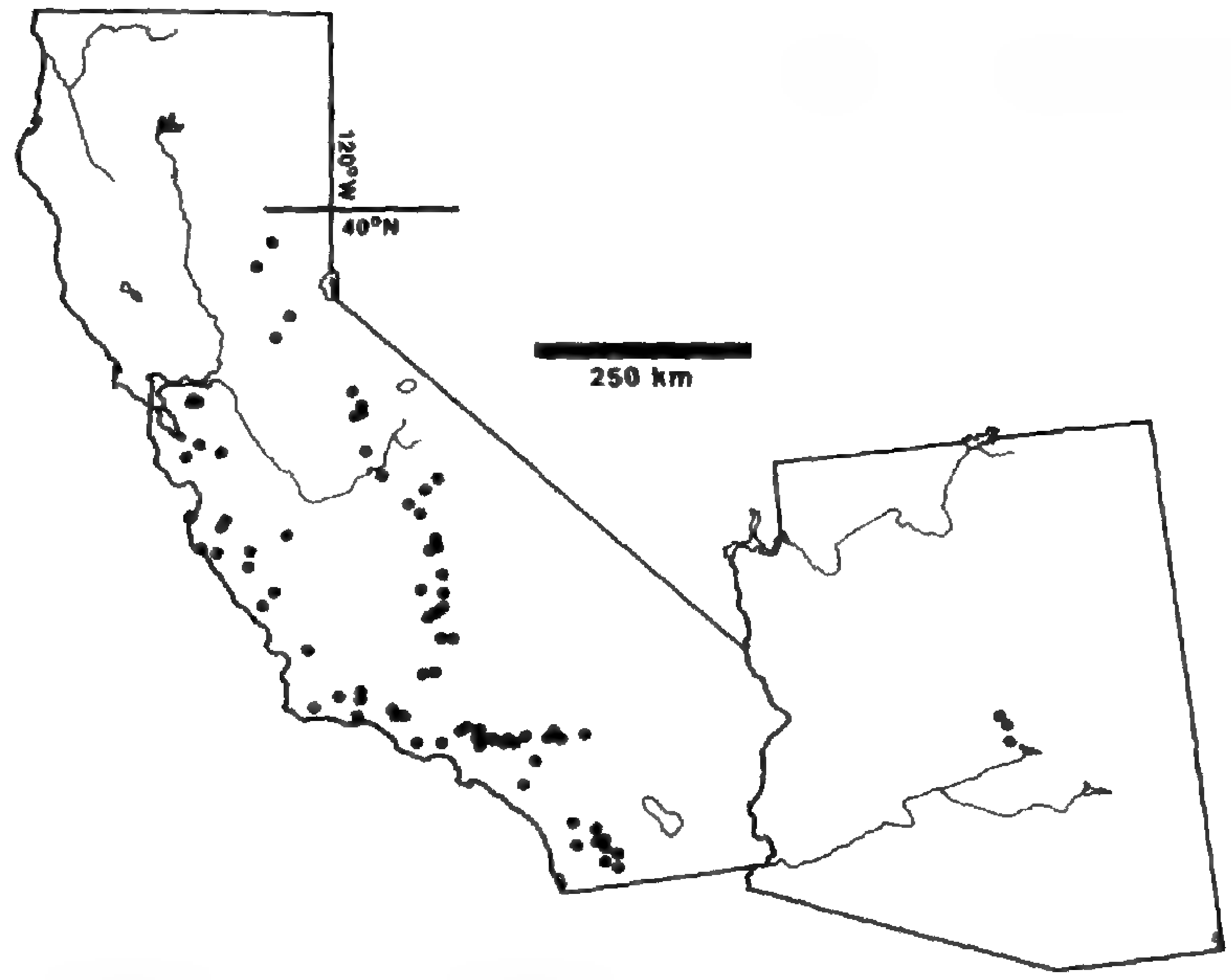


FIGURE 16. Geographic distribution of *Osmorhiza brachypoda.*

(Fig. 16), although they have not been collected since 1938.

Osmorhiza mexicana has an extended, although interrupted, range from southwestern Texas to northern Argentina. *Osmorhiza mexicana* subsp. *bipatriata* is known from only three localities: Madera del Carmen, Coahuila, and Cerro Potosí, Nuevo León, Mexico, and Mount Livermore, Jeff Davis Co., Texas. It is very possible, however, that this taxon also occurs on some of the other, as yet unexplored, mountains of Coahuila and Nuevo León. *Osmorhiza mexicana* subsp. *mexicana* reaches its northern limit in the Sierra Mohinora of Chihuahua and occurs together with subspecies *bipatriata* on Cerro Potosí. The typical subspecies ranges southward through the mountains of Mexico, Guatemala, and Costa Rica, into South America, where it occurs from the Páramo de Ruiz in Tolima, Colombia, through the Cordillera Oriental of southern Peru and adjacent Bolivia, and the mountains of northwestern Argentina, reaching its southern limit in the Sierra Grande of Córdoba, Argentina (Fig. 17).

Osmorhiza glabrata is restricted to the central Andes, ranging over a distance of less than 750 km from Prov. Santiago, Chile, to southern Neuquén, Argentina (Fig. 18).

The members of *Osmorhiza* sect. *Mexicanae* form a more or less continuous chain between northern California and central Argentina, "substantially bridging the gap which separates the discrete populations of the amphitropical taxa" in North and South America (Constance, 1963: 113). As Constance pointed out, however, it is difficult to imagine a polytopic origin of both *O. chilensis* and *O. depauperata* from an extant or extinct member of the section *Mexicanae* both to the north and south of the equator.

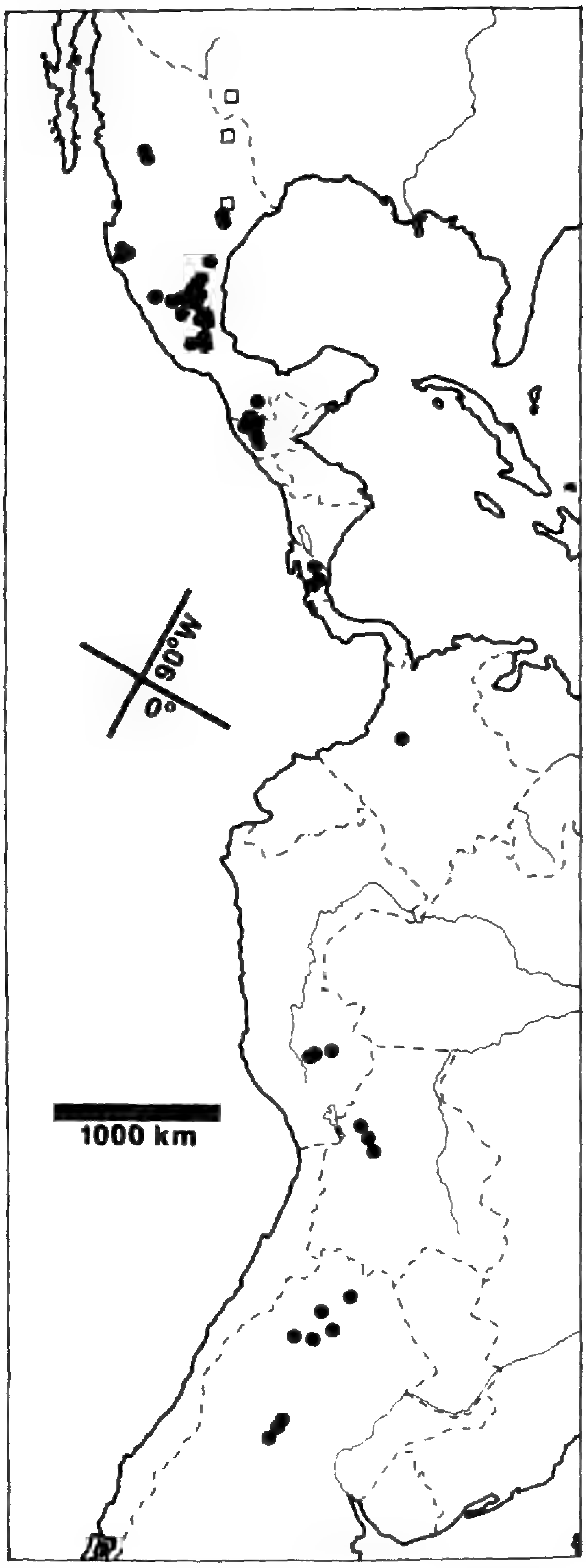


FIGURE 17. Geographic distribution of *Osmorhiza mexicana.*—*O. mexicana* subsp. *mexicana* (●).—*O. mexicana* subsp. *bipatriata* (☐).

Although one may be tempted to think of *O. brachypoda* and *O. glabrata* as northern and southern derivatives, respectively, of *O. mexicana,* there is no evidence to support this idea. A more plausible hypothesis is that all three species are derivatives of a once widespread common ancestral population whose distribution spanned the tropics, much as *O. mexicana* does today. According to Constance (1963), the

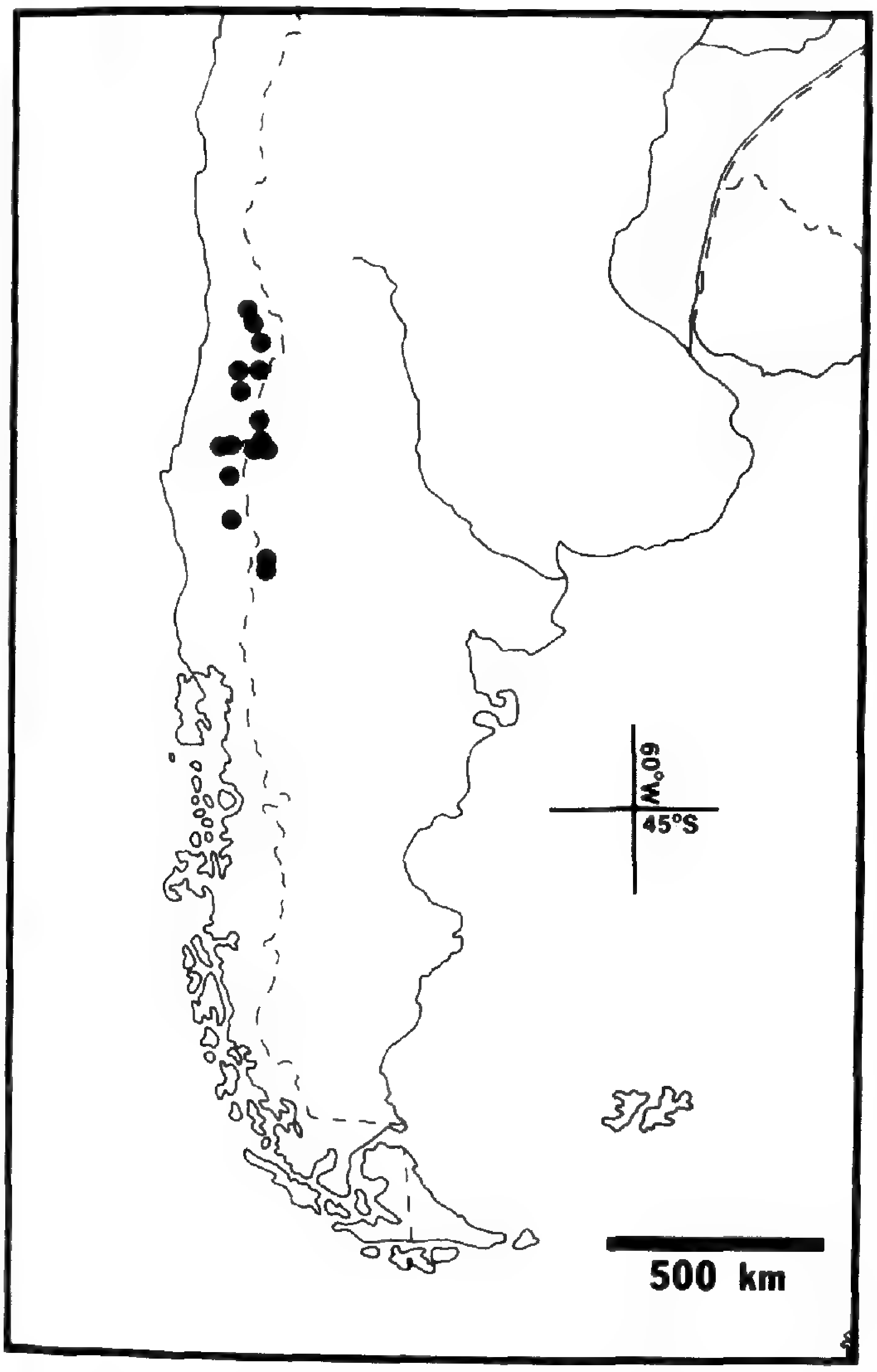


FIGURE 18. Geographic distribution of *Osmorhiza glabrata.*

mountains of Mexico and Central America were uplifted during the Pliocene or Pleistocene, orogenic movements that would have provided a chain of mountain tops with temperate climatic conditions suitable for the survival of such ancestral plants.

OSMORHIZA SUBG. *GLYCOSMA.* The sole member of this subgenus, *O. occidentalis,* is quite common in the somewhat drier areas throughout much of the western United States and adjacent Canada. It is widely distributed in the Rocky Mountains, ranging from southern Utah and southwestern Colorado northward to extreme southwestern Alberta and southern British Columbia, with eastward extensions into the Big Horn Mountains of Wyoming and the Big Snowy Mountains of Montana. To the west, the range of *O. occidentalis* extends through the mountains of the Great Basin in Nevada, eastern Oregon, and southwestern Idaho, to the northern Sierra Nevada, and the Coast Ranges of northern California and Oregon. This species also occurs in the Olympic and Cascade Mountains of Washington, the Blue Mountains of Oregon, Washington, and Idaho, and in the Willamette Valley and western foothills of the Cascade Mountains in Oregon, but it has not been recorded in the central and eastern parts of the Cascades.

No major disjunctions occur in the range of *O. occidentalis,* but this is not surprising when one considers how poorly adapted its fruits seem to be for long-distance dispersal; the schizocarps are relatively large; they lack caudate appendages and retrorse bristles (Fig. 9d).

Constance and Shan (1948) erroneously included *Osmorhiza glabrata* in their section "*Glycosmae*" (= subg. *Glycosma*), leaving the group with a large North American–South American disjunction that is difficult to explain. If the affinities of *O. glabrata* are, however, recognized as lying with members of the section *Mexicanae,* the problem is eliminated.

The phytogeographic evidence presented here indicates that North America is the center of diversity, distribution, and possibly also the center of origin for the genus *Osmorhiza.* Although none of the presumably related genera (e.g., *Myrrhis, Chaerophyllum, Scandix*) occurs in the area, both subgenera of *Osmorhiza,* and eight of ten species, are represented here. Furthermore, *O.* subg. *Glycosma,* which appears to have retained many ancestral characters, is restricted to western North America, and all three sections of the typical subgenus have members in this continent.

SYSTEMATIC TREATMENT

Osmorhiza Raf., Amer. Monthly Mag. & Crit. Rev. 4: 192. Jan. 1819, nom. cons. prop. TYPE: *Myrrhis claytonii* Michaux [= *Osmorhiza claytonii* (Michaux) C. B. Clarke].

Washingtonia Raf., Amer. Monthly Mag. & Crit. Rev. 2: 176. 1818, nom. nud., non *Washingtonia* H. Wendland (1879), nom. cons.
Osmorhiza Raf., Amer. Monthly Mag. & Crit. Rev. 2: 176. 1818, nom. nud.
Gonatherus Raf., Amer. Monthly Mag. & Crit. Rev. 2: 176. 1818, nom. nud.
Uraspermum Nutt., Gen. Amer. pl. 192. 1818, nom. rejic. prop.
Osmorhiza Raf., J. Phys. Chim. Hist. Nat. Arts 89: 157. 1819. nom. cons. prop. (cf. Lowry, 1985).
Spermatura Reichb., Consp. Reg. Veg. 141. 1828.
Glycosma Nutt. in Torrey & A. Gray, Fl. N. Amer. 1: 639. 1840.
Schudia Molina ex C. Gay, Fl. Chilena 143. 1874, pro syn.
Elleimataenia Koso-Poljansky, Bull. Soc. Imp. Naturalistes Moscou 29: 164. 1916.

Plants andromonoecious, slender to robust, perennial, herbaceous, aromatic, caulescent, dying back to a basal rosette of leaves; stems erect to spreading-ascending or decumbent, solitary to densely clustered, branching, fistulose, pubescent to glabrous. Roots fusiform, thick, fascicled, diffusely to extensively branched, surmounted by a branched caudex. Leaves alternate, basal and cauline, membranaceous, bipinnate or 2–3-ternate; leaflets lanceolate to orbicular, serrate to pinnately divided, with mucronate ultimate segments; petiole bases sheathing the stem, with their membranous margins densely ciliate to glabrous. Umbels twice compound, loose to somewhat constricted; peduncles terminal and lateral, erect to ascending or spreading, usually exceeding the leaves; involucre wanting, or composed of 1–several narrow, foliaceous, ciliate bracts; rays ascending to widely divaricate or reflexed, slender, unequal, the peripheral ones being longer; umbellets few to numerous, often of two kinds, those bearing hermaphrodite flowers or a mixture of hermaphrodite and staminate flowers (referred to as "hermaphrodite" umbellets), and those bearing only staminate flowers (referred to as "staminate" umbellets); involucel wanting, or of several linear to ovate, acuminate, ciliate, spreading to reflexed bractlets; pedicels ascending to widely divaricate, those of the hermaphrodite flowers longer than those of the staminate flowers. Hermaphrodite flowers in each umbellet borne peripherally to the staminate flowers (if any), sometimes slightly irregular; calyx wanting; corolla white, greenish white, or yellow, or tinged with green, pink, or purple, the petals spatulate to ovate, the apex with an inflexed appendage; anthers about 0.5 mm long, smaller in the staminate flowers, inflexed before anthesis, spreading as the flower opens; styles spreading to divaricate, variable in length depending on the species, but wanting in the staminate flowers; stylopodium conic to depressed, sometimes with a conspicuous disc, often nectariferous; carpophore 2-cleft from one-quarter to nearly one-half of its length. Fruit a schizocarp, deep brown to black at maturity, linear to oblong, fusiform to clavate, beaked to obtuse at the apex, sometimes constricted just below the stylopodium, shallowly to deeply concave furrowed, slightly compressed laterally, the ribs filiform, equidistant, moderately to sparingly hispid with retrorse bristles, or glabrous, the base rounded or with two caudate appendages; oil tubes (vittae) obscure or wanting; seeds subterete or unequally pentagonal in cross section, the face shallowly concave or sulcate.

Osmorhiza is clearly distinct from the monotypic European genus *Myrrhis* (apparently its closest relative) on the basis of the following characters: the leaves are 2–3-ternate or bipinnate (they are 2–4 times pinnatisect in *Myrrhis*), the umbels are definite in number (numerous in *Myrrhis*), the rays are glabrous (densely pubescent in *Myrrhis*), and the fruit are relatively small and lack winged ribs (fruit larger and strongly winged in *Myrrhis*).

Drude (1897), in his classic treatment of the Umbelliferae, placed *Osmorhiza* in his subfamily Apioideae, tribe Scandicineae, subtribe Scandicinae, along with the clearly related genera *Chaerophyllum* L., *Myrrhis* Miller, and *Scandix* L. A number of other genera, many of which are likely related to *Osmorhiza,* but some of which clearly are not, were also included in this subtribe. Bentham (1867) placed *Osmorhiza* in his series Heterosciadiae, tribe Ammineae, subtribe Scandicineae, along with the three genera mentioned above, as well as some others.

ANALYTICAL KEY

1a. Fruit glabrous, lacking caudate appendages; staminate umbellets 3–10 per umbel; staminate flowers (75–)90–225 per umbel; plants very robust; stems (1–)3–6(–8), densely clustered; leaves bipinnate; corolla yellow to greenish yellow .... (*Osmorhiza* subg. *Glycosma*)
One species .... 1. *Osmorhiza occidentalis*

1b. Fruit hispid with retrorse bristles (glabrous in *O. mexicana* subsp. *bipatriata*), with caudate appendages; staminate umbellets 0–4(–6) per umbel; staminate flowers 0–90(–125) per umbel; plants slender to rather stout; stems 1–3(–5), not densely clustered; leaves 2–3-ternate; corolla white, or tinged with green, pink, or purple .... (*Osmorhiza* subg. *Osmorhiza*)

  2a. Involucel conspicuous, composed of 1–6 spreading to reflexed, foliaceous bractlets.

    3a. Styles (including stylopodium) 1–3.6 mm long; stylopodium high-conic; involucre composed of (1–)2–3(–5) bracts .... (*Osmorhiza* sect. *Osmorhiza*)

      4a. Pedicels of the hermaphrodite flowers (5–)9–30 mm long; rays 4.5–11 cm long; fruit linear-clavate, obtuse or abruptly acute at the apex; plants restricted to Asia .... 2. *Osmorhiza aristata*

4b. Pedicels of the hermaphrodite flowers 4–10(–15) mm long; rays 1.5–8 cm long; fruit oblong-fusiform, strongly acute to attenuate at the apex; plants of North America.

5a. Styles 1–1.5(–1.7) mm long; flowers 4–7(–8) per umbellet; staminate flowers (2–)7–17(–23) per umbel; umbels loose and uncongested; roots rank-smelling, or sometimes weakly anise-scented .... 3. *Osmorhiza claytonii*

5b. Styles 2–3.6 mm long; flowers (7–)9–18 per umbellet; staminate flowers (23–)35–75(–86) per umbel; umbels dense and congested; roots with a strong, sweet, anise-like smell .... 4. *Osmorhiza longistylis*

3b. Styles 0.5–1.2 mm long; stylopodium low-conic to somewhat depressed; involucre wanting, or sometimes composed of 1–2(–3) reduced bracts .... (*Osmorhiza* sect. *Mexicanae*)

6a. Leaves laciniately lobed or pinnatifid; styles (incl. stylopodium) (0.9–)1–2 mm long; stylopodium 0.4–0.8 mm long; plants restricted to the central Andes of Chile and Argentina .... 5. *Osmorhiza glabrata*

6b. Leaves coarsely serrate to pinnately lobed or divided at the base, never laciniate; styles (incl. stylopodium) 0.5–1.2 mm long; stylopodium 0.2–0.5 mm long; plants occurring in North, Central, and South America.

7a. Pedicels of the hermaphrodite flowers 1–4.5 mm long, ascending; plants restricted to southern California and central Arizona .... 7. *Osmorhiza brachypoda*

7b. Pedicels of the hermaphrodite flowers (2–)3.5–7.5 mm long, spreading to spreading-ascending; plants occurring from southwestern Texas and northern Mexico to northern Argentina .... 6. *Osmorhiza mexicana*

8a. Fruit (10–)11–20 mm long, moderately to densely hispid with retrorse bristles, the appendages (1.5–)2–10 mm long; staminate flowers (0–)5–25(–35) per umbel; plants rather widespread from northern Mexico southward .... 6a. *Osmorhiza mexicana* subsp. *mexicana*

8b. Fruit 9–11(–12) mm long, glabrous, or occasionally with a few bristles toward the base, the appendages lacking, or to 1.8 mm long; staminate flowers (33–)40–70(–125) per umbel; plants restricted to three localities in southwestern Texas and adjacent Mexico .... 6b. *Osmorhiza mexicana* subsp. *bipatriata*

2b. Involucel wanting, or very rarely composed of 1(–2) minute bractlets .... (*Osmorhiza* sect. *Nudae*)

9a. Fruit linear-fusiform to linear-oblong, beaked at the apex; rays and pedicels spreading-ascending.

10a. Stylopodium high-conic to somewhat gibbous, lacking a disc, (0.2–)0.3–0.6 mm long; fruit tapering below the stylopodium, not constricted, 12–21(–25) mm long, the appendages 2.5–8.5(–10) mm long .... 8. *Osmorhiza chilensis*

10b. Stylopodium strongly depressed, with a conspicuous disc, 0.1–0.4 mm long; fruit constricted below the stylopodium, 8–15(–16) mm long, the appendages 1–5 mm long .... 9. *Osmorhiza purpurea*

9b. Fruit clavate, obtuse at the apex; rays and pedicels strongly divaricate to nearly reflexed .... 10. *Osmorhiza depauperata*

I. **Osmorhiza** Raf. subg. **Glycosma** (Nutt.) Drude. *Glycosma* Nutt. in Torrey & A. Gray, Fl. N. Amer. 1: 639. 1840. *Myrrhis* § [sect.] *Gycosma* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 7: 346. 1868. *Osmorhiza* subg. *Glycosma* (Nutt.) Drude in Engl. & Prantl, Nat. Pflanzenfam. 3^{8}: 153. 1897. *Washingtonia* subg. *Glycosma* (Nutt.) Coult. & Rose, Contr. U.S. Natl. Herb. 7: 62. 1900. *Osmorhiza* sect. *Glycosmae* (Nutt.) Constance & Shan, Univ. Calif. Publ. Bot. 23: 112. 1948, nom. nud. TYPE: *Glycosma occidentalis* Nutt. [= *Osmorhiza occidentalis* (Nutt.) Torrey].

Plants robust; stems densely clustered, (1–)3–6(–8), often glaucous. Root system deep, extensively branched. Leaves bipinnate; petiole bases finely ciliate to glabrous. Primary umbel with fewer hermaphrodite and more staminate flowers than the secondary and later flowering umbels; staminate umbellets 3–10 per umbel; staminate flowers (75–)90–225 per umbel; corolla yellow to greenish yellow. Fruit glabrous, without caudate appendages.

When *Osmorhiza occidentalis* was first described, Nuttall (in Torrey & Gray, 1840) placed it in a new, monotypic genus *Glycosma*. Plants belonging to this genus were distinguished from those of *Osmorhiza* by having unappendaged, glabrous fruit. Torrey (1859), Drude (1897), and Coulter and Rose (1900) united these genera, although in the latter two treatments *Glycosma* was retained as a separate subgenus.

Osmorhiza occidentalis is quite distinct from the other members of the genus. However, the morphological differences between *O. occidentalis* and the other species of *Osmorhiza* are much less pronounced than those between either of these groups and related genera such as *Myrrhis*, *Chaerophyllum*, and *Scandix*. Furthermore, *Os-*

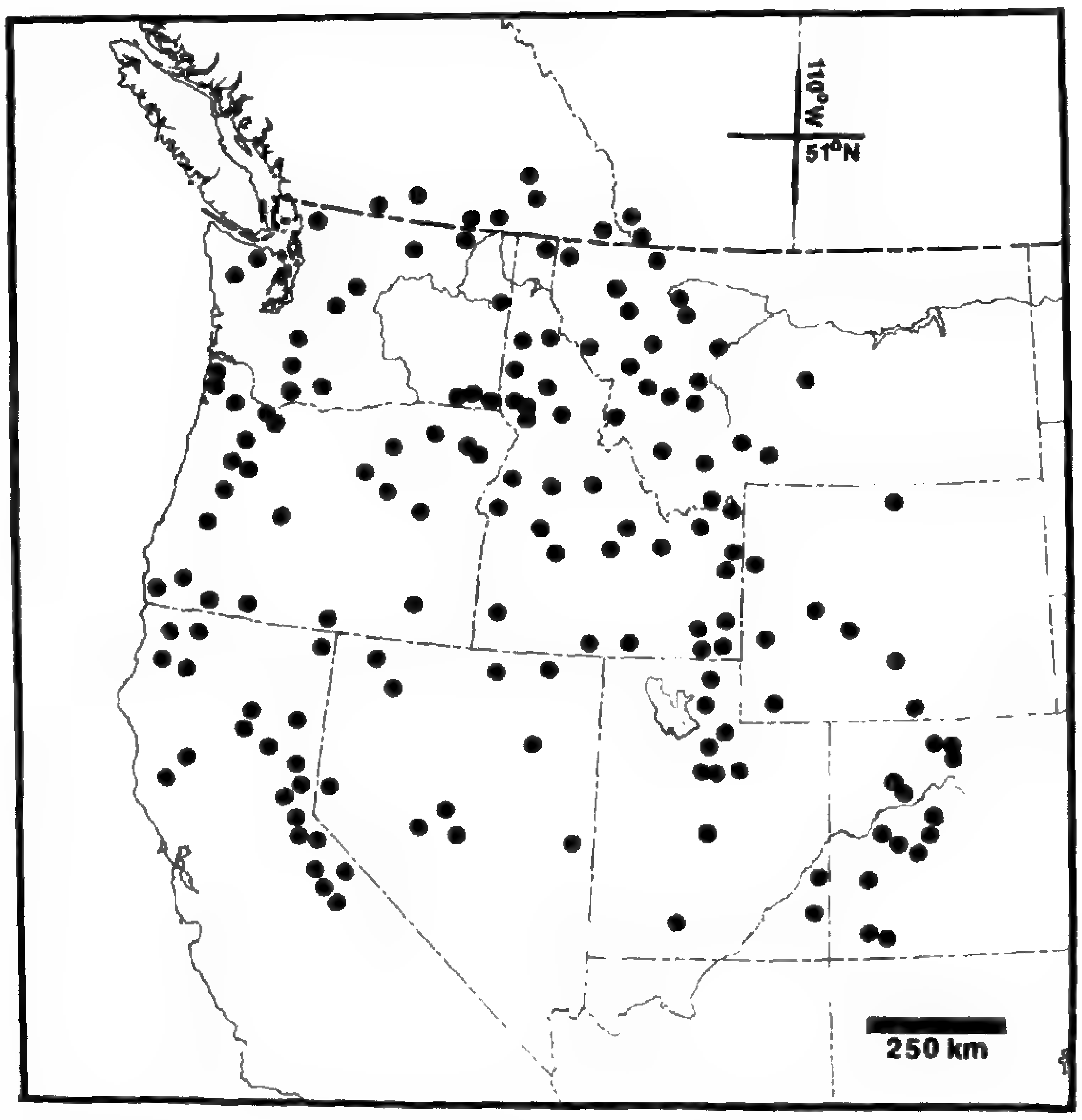


FIGURE 19. Geographic distribution of *Osmorhiza occidentalis.*

morhiza, as treated here, is considered to represent a distinct monophyletic group. For these reasons, *Glycosma occidentalis* is included in *Osmorhiza* and placed in the monotypic subgenus *Glycosma.*

1. **Osmorhiza occidentalis** (Nutt.) Torrey. *Glycosma occidentalis* Nutt. in Torrey & A. Gray, Fl. N. Amer. 1: 639. 1840. *Osmorhiza occidentalis* (Nutt.) Torrey, Bot. Mex. bound. surv. 71. 1859. *Myrrhis occidentalis* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 7: 346. 1868. *Washingtonia occidentalis* (Nutt.) Coult. & Rose, Contr. U.S. Natl. Herb. 7: 67. 1900. TYPE: U.S.A. Oregon: "Western side of the Blue Mountains," *Nuttall s.n.* [lectotype, NY! (designated by Coulter & Rose, Contr. U.S. Natl. Herb. 7: 67. 1900); isolectotypes, BM!, GH!].

Myrrhis bolanderi A. Gray, Proc. Amer. Acad. Arts 7: 346. 1868. *Glycosma bolanderi* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 8: 386. 1872. *Osmorhiza occidentalis* var. *bolanderi* (A. Gray) Jepson, Madroño 1: 120. 1922. TYPE: U.S.A. California: Mendocino Co., Lambert's Lake, *Bolander 6525* [lectotype, GH! (designated by Coulter & Rose, Contr. U.S. Natl. Herb. 7: 68. 1900); isolectotypes, K!, MO!, NY!].

Glycosma ambiguum A. Gray, Proc. Amer. Acad. Arts 8: 386. 1872. *Osmorhiza ambigua* (A. Gray) Coult. & Rose, Rev. N. Amer. Umbell. 119. 1888. *Myrrhis ambigua* (A. Gray) E. Greene, Fl. francisc. 332. 1892. *Washingtonia ambigua* (A. Gray) Coult. & Rose, Contr. U.S. Natl. Herb. 7: 69. 1900. TYPE: U.S.A. Oregon: Marion Co., foot of the Cascade Mts., Wolford's Orchard, Silver Creek, *Hall 217* [lectotype, GH! (designated by Coulter & Rose, Contr. U.S. Natl. Herb. 7: 69. 1900); isolectotypes, F!, GOET!, K!, MO!, NY!].

Glycosma maxima Rydb., Bull. Torrey Bot. Club 40: 67. 1913. TYPE: U.S.A. Utah: Juab Co., Mt. Nebo, *Rydberg & Carlton 7585* (holotype, NY!; isotype, RM!).

Plants robust, (3–)4–12 dm high; stems (1–)3–6(–8), erect or slightly ascending at the base, villous to hirsute just below the nodes, villosulous to glabrous elsewhere, and often glaucous. Root system deep, extensively branched, the roots with a strong, heavy anise-like fragrance. Leaves bipinnate, oblong to ovate, (8–)10–22 cm long, hirsutulous or more often glabrous; leaflets broadly lanceolate to ovate, 2–10(–12) cm long, 1–4(–5) cm wide, acute, serrate and incised or lobed at the base; petioles 5–25(–30) cm long. Umbels rather constricted; peduncles 2–4(–5), terminal and lateral, 6–18(–22) cm long; involucre wanting, or occasionally composed of 1–2 minute, linear, foliaceous, ciliate, spreading bracts; rays spreading-ascending to nearly erect, (2.8–)3–8(–9.5) cm long; umbellets (3–)5–15 per umbel, (1–)3–10(–12) of them producing only staminate flowers; involucel wanting, or sometimes of 1(–2) minute, linear-lanceolate, acuminate, ciliate bractlets; pedicels (7–)9–22(–25) per hermaphrodite umbellet, (6–)8–16(–18) per staminate umbellet, spreading to ascending, those of the hermaphrodite flowers (2–)2.5–7(–10) mm long, those of the staminate flowers 2–4.5(–6) mm long. Hermaphrodite flowers (1–)2–6 per umbellet, (1–)8–20(–45) per umbel, staminate flowers (6–)8–20(–22) per hermaphrodite umbellet, (73–)100–200(–225) per umbel; corolla yellow to greenish yellow, rather showy; styles plus stylopodium (0.7–)0.9–1.4(–1.8) mm long, stylopodium (0.1–)0.3–0.6 mm long, low-conic, with a conspicuous disc; carpophore cleft about one-third of its length. Fruit linear-fusiform, slightly constricted below the apex, rather deeply concave furrowed, (12–)13–22 mm long, the ribs glabrous throughout, the caudate appendages lacking, or very rarely to 1.5 mm long. $n = 11$ (Bell & Constance, 1957). Figures 9d and 19.

Flowering period. May to early July.

Habitat. Moist to rather dry forests, thickets, and open slopes.

Common names. Bald cicely, Mountain

sweet cicely, Sheep cicely, Sierra sweet cicely, Sweetanise, Sweetroot, Western sweet cicely, Western sweetroot.

Representative specimens. U.S.A. CALIFORNIA: Alpine Co., Red Lake, 2,440 m, *Johnson 130* (CS, NY, UC); Humboldt Co., NW slope of Black Mt., 760 m, *Tracy 8810* (CAS, JEPS, MO, NY, UC); Modoc Co., S slope of Eagle Peak, 2,440 m, *Alexander & Kellogg 5101* (UC); Mono Co., Sweetwater Canyon Creek, Sweetwater Mts., 2,440 m, *Alexander & Kellogg 3924* (JEPS, MO, UC); Nevada Co., S of Donner Pass, 2,600 m, *Heller 7183* (CAS, MICH, MO, NY, P, RM, UC); Sierra Co., *Lemmon 89* (MO, NY); *Rose 34375* (K); Siskiyou Co., Shackelford Creek, 1,220 m, *Butler 1668* (CAS, MO, NMC, RM, UC); Tehama Co., 1 km S of Lassen Chalet, *Lowry 849* (ILL, UC). COLORADO: Garfield Co., 10 km W of Triangle Park, *Klinger & Blumquist,* 10 July 1959 (CS); Gunnison Co., Ruby, *Baker 723* (MO, NY, UC); La Plata Co., Bob Creek, W La Plata Mts., 3,050 m, *Baker et al. 177* (MICH, MO, NY, RM, UC); Larimer Co., Rabbit Ears, *Goodding 1563* (MO, NY, RM, UC); Montezuma Co., 19 km N of Mancos, *Colyer 26* (CS); Pitkin Co., Maroon Lake, White River Natl. Forest, 2,900 m, *R. A. Nelson 7720* (CS); Rio Blanco Co., 1 km SW of Wilson Creek Camp, 2,350 m, *S. Tabar & J. Walker 368* (CS); Routt Co., Mts. S of Steamboat Springs, 2,595 m, *Porter 5960* (MO, NY, RM, SMU, TEX, UC). IDAHO: Bannock Co., Mint Creek Canyon, S of Pocatello, *Lingenfelter 685* (NY, UC, WTU); Blaine Co., Boulder Creek Canyon, 2,440 m, *Thompson 14092* (CAS, MICH, MO, NY, UC, WTU); Bonneville Co., 17.5 km SW of Victor, *Lowry 1118* (ILL, UC); Cassia Co., Black Pine Mts., 2,135 m, *N. H. Holmgren 3798* (NY, UC); Elmore Co., Dog Mt., N of Pine, 2,440 m, *Hitchcock & Muhlick 8726* (NY, UC, WTU); Fremont Co., above Blair Lake, Centennial Mts., 2,665 m, *Lowry 2609* (ILL, MONT, MONTU, UC); Lemhi Co., Quartzite Mt., *Hitchcock 14218* (MO, NY, WTU); Owyhee Co., 3 km S of Silver City, *Baker 8248* (NY, WTU); Teton Co., S of Victor, *Christ 5302* (NY); Twin Falls Co., 1.5 km S of Magic Mt. Ski Area, *Holmgren & Holmgren 6013* (UC). MONTANA: Beaverhead Co., Red Rock Lakes, *Lowry 1325* (ILL, MO, UC); Cascade Co., *Hawkins s.n.* (MONT); Fergus Co., Half Moon Ridge, Big Snowy Mts., *Hitchcock 16083* (CAS, MO, MONT, NY, RM, UC, WTU); Gallatin Co., Bridger Mts., *Rydberg & Bessey 4597* (K, MONT, RM, UC); Glacier Co., Midvale, *Umbach 389* (CAS, MONT, WIS); Granite Co., 3 km W of Skalkaho Rd. Summit, *Hitchcock & Muhlick 14479* (MO, NY, UC, WTU); Missoula Co., Missoula, *Kirkwood 1228* (CAS, MO, MONT, UC); Park Co., 3 km S of Livingston, *Booth 62156* (MONT); Silver Bow Co., Humbug Spires, *Lowry 2886, 2913* (ILL, MONT, MONTU, UC). NEVADA: Elko Co., Ruby Mts., *Gentry & Davidse 1806* (ILL, NY, RM, TEX, UC); Humboldt Co., Pine Forest Range, *Holmgren & Reveal 1202* (MICH, NY, TEX, UC); Lander Co., Kingston Canyon, Toiyabe Mts., *Tidestrom 10889* (MO); Nye Co., N Kawich Range, 2,045 m, *Beatley & Reveal 11221* (CAS, NY, UC); Washoe Co., Hunter Creek, W of Reno, 1,830 m, *Kennedy 1861* (CAS, MO, NY, RM, UC); White Pine Co., Snake Range, *Holmgren & Reveal 1097* (NY, TEX, UC). OREGON: Baker Co., Powder River, *Cusick 1819* (JEPS, UC); Clackamas Co., *Goodding & Evinger,* 27 June 1927 (OSC); Clatsop Co., Saddle Mt., 715 m, *Chambers 3461* (OSC, NY); Crook Co., 3 km W of Ochoco Summit, *Kruckeberg 2153* (RM, UC, WTU); Deschutes Co., *Ireland 2663* (ORE); Grant Co., 7 km S of Long Creek, *Lowry 1094* (ILL, MO, NY, OSC, UC); Harney Co., Steens Mt., *Lowry 894* (ILL, OSC, UC); Jackson Co., Green Springs Mt., *Constance et al. 3629* (NY, SMU, UC); Klamath Co., 1.5 km N of Keno, *Peck 9426* (CAS, MO, NY); Lake Co., Crane Mt., *Thompson 13236* (CAS, MO, NY, WTU); Marion Co., Silver Creek, *Hall 217* (F, GH, GOET, K, MO, NY); Tillamook Co., *Chambers 4096* (OSC); Washington Co., Gales Creek, near Forest Grove, *Thompson 615* (CAS, MO, WTU); Wheeler Co., Wolf Mt., *Cronquist 7540* (CAS, K, NY, RM, UC, WTU). UTAH: Cache Co., Spring Hollow Canyon, 1,615 m, *Maguire 13739* (RM, UC); Garfield Co., 16 km E of Cedar Breaks, 2,450 m, *Graham 8679* (MO); San Juan Co., Abajo Mts., *Goodman & Hitchcock 1399* (MO); Summit Co., W Fork Bear River, Uintah Mts., *Payson & Payson 4936* (CAS, MO, RM, UC); Utah Co., Provo, 2,440 m, *M. E. Jones 5587* (MO, NY, RM, UC). WASHINGTON: Asotin Co., Blue Mts., above Indian Tom Cr., *Cronquist 5900* (MICH, NY, SMU, UC); Chelan Co., Tumwater Canyon, near Leavenworth, *Thompson 8451* (CAS, MO, NY, UC, WTU); Clallam Co., Mt. Angeles, 1,525 m, *Thompson 7470* (CAS, K, MO, UC, WTU); Jefferson Co., Hurricane Ridge, *Kuramoto,* 18 July 1966 (ILL); Kittitas Co., Upper Cle Elum River, *Kruckeberg 2976* (CAS, NY, RM, UC, WTU); Okanogan Co., Billy Goat Pass, 1,525 m, *Thompson 10881* (MO, NY, WTU); Spokane Co., Mt. Carleton, *Kraeger 282* (NY, UC); Yakima Co., Mt. Aix, 1,830 m, *Thompson 15056* (CAS, MICH, MO, NY, SMU, UC, WTU). WYOMING: Big Horn Co., Big Horn Mts., 2,835 m, *Gierisch 1790* (CS); Carbon Co., Lost Creek, Medicine Bow Mts., *Porter 4076* (CAS, RM, SMU, TEX, UC); Sublette Co., Middle Piney Lake, 2,500 m, *Porter 5034* (CAS, MO, RM, SMU, TEX); Teton Co., 5 km W of Teton Pass, *Lowry 1123* (ILL, UC); Uinta Co., Teton Mts., *Nelson & Nelson 6472* (BM, ILL, K, MO, NY).

CANADA. ALBERTA: Chief Mt. Int'l. Hwy., Waterton Lakes Nat'l. Park, 1,375 m, *Breitung 15930* (NY, UC); Red Rock Canyon, Waterton Lakes, 1,525 m, *de Vries 2102* (DAO); Mountain Hill, W of Pincher Creek, *Moss 56* (DAO); W of Beaver Mines, *Moss 825* (DAO). BRITISH COLUMBIA: near int'l. boundary, between Columbia River and Kettle River, 1,220 m, *Macoun 64628* (NY); near Ainsworth, 1,525 m, *Macoun,* 10 July 1890 (NY); Lightning Lake, Manning Prov. Park, 1,220 m, *Beamish & Vingtman 60770* (DAO, ILL); km 30, Flathead Rd., *Bell & Davidson 150* (DAO); 9 km SW of Rossland, *Calder et al. 9460* (DAO); Mt. Apex, SW of Penticton, *Calder & Savile 11750* (DAO, UC); 1.5 km E of Phoenix, *Calder & Savile 33076* (DAO); 21 km W of Kaslo, 900 m, *McCabe 6572* (UC); 3 km N of Howell Creek Bridge on Flathead Rd., 1,525 m, *Taylor & Ferguson 1018* (DAO, UC); 13 km N of Flathead Customs, *Taylor & Ferguson 2039* (DAO).

II. **Osmorhiza** Raf. subg. **Osmorhiza**

Osmorhiza subg. *Euosmorhiza* Drude in Engl. & Prantl,
Nat. Pflanzenfam. 3^{8}: 153. 1897. nom. illeg.

Scandix subg. *Uraspermum* (Nutt.) Koso-Polj., Bull. Soc. Imp. Naturalistes Moscou 29: 143. 1916.

Plants slender to rather stout; stems not densely clustered, 1–3(–5), never glaucous. Root system shallow to deep, diffusely branched. Leaves 2–3-ternate; petiole bases moderately to densely ciliate. Primary umbel with more hermaphrodite and fewer staminate flowers than the secondary and later flowering umbels; staminate umbellets 0–4(–6) per umbel; staminate flowers 0–90(–125) per umbel; corolla white, or variously tinged with green, pink, or purple. Fruit hispid with retrorse bristles, or occasionally glabrous, with short to very long caudate appendages (rarely lacking).

IIa. **Osmorhiza** Raf. sect. **Osmorhiza**

Uraspermum § [sect.] *Osmorhiza* (Raf.) Kuntze, Lexicon 582. 1904, pro parte.
Scandix 2. [sect.] *Urascandix* Koso-Polj., Bull. Soc. Imp. Naturalistes Moscou 29: 143. 1916, pro parte.
Osmorhiza sect. *Aristatae* Constance & Shan, Univ. Calif. Publ. Bot. 23: 112. 1948, nom. nud.

Involucre composed of (1–)2–3(–5) linear to lanceolate, reflexed bracts; involucel conspicuous, composed of 3–6 reflexed bractlets. Styles (including stylopodium) 1–3.6 mm long, stylopodium 0.4–0.8 mm long, high-conic, lacking a disc.

There is no doubt that the three members of *Osmorhiza* sect. *Osmorhiza* (*O. claytonii, O. aristata,* and *O. longistylis*) are very closely related, and constitute a monophyletic assemblage; many authors (e.g., Gray, 1859; Clarke, 1879; Kuntze, 1891; Boivin, 1968) have even treated them as conspecific. These taxa, however, appear to represent distinct, natural populations. The Asian *O. aristata* is intermediate between the North American *O. claytonii* and *O. longistylis* for many characters but is clearly distinct for a number of others, including pedicel length and fruit shape.

The North American representatives of this section are completely separable from each other by many characters, including style length, total number of flowers per umbel, number of staminate flowers per umbellet, and pollen grain morphology (Lowry, 1976; Lowry & Jones, 1979a). Every one of the more than 2,250 herbarium specimens examined was clearly referable to one or the other of the two species; not a single individual exhibiting an intermediate combination of characters has been found. While pollen flow is likely in the numerous sympatric populations, there is no indication of any natural hybridization or gene flow between *O. claytonii* and *O. longistylis.*

Palynological evidence also supports the treatment of *Osmorhiza claytonii* and *O. longistylis* as distinct at the specific level (Lowry, 1976; Lowry & Jones, 1979a). The pollen grains of the two species have significantly different ratios of polar axis length to equatorial diameter (P/E ratio). Those of *O. claytonii* are generally prolate in shape, i.e., their P/E ratios are between 1.33 and 2.00 (Erdtman, 1969; Kapp, 1969). By contrast, the grains of *O. longistylis* are perprolate, with P/E ratios greater than 2.00.

2. **Osmorhiza aristata** (Thunb.) Rydb. *Chaerophyllum aristatum* Thunb., Fl. Jap. 119. 1784. *Myrrhis aristata* (Thunb.) Sprengel, Pl. Umbell. 29. 1813. *Uraspermum aristatum* (Thunb.) Kuntze, Revis. gen. pl. 1: 270. 1891, pro parte. *Osmorhiza aristata* (Thunb.) Rydb., Bot. surv. Nebr. 3: 37. 1894, pro parte (exclusive of North American populations). *Scandix aristata* (Thunb.) Koso-Polj., Bull. Soc. Imp. Naturalistes Moscou 29: 143. 1916. TYPE: Japan. *Thunberg s.n.* (holotype, UPS!).

Osmorhiza laxa Royle, Ill. bot. Himal. 233, pl. 52, fig. 1. 1839. *Washingtonia laxa* (Royle) Koso-Polj. in Fedtschenko, Fl. Asiat. Ross. 15: 52. 1920. *Washingtonia longistylis* var. *laxa* (Royle) Koso-Polj. in Fedtschenko, Fl. Asiat. Ross. 15: 52. 1920, pro syn. *Osmorhiza aristata* var. *laxa* (Royle) Constance & Shan, Univ. Calif. Publ. Bot. 23: 130. 1948. TYPE: India. Punjab: "Simore [Sirmur] in the Himalayan Mountains," *Royle s.n.* [lectotype (designated herein), K!; isolectotype, K!].
Osmorhiza japonica Siebold & Zucc., Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. IV. 2: 203. 1843. Based on *Chaerophyllum aristatum* Thunb.
Osmorhiza amurensis F. Schmidt ex Maxim., Pr. fl. Amur. 129. 1859. *Scandix amurensis* (Maxim.) Koso-Polj., Bull. Soc. Imp. Naturalistes Moscou 29: 143. 1916. *Washingtonia amurensis* (Maxim.) Koso-Polj. in Fedtschenko, Fl. Asiat. Ross. 15: 50. 1920, pro syn. TYPE: U.S.S.R. Khabarovsk Krai: on the lower Amur River, near the vicinity of the mouth of the Dondon, at Dshare, in deciduous woodland places, scattered, *K. I. Maximowicz,* 18 July 1855 [holotype, LE; photograph of holotype, ILL!; plus two authentic specimens (possibly isotypes), K!, LE, photographs at ILL!].
Osmorhiza claytonii (Michaux) C. B. Clarke in Hook., Fl. Brit. India 2: 690. 1879, pro parte (exclusive of *M. claytonii* Michaux and *M. longistylis* Torrey).
Osmorhiza aristata var. *montana* Makino, J. Jap. Bot. 2: 7. 1918. *Osmorhiza montana* (Makino) Makino, J. Jap. Bot. 5: 28. 1928. *Osmorhiza amuren-*

sis var. *montana* (Makino) Kitagawa, Rep. Inst. Sci. Res. Manchoukuo 2: 279. 1938. TYPE: Japan. Honshu: Totigi, Nikko, Shimotsuke, *T. Makino s.n.* (The holotype has not been located.)

Washingtonia claytonii subsp. *orientalis* Koso-Polj. in Fedtschenko, Fl. Asiat. Ross. 15: 51. 1920. (No type material has been located.)

Washingtonia claytonii subsp. *occidentalis* Koso-Polj. in Fedtschenko, Fl. Asiat. Ross. 15: 51. 1920. (No type material has been located.)

Plants rather stout, 3–8(–10) dm high; stems 1–2(–3), erect to ascending, villous to glabrate. Root system rather deep, spreading, with an anise-like scent. Leaves 2–3-ternate, deltoid to broadly ovate, 7–20 cm long, hirsutulous (especially along the veins) to glabrescent; leaflets oblong-oval to ovate-deltoid, (1.5–)2.5–9 cm long, 1–6 cm wide, obtuse to acuminate, coarsely serrate, incised, sparsely lobed to deeply pinnatifid at the base; petioles 5–25 cm long. Umbels loose; peduncles 2–3(–4), terminal and lateral, (3.5–)5–25 cm long; involucre composed of 1–3(–5) linear to lanceolate, foliaceous, ciliate, reflexed bracts, or sometimes wanting, each (1–)2–10(–25) mm long, (0.3–)0.5–1.3(–4.5) mm wide; rays spreading to ascending, (3.5–)4.5–11 cm long; umbellets 3–6 per umbel; involucel of (3–)4–5 linear to lanceolate, acuminate, ciliate to hirsutulous bractlets, each (1–)2.5–10(–11) mm long, 0.5–1.7(–2) mm wide, strongly reflexed; pedicels (4–)5–15 per umbellet, spreading, those of the hermaphrodite flowers (5–)9–30(–33) mm long, those of the staminate flowers 2.5–9(–10) mm long. Hermaphrodite flowers 2–6(–7) per umbellet, (10–)15–30(–38) per umbel, staminate flowers (2–)3–7(–11) per umbellet, (7–)15–40 (–50) per umbel; corolla white, somewhat showy; styles plus stylopodium 1.5–2.2(–2.4) mm long, stylopodium (0.4–)0.45–0.7 mm long, high-conic, lacking a disc; carpophore cleft about to the middle. Fruit linear-clavate, obtuse or abruptly acute at the apex, concave furrowed, (13–)15–22(–23) mm long, the ribs sparingly to moderately hispid with retrorse bristles, especially toward the base, the caudate appendages (4.5–)5.5–11 mm long. $n = 11$ (Wanscher, 1932). Figures 9a and 12.

Flowering period. April to early June.

Habitat. Moist woods, at lower and middle elevations.

Common names. Ihari (Nepalese), Hsiang Kên Ts'ao Shu (Chinese), Miyama-yabu-ninzin, Nagajirami, Nagazirami, Onaga-yabu-ninzin, Yabu-ninjin, Yabu-ninzin (all Japanese).

Representative specimens. CHINA. GUIZHOU: *Cavalerie & Fortunat 2961* (K, P, UC). HUBEI: *Henry 5789* (BM, K, P); S of Wushan, *Wilson 1044, pars* (K, NY, P); Paok'ang, *Wilson 1044, pars* (P). JIANGSU: P'ang-huang-chen, *Chiao & Cheo 3541* (NY). JIANGXI: Lushan Mts., *Chung & Sun 295* (NY). JILIN: Manchuria, *Komarov 1158* (BM, K, P). SICHUAN: Pao-hsing-hsien, *Chu 3336, 3495* (BM); Tchen-keou-tin, 1,400 m, *Farges 72* (K, P, UC); Cheto Valley, Kangting (Tachienlu) Dist., 3,100 m, *Smith 10963* (BM); Kiala, *Soulié 1143* (P); S of Wushan, *Wilson 1044, pars* (K). XIZANG: Rongshar Valley, N of Mt. Everest, 2,900 m, *Hingston 183* (K); 28°25′N, 97°55′E, 3,250 m, *Kingdon-Ward 10092* (BM); Valley of Lilung Chu, between Charko and Lilung, 29°04′N, 93°56′E, 3,100 m, *Ludlow et al. 4460* (BM); Peding, Tsangpo Valley, 29°30′N, 94°20′E, 3,000 m, *Ludlow et al. 4533* (BM); Pe, 29°31′N, 94°54′E, 2,960 m, *Ludlow et al. 5320* (BM). YUNNAN: Ma-eul-chan, 3,000 m, *Delavay 3902* (P); Yungning, *Handel-Mazzetti 7049* (N—not seen; reported in Constance & Shan, 1948); N of Mengzi, 2,600 m, *Henry 10233* (K, MO, NY). ZHEJIANG: W of Tien-mu, *Hu 1654* (UC).

JAPAN. HOKKAIDO: Hakodate-si, Jesso Island, near Hakodate, *Albrecht s.n.* (K); Hakodate, *Faurie 473* (P); Iwanai-tyo, Iwanai, *Faurie 7024* (P); Kamikawa-tyo, foot of Mt. Kuro-dake, *Hiroe 6628* (UC); Minami-huramo-tyo, Mt. Tomamu, *Hiroe 6730* (UC); Monbetu-tyo, Monbetu, *Faurie 709* (K, P); Rebun-tyo, Rebun Island, *Hiroe 7611* (UC); Risiri-tyo, Mt. Rishiri, Rishiri Island, *Hiroe 7541* (UC); Rubesibe-tyo, Onneyu, *Okamoto,* 18 Aug. 1958 (UC); Sapporo-si, Sapporo, *Tokubuchi,* 26 June 1891 (MO, NY); Yubari-si, foot of Mt. Yubari, *Hiroe 6630* (UC). HONSHU: Akita-ken, Yokobori, *Yushun,* 23 July 1905 (NY); Aomori-ken, Moura, W coast of Natsudomari-hanto, *Mimoro et al. 3551* (MO); Gunma-ken, Ikao, *Lyle,* May 1908 (BM); Hukusima-ken, Asakawa, *Mizushima,* 27 Apr. 1952 (UC); Ibaraki-ken, foot of Mt. Tsukuba, *Furuse,* 18 Apr. 1956 (UC); Iwate-ken, Nagamachi, *Iishiba,* 16 May 1926 (UC); Kanagawa-ken, Yamakita, *Faurie 3303* (P); Kyoto-hu, Mt. Otoko, *Hiroe 13565* (NY, UC, WIS); Miyagi-ken, Ninomaru, *Mori & Yashima,* 24 May 1973 (MO); Nagano-ken, Mt. Kiso-ontake, *Okuhara,* 28 Aug. 1955 (UC); Nara-ken, Mt. Kasuga, *Hiroe 16236* (UC); Niigata-ken, Niigata, *Faurie 79* (P); Osaka-hu, Mt. Chihaya, 600 m, *Hiroe 13159* (NY, UC, WIS); Saitama-ken, Karisaka Pass, *Kobayashi,* 3 Aug. 1961 (UC); Siga-ken, foot of Mt. Ibuki, *Hiroe 68* (K, NY, UC, WIS); Sizuoka-ken, ascent way of Fujinomiya, Mt. Fuji, 2,000 m, *Hiroe 12683* (UC); Tokyo-to, Komae, *Suzuki 77007* (UC); Totigi-ken, Lake Kirikomi, Nikko City, *Ono & Kobayashi,* 4 Aug. 1963 (UC); Toyama-ken, Yatsuo village, 17 km SW of Toyama, *Kirino 172* (MO); Yamagata-ken, Kabuto-iwa, *Ohashi et al. 708124* [sic] (BR, MO); Yamaguchi-ken, Hakusan Shrine, base of Castle Mt., 41 km W of Hiroshima, *Charette 1680* (UC). KYUSHU: Kagosima-ken, *Masamune,* 4 Apr. 1923 (NY); Kumamoto-ken, Aso Volcanos, Kamisikimi Takamori, 650 m, *Tokio 374* (WIS); Nagasaki-ken, Nagasaki, *Faurie 3302* (BM, P); Oita-ken, Mt. Yuhu, 1,200 m, *Tokio 1009* (WIS). SHIKOKU: Kagawa-ken, Mt. Ohtaki, 800 m, *Hiroe 15500* (UC).

KOREA. CHEJU DO: Cheju-do Island, *Jaquet 881* (K). KANGWON DO: Ullung Island, Kyongsang-Pukto, *Chung 2290* (MICH); Mt. Odae, *Chung 2728* (MICH). KYONGGI DO: Kwangnung, *Chung 2614, 7404* (MICH).

Bhutan. Chalimarphe Timpu, 2,290 m, *Cooper 1405* (BM); Drugge Dzong, 3,050 m, *Ludlow et al. 16209* (BM).

Nepal. pālpa: Lukarban Khola, W of Beni, 3,000 m, *Stainton et al. 451* (BM); Lete, S of Tukucha, Kali Gandahi Valley, 3,000–3,200 m, *Stainton et al. 1034, 5600* (BM).

India. himachal pradesh: Raiengarb Mut, 2,135 m, *Gamble 26799* (K); Swajaui Maidan, Parbatti Valley, 3,050 m, *Nath 123* (NY); Kulu-Lahoul, Punjab, *Drummond 23122, 23131, 23132* (K, UC); Nagzuda, Simla Hills, 2,250 m, *Hooker f. & Thomson,* 9 June 1849 (K, P). jammu: Jangla, 2,750 m, *Dudgeon & Kenoyer 386* (MO); Jammu, 2,000 m, *Hooker f. & Thomson,* 31 May 1868 (K). kashmir: Pahlgam, E Liddar River, 43 km N of Anantnag [Islamabad], 2,290 m, *Dickason 845* (MICH); Pahlgam, 2,200 m, *Stewart 9271* (NY). uttar pradesh: below Budhi, Byans, Kumaun, 2,600 m, *Duthie 5595* (BM, K); Bamon Valley, 2,135 m, *Duthie,* 15 May 1897 (P); Jaunsar Bahar, near Kinani Pani, 2,600 m, *Gamble 1136* (K); Jaunsar, Chaelipup, *Gamble 23589* (K); Kedar Kantah Mts., *Jacquemont 830* (P); Kumaon, Lahai, 2,285 m, *Strachey & Winterbottom s.n.* (BM, BR, K); Garhwal, *Thomson 1254* (K).

Pakistan. kashmir: Kishenganga Valley, Rd. to Nanga Parbat via the Gangabal Lakes, Keran, 1,850 m, *Stewart & Stewart 17544* (NY, UC).

U.S.S.R. altayskiy kray: Teletskoe Ozero Tulkuy, *Koshurnikova & Vishniovskya,* 19 July 1927 (NY). khabarovskiy kray: lower Amur River, at Dshare, *Maximowicz,* 18 July 1855 (K, LE). primorskiy kray: Kedrovaja Padj Reservation, SW of Vladivostok, *Gorovoy 8* (UC); S Ussuriysk, Pos'yet Dist., *Saberkin 890* (NY). sachalin: Sachalin Island, *Schmidt s.n.* (K).

Royle (1839) considered Himalyan populations of *Osmorhiza* conspecific with short-styled populations in North America now treated as *O. claytonii* (Michaux) C. B. Clarke, and accepted the name *O. brevistylis* DC. for them. Similarly, several authors (e.g., Gray, 1859; Hayata, 1911, 1912) incorrectly applied the name *O. longistylis* (Torrey) DC. to Asian populations of *Osmorhiza.*

Constance and Shan (1948) treated all the Asian representatives of *Osmorhiza* under *O. aristata,* although they distinguished two varieties on the basis of characters of the leaves. Quantitative evaluation of morphological characters, however, does not support the recognition of infraspecific taxa within *O. aristata* (Table 4).

3. **Osmorhiza claytonii** (Michaux) C. B. Clarke. *Myrrhis claytonii* Michaux, Fl. bor.-amer. 1: 170. 1803. *Chaerophyllum claytonii* (Michaux) Persoon, Syn. sp. pl. 1: 320. 1805. *Osmorhiza claytonii* (Michaux) C. B. Clarke in Hook., Fl. Brit. India 2: 690. 1879, sensu stricto (exclusive of *M. longistylis* Torrey and *O. laxa* Royle). *Washingtonia claytonii* (Michaux) Britt. in Britt. & Brown, Ill. fl. 2: 530. 1897. *Scandix claytonii* (Michaux) Koso-Polj., Bull. Soc. Imp. Naturalistes Moscou 29: 143. 1916. type: U.S.A. "*In montibus* Alleghanis," *A. Michaux s.n.* (holotype, P!).

Scandix dulcis Muhlenb., Cat. pl. 31. 1813. *Myrrhis dulcis* (Muhlenb.) D. Eaton, Man. bot. 326. 1818. *Uraspermum dulce* (Muhlenb.) Farwell, Amer. Midl. Naturalist 9: 273. 1925. Based on *Myrrhis claytonii* Michaux.

Uraspermum hirsutum Bigelow, Fl. boston. 112. 1824. type: U.S.A. Massachusetts: "Woods on the Concord turnpike," *Bigelow s.n.* (No type material has been located.)

Osmorhiza brevistylis DC., Prodr. 4: 232. 1830. *Myrrhis brevistylis* (DC.) Dietr., Syn. pl. 2: 984. 1840. *Uraspermum aristatum* α [subsp.] *brevistyle* (DC.) Kuntze, Revis. gen. pl. 1: 270. 1891. *Osmorhiza aristata* var. *brevistylis* (DC.) Boivin, Phytologia 17: 104. 1968. type: U.S.A. New York: Range Co., West Point, *Torrey s.n.,* 1828 [lectotype (designated herein), G-DC!; isolectotypes (2), G-DC!].

Osmorhiza villosa Raf., Med. fl. 2: 249. 1830 (as "*vilosa*"). (No type material has been located.)

Osmorhiza cordata Raf., Med. fl. 2: 249. 1830. (No type material has been located.)

Uraspermum aristatum α [subsp.] *brevistyle* [var.] *subintegrifoliolum* Kuntze, Revis. gen. pl. 1: 270. 1891. (No type material has been located.)

Uraspermum dulce var. *laevicaule* Farwell, Amer. Midl. Naturalist 9: 273. 1925. type: U.S.A. Michigan: Oakland Co., Pontiac, *O. A. Farwell 5267* [lectotype, BLH! (designated by McVaugh et al., Bull. Cranbrook Inst. Sci. 34: 79. 1953); isolectotype, GH].

Osmorhiza claytonii f. *brevipilosa* Salamun, nom. inval. Although this name was provided with a Latin diagnosis and citation of a type specimen, it was never effectively published, having only been proposed in Salamun's dissertation (1950: 82).

Plants rather stout, 4–8(–10) dm high; stems 1–2(–3), erect to ascending, villous, villosulous, or sometimes essentially glabrous. Root system shallow, more or less horizontally spreading, the roots fibrous and limber, rank smelling, or sometimes weakly anise-scented. Leaves 2–3-ternate, more or less broadly ovate, 10–30 cm long, hirsutulous; leaflets ovate to lanceolate, (3–)4–8 cm long, 1.5–3 cm wide, acute or acuminate, serrate-dentate, often parted or divided at the base; petioles 5–15 cm long. Umbels loose; peduncles 2–3 (–4), terminal and lateral, 3–10(–13) cm long; involucre wanting, or often composed of 1–2(–3) minute, linear-lanceolate, foliaceous, ciliate, reflexed bracts; rays ascending, 2–8(–10) cm long; umbellets 3–5 per umbel; involucel of 3–5 linear-lanceolate, attenuate, ciliate bractlets, each 2–5

(–6) mm long, 0.4–1 mm wide, strongly reflexed; pedicels 4–7(–8) per umbellet, ascending, those of the hermaphrodite flowers (4–)6–12(–15) mm long, those of the staminate flowers (3–)3.5–5.5 (–7) mm long. Hermaphrodite flowers 2–5(–7) per umbellet, (6–)10–23(–31) per umbel, staminate flowers 0–5(–6) per umbellet, (2–)7–17(–23) per umbel; corolla white, inconspicuous; styles (including stylopodium) 1–1.5(–1.7) mm long, stylopodium 0.5–0.75(–0.8) mm long, high-conic, lacking a conspicuous disc; pollen prolate in shape; carpophore cleft about one-fourth of its length. Fruit oblong-fusiform, tapering to a short, attenuate beak at the apex, concave furrowed, (10–)12–22(–25) mm long, the ribs sparingly to moderately hispid with retrorse bristles, especially toward the base, the caudate appendages 4.5–8.5 mm long. $n = 11$ (Bell & Constance, 1957). Figures 9b and 10.

Flowering period. April to early June.

Habitat. Dense to open deciduous forests, tending toward the more moist, lower areas.

Common names. Clayton sweetroot, Hairy sweet cicely, Sweet jarvil, Woolly sweet cicely.

Representative specimens. U.S.A. ALABAMA: Madison Co., Huntsville, *Baker,* 23 May 1897 (MO, NY). ARKANSAS: Independence Co., *Thomas 38940* (TENN). CONNECTICUT: Hartford Co., Southington, *Bissell 83* (NY). DELAWARE: Newcastle Co., near Wilmington, *Canby s.n.* (NY). GEORGIA: Union Co., *Duncan 22356* (GA). ILLINOIS: Bureau Co., *Evers 80102* (ILLS); Champaign Co., Brownfield Woods, N of Urbana, *Lowry 1206* (ILL); Crawford Co., *Evers 43236* (ILLS); Hancock Co., *M. J. Warnock 215* (ILL); Lake Co., Waukegan, *Umbach 5355* (UC); La Salle Co., Starved Rock State Park, *Greenman et al. 27* (GH, NY, UC); Lee Co., 5 km NE of Franklin Grove, *G. N. Jones 15839* (ILL, MO); Macon Co., Spittler Woods, Mt. Zion, *Lowry 545* (ILL, MO, UC); McLean Co., Funk's Grove, S of Bloomington, *Lowry 1140* (ILL); Piatt Co., Allerton Park, near Monticello, *Lowry 211* (ILL, MO). INDIANA: Adams Co., 3 km W of Geneva, *Deam 50233* (WIS); Fountain Co., Portland Arch, *Lowry 1208* (ILL); Lake Co., 6 km N of Schneider, *Salamun,* 5 Aug. 1947 (ILL, UC); Morgan Co., 4.5 km N of Martinsville, *Heiser & Smith,* 19 May 1950 (ILL, MO, UC); Parke Co., Turkey Run St. Park, *Salamun,* 6 Aug. 1947 (ILL, MO). IOWA: Clayton Co., Pike's Peak, McGregor, *Shimek,* 8 Aug. 1922 (UC); Dickinson Co., 3 km W of Milford, *Thorne 12907* (UC); Hardin Co., Iowa Falls, *Shimek,* 27 July 1922 (NY); Poweshiek Co., Grinnell, *M. E. Jones 146* (GOET, NY). KANSAS: Doniphan Co., *Stephens 58060* (KANU); Leavenworth Co., *A. S. Hitchcock 701* (GH, NY, RM). KENTUCKY: Carter Co., Carter Caves, *Brown 3940* (NY); Greenup Co., 4.5 km from Boyd Co. line, *Smith et al. 3580* (F, GH, NY, US); Madison Co., Berea, *McFarland 4294* (MO). MAINE: Aroostook Co., Fort Fairfield, *Fernald 51* (GH, MO, UC, US); Knox Co., Camden, *LeBean,* 13 Aug. 1913 (WIS); Somerset Co., Skowhegan, *Eaton,* 30 June 1903 (LL, NY). MARYLAND: Alleghany Co., Cumberland, *Shriver s.n.* (NY); Howard Co., Ellicott City, *Arsène,* 26 July 1916 (MO). MASSACHUSETTS: Berkshire Co., Florida, Deerfield River, *Fernald & Long 10088* (GH); Middlesex Co., Malden, *Manning,* 6 June 1881 (NY). MICHIGAN: Arenac Co., Mud Lake, *Sharp et al.,* 20 June 1961 (MICH); Baraga Co., Big Limestone Mt., L'Anse, *Fassett 21037* (WIS); Cheboygan Co., Monroe Lake, *Ehlers 374* (GH, MO, US); Emmet Co., 3 km W of Mackinac City, *McVaugh 9430* (MICH, MO); Gogebic Co., Gogebic Lake, *Fassett 19868* (F, MO, NY, WIS); Keweenaw Co., Isle Royale, *McFarlin 2149* (MONT); Schoolcraft Co., 8 km W of Gulliver, *Salamun,* 19 July 1946 (ILL, MO). MINNESOTA: Clearwater Co., Floating Bog Bay, *Grant 2885* (MO, NY, UC); Cook Co., Mineral Center, *Rosendahl & Butters 4590* (GH, NY); Saint Louis Co., Duluth, *Lakela 2071* (MO); Wabasha Co., 10 km N of Reed's Landing, *M. J. Warnock 1463* (ILL). MISSOURI: Dallas Co., 8 km SW of Bennett Springs, *Conrad 3496* (MO); Jackson Co., Kansas City, *MacKenzie,* 16 May 1896 (MO, NY); Lincoln Co., Mill Creek, NE of Silex, *Steyermark 25981* (F, MO); Mercer Co., 5 km NE of Saline, *Palmer & Steyermark 41324* (MO, NY). NEBRASKA: Cherry Co., NE of Valentine, *Churchill 4489* (MO, NY); Cuming Co., 2 km SSE of Beemer, *Churchill 5516* (NY); Dixon Co., Ponca, *Clements 2564* (US); Washington Co., 4 km NW of Fort Calhoun, *Churchill 5328* (MO). NEW HAMPSHIRE: Grafton Co., N Woodstock, *Fernald 386* (BM, BR, CAS, DUKE, G, GH, K, KANU, MO, MONTU, NY, PH, RM, SMU, TENN, TEX, UC, US). NEW JERSEY: Bergen Co., W of Englewood, *Wilson,* 19 July 1915 (NY); Middlesex Co., Plainfield, *Tweedy s.n.* (GOET). NEW YORK: Chautauqua Co., Bemus Pt., Lake Chautauqua, *Churchill,* 2 Aug. 1896 (MO); Greene Co., Big Hollow, *Barnhart 2344* (NY); Herkimer Co., 2.5 km SW of Dart Lake, *Smith 2504* (WIS); Monroe Co., Webster, *Matthews 4164* (UC); Rensselaer Co., Brunswick, *House 26381* (MO, TEX). NORTH CAROLINA: Haywood Co., 1 km NW of Blue Ridge Parkway on Hwy. 276, *Lowry 1153* (ILL); Macon Co., 1 km SW of Swain Co. line on Hwy. 19, *Lowry 1152* (ILL, UC); McDowell Co., Curtis Creek, Blue Ridge Parkway, 825 m, *Feddema 3028* (RM); Mitchell Co., 1 km S of Hwy. 226 on Penland Rd., *Lowry 1155* (ILL, NY, UC); Yancey Co., 6 km NNW of Swiss, *Lowry 1154* (ILL, NY, UC). NORTH DAKOTA: Cass Co., Fargo, *Shunk s.n.* (MONT); Grand Forks Co., *Facey s.n.* (reported in Rhodora 74: 393. 1972); Richland Co., Leonard, *Stevens 1343* (UC). OHIO: Athens Co., Athens, *Abbot 12* (NY); Cuyahoga Co., Cleveland, *Greenman 710* (GH, MO); Scioto Co., Camp Gordon, Friendship, *Demaree 10648* (CAS, GH, MO). PENNSYLVANIA: Armstrong Co., *Wahl 5315* (PH); Berks Co., 3 km W of Upper Black Eddy, *Fogg 8665* (MO, PH); Cambria Co., *Wahl 9325* (PH); Juniata Co., 1.5 km NE of Peru Mills, *Wahl 10730* (PH, UC); Warren Co., *Pohl 2461* (PH). SOUTH CAROLINA: McCormick Co., *Radford 31734* (KANU). SOUTH DAKOTA: Brookings Co., Warren's Woods, *Williams & Thordaer,* 17 June 1893 (MO); Roberts Co., Big Stone Lake, *Over 14409* (US). TENNESSEE: Davidson Co., Joelton, *Svenson 93* (GA, GH); Grainger Co., *Sharp 43562* (TENN); Greene Co., Paint Creek, 1 km N of French Broad River, *Bufford et al. 18119* (MO); Knox Co., Lane's Creek, *Sharp & Herster 584* (NY).

VERMONT: Bennington Co., Red Mt., Arlington, *Seymour 21637* (MO); Caledonia Co., Peacham, *Blanchard s.n.* (MO, NY, RM); Windsor Co., Norwich, *Brown,* 20 June 1946 (SMU). VIRGINIA: Fairfax Co., Dead Run, E of Plummer's Island, *Mathias 1394* (CAS, GH, MO, NY, RM, UC, US); Smythe Co., Chatham Hill Gap, Walker Mt., *Small,* 13 June 1892 (F, GH, K, MO, P, UC). WEST VIRGINIA: Cabell Co., Pleasant Valley, *Williams & Gilbert 445* (F, GH, MO, NY, SMU); Ohio Co., Wheeling, *Mertz 1042* (F). WISCONSIN: Bayfield Co., *Koch 6881* (KANU); Forest Co., 13 km SE of Crandon, *Stearns,* 23 June 1946 (NY); Green Co., 7 km W of Monticello, *Salamun,* 10 July 1947 (ILL, MO); Outagamie Co., Appleton, *Chandler,* 18 May 1896 (UC); Trempeauleu Co., NW of Trempeauleu, *M. J. Warnock 1470* (ILL).

CANADA. MANITOBA: 6.5 km N of Moon Lake, Riding Mt. Nat'l. Park, *Mosquin 6066* (DAO). NEW BRUNSWICK: Albert Co., *Roberts 64-1655* (DAO); Charlotte Co., Grand Manan, *Weatherby & Weatherby 7327* (GH, US); Westmorland Co., *Dore 45235* (DAO). NOVA SCOTIA: Cape Breton Co., George River, *Bissell & Linder 22050* (GH); Inverness Co., Mabou, *Robinson 229* (NY); Victoria Co., Dingwall, Aspy Bay, *Churchill,* 7 July 1909 (MO). ONTARIO: Algoma Dist., *Jenkins 4909* (DAO); Carleton Co., March Twp., *Cody & Calder 480* (DAO, MO); Grey Co., 1.5 km SW of Meadford, *Soper & Shields 4603* (MO); Manitoulin Dist., Manitoulin Island, *Salamun,* 20 July 1946 (ILL, MO); Muskoka Dist., *Minshall 3076* (DAO); Oxford Co., 8 km N of Thamesford, *Soper & Shields 4506* (MO); Rainy River Dist., 8 km below Rainy River, *Garton 8670* (DAO); Russell Co., 1.5 km SE of Cumberland, *Cody & Calder 540* (DAO, MO); Thunder Bay Dist., N bank of Pigeon River at Middle Falls, *Garton 2062* (DAO, MO). PRINCE EDWARD ISLAND: Kings Co., Bear River, *Fernald & St. John 11140* (GH, UC, US). QUÉBEC: Charlevoix Co., *Cayouette 57-247* (DAO); Gaspé Co., *Lemieux 14506* (DAO); Labelle Co., Bellerive, *Lucien & Eloi 248* (UC); Lac-Saint-Jean Co., *Bouchard 70-520* (DAO, G); Matane Co., Mt. Nicolabert, Joffre, *Fernald & Pease 25208* (GH); Richmond Co., Cleveland, *Chamberlain & Knowlton,* 26 July 1923 (GH, MO); Terrebonne Co., Lac Tremblant, *Churchill,* 8 Aug. 1922 (GH, MO).

Osmorhiza claytonii is fairly uniform throughout its range. Although two varieties have been recognized on the basis of quantity of pubescence (Farwell, 1925; Salamun, 1950), examination of a large number of specimens shows that this character is highly variable in *O. claytonii,* and neither variety is upheld in this interpretation (Lowry, 1976; Lowry & Jones, 1979a).

4. **Osmorhiza longistylis** (Torrey) DC. *Myrrhis longistylis* Torrey, Fl. U.S. 310. 1824. *Osmorhiza longistylis* (Torrey) DC., Prodr. 4: 232. 1830. *Uraspermum aristatum β* [subsp.] *longistyle* (Torrey) Kuntze, Revis. gen. pl. 1: 270. 1891, pro parte (with two varieties: *laciniatum* and *subintegrifoliolum*). *Washingtonia longistylis* (Torrey) Britt. in Britt. & Brown, Ill. fl. 2: 530. 1897. *Scandix longistylis* (Torrey) Koso-Polj., Bull. Soc. Imp. Naturalistes Moscou 29: 143. 1916. *Osmorhiza aristata* var. *longistylis* (Torrey) Boivin, Phytologia 17: 104. 1968. TYPE: "In wet meadows near Albany, N.Y. *Tracy.* Near Geneva, N.Y. *Paine.* June. Near Hudson, N.Y. Alsop & c." (None of these syntypes has been located; only an authentic specimen collected by Paine was found, and is herein designated the neotype.) Canada. Québec: Montreal, *Paine s.n.* (neotype, NY!).

Osmorhiza dulcis Raf., Med. fl. 2: 249. 1830. *Myrrhis dulcis* (Raf.) Raf., Good book 53. 1840, pro syn., non *Scandix dulcis* Muhlenb. TYPE: U.S.A. "Mts Alleghy [sic]," *Rafinesque s.n.* [lectotype, PH! (designated by Lowry & Jones, Amer. Midl. Naturalist 101: 26. 1979); possible syntypes, G!, PH!].

Chaerophyllum dulce Fischer ex Steud., Nom. bot. 1: 339. 1841, non *Scandix dulcis* Muhlenb. (No type material has been located.)

Osmorhiza claytonii (Michaux) C. B. Clarke in Hook., Fl. Brit. India 2: 690. 1879, pro parte (exclusive of *M. claytonii* Michaux and *O. laxa* Royle).

Osmorhiza aristata (Thunb.) Rydb., Bot. surv. Nebr. 3: 37. 1894, pro parte (exclusive of Asian populations).

Osmorhiza longistylis var. *villicaulis* Fern., Rhodora 10: 52. 1908. *Washingtonia longistylis* var. *villicaulis* (Fern.) Coult. & Rose, Contr. U.S. Natl. Herb. 12: 443. 1909. *Uraspermum aristatum* var. *villicaulis* (Fern.) Farwell, Pap. Michigan Acad. Sci. 1: 96. 1931. TYPE: U.S.A. Pennsylvania: Lancaster Co., On the Conestoga, near Binkley's Bridge, in limestone, *A. A. Heller,* 21 June 1901 (holotype, GH!; isotypes, F!, G!, US!).

Osmorhiza longistylis var. *brachycoma* S. F. Blake, Rhodora 25: 110. 1923. *Washingtonia longistylis* var. *brachycoma* (S. F. Blake) House, Bull. New York State Mus. 254: 529. 1924. TYPE: U.S.A. Maryland: Montgomery Co., slope in woods, vicinity of Cabin John, *S. F. Blake 6902* (holotype, US!; isotypes, GH!, TEX!).

Osmorhiza longistylis var. *imbarbata* Salamun, Amer. Midl. Naturalist 47: 253. 1952. TYPE: U.S.A. South Dakota: Lawrence Co., wooded bank of Spearfish Creek in Spearfish Canyon, approx. ¼ mi. N of Bridal Veil Falls, *A. L. Thorne,* 12 Aug. 1949 (holotype, UWM!; isotype, WIS!).

Plants rather stout, 6–10(–12) dm high; stems 1–2(–3), erect, densely pilose to villous, or often glabrous. Root system rather deep, tending toward vertical orientation, the roots carnose (breaking with a snap), with a sweet, anise-like scent. Leaves 2–3-ternate, broadly ovate, 8–25 cm long, sparsely hirsutulous (especially along the veins) to glabrescent; leaflets ovate to oblong-lanceolate, (3–)4–10 cm long, 2–5 cm wide, acute, serrulate-dentate, often incised or parted at the base; petioles 5–16 cm long. Umbels loose; peduncles 2–4, terminal and lateral, 5–13 cm long; involucre composed of 1–3(–4) linear to lanceolate, foliaceous, ciliate, reflexed bracts, each 5–10(–15) mm long, 1–1.5 mm wide; rays ascending, 1.5–5(–7.5) cm long; umbellets 4–6(–8) per umbel, (0–)1–3 of them producing only staminate flowers; involucel of 4–6 linear-lanceolate to ovate, acuminate, ciliate bractlets, each 2.5–6(–7) mm long, 0.7–1.8 mm wide, often strongly reflexed; pedicels (7–)9–18 per hermaphrodite umbellet, 3–13 per staminate umbellet, ascending, those of the hermaphrodite flowers 4–8(–9) mm long, those of the staminate flowers 3–6(–8) mm long. Hermaphrodite flowers (2–)3–5(–7) per umbellet, (8–)15–30(–33) per umbel, staminate flowers (3–)4–10(–14) per hermaphrodite umbellet, (23–)35–75(–86) per umbel; corolla white, showy; styles (including stylopodium) 2–3.6 mm long, stylopodium (0.4–)0.5–0.75(–0.8) mm long, high-conic, lacking a disc; pollen perprolate in shape; carpophore cleft about one-third of its length. Fruit oblong-fusiform, acute at the apex, concave furrowed, (10–)15–21(–22) mm long, the ribs sparsely to moderately hispid with retrorse bristles, especially toward the base, the caudate appendages 4–8 mm long. $n = 11$ (Wanscher, 1932; Bell & Constance, 1957). Figures 9c and 11.

Flowering period. April to early June.

Habitat. Dense to open deciduous forests, tending toward the somewhat drier, upland sites.

Common names. Aniseroot, Longstyle sweetroot, Smoother sweet cicely.

Representative specimens. U.S.A. ALABAMA: Lauderdale Co., *Murchison 171* (AUA); Tuscaloosa Co., Warrior River above Hurricane Creek, *Harper 144* (F, GH, MO, NY, US). ARKANSAS: Benton Co., Sulphur Springs, *Demaree 4974* (GH, MO, ORE); Fulton Co., Salem, *Demaree 26020* (UC); Hot Springs Co., Dripping Springs, *Scully 938* (UC, US). COLORADO: Boulder Co., Boulder Creek, Boulder, 1,615 m, *Weber,* 7 July 1954 (CAS, UC); Larimer Co., Spring Canyon, *Osterhout 344* (F, RM). CONNECTICUT: Fairfield Co., vicinity of Green's Farm, *Pollard 37* (US); Newcastle Co., Mt. Cuba, *Commons,* 25 June 1875 (MO). DISTRICT OF COLUMBIA: Washington, *Pennell 15005* (PH). GEORGIA: Burke Co., Shell Bluff, *Pyron & McVaugh 2494* (GA); Decatur Co., *Anderson,* 30 May 1923 (RM). ILLINOIS: Champaign Co., Brownfield Woods, N of Urbana, *Lowry 1207* (ILL); Cook Co., Riverdale, *Greenman 2627* (GH, MO); Du Page Co., Naperville, *Umbach,* 8 June 1897 (MO); Grundy Co., *Evers 72569* (ILLS); Jo Daviess Co., Apple River Canyon State Park, *G. N. Jones 15859* (ILL, MO); Macon Co., Spittler Woods, Mt. Zion, *Lowry 546* (ILL, MO, NY, UC); McLean Co., Funk's Grove, S of Bloomington, *Lowry 1141* (ILL); Piatt Co., Allerton Park, near Monticello, *Lowry 540* (ILL). INDIANA: Blackford Co., Hartford, *Deam 1078* (NY); Lawrence Co., Bedford, *Kriebel 1879* (DUKE, GH); Marion Co., Indianapolis, *Friesner 16672* (GH, MO, NY, SMU). IOWA: Appanoose Co., Sedan, *Shimek,* 15 May 1902 (WIS); Decatur Co., *Fitzpatrick & Fitzpatrick,* 24 May 1897 (F, GH, NY); Dubuque Co., NW of Luxembourg, *Shimek,* 2 July 1929 (UC); Emmet Co., Ft. Defiance St. Park, *Hayden 9426* (MO); Poweshiek Co., Grinnell, *M. E. Jones 145* (CAS, GOET, NY, RM, UC). KANSAS: Cowley Co., Winfield, *White s.n.* (MO); Crawford Co., *Holland 381* (KANU); Douglas Co., N of Baldwin, *Croat 116* (MO); Greenwood Co., *Stephens 2925* (KANU, SMU); Miami Co., 5 km SSE of Fontana, *Brooks et al. 11958* (KANU, MO); Riley Co., *Norton 700* (GH, MO, NY, P, RM, US). KENTUCKY: Fayette Co., Lexington, *Short s.n.* (GH, NY, UC); Greenup Co., Big Woods, 4.5 km from Boyd Co. line, *Smith et al. 3581* (GH, NY, US); Henry Co., 0.5 km N of Sand Ripple Creek, *Gentry 932* (NY); Union Co., McCotrey School, *Shacklett 296* (GH, NY, SMU). MAINE: Aroostook Co., Ft. Fairfield, *Fernald 2020* (GH); Hancock Co., Somersville, *Rand,* 18 July 1898 (UC); Kennebeck Co., Vassalboro, *Chamberlain s.n.* (GH). MARYLAND: Montgomery Co., near Cabin John, *Blake 6902* (GH, TEX, US). MASSACHUSETTS: Berkshire Co., New Marlboro, *Churchill,* 13 June 1919 (GH, MO); Essex Co., Manchester, *Chamberlain s.n.* (NY); Suffolk Co., Waverley, *Andrews,* 16 July 1892 (ILL). MICHIGAN: Emmet Co., 3 km S of Good Hart, *McVaugh 9282* (MICH, MO); Houghton Co., Calumet, *Minns s.n.* (GH); Ingham Co., E Lansing, *Lowry 1142* (ILL); Monroe Co., 5.5 km SE of Milan, *Robertson 109* (MICH). MINNESOTA: Chisago Co., Center City, *Taylor s.n.* (NY, RM, UC, US); Clearwater Co., Bear Pt., *Moyle 207* (GH, NY, UC, US); Pipestone Co., Pipestone Nat'l. Mon., *Moore 23192* (ILL). MISSISSIPPI: Desoto Co., *Kral 8582* (LAF); Oktibbeha Co., *Lott,* 28 Apr. 1940 (MISSA); Tate Co., *Pullen 64276* (GA, LAF). MISSOURI: Franklin Co., Arboretum, Gray's Summit, *Sharp 201* (MO); Grundy Co., 20 km W of Spickard, *Steyermark 11036* (MO); Harrison Co., W of Blythedale, *Steyermark 10976* (MO); Osage Co., S of Meta, *Steyermark 69719* (MO); Phelps Co., 6.5 km SE of St. James, *Steyermark 22179* (UC); Wright Co., 3 km SE of Cedar Gap, *Steyermark 23671* (F, MO, UC). MONTANA: Cascade Co., Lower Falls of the Missouri, *Williams 275* (MONT, US); Fallon Co., *Stephens 23282* (KANU); Gallatin Co., Bozeman, *Blankinship,* 18 Aug. 1898 (MO, MONT); Stillwater Co., Absarokee, *Hawkins,* 15 June 1918 (MONT, WIS). NEBRASKA: Antelope Co., Neligh, *Harper,* 30 May 1888 (WIS); Blaine Co., Halsey, *Pool,* 21 June 1912 (MO); Richardson Co., 1.5 km N of Barada, *Reynolds 3085* (MO, UC); Sioux Co., *Stephens 16324* (KANU). NEW HAMPSHIRE: Cheshire Co., Walpole, *Fernald 417* (GH); Grafton Co., Lebanon, *Kennedy s.n.* (GH). NEW JERSEY: Burlington Co., Vincetown, *Long 9790* (GH); Gloucester Co., *Fogg 8564* (PH). NEW YORK: Delaware Co., N Harpersfield, *Topping 166* (ILL, US); Erie Co., Buffalo, *Kinnicutt s.n.* (NY); St. Lawrence Co., Hermon, *Phelps 1615* (GH, US); Suffolk Co., Cold Spring Harbor, *Banker 2830* (NY). NORTH CAROLINA: Buncombe Co., 1.5 km N of Warren Wilson College, *Lowry 1144* (ILL); Lee Co., 3 km E of Moncure, *Wood 857* (MO). NORTH DAKOTA: Benson Co., Peninsula of Lake Ibsen, *Lunell,* 8 July 1901 (NY, RM, US); Golden Valley Co., *Ste-*

phens 49996 (KANU); Pembina Co., 3 km S of Walhalla, *Willenbring 687* (MO); Richland Co., Abercrombie, *Bergman 1769* (MO, RM, UC). OHIO: Coshocton Co., *Moldenke 12516* (UC); Hamilton Co., Madisonville, Cincinnati, *Lowry 547* (ILL, MO, UC); Preble Co., Devil's Backbone, near Camden, *Cobbe 104* (CAS, G, UC); Scioto Co., Camp Gordon, Friendship, *Demaree 10647* (CAS, GH, MO, SMU, UC). OKLAHOMA: Canadian Co., Devil's Canyon, *Goodman 5060* (OKL, UC); Cherokee Co., Camp Egan, E of Tahlequah, *Goodman 6811* (ILL, OKL); Creek Co., Sapulpa, *Bush 1059* (MO, NY). PENNSYLVANIA: Berks Co., *Berkheimer 16799* (PH); Centre Co., *Wahl 17229* (PH); Elk Co., Benezett, *Wahl 612* (GH, PH); Lancaster Co., Conestoga, near Binkley's Bridge, *Heller,* 21 June 1901 (F, G, GH, US); Lebanon Co., *Wherry,* 23 May 1959 (PH); Somerset Co., *Pohl 5574* (PH). RHODE ISLAND: Kent Co., Warwick, *Congdon,* 3 June 1877 (CAS, MO, NY). SOUTH CAROLINA: Lancaster Co., *Bozeman et al. 8812* (AUA, CAS). SOUTH DAKOTA: Brookings Co., Brookings, *Thornber,* 4 July 1894 (ARIZ, MO, UC); Harding Co., W Short Pines, *Visher 459* (F); Lawrence Co., NW of Whitewood, *D'Arcy 5761* (MO). TENNESSEE: Cheatham Co., 2.5 km SE of Ashland City, *Kral 26796* (UC); Davidson Co., Nashville, *Gattinger,* 28 Mar. 1886 (F, NY, US); Knox Co., Knoxville, *Ruth 442* (MO); Lauderdale Co., *Sharp 12115* (TENN). TEXAS: Tarrant Co., near Trinity, *Ruth 601* (NY, PH, US). VERMONT: Addison Co., Hancock, *Dutton,* 21 June 1914 (GH, MO); Lamoille Co., *Knowlton,* 18 July 1916 (PH). VIRGINIA: Fairfax Co., Dead Run, E of Plummer's Island, *Mathias 1392* (CAS, GH, MO, NY, UC, US); James City Co., 1 km W of Williamsburg, *Grimes 3601* (NY); Surry Co., Claremont Wharf, *Fernald & Long 8386* (GH, MO, NY, US). WEST VIRGINIA: Berkeley Co., E of Martinsburg, *A. G. Jones 4218* (ILL, MO); Monongalia Co., Monongahela River, *Millspaugh 173* (NY); Pendleton Co., Snowy Mt., *Rydberg 9122* (NY, PH). WISCONSIN: Brown Co., Green Bay, *Schuette s.n.* (F); Iowa Co., Blue Mounds, *Clikenian et al.,* 5 June 1932 (UC); Walworth Co., *Salamun,* 12 June 1948 (ILL, MO). WYOMING: Big Horn Co., mouth of Dry Medicine Lodge Canyon, *Dueholm 9509* (RM); Converse Co., 16 km W of Douglas, *Porter 4511* (RM, WTU); Sheridan Co., Tongue Creek, N of Big Horn Coal Mine, 1,100 m, *Brink 1366* (ILL, MO).

CANADA. ALBERTA: Edmonton Dist., *Moss 6363* (DAO); Medicine Hat Dist., *Macoun 858* (GH). MANITOBA: Portage-la-Prairie Dist., 4 km N of Portage-la-Prairie, *Boivin & Breitung 6501* (DAO); Winnipeg Dist., Winnipeg, *Johnson 1044* (NY); Thalberg, *Krivda,* 20 June 1960 (NY); Ft. Ellice, *Macoun & Herriot 77116* (NY). NEW BRUNSWICK: Charlotte Co., St. Andrews, *Malte 843/29* (GH, US); Kent Co., Bass River, *Fowler,* 5 July 1873 (GOET, WIS). NOVA SCOTIA: Cumberland Co., Clay, Green Bay, *Roland 41583* (GH). ONTARIO: Elgin Co., St. Thomas, *Macoun 81729* (F); Hastings Co., Ox Pt., near Point Anne, *Soper & Shields 4656* (MO); Manitoulin Dist., S of Little Current, Manitoulin Island, *Fernald & Pease 3448* (GH, US); Northumberland Co., Presqu'ile Park, *Soper & Shields 4644* (MO); Rainy River Dist., *Garton 8862* (DAO); Thunder Bay Dist., Middle Falls on Hwy. 61, *Garton 2061* (MO, DAO). QUÉBEC: Bonaventure Co., Restigouche River, Matapedia, *Collins & Fernald s.n.* (GH); Gaspé Co., *Dansereau 180* (DAO); Missisquoi Co., *Perron 66-210* (DAO); Papineau Co., *Charlebois 1401* (DAO); Temiscamingue Co., Baie Girard, *M.-Victorin 8546* (GH, NY); Vaudreuil Co., *Gervais & Lavigne,* 4 June 1959 (G). SASKATCHEWAN: Assiniboia Dist., 8 km S of Estevan, *Boivin & Perron 11823* (DAO); Lake Centre Dist., Outlook, *Boivin & Alex 9848* (DAO); Moose Jaw Dist., Moose Jaw Creek, *Macoun 858* (NY); Qu'Appelle Dist., Qu'Appelle River, near mouth of Lake Katepwe, *Boivin & Dore 7591* (DAO); Wood Mountain Dist., 1.5 km S of Willowbunch, *Boivin & Gillett 8838* (DAO); Cypress Hills, *Breitung 4719* (DAO, MO).

Clarke (1879) included all representatives of *Osmorhiza* sect. *Osmorhiza,* including *O. longistylis,* under the name *O. claytonii.* Similarly, MacMillan (1892) included *O. longistylis* in his broad concept of *Myrrhis aristata.*

Three varieties of *Osmorhiza longistylis* have been described on the basis of quantity of indument (Fernald, 1908; Blake, 1923; Salamun, 1952). This character, however, was found to be highly variable, and thus none of these infraspecific taxa is upheld (Lowry, 1976; Lowry & Jones, 1979a).

IIb. **Osmorhiza** Raf. sect. **Mexicanae** Constance & Shan ex Lowry & Jones, sect. nov. TYPE: *O. mexicana* Griseb.

Uraspermum § *Osmorhiza* (Raf.) Kuntze, Lexicon 582. 1904, pro parte.

Scandix 2. [sect.] *Urascandix* Koso-Polj., Bull. Soc. Imp. Naturalistes Moscou 29: 143. 1916, pro parte.

Osmorhiza sect. *Mexicanae* Constance & Shan, Univ. Calif. Publ. Bot. 23: 112. 1948, nom. nud.

Involucrum deficiens vel interdum ab 1–3 bracteis parvis constitutum; bracteae lineares vel lanceolatae, patentes vel reflexae; involucellum generaliter conspicuum, ab 1–6 bracteolis patentibus vel reflexis constitutum. Styli cum stylopodio 0.5–1.2 mm longi, stylopodium 0.2–0.8 mm longum, depresso-conicum vel depressum, saepe cum disco conspicuo.

Involucre wanting, or sometimes composed of 1–3 small, linear to lanceolate, spreading to reflexed bracts; involucel generally conspicuous, composed of 1–6 spreading to reflexed bractlets. Styles plus stylopodium 0.5–1.2 mm long, stylopodium 0.2–0.8 mm long, low-conic to somewhat depressed, often with a conspicuous disc.

5. **Osmorhiza glabrata** Philippi. Linnaea 28: 653. 1856. *Uraspermum glabratum* (Philippi) Kuntze, Revis. gen. pl. 1: 270. 1891. TYPE: Chile. Bío-Bío: Santa Barbara, *C. Gay 1514* (holotype, SGO; photograph of holotype, ILL!; 2 possible syntypes, P!).

Myrrhis renjifoana Philippi, Anales Univ. Chile 85: 725. 1894. *Elleimataenia renjifoana* (Philippi)

Koso-Polj., Bull. Soc. Imp. Naturalistes Moscou 29: 164. 1916. TYPE: Chile. Ñuble: Valle de las Nieblas, near Termas de Chillán, *F. Philippi 2029* [lectotype, SGO (no. 053472) (designated herein); photographs of lectotype, ILL!, UC!; isolectotype, SGO (no. 041594); photograph of isolectotype, ILL!].

Plants rather stout, 1–5(–6) dm high; stems 1–2(–3), erect to ascending, villous to hirsutulous, or often glabrate. Root system rather deep. Leaves ternate-bipinnate, deltoid to broadly ovate, 5–10(–13) cm long, glabrous to hirsutulous along the veins and rachis; leaflets ovate, (0.6–)1–2.5 cm long, 0.5–1.3 cm wide, acute or acuminate, laciniately lobed to parted or pinnatifid, with linear to linear-lanceolate ultimate divisions; petioles 4–12(–15) cm long. Umbels loose to somewhat congested; peduncles 2–3, terminal and lateral, 4–15 cm long; involucre wanting; rays stiffly ascending, (1–)1.5–8(–9.5) cm long; umbellets (2–)3–13 per umbel, 1–5(–6) of them producing only staminate flowers; involucel of (0–) 1–2 minute, linear, acuminate, ciliate bractlets; pedicels (3–)4–10 per hermaphrodite umbellet, 2–7(–9) per staminate umbellet, stiffly ascending to nearly erect, those of the hermaphrodite flowers (2–)2.5–7(–9) mm long, those of the staminate flowers (1.5–)2.3–5.5(–6.5) mm long. Hermaphrodite flowers (2–)3–5 per umbellet, (9–)15–30(–38) per umbel, staminate flowers (1–)2–7(–9) per hermaphrodite umbellet, (7–)15–60(–82) per umbel; corolla white, rather inconspicuous; styles (including stylopodium) (0.9–)1–2 mm long, stylopodium 0.4–0.8 mm long, conic, often with a conspicuous disc; carpophore cleft about one-third of its length. Fruit linear-fusiform, acute at the apex, concave furrowed, (13–)14–20(–25) mm long, the ribs glabrous to moderately hispid with retrorse bristles, especially toward the base, the caudate appendages (0.5–)1–6 mm long. Figures 9e and 18.

Flowering period. November to January (with one collection flowering in April).

Habitat. Seasonally moist *Nothofagus* forests to open, grassy slopes.

Common names. Glabrate sweet cicely, Andean sweet cicely.

Representative specimens. ARGENTINA. NEUQUÉN: Dept. Alumine, Parque Nac. Lanin, *Eskuche 934* (UC, WIS); Dept. Huiliches, Lago Huechu-Lauquen, *Castellanos 20507* (UC); Dept. Minas, Lagunas Epu-laquén, 1,600 m, *Boelcke et al. 10978* (UC); Cordillera del Viento, 2,000 m, *Boelcke et al. 11634* (UC); Paso del Macho, 2,280 m, *Boelcke et al. 13955* (UC).
CHILE. BÍO-BÍO: Sierra Velluda, *Poeppig 905* (BM, BR, P). COLCHAGUA: San Fernando, Termas Vegas del Flaco, *Montero O. 1214* (UC); Cordillera de Colchagua, *Pirian 159* (GH); Termas Vegas del Flaco, 2,500 m, *Zöllner 6430* (UC). CURICÓ: hills NE of Los Baños, the Quebrada, 2,500 m, *Aravena 33301* (UC). MALLECO: Volcán Longuimay, 1,500 m, *Constance & Sparre 3580* (BM, F, K, MICH, MO, UC, US). ÑUBLE: Cordillera de Chillán, *Germain s.n.* (BM, G, K); Termas de Chillán, *Jaffuel 2035, 2837, 3715, 3717* (GH); Chillán, *Philippi 3469* (UC), *s.n.* (photographs in F, NY, UC); Baños de Chillán, *Philippi & Borchers s.n.* (BM), *Werdermann 1571* (NY). SANTIAGO: Río Yeso, Lag. Pinquenes, 2,500 m, *Biese 800* (NY); Maipo, 2,700 m, *Claude-Joseph 2964* (US); Valdes-Tál (Volcántal), 2,800 m, *Grandjot s.n.* (MO, UC); valley of the Maipo River, near the Baths of Colima, 2,500 m, *Zöllner 9715* (ILL). TALCA: Laguna Maule, 2,400 m, *Zöllner 5824* (ILL, UC).

Constance and Shan (1948: 120) included *Osmorhiza glabrata* in their section "*Glycosmae*" [= subg. *Glycosma*], stating that it "is remarkable for its close similarity to *O. occidentalis.*" However, the evidence presented here indicates that the affinities of *O. glabrata* lie with *O. mexicana* and *O. brachypoda* rather than with *O. occidentalis.* Constance and Shan's misinterpretation of the relationships of *O. glabrata* most likely was due to the very limited amount of material available to them; they cite only nine collections of this species.

In their discussion of *Osmorhiza glabrata,* Constance and Shan (1948: 120) stated, "The single specimen which caused the most trouble in our study was *Pennell 12487,* from Baños de Chillán, Chile. This plant has the ascending rays and long styles of *O. glabrata,* but combines these characteristics with appendaged, bristly fruit and subentire leaflets. We can only suggest that the plant in question may be the result of interbreeding between *O. glabrata* and either *O. chilensis* or *O. obtusa* [= *O. depauperata*], all three of which occur in this area." We have tried to locate this specimen, with no success. In any case, Pennell's collection is probably much less of an anomaly than Constance and Shan suggest; appendaged, bristly fruits are not at all uncommon in *O. glabrata.* Furthermore, the occurrence of subentire leaflets in this specimen may represent an intermediate between *O. glabrata* and *O. mexicana* subsp. *mexicana.* The existence of such a specimen would not be surprising because the two taxa involved are closely related, and this would seem a more reasonable explanation than assuming intersectional hybridization involving *O. glabrata* and either *O. chilensis* or *O. depauperata.*

Clos (1848) erroneously interpreted plants referable to *O. glabrata* as being conspecific with the European species *Myrrhis odorata* (L.) Scopoli.

6. Osmorhiza mexicana Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 147. 1879. *Washingtonia mexicana* (Griseb.) Rose, Contr. U.S. Natl. Herb. 8: 337. 1905. TYPE: Mexico. *Schaffner 37* (holotype, GOET!; 2 isotypes, P!). [The holotype is marked in Grisebach's hand "*Osmorhiza mexicana m*(*ihi*)," his annotation for the original material. Several paratypes in GOET are marked by Grisebach "*Osmorhiza mexicana* Gr.," his annotation for authentic material other than the holotype, according to G. Wagenitz, GOET.]

Uraspermum aristatum β [subsp.] *brevistyle* var. *laciniatum* Kuntze, Revis. gen. pl. 1: 270. 1891. (No type material has been located.)

Plants slender to rather stout, stems 1–2, erect to ascending. Leaves 2–3-ternate, villous or pilose, especially on the veins below; leaflets ovate to ovate-oblong, acute to acuminate, coarsely serrate to divided at the base. Umbels loose to rather open; involucre wanting, or often composed of 1–2 linear, foliaceous, ciliate bracts; rays spreading-ascending; involucel of 1–4 linear, acuminate, ciliate bractlets. Styles (including stylopodium) 0.5–1 mm long, stylopodium low-conic to somewhat depressed, often with a disc; carpophore cleft about one-fourth of its length. Fruit variable in characters depending on the subspecies.

At their morphological extremes, the two subspecies of *Osmorhiza mexicana* (subsp. *mexicana* and subsp. *bipatriata,* see below) are very distinct. A number of truly intermediate collections, however, mark a transition between these taxa. For example, two specimens from Cerro Potosí, Nuevo León, Mexico (*C. H. Mueller 2231* and *R. A. Schneider 1108*) have fruit with retrorse bristles and short caudate appendages, but are in most other respects similar to specimens of the subspecies *bipatriata.* Typical representatives of both subspecies also occur on Cerro Potosí. Another collection, *G. C. Rzedowski 22915,* from Hidalgo, exhibits a similar intermediate combination of characters. Also, a number of collections from northern Mexico clearly referable to the subspecies *mexicana* have remarkably short fruit, indicating a certain similarity to the subspecies *bipatriata.* Furthermore, many individuals of otherwise typical *O. mexicana* subsp. *bipatriata* observed on Cerro Potosí (*Lowry & M. J. Warnock 3182, 3188*) have fruit armed with a few bristles toward the base, while others have completely glabrous fruit.

The strong similarity and intermediacy observed between the two subspecies of *Osmorhiza mexicana* has not gone unnoticed in the past. Constance and Shan (1948: 121) stated that *O. mexicana* subsp. *bipatriata* "was not included in the 'North American Flora,' because only the Mexican specimens had come to the attention of Mathias and Constance at the time that account was published (1944), and these had been regarded as somewhat aberrant representatives of *O. mexicana* (subsp. *mexicana*)."

Although Constance and Shan (1948) described the taxon *Osmorhiza bipatriata* as a distinct species they, too, recognized its strong resemblance to the plants of *O. mexicana,* citing two of the intermediates mentioned above (*Mueller 2231* and *Schneider 1108*).

6a. Osmorhiza mexicana Griseb. subsp. **mexicana**

Plants slender to rather stout, 4–8(–10) dm high; stems hirsutulous throughout. Root system rather deep, the roots weakly to rather strongly anise-scented. Leaves 2–3-ternate, broadly ovate to deltoid, 5–12(–15) cm long, villous or pilose, especially below; leaflets ovate, (1.5–)2–4 cm long, 1.5–2.5 cm wide, acute to acuminate, coarsely serrate to incised and pinnately lobed at the base; petioles 6–14 cm long. Umbels rather loose; peduncles 2–3(–4), terminal and lateral, 7–15 cm long; involucre wanting, or sometimes composed of 1–2 linear, foliaceous, ciliate bracts, each (2–) 5–10 (–13) mm long, 0.3–1 mm wide; rays spreading-ascending, 2.2–10(–11) cm long; umbellets 2–5(–7) per umbel; involucel of (1–)2–4 linear, acuminate, ciliate bractlets, each (1.5–)2.5–9.5 mm long, 0.3–1 mm wide, spreading to reflexed; pedicels (2–)5–11 per umbellet, spreading-ascending, those of the hermaphrodite flowers (1–)2–8.5(–12) mm long, those of the staminate flowers 2–5(–6) mm long. Hermaphrodite flowers (2–)3–6 per umbellet, (8–)12–32 (–41) per umbel, staminate flowers (0–)2–7 per umbellet, (0–)5–25(–35) per umbel; corolla white or greenish white, somewhat showy; styles (including stylopodium) 0.6–1 mm long, stylopodium 0.2–0.5(–0.6) mm long, low-conic to somewhat depressed, often with a conspicuous disc.

Fruit linear-oblong, tapering to a short beak at the apex, concave furrowed, (10–)11–20 mm long, the ribs moderately to densely hispid with retrorse bristles, especially toward the base, the caudate appendages (1.5–)2–8.5(–10) mm long. $n = 11$ (Bell & Constance, 1966; Constance et al., 1976). Figures 9f and 17.

Flowering period. Late May to July (Mexico); July (Central America); November and December (South America).

Habitat. Moist forests, at middle and higher elevations.

Common names. Mexican sweet cicely, Mexican sweetroot, Cillandrillo (Mexican Indian; Oaxaca).

Representative specimens. ARGENTINA. CATAMARCA: Dept. Andalgalá, Comné Esquina Grande, *Jörgensen 1812* (F, GH, MO, US). CÓRDOBA: Dept. Calamuchita, Sierra Arhala de Córdoba, *Hieronymus,* 3 Dec. 1878 (UC); El Vallecito, Sierra Grande, 2,000 m, *A. T. Hunziker 8651* (UC, WTU); La Cumbrecita, 1,500 m, *Roig 17767* (UC). JUJUY: Dept. Santa Bárbara, Sierra El Centinela, 1,950 m, *Cabrera et al. 17299* (UC, WIS). SALTA: Dept. Guachipas, Alemania, 1,300 m, *Venturi 9810* (GH, K, MO). TUCUMÁN: Questa del Garabatal, Sierra del Tucumán, *Lorentz & Hieronymus 863* (GOET); near la Cienega, *Lorentz & Hieronymus 668* (GOET).

BOLIVIA. COCHABAMBA: N of Yungas, 3,200 m, *Buchtien 659* (GH, NY, US). LA PAZ: Prov. Murillo, upper Valle de Zongo, 3,500 m, *Solomon 5228* (MO), *Tate 194* (NY); near Sorata, 3,100 m, *Mandon 594* (BM, G, GH, GOET, K, NY, P, UC).

COLOMBIA. TOLIMA: Paramó de Ruiz, 3,500 m, *Lehmann 3074* (BM, K, US), *Pennell 3101* (NY, US).

COSTA RICA. ALAJUELA: San Juan, Cerrido, *Brenes,* 21 Jan. 1906 (NY). CARTAGO: Volcán de Irazú, 2,750 m, *Kuntze 2270* (K, NY); 3,000 m, *Pittier & Durand 4073* (US); Chicuá, Irazú, 2,750 m, *J. León 2680* (CR); Près du sommet de l'Irazú, 3,000 m, *Tonduz 4273* (BR, CR); Sabana larga, S of Volcán de Irazú, 2,900 m, *Pittier 44* (K), *200* (BR, CR, US). SAN JOSÉ: Cerro de las Vueltas, 2,800 m, *Standley & Valerio 43592* (K, US), *43669* (US).

GUATEMALA. CHIMALTENANGO: Chichavac, 2,500 m, *Skutch 499* (CAS, MICH); Volcán de Agua, 2,450 m, *Johnston 809* (F). HUEHUETENANGO: near Hacienda de Chaucol, Sierra de los Cuchumatanes, 3,350 m, *Nelson 3645* (GH, NY, US), *Skutch 1210* (F, GH); near Tunima, Sierra de los Cuchumatanes, 3,450 m, *Steyermark 48383* (F, UC); Cerro Chémal, Sierra de los Cuchumatanes, 3,750 m, *Steyermark 50307* (F). QUEZALTENANGO: Volcán Santo Tomás, *Steyermark 34714* (F, UC); 5 km N of Ostuncalco, Sierra Madre, 2,600 m, *Williams et al. 25467* (GH, NY, US). SACATEPEQUEZ: Volcán de Agua, above Santa María, *Bell & Duke 16987* (UC). SAN MARCOS: San Luis, 3.8 km W of Ixchiguan on road to Tacana, 3,450 m, *Beaman 3247* (GH, UC, US). SOLOLÁ: Volcán Tolimán, side facing Volcán Atitlán, 2,900 m, *Steyermark 47581* (F).

MEXICO. CHIAPAS: near San Cristobal, *Nelson 3188* (US). CHIHUAHUA: La Rocha, Sierra Mohinora, 2,300 m, *Correll & Gentry 23138* (GH, LL), *Nelson 4864* (GH, US); 16 km SW of Guadalupe y Calvo, Cerro Mohinora, *Straw & Forman 2013* (UC). DISTRITO FEDERAL: Miguel-Hidalgo Park, 3,200 m, *Bell & Duke 16778* (GH, K, MICH, MO, NY, TEX, UC); Desierto de los Leones, *Kenoyer 562* (MICH), 9 July 1938 (ARIZ), *MacDaniels 83* (F), *Sharp & Gilly 22* (MICH); Contreras, *Lyonnet 1623* (US); Sierra de Ajusco, 2,450 m, *Pringle 6615* (BM, BR, CAS, F, G, GH, GOET, K, MO, NY, P, PH, RM, UC, US); Cuarto Dinamo, 3,100 m, *A. Ventura A. 3586* (G); Los Dinamos, 3,000 m, *A. Ventura A. 3492* (G). HIDALGO: 3.8 km SW of Cabrera on Hwy. 105, 2,800 m, *Bell & Duke 16813* (MICH, TEX, UC); El Chico Nat'l. Park, 16 km NE of Pachuca, 2,750 m, *Weller 582* (UC); Real del Monte, 2,800 m, *Hernandez X. 464* (LL), *Sharp 44593* (UC); Cerro de las Ventanas, 6 km N of Pachuca, 2,900 m, *Rzedowski 26813* (CAS, MICH). JALISCO: Nevado de Colima, 2,700 m, *McVaugh 10047* (MICH, UC), *12853* (K, MICH, SMU, UC, US), *Gregory & Eiten 295* (GH, MICH, MO). MÉXICO: Valleé de Mexico, *Bourgeau 781* (BR, GH, K, UC, US); Méson Viejo, Temascaltepec, *Hinton 1308* (F, GH, K, US); Las Cruces, Temascaltepec, 3,260 m, *Hinton 4899* (BM, K, US), *Pringle 5208* (MO, US); Crucero-Agua Blanca, Temascaltepec, *Hinton et al. 8324* (ARIZ, BM, G, GH, K, LL, MO, NY, PH, TEX, UC, WTU); Vaqueria del Jacal, 3,000 m, *Liebermann 12240* (F, MO, US); Ixtapaluca, above Río Frio, 3,000 m, *Sharp & Gilly 69* (MICH). MICHOACAN: *Arsène s.n.* (CAS). MORELOS: 9.25 km W of Tres Cumbres, 2,800 m, *Steingraeber & Steingraeber 150* (UC, WIS). NUEVO LEÓN: Cerro El Infernillo, S of Galeana, 2,750 m, *Bell & Duke 16563* (UC); Hwy. 51, 40 km S of junction with Hwy. 54, 2,400 m, *Lowry & Warnock 3181a* (MO); Ojo de Agua, foot of Cerro Potosí, 2,000 m, *Sharp 45711* (NY, UC). OAXACA: Cerro de Cabeza de Vaca, trail to Cerro San Felipe, 2,750 m, *Bell & Duke 16884* (UC); Sierra San Felipe, 3,000 m, *Pringle 5547* (F, US); Cordillera de Oaxaca, 2,750 m, *Galeotti 2751* (G, K); 21 km N of Ixtlán de Juárez, 2,800 m, *Weller 566* (UC). PUEBLA: Orizaba, 3,000 m, *Liebmann 12241* (F, GH, US), *Müller 1722* (GH, NY), *Rose & Hay 5726* (US), *Standley 12241* (UC); 3,650 m, *Seaton 195* (F, GH, US); Popocatepetl, *Rose & Hay 6249* (US); Esperanza, *Purpus 7456* (MO, NY, UC, US). SAN LUIS POTOSÍ: Sierra de Alvarez, Sierra Madre Oriental, 2,300 m, *Palmer 127* (US), *Pennell 17883* (PH, US). VERACRUZ: near El Puerto, 2,350 m, *Sharp 44680* (GH, NY).

PERU. CUZCO: Ollantiatambo, 3,000 m, *Cook & Gilbert 747* (US); Veronica, between Cuzco and Machupichu, 3,500 m, *Rauh & Hirsch P1026* (UC); between Cachu-pampa and Chile-chile, 2,500 m, *Vargas 9697* (GH, K, MO, UC), 3,000 m, *Vargas 1352* (F).

Weddell (1861) and Hemsley (1880) considered Central and South American populations as *Osmorhiza brevistylis* DC.

6b. Osmorhiza mexicana Griseb. subsp. **bipatriata** (Constance & Shan) Lowry & Jones, comb. et stat. nov. *Osmorhiza bipatriata* Constance & Shan, Univ. Calif. Publ. Bot.

23: 121. 1948. TYPE: U.S.A. Texas: Jeff Davis Co., in wet ground at spring, W branch Madera Canyon on slope of Mt. Livermore, Davis Mts., *L. C. Hinckley,* 26 July 1937 (holotype, NY!; isotypes, or possibly paratypes, because label data are not identical to those of the holotype, ARIZ!, GH!).

Plants slender, 2–7 dm high; stems sparingly hirsutulous to glabrescent. Root system somewhat shallow, with a weak anise-like scent. Leaves 2–3-ternate, ovate to broadly ovate, 4–10(–14) cm long, villous or pilose, especially on the veins below; leaflets ovate to ovate-oblong, (0.7–)1.2–4 cm long, 0.5–3 cm wide, acute to acuminate, coarsely serrate-laciniate to lobed or divided at the base; petioles 4–10(–12) cm long. Umbels loose and rather open; peduncles 1–3, terminal and often lateral, 3–15(–18) cm long; involucre wanting, or often composed of 1(–2) linear, foliaceous, ciliate bracts, each 4–10 mm long, 0.5–0.8 mm wide; rays spreading-ascending, (1.4–) 1.6–6.5 (–7.5) cm long; umbellets (2–)3–9 per umbel, (0–)1–4(–6) of them producing only staminate flowers; involucel of 1–4 linear, acuminate, ciliate bractlets, each (2–)3–4.5 mm long, 0.3–1 mm wide, spreading; pedicels (3–)4–20 (–22) per hermaphrodite umbellet, (3–)4–17 per staminate umbellet, spreading, those of the hermaphrodite flowers (3–)4–7.5(–8) mm long, those of the staminate flowers (1.5–)2–3.5(–4) mm long. Hermaphrodite flowers 1–3 per umbellet, (2–)5–10 per umbel, staminate flowers (4–)6–21 per hermaphrodite umbellet, (33–)40–70(–125) per umbel; corolla white, or sometimes tinged with purple, pink, or green, rather inconspicuous; styles (including stylopodium) 0.5–0.75 mm long, stylopodium 0.25–0.3 mm long, low-conic, often with a conspicuous disc. Fruit linear-fusiform, tapering into a short beak at the apex, concave furrowed, 9–11(–12) mm long, the ribs glabrous, or with a few retrorse bristles at the base, the caudate appendages lacking, or sometimes to 1.8 mm long. Figures 9g and 17.

Flowering period. June and July.

Habitat. Moist, generally shaded ravines and canyons, from 2,100 to over 2,750 m.

Common names. None.

REPRESENTATIVE SPECIMENS. U.S.A. TEXAS: Jeff Davis Co., Upper Madera Canyon, NW side of Mt. Livermore, 2,300 m, *Hinckley 408* (F, NY), *3589* (NY, UC), *B. H. Warnock & Hinckley 4147* (NY), *B. H. Warnock 7479* (SMU, TEX).

MEXICO. COAHUILA: NW of Campo Cinco, Madera del Carmen, 2,400 m, *Lowry & M. J. Warnock 3130, 3149* (ILL, MEXU, MO, NY, TEX, UC), *Fryxell 2689* (UC), *2703* (CAS); Upper Dos Canyon, Madera del Carmen, 2,450 m, *Fryxell 2722* (MO, UC). NUEVO LEÓN: 2.2 km below microwave tower, Cerro Potosí, 3,000 m, *Lowry & M. J. Warnock 3188* (ILL, MEXU, MO, NY, TEX, UC); microwave tower, Cerro Potosí, 3,200 m, *McGregor et al. 252* (UC), *339* (NY, SMU, UC); Cerro Potosí, *Schneider 1043* (F).

The following collections exhibit combinations of characters intermediate between *O. mexicana* subsp. *mexicana* and subsp. *bipatriata*:

MEXICO. HIDALGO: Penas Largas, near Tezoantla, 2,750 m, *Rzedowski 22915* (CAS, MICH, ORE, TEX). NUEVO LEÓN: Canyon below Las Canoas, Cerro Potosí, *Mueller 2231* (GH); Hacienda La Jolla, 2,600 m, *Schneider 1108* (F).

7. **Osmorhiza brachypoda** Torrey in Durand, J. Acad. Nat. Sci. Philadelphia II, 3: 89. 1855. *Myrrhis brachypoda* (Torrey) E. Greene, Fl. francisc. 332. 1892. *Washingtonia brachypoda* (Torrey) A. A. Heller, Cat. N. Amer. pl. 5. 1898. *Scandix brachypoda* (Torrey) Koso-Polj., Bull. Soc. Imp. Naturalistes Moscou 29: 143. 1916. TYPE: U.S.A. California: Nevada Co., near the banks of Deer Creek, Nevada City, *H. Pratten,* July 1851. (This specimen has not been located.)

Osmorhiza brachypoda var. *fraterna* Jepson, Fl. Calif. 2: 670. 1936. TYPE: U.S.A. California: San Bernardino Co., Arroyo Seco, San Gabriel Mts., 600 m, *F. W. Peirson 451a* (holotype, JEPS!).

Plants rather stout, 3–8 dm high; stems 1–2 (–3), erect, villous to hirsutulous. Root system rather deep, the roots weakly to moderately anise-scented. Leaves 2–3-ternate, ovate to deltoid, 10–18(–20) cm long, hirsutulous, especially below and along the veins; leaflets ovate, 2–6(–8) cm long, 1–4 cm wide, acute or obtuse, coarsely serrate, incised and pinnately lobed at the base; petioles 5–18(–22) cm long. Umbels somewhat congested, peduncles 2–4, terminal and lateral, 9–18 cm long; involucre wanting, or often composed of 1–3 small (or very rarely large and leaf-like), linear-lanceolate, foliaceous, ciliate bracts; rays spreading-ascending, (3.3–)3.8–12(–12.5) cm long; umbellets 2–5 per umbel; involucel of 2–6(–7) linear to lanceolate, acute, ciliate bractlets, each (1–)2–9.5(–15) mm long, (0.3–)0.5–1.3(–5) mm wide, spreading or reflexed; pedicels (2–)4–14(–16) per umbellet, ascending, those of the hermaphrodite flowers 1–4.5(–7.5) mm long, those of the staminate flowers (2–)2.8–6(–6.5) mm long.

Hermaphrodite flowers (1–)2–10 per umbellet, (6–)10–35(–43) per umbel, staminate flowers (0–)1–6(–8) per umbellet, (0–)5–30(–40) per umbel; corolla greenish white, somewhat inconspicuous; styles (including stylopodium) (0.6–)0.7–1.2(–1.3) mm long, stylopodium 0.2–0.5(–0.6) mm long, low-conic to somewhat depressed, often with a conspicuous disc; carpophore cleft about one-third of its length. Fruit oblong-fusiform, tapering to a narrow beak at the apex, deeply concave furrowed, (12–)13–18(–20) mm long, the ribs densely hispid with retrorse bristles, especially toward the base, the caudate appendages (0.5–)0.9–3.8(–4) mm long. $n = 11$ (Constance et al., 1976). Figures 9h and 16.

Flowering period. March to early May.

Habitat. Seasonally moist forests at lower to fairly high elevations in the mountains.

Common names. California cicely, California sweet cicely, Orris root, Sweet cicely.

Representative specimens. U.S.A. ARIZONA: Gila Co., Collom Camp, base of Mazatzal Mts., 1,200 m, *Collom 866* (ARIZ, UC); Hells Canyon, Mazatzal Mts., *Harrison et al. 7815, 7830* (ARIZ). CALIFORNIA: Amador Co., 2.5 km E of Oleta, *Raven 9123* (CAS, JEPS); Contra Costa Co., Mt. Diablo, 300 m, *Bowerman 2108* (CAS, UC); Kern Co., mouth of Kern Canyon, Greenhorn Mts., *Benson 3342* (CAS, NY, RM); Los Angeles Co., Evey Canyon, N of Claremont, *Lowry 1481, 1482* (ILL); Monterey Co., Arroyo Seco Camp, 29 km NW of Greenfield, Santa Lucia Mts., 760 m, *Constance 3311* (ARIZ, CAS, G, K, MO, NY, RM, UC); Orange Co., Silverado Canyon, Santa Ana Mts., 380 m, *Munz & Harwood 3722* (NY, RM); Riverside Co., Temescal, *Hall 886* (UC); San Benito Co., Idria, *Ferris 7028* (CAS, NY); San Bernardino Co., near San Bernardino, 350 m, *Parish 4165* (BM, K, NY, UC); San Diego Co., Cuyamaca, *Abrams 3838* (BM, CAS, G, K, MO, NY, UC, Z); Santa Barbara Co., Santa Barbara, *Elmer 3879* (CAS, K, MO, NY, WIS, Z); Santa Clara Co., Alum Rock Park, *Heller 8481* (G, MO, NY, WIS); Sierra Co., Downieville, *Bigelow s.n.* (NY); Tuolumne Co., Hetch-Hetchy Trail, Yosemite Nat'l. Park, 1,500 m, *Hall & Babcock 3379* (ARIZ, NY, RM, UC); Ventura Co., Sulphur Mt. Spring, Sulphur Mts., *Abrams & McGregor 24* (CAS, G, NY, Z).

IIc. **Osmorhiza** Raf. sect. **Nudae** Constance & Shan ex Lowry & Jones, sect. nov. TYPE: *O. chilensis* Hook. & Arn.

Uraspermum § *Osmorhiza* (Raf.) Kuntze, Lexicon 582. 1904, pro parte.

Scandix 2. [sect.] *Urascandix* Koso-Polj., Bull. Soc. Imp. Naturalistes Moscou 29: 143. 1916, pro parte.

Osmorhiza sect. *Nudae* Constance & Shan, Univ. Calif. Publ. Bot. 23: 113. 1948, nom. nud.

Involucrum deficiens vel raro ab 1(–2) bracteis minutis constitutum; involucellum deficiens vel raro ab 1(–2) bracteolis minutis constitutum. Styli cum stylopodio 0.2–1.1 mm longi, stylopodium 0.1–0.6 mm longum, conicum vel leviter depressum, saepe cum disco conspicuo.

Involucre wanting, or rarely composed of 1(–2) minute bracts; involucel wanting, or rarely composed of 1(–2) minute bractlets. Styles (including stylopodium) 0.2–1.1 mm long, stylopodium 0.1–0.6 mm long, conic to somewhat depressed, often with a conspicuous disc.

8. **Osmorhiza chilensis** Hook. & Arn., Bot. Beechey Voy. 26. 1830. TYPE: Chile. Concepción: Concepción, *Lay & Collie,* 9–20 Oct. 1825. (This specimen has not been located.)

Osmorhiza berterii DC., Prodr. 4: 232. 1830. *Myrrhis berterii* (DC.) Dietr., Syn. pl. 2: 984. 1840. *Uraspermum berteroi* [sic] (DC.) Kuntze, Revis. gen. pl. 1: 270. 1891. TYPE: Chile. "*in sylvis umbrosis prope Tagua-Tagua,*" *C. Bertero 446* (holotype, G-DC!; isotypes, G!, GH!, P!).

Schudia chilensis Molina ex Clos in C. Gay, Fl. chil. 3: 143. 1848, pro syn.

Scandix clavata Banks & Sol. ex Hook. f., Fl. antarct. 2: 288. 1846, pro syn.

Osmorhiza nuda Torrey, Pacific railroad rep. 4^1: 93. 1857. *Uraspermum nudum* (Torrey) Kuntze, Revis. gen. pl. 1: 270. 1891. *Myrrhis nuda* (Torrey) A. A. Heller, Cat. N. Amer. pl. 5. 1898. *Osmorhiza divaricata* var. *nuda* (Torrey) M. E. Jones, Bull. Montana State Univ., Biol. Ser. 15: 42. 1910. *Scandix nuda* (Torrey) Koso-Polj., Bull. Soc. Imp. Naturalistes Moscou 29: 143. 1916. TYPE: U.S.A. California: Napa Co., Shady woods, *J. M. Bigelow,* 27 Apr. 1853 or 1854 [lectotype, NY! (designated by Coulter & Rose, Contr. U.S. Natl. Herb. 7: 66. 1900); isolectotypes, GH!, K!].

Osmorhiza berterii var. *glacilior* Philippi, Anales Univ. Chile 85: 726. 1894. TYPE: Chile. "In Andibus provinciae l. d." Chihuim, *O. Philippi,* Jan. 1887 (holotype, SGO; photograph of holotype, ILL!).

Osmorhiza divaricata Nutt. ex Britt. in Britt. & Brown, Ill. fl. 2: 531. 1897, pro syn. *Washingtonia divaricata* (Nutt. ex Britt.) Britt. in Britt. & Brown, Ill. fl. 2: 531. 1897. *Scandix divaricata* (Nutt. ex Britt.) Koso-Polj., Bull. Soc. Imp. Naturalistes Moscou 29: 143. 1916. *Osmorhiza nuda* var. *divaricata* (Nutt. ex Britt.) Jepson, Madroño 1: 119. 1923. *Uraspermum divaricata* [sic] (Nutt. ex Britt.) Farwell, Amer. Midl. Naturalist 12: 70. 1930. TYPE: U.S.A. "Oregon woods," *Nuttall s.n.* [lectotype, NY! (designated by Coulter & Rose, Contr. U.S. Natl. Herb. 7: 65. 1900); plus two authentic specimens (likely syntypes): "Columbia plains," *Nuttall s.n.* (BM!); "Columbia woods," *Nuttall s.n.* (GH!)].

Washingtonia brevipes Coult. & Rose, Contr. U.S. Natl. Herb. 7: 66. 1900. *Osmorhiza brevipes* (Coult. & Rose) Suksd., Allg. Bot. Z. Syst. 12: 5. 1906. *Os-*

morhiza nuda var. *brevipes* (Coult. & Rose) Jepson, Madroño 1: 119. 1923. *Urasperum* [sic] *brevipes* (Coult. & Rose) Farwell, Amer. Midl. Naturalist 12: 70. 1930. TYPE: U.S.A. California: Siskiyou Co., Mt. Shasta and vicinity, *E. Palmer 2481* (holotype, US!).

Washingtonia intermedia Rydb., Mem. New York Bot. Gard. 1: 289. 1900. *Osmorhiza intermedia* (Rydb.) A. A. Heller, Mont. Coll. Agric. Sci. Stud., Bot. 1: 93. 1905. TYPE: U.S.A. Montana: Gallatin Co., Bridger Mts., 2,150 m, *P. A. Rydberg & E. A. Bessey 4595* [lectotype, NY! (designated by Constance & Shan, Univ. Calif. Publ. Bot. 23: 139. 1948); isolectotypes, K!, MONT!, US!].

Uraspermum barbatum Farwell, Amer. Midl. Naturalist 12: 70. 1930. TYPE: U.S.A. Michigan: Keweenaw Co., rocky woods, Copper Harbor, *O. A. Farwell 8490* [lectotype, BLH! (designated by McVaugh et al., Bull. Cranbrook Inst. Sci. 34: 79. 1953); isolectotype, GH! ("isotype" fide Constance & Shan, Univ. Calif. Publ. Bot. 23: 139. 1948)].

Plants slender to rather stout, 3–12(–15) dm high; stems 1–3(–4), erect, villous to hirsutulous, or sometimes essentially glabrous. Root system rather deep, well developed, the roots with a weak carrot- or anise-like scent. Leaves biternate, orbicular to broadly ovate, 4–18(–23) cm long, appressed-hispidulous to villosulous (especially along the veins), or sometimes nearly glabrous; leaflets ovate-lanceolate to nearly orbicular, (2–)3–8(–10) cm long, 1–5 cm wide, obtuse or acute, coarsely serrate to incised, parted or divided at the base; petioles 5–16 cm long. Umbels rather loose; peduncles 2–4, terminal and lateral, 5–25 cm long; involucre wanting, or rarely composed of 1(–2) minute (to very rarely large and leaf-like), linear-lanceolate, foliaceous, ciliate, spreading bracts; rays spreading-ascending, (1.5–) 2–12(–13) cm long; umbellets 3–8 per umbel; involucel wanting, or rarely of 1(–2) minute, linear-lanceolate, foliaceous, ciliate bractlets; pedicels (2–)3–9 per umbellet, spreading-ascending, those of the hermaphrodite flowers 4–20(–25) mm long, those of the staminate flowers (1–)2–7(–9) mm long. Hermaphrodite flowers (1–)2–6 per umbellet, (5–)9–30(–39) per umbel, staminate flowers 0–4 per umbellet, 0–18(–25) per umbel; corolla greenish white (rarely pink?), rather inconspicuous; styles (including stylopodium) 0.4–1.1(–1.2) mm long, stylopodium (0.2–)0.3–0.6 mm long, high-conic to somewhat gibbous, lacking a disc; carpophore cleft about one-fourth of its length. Fruit linear-oblong, tapering to a slender beak at the apex, concave furrowed, (11–) 12–21(–25) mm long, the ribs moderately to densely hispid with retrorse bristles, especially toward the base, the caudate appendages (2–)2.5–8.5(–10) mm long. $n = 11$ (Bell & Constance, 1957; Constance et al., 1976). Figures 9j and 15.

Flowering period. April to early July (North America), November and December (South America).

Habitat. Moist forested areas to somewhat drier, open, often disturbed areas.

Common names. Common sweet cicely, Mountain sweet cicely, Mountain sweetroot, Spreading sweetroot, Sweet cicely, Sweetroot, Western sweet cicely, Western sweetroot, Wood cicely, Asta de Cabra.

Representative specimens. U.S.A. ALASKA: Hyder, *McCabe 8426* (UC); Salmon River, W of Hyder, *Robuck 1348* (RM); Deer Mt., 2 km E of Ketchikan, *McCabe 8644* (UC); Sitka, *Eastwood 966* (CAS); Todd, SE Chichagof Island, *Scamman 328* (DAO, photograph); Haines Hwy., mile 31, *Walsh & Moore 6113* (NY); Yakutat, *Piper 4280, 4283* (UC); Shaw Island, N of Cape Douglas, *Anderson 1382* (US); Unalaska Island, *Eyerdam 2256* (cited in Hultén, 1947). ARIZONA: Coconino Co., Oak Creek Canyon, 1,375 m, *Demaree 41249* (NY); Gila Co., under Mogollon Rim, 1,800 m, *Collom 753* (MO, US); Graham Co., Mt. Graham, *Peebles et al. 4483* (US). CALIFORNIA: Butte Co., Jonesville, 1,550 m, *Copeland 391* (ARIZ, BM, BR, CAS, K, MO, NY, RM, UC, WIS); Fresno Co., Huntington Lake, 2,135 m, *Grant 1173* (ARIZ, JEPS); Humboldt Co., Lady Bird Johnson Grove, Redwood Nat'l. Park, *Lowry 791, 795* (ILL); Lake Co., Summit Lake, near Mt. Sanhedrin, *Heller 5879* (CAS, G, ILL, NY, RM, UC); Lassen Co., Diamond Mt., near Susanville, 2,000 m, *M. E. Jones,* 28 June 1897 (BM, CAS, MO); Los Angeles Co., Lily Spring, Mt. Hawkins, San Gabriel Mts., *Thorne 41257* (RSA, UC); Mendocino Co., Noyo, *Constance 2518* (BM, CAS, NY, RM, UC); Modoc Co., Deep Creek, Warner Mts., 1,825 m, *Constance 3103* (K, MO, NY, UC); Monterey Co., Pfeiffer St. Park, *Mathias 1300* (RM, SMU, UC); Placer Co., Emigrant Gap, *M. E. Jones 2734* (BM, BR, CA, MO, NY, UC); San Diego Co., Stonewall Mine, Cuyamaca Mts., 1,400 m, *Parish 4421* (BM, CAS, JEPS, K, MO, NY); Santa Clara Co., W of Los Gatos, *Heller 7430* (CAS, G, MO, NY, UC, WIS); Siskiyou Co., NE base of Mt. Eddy, *Heller 12467* (CAS, G, ILL, MO, NY, UC, WIS); Sonoma Co., Petrified Forest, *Heller 5737* (CAS, G, MO, NY, RM, UC); Tehama Co., 1 km S of Lassen Chalet, *Lowry 851* (ILL); Tuolumne Co., Sullivan Creek, 1 km W of Twain Harte P.O., 1,220 m, *Alexander & Kellogg 3673* (JEPS, NY, UC). COLORADO: Archuleta Co., Piedra River, 11 km N of Arboles, 2,250 m, *H. D. Harrington 4108* (CS); Boulder Co., Boulder, 1,650 m, *Hanson C262* (ARIZ, MO); Garfield Co., 1.5 km N of Douglas Pass, *M. J. Warnock 1699* (ILL); Mesa Co., SW slope of Hightower Mt., *Kufeld K-73* (CS); Moffat Co., NE of Five Springs (Douglas Mountain) overlooking Conway Draw, 2,300 m, *J. Walker & S. Tabar 349* (CS); Rio Blanco Co., Cow Creek, 4.5 km from confluence with Piceance Creek Road, 2,195 m, *W. R. Erickson & D. Bartman 688* (CS). IDAHO: Bannock Co., Mt. Putnam, *Davis 4672* (NY); Benewah Co., 16 km S of St. Maries, *Christ 10927* (NY, UC); Bonneville Co., 17.5 km SW of Victor, *Lowry 1116* (ILL, MO, NY, RM, UC); Clearwater Co., E Fork Potlatch River, *Cronquist & Jones 5977* (CAS, NY, SMU, TEX, UC); Custer Co., Morse Canyon, Lemhi Mts., *Hitchcock & Muhlick 11275* (NY, UC); Idaho Co., Clearwater River, 6.5 km below Lowell, *Constance & Rollins 1608* (MO, UC, WTU); Lemhi Co., Jessie Creek, 1,375 m, *Payson & Payson 1884* (CAS, MO, NY, RM); Lewis Co., Mission Creek, *St. John et al. 6345* (NY, WTU); Nez Perce Co., Potlatch River, *Heller & Heller 7006* (ILL, WIS). MAINE: Aroostook Co., Ft. Kent, *MacKenzie 3509* (MO, NY); Somerset Co., E of Knight's Pond, Squaretown, *Fassett 3658* (WIS). MICHIGAN: Alger Co., Miner's Falls, near Munising, *Fernald & Pease 3450* (MICH, NY); Alpena Co., Thunder Bay Island, *Dodge*, 23 June 1907 (MICH); Baraga Co., Big Limestone Mt., L'Anse, *Fassett 21055* (WIS); Gogebic Co., 17 km NW of Ironwood, *Voss 6238* (MICH); Keweenaw Co., Copper Harbor, *Fernald & Pease 3452* (K, MICH, WIS); Wayne Co., Livonia, *Farwell 9442* (BLH). MONTANA: Beaverhead Co., Red Rock Lakes, 2,000 m, *Lowry 2580* (ILL, MONT, UC); Carter Co., 1.5 km S of Alzada, *Booth 2661* (MONT); Flathead Co., Columbia Falls, *Williams*, 22 June 1894 (MO, NY, RM); Glacier Co., Florence Falls, Glacier Nat'l. Park, 1,615 m, *Stickney 1764* (MONT); Lake Co., Flathead Lake, *Hitchcock 17734* (RM, UC, WTU); Madison Co., Bear Trap Canyon, 1,415 m, *Lowry 2560* (ILL, MO, MONT, MONTU, NY, RM, UC); Missoula Co., Grant Creek, *Kirkwood 1230* (MONT, NY); Silver Bow Co., Humbug Spires, 2,050 m, *Lowry 1999* (ILL). NEVADA: Elko Co., Lamoille Canyon, Ruby Mts., 2,285 m, *Holmgren 1354* (UC); Washoe Co., Little Valley, 2,000 m, *Baker 1363* (G, MO, NY, RM, UC). NEW HAMPSHIRE: Coos Co., Carter Notch, *Forbes s.n.* (GH); Alpine Cascade, Gorham, *Pease 16432* (GH). NEW MEXICO: Taos Co., 14.5 km S of Talpa, *Correll & Correll 33135* (TEX). OREGON: Clatsop Co., Lee Wooden Co. Park, *Lowry 1310* (ILL, MO, OSC, UC); Columbia Co., 16 km NW of Scapoose, *Lowry 593* (ILL); Douglas Co., Iverson Co. Park, *Lowry 1319* (ILL, MO, NY, OSC, UC); Grant Co., 7 km S of Long Creek, 1,460 m, *Lowry 1095* (ILL, MO, NY, OSC, UC); Harney Co., *Train*, 6 June 1935 (OSC); Hood River Co., Herman Creek Trail, *Lowry 706* (ILL, MO, OSC, UC); Jefferson Co., Jack Creek, 16 km W of Camp Sherman, *Lowry 747* (ILL, OSC); Marion Co., Silver Creek, *Hall 216* (GOET, MO, NY); Multnomah Co., Forest Park, Portland, *Lowry 626* (ILL, MO, OSC, UC); Tillamook Co., Bay City, *Morrill 162* (WTU); Wallowa Co., 0.5 km S of Wallowa Lake, 1,340 m, *Constance & Jacobs 1304* (MO, UC); Wheeler Co., 3 km NE of Ochoco Divide, *Lowry 1092* (ILL, OSC, UC). SOUTH DAKOTA: Lawrence Co., Deadwood, *Carr 130* (MO, NY, RM, WIS); Lead City, 1,800 m, *Rydberg 724* (NY). UTAH: Cache Co., Logan Canyon, 1,550 m, *Maguire 3637* (RM, UC); Salt Lake Co., City Creek Canyon, *M. E. Jones 1852* (BM, BR, G, NY, RM); Washington Co., 5 km E of Pine Valley, 2,135 m, *Gould 1846* (ARIZ, CAS, NY, UC). WASHINGTON: Chelan Co., Stehekin, 400 m, *Rose 48178* (SMU, UC); Columbia Co., Godman Spring, Blue Mts., 1,750 m, *Constance et al. 1162* (CAS, MO, UC, WIS); Grays Harbor Co., Montesano, *Heller & Heller 3975* (G, MO, NY, UC); Jefferson Co., N Fork Quinalt River, *Lowry 254a* (ILL); King Co., Seattle, *Thompson 10395* (CAS, MO, NY, WTU); Kittitas Co., 5 km W of Teanaway Junction, Wenatchee Mts., *Hitchcock 17258* (RM, UC, WTU); Klickitat Co., Bingen, *Suksdorf 10037* (BM, CAS, ILL, K, MO, NY, UC); San Juan Co., Friday Harbor, *Zeller & Zeller 768* (CAS, K, MO, NY); Skamania Co., 50 km E of Camas, *Lowry 713* (ILL); Spokane Co., Clarks Spring, N of Spokane, *Kreager 44* (NY, UC, WTU); Whatcom Co., Fairhaven Coll., Bellingham, *Lowry 629* (ILL, MO, NY, UC). WISCONSIN: Bayfield Co., 4 km S of Little Sand Bay, *Iltis & Kawano 20503* (BM, UC). WYOMING: Campbell Co., 4 km SW of Rockypoint, *Dueholm 2962* (RM); Carbon Co., S Brush Creek Campground, *Lowry 1131* (ILL, MO, NY, RM, UC); Fremont Co., Sinks Canyon, Popo Agie River, W of Lander, 2,200 m, *Scott 909* (NY, RM); Lincoln Co., Cottonwood Lake, SE of Afton, *Porter 3776* (CAS, RM, TEX); Teton Co., 5 km W of Teton Pass, *Lowry 1120* (ILL, RM, UC); Uinta Co., Teton Mts., *Nelson & Nelson 6473* (G, ILL, MO, NY, RM).

CANADA. ALBERTA: Cameron Lake, Waterton Lakes Nat'l. Park, 1,660 m, *Breitung 16175* (DAO, UC); Chief Mt., Waterton Lakes, 1,525 m, *Breitung 16842* (SMU, UC); Nordegg River, *Brinkman 4072* (DAO); Olds, *Fletcher 739* (DAO); 13 km W of Pincher Creek, *Moss 86* (DAO). BRITISH COLUMBIA: 13 km N of Flathead Customs Sta., 1,370 m, *Taylor & Ferguson 2044* (DAO); 5 km NNE of Nelson, *Calder & Savile 9405* (DAO, UC); Carbonate, Selkirk Mts., 820 m, *Shaw 219* (MO, NY, RM); Glacier Nat'l. Park, *Lowry 1012* (ILL, MO, NY, UC); 13 km W of Revelstoke, *Lowry 1016* (ILL); Friday Creek, S of Princeton, *Lowry 1020* (ILL, UC); Manning Prov. Park, *Lowry 1026a* (ILL); 11 km N of Boston Bar, *Taylor & Staudt 4197* (DAO, UC); 11 km SE of Vedder's Crossing, *Lowry 1036* (ILL, MO, NY, UC); 3 km S of Pemberton, *Lowry 644* (ILL); NW tip Saturna Island, Gulf Islands, *Calder & MacKay 28775* (DAO); Cowitcham Lake, Vancouver Island, *Rosendahl & Johnson 1857* (DAO); Ucluelet, *Macoun 78607* (NY); 16 km NE of 150 Mile House, 1,000 m, *Calder et al. 19030* (DAO); Bella Coola, *McCabe 123, 1402* (UC); Reid Lake, NW of Prince George, *Eastham 14780* (DAO); 5.5 km SW of Telkwa, *Calder et al. 15259* (DAO); 4 km W of Skeena Crossing, 250 m, *Calder et al. 13021* (DAO, UC); Skidegate Mission, Graham Island, *Calder 21427* (DAO, UC); Haines Rd., km 73.5, NW of Haines, 200 m, *Taylor et al. 1406* (DAO). NEW BRUNSWICK: Albert Co., Goshen, *Squires & Christie*, 26 June 1963 (DAO); Restigouche Co., 1 km SE of Summit Depot, *Cunningham*, 21 July 1960 (DAO). NEWFOUNDLAND: N of Doctor Hill, *Fernald & Long 28771* (K); Frenchman's Cove, Bay of Islands, *Waghorne*, 24 June 1895 (DAO, photo ex QK). NOVA SCOTIA: Inverness Co., Brigend, *Smith et al. 2589* (DAO, UC); Kings Co., Kentville, *Prince & Atwood 1011* (CAS, WIS). ONTARIO: Algoma Dist., Garden River, *Fassett 13282* (WIS); Bruce Co., Kincardine, *Anderson & Fassett 21585* (UC, WIS); Manitoulin Dist., Excelsior, Manitoulin Island, *Fassett 14833* (WIS); Thunder Bay Dist., Talus Lake, Sibley Twp., *Taylor et al. 1146* (UC). QUÉBEC: Charlevoix Co., St. Chrétien, *Cinq-Mars et al. C69-25* (DAO); Gaspé Co., Percé, *Collins & Fernald 119* (ILL, K, LL, NY, UC); Matane Co., 8 km S of Mt. Joli, *Scoggan 13595* (NY, UC); Rivière-du-Loup Co., Rivière-du-Loup, *Churchill*, 8 Aug. 1902 (SMU). SAS-

KATCHEWAN: Cypress Hills Park, *Breitung 4720, 8102* (DAO, UC).

ARGENTINA. CHUBUT: Futaleufu, Lago Futalaufquen, *Burkart 19823* (P, UC); Río Futaleufu, *Castellanos,* 24 Jan. 1945 (NY); Colonia 16 de Octobre, *Lahitte 52212* (UC); Senguerr, Lago Fontana, *Moreno s.n.* (NY); Languiñeo, Pa pa Chica, *Soriano 2488* (UC). MENDOZA: Tunuyan, Cerro de las Piedras, *Ruiz Leal 3106* (BM, UC). NEUQUÉN: Aluminé, Lago Quillén, *Valle et al. 3074* (K); Huiliches, Lago Huechulafquen, Parque Nac. Lanín, *Correa 5537* (UC); Laguna Verde, Parque Nac. Lanín, 980 m, *Correa et al. 5774* (UC); Lacár, Hua Hum, *Cabrera 11229* (UC), *DeBarba 1754* (BR, MO, TEX), *O'Donell 2331* (NY); San Martín de los Andes, *Hunziker 6910* (UC), *Ruiz Leal & Roig 18128* (UC), *Ruiz Leal 20265* (UC), *O'Donell 2399* (NY); Los Lagos, Parque Nac. Nahuel Huapí, *DeBarba 1548* (TEX), *2110* (K); Minas, Lagunas Epu-Lauquén, Aduana Vieja, 1,300 m, *Boelcke et al. 10826* (UC). RIO NEGRO: Bariloche, Parque Nac. Nahuel Huapí, *Boelcke 5246, 5659, 5842* (UC), *Boelcke & Hunziker 3417* (UC), *Cabrera & Job 98* (NY), *DeBarba 95* (NY, UC), *1127* (P), *Descole 25* (NY), *Meyer 7456* (NY); Entre Llao-Llao y Bahia López, *Meyer 8002* (NY). SANTA CRUZ: Lago Argentino, Parque Nac. "Los Glaciares," *Correa et al. 2998* (UC); Cerro Mayo, *James 3002* (BM, UC); Lago Argentino, *Ruiz Leal 26558* (UC); Lago Buenos Aires, Río Jeinemeni, entre Lago Buenos Aires y Codo Río Mayer, 500 m, *von Platen & Greiner 150* (MO, Z). TIERRA DEL FUEGO: Ushuaia, Estancia Harberton, *Constance et al. 3860* (UC), *Goodall 481* (MICH), *549* (MICH, NY), *3585* (UC); Lago Roca, *Goodall 2439* (UC); Estancia Fique, *Ruiz Leal & Roig 15117* (UC).

CHILE. ACONCAGUA: Los Ojos de Agua, *Bridger 475* (K); Zapallar (El Tigre), *Johow,* Nov. 1908 (ILL), *Looser,* 13 Oct. 1953 (UC), *Möller,* 8 Dec. 1951 (UC). ARAUCO: Contulmo, Cerro Santa Elena, *Ricardi 9248* (UC). AYSÉN: Coihaique, cercanías del Lago Seco, 750 m, *Schlegel 2321* (F); Pto. Puyuhuapi, Río Pascue, 8 m, *Schwabe 45* (NY). CAUTÍN: Temuco, *Elliot 276* (BM, NY); Temuco, Truf-Truf, *Montero O. 6371* (UC); Temuco, Fundo Huilquilco, 2 km S of Quepe, *Moore 312* (K, UC); Vilcún, 330 m, *Hollermayer 334* (UC); Pucón, La Peninsula Entrada, 250 m, *Mahu 11425* (ILL); Victoria, 16 km from Termas de Tolhuaca on rd. to Curacautin, 950 m, *Morrison & Wagenknecht 17486* (G, K, UC); Volcán Llaima, 1,100 m, *Werdermann 1246* (BM, CAS, F, G, K, MO, NY, UC, Z); Pass to Longuimay, 1,000 m, *Zöllner 5617* (ILL). CHILOÉ: Ancud, Chiloé Island, *MacMillan & Erlanson 11* (MICH); Cucao Laguna, Chiloé Island, *Philippi & Borchers,* 2 Feb. 1885 (BM). CONCEPCIÓN: Lota, *Brooke 6964* (BM); Concepción, *D'Urville 289* (P), *Holway 139* (NY); probably Talcahuano, *Poeppig s.n.* (UC). LLANQUIHUE: 10 km W of Los Muermos, *Constance & Sparre 3573* (UC); Valle Cayutue, *Rudolph 4925* (UC). MAGALLANES: 50 km SW of Puerto Natales, rd. to Punta Arenas, 30 m, *Eyerdam et al. 24181* (K, MO, UC); Sandy Point, *Lechler 1186* (GOET); Estancia Vicuña, 200 m, *Moore 2178* (K, UC); Seno Almirantazgo, ca. 8 km from mouth of Río Azopardo, 20 m, *Moore 2307* (UC). MALLECO: Fundo Solano, Los Alpes, Cord. Nahuelbuta, 1,200 m, *Eyerdam 10333* (F, UC); 1 km W of Agua Fria, W of Angol, Sierra Nahuelbuta, 650 m, *Hutchison 293* (K, UC); Termas de Tolhuaca, 1,100 m, *Looser 2746* (UC), *Solomon & Solomon 4479* (MO), *Zöllner 10201* (MO); Parque Nac. de Nahuelbuta, *Mahu 5767, 8272, 8417, 8733, 8734, 8735, 11451* (ILL), *Pincheira 7881, 8218* (ILL). ÑUBLE: Termas (Baños) de Chillán, 1,750 m, *Moore 414* (UC), *Philippi & Borchers s.n.* (BM). O'HIGGINS: La Leona, Rancaque, *Bertero 446* (P), *Guillemin 446* (P); Agua de la Vida, *Borchers s.n.* (GOET); Baños, Cauquenes, *Philippi,* Sept. 1896 (BM); upper valley of River Cachapoal, *Zöllner 9892* (ILL). OSORNO: Termas de Puyehue, 350 m, *Sparre 2128* (K). SANTIAGO: Manzano, *Looser,* 11 Nov. 1928 (UC); Quebrada de Macul, 1,100 m, *Pisano V. & Baraona L. 1572* (UC); Los Valdes, near Río Maipo, 2,500 m, *Zöllner 2079* (ILL). VALDIVIA: Valdivia, *Bridges 768* (K), *DeCandolle m. 418* (P), *Gay 124* (P), *Hohenacher 481* (K), *Hollermayer 334* (BR); Cabo Blanco, Río Cruces, *Klempau s.n.* (UC); La Unión Reserva Forestal Llancacura, *Mahu 11424* (ILL). VALPARAÍSO: Valparaíso, *Bertero 74* (F, NY, UC—all photos ex B), *Cuming 335* (K); Limache (Lliu-Lliu), *Garaventa H. 2270* (UC), *Bertero,* Oct. 1828 (BM), *Bertero 1163* (G, P), *Steudel 1163* (P); Laguna Verde, *Garaventa H. 2378* (UC); Granizo, Cajón Grande, foot of Cerro Campana, near Olmue, 15 km E of Limache, *Meyer 9704* (MO, UC), *Zöllner,* Nov. 1977 (ILL); 8 km from La Dormida on trail to Las Vizcachas, 1,100 m, *Morrison 16832* (G, K, MO, UC); Quilpué, *Zöllner 8353* (MO).

Constance and Shan (1948) were the first to recognize the conspecificity of North and South American populations of *Osmorhiza chilensis.* Previous to that, the North American material had been referred to a variety of names, including *Osmorhiza brevipes, O. divaricata, O. intermedia, O. nuda,* and *Uraspermum barbatum,* while South American specimens were identified as either *O. berterii* or *O. chilensis.* However, the similarity of plants from the two areas was mentioned by Coulter and Rose (1895) and Reiche (1902).

It has been established that the names *Osmorhiza chilensis* and *O. berterii* were both published in 1830 (Constance & Shan, 1948; cf. also Jackson, 1893; Rickett, 1945). While the month of publication for *O. berterii* most likely is September, that for *O. chilensis* is not known. However, Hooker and Arnott (1833), J. D. Hooker (1846), and Gray (1854) accepted the name *O. chilensis,* placing *O. berterii* in synonymy under it, and it was on this basis that Constance and Shan (1948) adopted the former name. We have uncovered no additional evidence that would require a different interpretation.

Bongard (1833) included Alaskan populations of *Osmorhiza chilensis* in *O. brevistylis* DC. Similarly, W. J. Hooker (1840) used an expanded concept of *O. brevistylis* to include populations from western North America now included in *O. chilensis.*

9. Osmorhiza purpurea (Coult. & Rose) Suksd., Allg. Bot. Z. Syst. 12: 5. 1906. *Washingtonia purpurea* Coult. & Rose, Contr. U.S. Natl. Herb. 7: 67. 1900. *Osmorhiza chilensis* var. *purpurea* (Coult. & Rose) Boivin, Naturaliste Canad. 93: 644. 1966. TYPE: U.S.A. Alaska: Sitka, *F. V. Coville & T. H. Kearney, Jr.*, 14–17 June 1889 (holotype, US!).

Washingtonia leibergii Coult. & Rose, Contr. U.S. Natl. Herb. 7: 66. 1900. *Osmorhiza leibergii* (Coult. & Rose) Blankinship, Mont. Coll. Agric. Sci. Stud., Bot. 1: 93. 1905. TYPE: U.S.A. Washington: Chelan (formerly Okanogan) Co., Sandy slopes of Nason Creek, (branch of the Wenatchee River) 1,370–2,133 m, *J. H. Sandberg & J. B. Leiberg 666* [holotype, US!; isotypes, BM!, BR!, CAS!, MO!, NY!, ORE!, P!, UC! (or possibly paratypes, as label data are not identical to those of the holotype)].

Plants slender, 2–6(–8) dm high; stems 1–2(–3), erect to ascending, sparingly hirsutulous to glabrescent. Root system relatively deep, well developed, the roots with a weak carrot- or anise-like scent. Leaves (1–)2–3-ternate, orbicular to deltoid or broadly ovate, 3–10(–12) cm long, sparingly hirsutulous along the veins and margins, to glabrous; leaflets lanceolate to ovate, 1.5–6(–8) cm long, 0.5–4 cm wide, acute or acuminate, coarsely serrate to incised, lobed or deeply divided at the base; petioles 5–10(–12) cm long. Umbels rather loose; peduncles 2–3(–4), terminal and lateral, 3–9(–11) cm long; involucre wanting, or very rarely consisting of 1 minute, linear-lanceolate, foliaceous, ciliate, spreading bract; rays spreading-ascending, (2.7–)3–9.5(–11) cm long; umbellets (2–)3–7 per umbel, sometimes 1–2 of them producing only staminate flowers; involucel wanting; pedicels (2–)3–9 per hermaphrodite umbellet, 3–5 per staminate umbellet (when present), spreading-ascending, those of the hermaphrodite flowers (8–)9–25(–33) mm long, those of the staminate flowers 2–5(–6) mm long. Hermaphrodite flowers (1–)2–6 per umbellet, (6–)10–22(–29) per umbel, staminate flowers 0–5 per hermaphrodite umbellet, 0–18(–24) per umbel; corolla purplish or greenish white, somewhat inconspicuous; styles (including stylopodium) (0.3–)0.4–0.8(–0.9) mm long, stylopodium 0.1–0.4 mm long, strongly depressed, with a conspicuous disc; carpophore cleft about one-fourth of its length. Fruit linear-fusiform, with an apical beak that is strongly constricted below the stylopodium, concave furrowed, (7–)8–15(–16) mm long, the ribs glabrous above and slightly to moderately hispid with retrorse bristles below, the caudate appendages 1–5(–6) mm long. $2n = 22$ (Taylor & Mulligan, 1968). Figures 9i and 13.

Flowering period. Late April to July.

Habitat. Moist coniferous forests in areas with considerable, regular precipitation.

Common names. Purplish sweet cicely, Purple sweet cicely, Purple sweetroot.

Representative specimens. U.S.A. ALASKA: Deer Mt., Revillagigedo Island, *McCabe 8644* (UC); Loring, *Chamberlain 20* (US); Yes Bay, *Gorman 23* (K, NY); Texas Creek Summit, NW of Hyder, *McCabe 8934* (UC); Misty Fjords Nat'l. Mon., *Vorobik 413* (ORE); Mt. Dewey, Wrangell Island, *Cowles 1288* (ILL); Washington Bay, Kuiu Island, *Eyerdam 8340* (G, SMU); Sitka, *Jepson 489* (JEPS); Young Bay, Admiralty Island, *Robuck 1311* (RM); Douglas Island, S of Juneau, *Trelease 4527* (US); Juneau, *Anderson 6322* (DAO, RM, TEX); Mt. Harris, St. Elias Mts., *Cowles 1402* (ILL, MO); Thum Bay, Knight Island, Prince William Sound, 300 m, *Eyerdam 3425* (ILL, K, MO, UC); Port San Juan, Evans Island, *Eyerdam 5969* (ILL, MO); Mt. Marathon, W of Seward, *Calder 5096* (DAO, NY, UC); Stetson Creek Valley, NW of Seward, *Calder 6479* (DAO, WTU); Three Saints Bay, Kodiak Island, *Eyerdam 386* (K). CALIFORNIA: Del Norte Co., Wilson Creek, between Requa and Crescent City, *Abrams & Bacigalupi 8323* (CAS, RM); Redwood Nat'l. Park, *Lowry 785a* (ILL, UC); Siskiyou Co., *Muth 396* (CAS). IDAHO: Bonner Co., Hope, *Dunkle 457* (NY); Kootenay Co., Packsaddle Peak, 2,600 m, *Sandberg et al. 845* (BM, K, MO, NY); Shoshone Co., Sohons Pass, 1,650 m, *Leiberg 1427* (CAS, K, NY, RM, UC). MONTANA: Glacier Co., Midvale, *Umbach 249* (MONT, RM, WIS); Park Co., 10 km W of Four Mile Ranger Sta., Boulder River Canyon, *Hitchcock 16381* (CAS, NY, UC, WTU). OREGON: Clackamas Co., S slope of Mt. Hood, 1,250 m, *Lowry 1073* (ILL, MO, OSC, UC); Clatsop Co., 1 km W of Washington Co. line on Hwy. 26, *Lowry 3092* (ILL, MO, OSC, UC); Jefferson Co., E base of Three Fingered Jack, 2,100 m, *Constance 3465* (BM, ILL, NY, RM, UC, WIS); Klamath Co., Crater Lake, *Baker 7126* (NY, WTU); Tillamook Co., Neahkahnie Mt., *Lowry 910* (ILL, MO, NY, OSC, UC). WASHINGTON: Chelan Co., Stevens Pass, *Sandberg & Leiberg 4028* (ILL, MICH, MO, NY, US, WIS, WTU); Grays Harbor Co., Colonel Bob Lookout, 1,250 m, *Thompson 7275* (CAS, K, MO, UC, WTU); Jefferson Co., N Fork Quinault River, *Lowry 254* (ILL); Okanogan Co., Mt. Bonaparte, *St. John et al. 5341* (MO, UC, WTU); Snohomish Co., Perry Creek Trail, 1,000 m, *Thompson 14712* (MICH, MO, NY, UC, WTU).

CANADA. ALBERTA: Cameron Lake, Waterton Lakes Nat'l. Park, 1,650 m, *Boivin & Gillett 8979* (DAO). BRITISH COLUMBIA: 16 km N of Bull River, *Taylor & Ferguson 2714* (DAO); S Fork Kaslo Creek, near Kokanee Glacier, *McCabe 4779* (UC); Glacier Nat'l. Park, *Haber & Shchpanek 1492A* (CAS, NY); Illecillewaet Valley, Selkirk Mts., *Brown 273* (MO, NY); Quiniscoe

Lake, Ashnola Range, *Calder et al. 19635* (DAO, NY, UC); Manning Prov. Park, *Lowry 1026* (ILL, UC); Copper Canyon, 800 m, *Schmidt 51-53* (DAO); Lake Bootahnie, Marble Mts., 1,500 m, *Thompson & Thompson 122* (WTU); Moat Lake, Forbidden Plateau, Vancouver Island, *Calder & MacKay 32303* (DAO, UC); Indianpoint Lake, NE of Bakerville, *McCabe 319* (UC); Mt. Fougner, Bella Coola, *Calder et al. 20417* (DAO); Safety Cove, Calvert Island, *McCabe 4189* (UC); Swanson Bay, Graham Reach, *McCabe 3458* (UC); 5 km WNW of Tyee, E of Prince Rupert, *Calder et al. 15038* (DAO); Bigsby Inlet, Moresby Island, *Calder et al. 34908* (DAO); trail to Mercer Lake from Empire Anchorage, Graham Island, *Calder & Savile 21494* (DAO, UC); Stewart, *Whited 1226* (MO).

Osmorhiza purpurea is clearly a distinct species, although it is often confused with the closely related *O. chilensis. Osmorhiza purpurea* is the only taxon in the section *Nudae* that does not exhibit disjunctions to the Great Lakes region, northeastern North America, and southern South America. Constance and Shan (1948) noted that the fruits of this species seem equally well adapted for long-distance dispersal as those of *O. chilensis* and *O. depauperata. Osmorhiza purpurea,* however, has a very restricted habitat preference, occurring only in areas with substantial, regular precipitation, often at higher elevations or along the Pacific Coast, in sharp contrast with its more widespread relatives.

Coulter and Rose (1900) published two names for plants now included in *O. purpurea*: *Washingtonia leibergi* and *W. purpurea.* When these taxa were combined by Mathias and Constance (1944), they adopted the name *Osmorhiza purpurea,* and accordingly, under Art. 57 of the "Code" (Voss et al., 1983), this choice of epithet must be followed.

10. Osmorhiza depauperata Philippi, Anales Univ. Chile 85: 726. 1894. TYPE: Chile. Ñuble: Valle de las Nieblas, near Termas de Chillán, *F. Philippi 2030* [lectotype (designated herein), SGO (no. 041589); photograph of lectotype, ILL!; isolectotype, SGO (no. 053461); photograph of isolectotype, ILL!].

Washingtonia obtusa Coult. & Rose, Contr. U.S. Natl. Herb. 7: 64. 1900. *Osmorhiza obtusa* (Coult. & Rose) Fern., Rhodora 4: 154. 1902. TYPE: U.S.A. Wyoming: Park Co., Ishawood (i.e., Ishawooa) Creek, *J. N. Rose 476* (holotype, US!).

Osmorhiza obtusa var. *cupressi-montanum* Boivin, Canad. Field-Naturalist 65: 20. 1951. *Osmorhiza chilensis* var. *cupressimontana* (Boivin) Boivin, Naturaliste Canad. 93: 644. 1966. TYPE: Canada. Saskatchewan: Cypress Hills Park, aspen woods, *A. J. Breitung 4742* (holotype, DAO!).

Plants slender, 1.5–6.5(–8) dm high, stems 1–3(–5), erect to spreading-ascending or decumbent, sparsely to rather densely hirsutulous, or sometimes glabrescent. Root system rather deep, well developed, the roots with a weak carrot- or anise-like scent. Leaves 2–3-ternate, orbicular to broadly ovate, 4–10(–12) cm long, sparingly hispidulous to glabrous; leaflets broadly lanceolate to ovate, 1.5–5(–6) cm long, 1–3 cm wide, obtuse or acute, coarsely serrate to incised, parted, or divided at the base; petioles 3–20(–23) cm long. Umbels open, peduncles 1–3, terminal and often lateral, 5–15 cm long; involucre wanting, or rarely consisting of 1 minute (to very rarely large and leaf-like), linear-lanceolate, foliaceous, ciliate, spreading bract; rays widely spreading to nearly reflexed, (2.5–)3–9(–10) cm long; umbellets 2–6 per umbel; involucel wanting, or rarely of 1–2 small, linear-lanceolate, foliaceous, ciliate bractlets, each 0.3–2.5 mm long, 0.2–0.4 mm wide; pedicels (2–)3–7 per umbellet, widely divaricate, those of the hermaphrodite flowers (4–)8–12(–32) mm long, those of the staminate flowers 2–12 (–13) mm long. Hermaphrodite flowers 2–6 per umbellet, (3–)7–20(–25) per umbel, staminate flowers 0–2(–3) per umbellet, 0–10(–15) per umbel; corolla greenish white, rather inconspicuous; styles (including stylopodium) 0.3–0.6(–0.7) mm long, stylopodium (0.1–)0.2–0.4(–0.5) mm long, low-conic to depressed, with or without a disc; carpophore cleft about one-third of its length. Fruit clavate, obtuse at the apex, concave furrowed, (9–)10–18(–19) mm long, the ribs moderately to densely hispid with retrorse bristles, especially toward the base, the caudate appendages (2.5–)3–8.5(–9) mm long. $n = 11$ (Bell & Constance, 1960; Constance et al., 1976); $2n = 22$ (Crawford & Hartman, 1972). Figures 9k and 14.

Flowering period. April to early July (North America); November and December (South America).

Habitat. Moist to fairly dry forests, woodlands, and open slopes.

Common names. Blunt-fruit sweet cicely, Blunt-fruit sweetroot, Blunt-fruited sweet cicely, Bluntseed sweetroot, Snub cicely, Sweet cicely.

Representative specimens. U.S.A. ALASKA: Denver Trail, E of Skagway, *Anderson 1735* (K); Pt. Gustavus, Glacier Bay, *Coville & Kearney 729* (US); Valdez, *Piper 4288* (US); Kenai Lake, *Calder 5688* (DAO); Cooper

Landing, W of Kenai Lake, *Anderson 6882* (RM); 12 km E of mouth of Moore River, Kenai Peninsula, *Lutz 105* (RM). ARIZONA: Apache Co., Lukachukai Mts., 2,700 m, *Goodman & Payson 2816* (CAS, MONT, MONTU, NY, UC, WTU); Cochise Co., Chiricahua Mts., *Ferris 9950* (MICH, TEX, UC); Coconino Co., Humphreys Peak, San Francisco Mts., *MacDougal 397* (ARIZ, G, NY, P, RM, UC); Pima Co., Santa Catalina Mts., *Goodman & Hitchcock 1253* (MO, NY, RM). CALIFORNIA: Modoc Co., Warner Mts., 1,850 m, *Constance 3104* (K, MO, NY, UC). COLORADO: Boulder Co., Boulder Creek, below Eldora, 2,500 m, *G. N. Jones 33299* (CS, ILL); Clear Creek Co., Georgetown, 2,500 m, *M. E. Jones 514* (BR, CAS, MISSA, NY, UC); Delta Co., Cedaredge, 2,150 m, *Baker 240* (K, RM, UC); El Paso Co., Jack Brook, 2,600 m, *Clements & Clements 236* (NY, RM); Garfield Co., S of Rifle, *Osterhout 2151* (NY, RM, WIS); Gunnison Co., Elko Park, N of Gothic, *Mathias 3264* (UC); La Plata Co., La Plata, *Baker et al. 849* (BM, K, MICH, MO, NY, RM); Mineral Co., near Pagosa Peak, 2,750 m, *Porter 3932* (CAS, RM, UC, WTU); Montezuma Co., Upper W Mancos Canyon, 3,000 m, *Baker et al. 188* (BM, G, K, MICH, MO, NY, RM); Rio Blanco Co., Black Sulphur Creek, 5.5 km SW of confluence with Swizer Gulch, 2,115 m, *W. R. Erickson 594* (CS); Summit Co., near Breckenridge, *MacKenzie 295* (MO, RM, WIS). IDAHO: Bingham Co., Wolverine Creek, Blackfoot Mts., *Holmgren & Murttala 5415* (NY, UC); Bonneville Co., 18 km SW of Victor, *Lowry 1114* (ILL); Cassia Co., Pole Canyon, SE of Burley, 2,000 m, *Holmgren & Jensen 3499* (NY, WTU); Clark Co., Centennial Mts., 2,350 m, *Lowry 2485* (ILL, MONT, UC); Custer Co., Challis Creek, 1,800 m, *Macbride & Payson 3332* (CAS, K, MO, NY, RM, UC); Fremont Co., Henry's Lake, 1,800 m, *Payson & Payson 1946* (CAS, MO, NY, RM). MICHIGAN: Keweenaw Co., Isle Royale, *McFarlin 2049* (MICH, MONT); Leelanau Co., E end of Manitou Island, *Richards 3123* (MICH). MINNESOTA: Cook Co., Mountain Lake, *Butters et al. 303* (NY). MONTANA: Beaverhead Co., Centennial Mts., 2,450 m, *Lowry 2426* (ILL, MO, MONT, MONTU, NY, RM, UC); Carbon Co., Red Lodge, *Hawkins,* 22 July 1919 (MONT); Deerlodge Co., Storm Lake, *Hitchcock & Muhlick 14845* (MO, NY, UC, WTU); Gallatin Co., Mystic Lake, *Blankinship 220* (BM, MO, MONTU); Silver Bow Co., Humbug Spires, 1,900 m, *Lowry 2269* (ILL, MONT, UC). NEVADA: Clark Co., Little Falls, Charleston Mts., 2,400 m, *Clokey 8050* (ARIZ, CAS, ILL, MO, MONTU, NY, RM, UC, WTU); Elko Co., Lamoille Canyon, 2,450 m, *Millan & McKnight 168* (NY); White Pine Co., Snake Creek, Snake Range, 2,950 m, *Holmgren & Reveal 1627* (NY). NEW MEXICO: Grant Co., Hillsboro Peak, Black Range, 3,050 m, *Metcalfe 1206* (MO, NY); Lincoln Co., 11 km W of Ruidoso, 2,750 m, *Hinckley 726* (ARIZ, NY, TEX, UC); Otero Co., Cloudcroft, *Wooton,* 30 June 1899 (ILL, MO, NMC, NY, RM); Santa Fe Co., Santa Fe Canyon, E of Santa Fe, *Heller & Heller 3822* (BM, CAS, K, MO, NY, P, UC). OREGON: Deschutes Co., Paulina Creek, 2,090 m, *Leiberg 555* (K, NY, UC); Jackson Co., Wimer, *Hammond 157a* (CS); Klamath Co., Crater Lake Nat'l. Park, 1,850 m, *Heller 13469* (CAS, ILL, WTU). SOUTH DAKOTA: Lawrence Co., S of Deadwood, *Churchill 5707* (MO, NY). UTAH: Duchesne Co., 6 km S of Moon Lake, 2,350 m, *Harrison & Larsen 7612* (MO, RM); Garfield Co., Henry Mts., 2,400 m, *McVaugh 14681* (CAS, MICH, NY, SMU, TEX); Grand Co., Post Canyon, Uintah and Ouray Ind. Res., 110 km S of Ouray, 2,650 m, *Holmgren et al. 2313* (ARIZ, CAS, ILL, NY, TEX, UC, WIS, WTU); San Juan Co., Abajo Mts., *Goodman & Hitchcock 1437* (BM, MO, NY, RM); Utah Co., Slate Canyon, E of Provo, 2,450 m, *M. E. Jones 5580* (BM, MO, NY, RM, UC); Washington Co., 4.5 km E of Pine Valley, 2,150 m, *Gould 1793* (NY). VERMONT: Chittenden Co., Mt. Mansfield, *Greenman 691* (MO). WASHINGTON: Asotin Co., *Cronquist & Jones 5860* (WTU); Chelan Co., Wenatchie region, *Brandegee 794* (NY, UC); King Co., Seattle, *Talcott,* 15 May 1891 (MICH); Okanogan Co., Myers Creek, Chesaw, *St. John et al. 5186* (MO, NY, UC, WTU). WYOMING: Albany Co., Laramie Range, 2,500 m, *Hartman 3122* (RM); Big Horn Co., 42 km W of Burgess Junction, Big Horn Mts., *Lowry 1423* (ILL); Carbon Co., S Brush Creek Campground, Medicine Bow Mts., *Lowry 1132* (ILL, MO, NY, RM, UC); Sublette Co., Middle Piney Lake, 2,600 m, *Meyer & Meyer 2402* (MO, NY, UC); Teton Co., 5 km W of Teton Pass, *Lowry 1119* (ILL, MO, NY, RM, UC).

CANADA. ALBERTA: Cypress Hills, 1,450 m, *Boivin & Gillett 8929* (DAO); Chief Mt. Hwy., Waterton Lakes Nat'l. Park, 1,450 m, *Breitung 15881* (NY, UC); W face of Sandhills, *Brinkman 5470* (DAO, SMU); Elbow River Valley, Calgary, *Moodie 1056* (NY, UC); 3 km below Canmore, 1,300 m, *Ewan 18685* (UC); Elk Island Park, E of Ft. Saskatchewan, *Turner 4498* (DAO); Battle Lake, SW of Pigeon Lake, *Turner 5907* (DAO); Elysium Pass Trail, Jasper Nat'l. Park, *Lowry 944* (ILL, UC); Geraldine Lakes Trail, Jasper, *Lowry 961* (ILL, UC); near Atauwan Cabin, Slave Lake Dist., *Brinkman 4335* (NY); SW of Spirit River, *Moss 8415* (DAO); Saddle Hills, N of Sexsmith, *Moss 9948* (WIS); Wembley, *Wallace for Jenkins 734* (DAO). BRITISH COLUMBIA: Starvation Park, W of Waterton Lakes, 1,550 m, *Calder et al. 3416* (DAO); Sheep Mt., 55 km N of Natal, *Weber 2373* (NY, UC); 7 km WSW of Wycliffe, 950 m, *Taylor et al. 2635* (DAO, UC); 5 km W of Needles, *McCabe 6663* (UC); Friday Creek, 25 km S of Princeton, *Lowry 1021* (ILL, UC); Yoho Nat'l. Park, *Lowry 1005* (ILL, MO, RM, UC); 1.5 km NW of Falkland, 600 m, *Hitchcock & Martin 7466* (NY, RM); Botanie Valley, 1,200 m, *Beamish et al. 8204* (DAO); Three Mile, on Lac La Hache-Williams Lake Rd., *Calder et al. 18970* (DAO); 24 km SW of Kleena Kleene, *McCabe 606* (UC); 21 km W of Puntataenkut Lake, W of Quesnel, 1,150 m, *Calder et al. 18212* (DAO); Tezsli, Kluskus Lakes, *Lewicki 79* (WIS); Prince George, 600 m, *Florian 94* (DAO); 25 km W of Burns Lake, *Calder et al. 12780* (DAO); 5 km S of Ft. McLeod, *Calder et al. 12445* (DAO, UC); Pine River, 67 km W of Bissett Creek Bridge, W of Dawson Creek, *Taylor & Staudt 4169* (DAO, UC); near Hudson's Hope, *Raup & Abbe 3640* (NY); Wicked River, near Peace River, 600 m, *Raup & Abbe 3878* (NY); Wolverine Ridge, near Manson Creek Village, 1,050 m, *Calder et al. 13702* (DAO); 5 km S of Takla Landing, *McCabe 7916* (UC); Bear Lake, 40 km NW of Takla Lake, *McCabe 7998* (UC); Fairy Lake, SSW of Ft. Nelson, 1,400 m, *Calder & Kukkonen 27162* (DAO, UC); Laird Hotsprings, 500 m, *Calder & Gillett 25575* (CAS, DAO, UC); mile 578, Alaska Hwy., 550 m, *Calder & Gillette 25655* (DAO). MANITOBA: Mont Dauphin, Norgate, *Boivin et al. 10682* (DAO); 13 km W of Norgate, Riding Mt. Nat'l. Park, *Löve & Löve 6563* (DAO); Forestry Camp, Riding Mt. Nat'l. Park, *Rowe 305* (DAO). NORTHWEST TERRITORIES: Charlton Island, James Bay, *Porsild 4506* (DAO—photo ex CAN); Mt. Coty, 750 m, *Cody & Spicer 11787* (NY, SMU, UC). NEW BRUNSWICK: Madawaska Co., Claire, *Eaton M-89* (LL). NEWFOUNDLAND: Dildo, Notre Dame Bay, *Fernald & Wiegand 5952* (K, NY); Benoit's Cove, Humber Arm, Bay of Islands, *Fernald & Wiegand 3767* (BM); Frenchman's Cove, Bay of Islands, *Waghorne 15* (MO); Port au Port, *MacKenzie*, 30 July 1921 (NY, UC); Nameless Cove-Mistaken Cove, Straights of Belle Isle, *Wiegand et al. 28767* (GH, US); Forteau, Labrador, *Waghorne*, 8 Aug. 1893 (MO). NOVA SCOTIA: Inverness Co., Cape St. Lawrence, *Smith et al. 11183* (DAO). ONTARIO: Algoma Dist., *Marie-Victorin & Rolland-Germain 27340* (CAS); Thunder Bay Dist., Mortimer Island, Slate Islands, *Hosie et al. 2187* (UC); Pijitiwabik Bay, Lake Nipigon, *Garton 7248* (DAO). QUÉBEC: Gaspé Co., Grand River, *Fernald s.n.* (MICH, NY); Lac St. Jean—Ouest Co., Chambord, Roberval, *Leduc L-69-68* (DAO); Matane Co., Little Metis, *Fowler 25351* (MO, WIS); Rimouski Co., near Bic, Isle de Bic, *Forbes*, 25 June 1905 (RM); Rivière-du-Loup Co., Pt. de la Rivière du Loup, *Cayouette & Cinq-Mars*, 19 June 1944 (DAO); Saguenay Co., Rivière du Renard, Anticosti Island, *Marie-Victorin & Rolland-Germain 27139* (MO, WIS); Niapisca, Mingan Islands, *Hamel & Genereux 3140* (DAO). SASKATCHEWAN: Maple Creek Dist., Cypress Hills, *Hudson 1838* (DAO); Melfort Dist., McKague, *Breitung*, 30 Jan. 1935 (DAO); Qu'Appelle Dist., Cherry Lake, SE of Indian Head, *Jones & Ledingham 742* (DAO); Wallwort, *Breitung 651* (DAO, MO, UC).

ARGENTINA. CHUBUT: Río Senguerr, Lago La Plata, *Krapovickas 4241* (UC). NEUQUÉN: Los Lagos, Fortín Chacabuco, *Correa & Constance 3788* (UC); between Lago Correntoso and Lago Escondido, *Correa & Constance 3845* (G, K, UC); Correntoso, Lago Nahuel Huapí, *Edwards s.n.* (BM). RÍO NEGRO: Bariloche, Parque Nac. Nahuel Huapí, *Boelcke 5405, 5436* (UC); Estacis Lago Roca, 350 m, *James 411* (BM). SANTA CRUZ: Güer Aike, Estancia Stag River, Río Gallegos, *Tweedie 101a, 267* (K); Lago Argentino, Brazo Norte, valle de La Cristina, 850 m, *Vervoorst 4387* (MO). TIERRA DEL FUEGO: Ushuaia, Lago Fagnano, *Boelcke et al. 15236* (UC), *Moore 2845* (K); Harberton, *Constance et al. 3861* (UC), *Goodall 164, 1025* (UC); Bahía Aguirre, *Goodall 1422* (UC); Laguna Victoria, Isla de Los Estados, *Goodall 1579* (UC), *Moore 2079* (K); Estancia Viamonte, *Goodall 2823* (UC); Río Valdez, *Goodall 3405* (UC); Monte de las Carpas, *Goodall 4669* (UC); Ushuaia, *Hunziker 6522, 6560* (UC), *Vallerini 66* (UC), *Zöllner 8584* (MO), *Pennington 196 bis* (Z); Monte Olivia, *Hunziker 8206* (UC); Estancia la Esperanza, 210 m, *Mexia 7925* (BM, G, K, MO, NY, UC), *Moore 1540* (K); Sierra Alvaer, E of Paso Garibaldi, *Moore 1818* (K).

CHILE. MAGALLANES: Rosvig, 200 m, *Donat 346* (BM, CAS, K, NY); Sandy Pt., *Cunningham s.n.* (NY), *DeCandolle m. 1186* (P); Buncombe Bay, *Commerson s.n.* (P); Punta Arenas, 20 m, *Eyerdam et al. 24105* (G, K, UC), *Stafford 26* (NY), *Savatier 61, 76* (P), *McLean D.A.14* (BM), *Hatcher s.n.* (NY); Estancia Maria Cristina, 80 km NE of Punta Arenas, *Goodall 4018* (UC); Puerto Williams, Navarino Island, *Godley 884* (K, UC); Pecket Harbor, *Hombron s.n.* (P); Orange Harbor, *Hyades 472* (P), *U.S. S Pac. Expl. Exped.* (P); Port Famine, *Le Guillou s.n.* (P), *Marivault s.n.* (P); Estancia Cameron, NW shore Lago Blanco, *Moore 2145* (K, UC); Estancia Vicuña, 200 m, *Moore 2177* (UC); Port Galant, *Savatier s.n.* (P). ÑUBLE: Termas de Chillán, *Jaffuel 3765* (GH, cited in Constance & Shan, 1948). VALDIVIA: Valdivia, *Lechler 225* (GOET); *Philippi s.n.* (G).

Osmorhiza depauperata was described by Philippi (1894) from material collected in South America. At the time Constance and Shan (1948) prepared their treatment of *Osmorhiza*, they were uncertain as to the identity of this name, and tentatively placed it in synonymy under *O. chilensis*. Instead, they accepted the name *Osmorhiza obtusa* for the taxon with clavate fruit and divaricate rays and pedicels. In 1954, Constance visited the Museo Nacional de Historia Natural in Santiago, Chile, where he examined the type material of *Osmorhiza depauperata* (Constance, pers. comm.). Three years later, this name was first used for North American plants by Mathias and Constance (1957: 11), with the following footnote: "Examination of Philippi's type at Santiago, Chile, has verified the necessity of substituting this name [*O. depauperata*] for the heretofore accepted *O. obtusa* (C. & R.) Fernald." Although Philippi's type material is not available for loan, we were able to obtain photographs of the two specimens through the courtesy of Dra. Mélica Muñoz S., Curator of Botany at SGO. While examination of these photographs does not, by itself, reveal with certainty the identity of Philippi's specimens, information contained in Constance's notes on them indicates that the name *Osmorhiza depauperata* does indeed apply to the taxon earlier referred to as *O. obtusa*.

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A GUIDE TO COLLECTING PASSIONFLOWERS[1]

P. M. JØRGENSEN, J. E. LAWESSON, AND L. B. HOLM-NIELSEN[2]

ABSTRACT

Collections of passionflowers are often inadequate for taxonomic studies because of insufficient description of their complicated flower structures, i.e., corona, operculum, nectar ring, and limen. These structures are highly important to the taxonomy of *Passiflora*. Instructions are given here on how to make good, properly labelled collections of passionflowers.

Passifloraceae comprises four genera and about 400 species in the New World, most of which occur in South America. The four genera are: *Passiflora* (including *Tetrastylis*) with 390 species, *Dilkea* with five species, *Mitostemma* with three species, and *Ancistrothyrsus* with one or two species.

FLORAL MORPHOLOGY

Different terms have been used to describe the floral parts of Passifloraceae. The terminology of H. Harms (1893) and E. P. Killip (1938) is used. Variation in these characters is shown in Figure 1.

Corona. The corona usually consists of numerous elongate extensions. They are often differently colored than the sepals and petals and arranged in one to ten filament series or rows. Whether these extensions are filiform, liguliform, or spathulate; straight or falcate; terete or angled is important in distinguishing the species.

Operculum. The operculum is normally a membranous structure below the corona, which rarely has filiformous extensions. It represents a "closed door" to non-pollinating visitors. It is most important as a distinguishing character at the subgeneric and specific level. Whether it is curved, straight, recurved, or plicate should be noted when collecting because such details are difficult to see in dried specimens. The nature of the operculum margins (entire, serrulate, lobulate, or filiform) should also be noted.

Nectar ring. The nectar ring is a low narrow ring below the operculum, at the bottom of the tube. Its presence or absence (it is often absent) should be noted and, when present, its shape and color.

Limen. The limen may be similar to the nectar ring, or it may be a cup-shaped membrane more or less closely surrounding the base of the gynophore. Because the limen is not present in all species, its presence or absence should always be noted when collecting, as well as the nature of its margin (serrulate, lobulate, entire, denticulate).

HOW TO COLLECT

Information that should be gathered when collecting is listed in Table 1. Passifloras are herbaceous and woody vines, or sometimes scandent shrubs or treelets. Treelets and lianas show much variation in leaf size, the lower leaves often being several times larger than leaves of flowering and terminal branches. It is therefore important to collect both types of leaves.

Passifloras should always be examined carefully when collected. Do not wait a few hours because the flower will often collapse. Because of the importance of the inner floral characters, notes on these will help in identification. Large and long-tubed flowers (e.g., subg. *Granadilla* and *Tacsonia*) should be opened, or partly cut longitudinally, before pressing, so the internal structures are clearly visible. Small flowers (e.g., subg. *Plectostemma*) can be pressed without this sectioning, but should be pressed with the flowers open.

Whenever possible, flowering material should also be preserved in FAA, together with pieces of stem, leaves, etc. Large fruits should be cut

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[1] We are indebted to Mrs. Kirsten Tind who made the drawings and Dr. Robert R. Haynes for reading the manuscript.

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ANN. MISSOURI BOT. GARD. 71: 1172–1174. 1984.

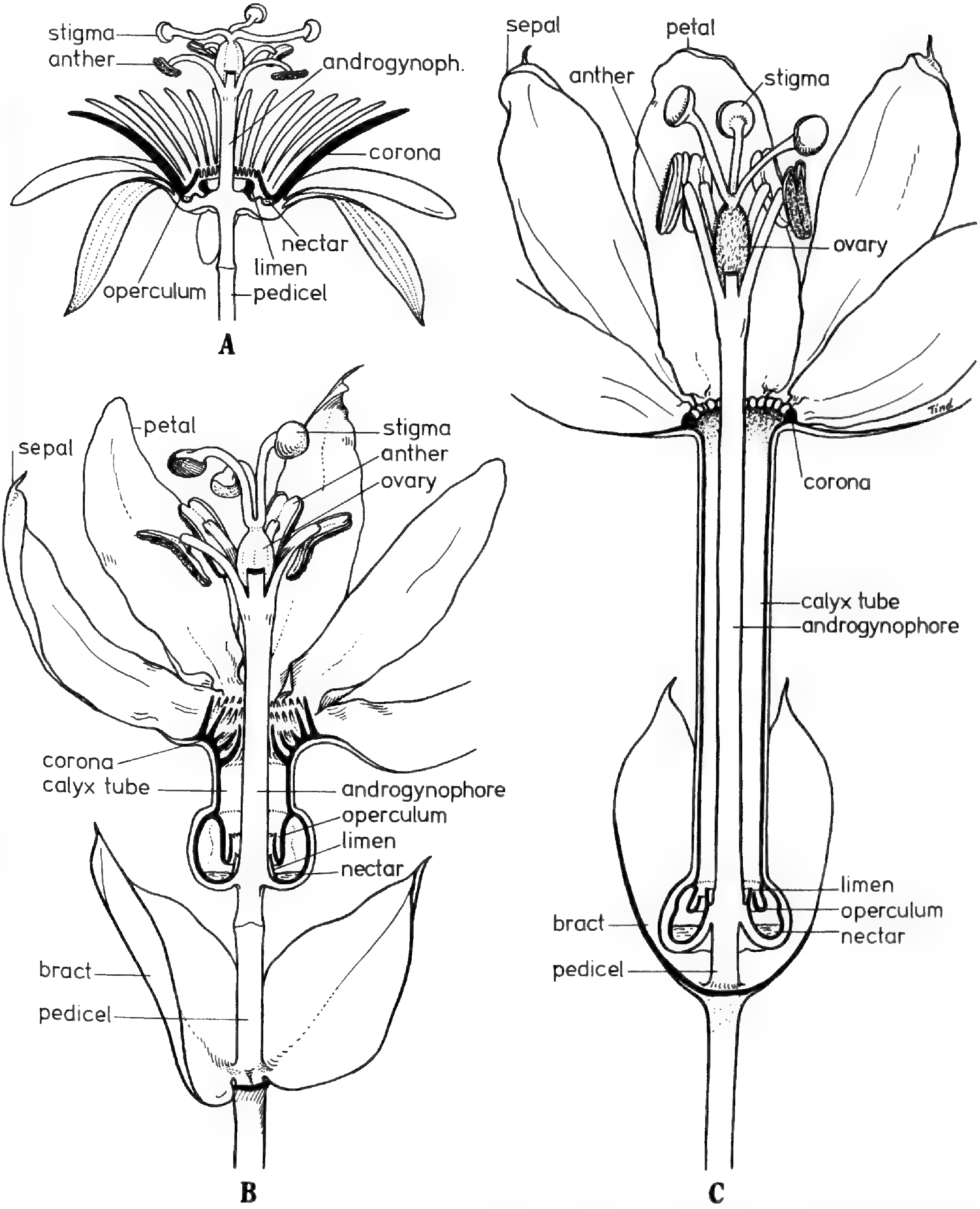

FIGURE 1. Variation in *Passiflora.*—A. subg. *Plectostemma. Passiflora capsularis* L.—B. subg. *Granadillastrum. P. manicata* (Juss.) Pers.—C. subg. *Tacsonia. P. mixta* L.

into halves or smaller slices, and some seeds dried separately.

Color photographs of the flower are valuable tools in the description of the flower and its colors.

LIVING MATERIAL

The easiest way of transferring passifloras into cultivation is by seeds, although these are sometimes difficult to germinate. Seeds from mature fruits are removed from the pulp and dried. Cuttings of *Passiflora* are very easy to grow if planted within a few days of collection.

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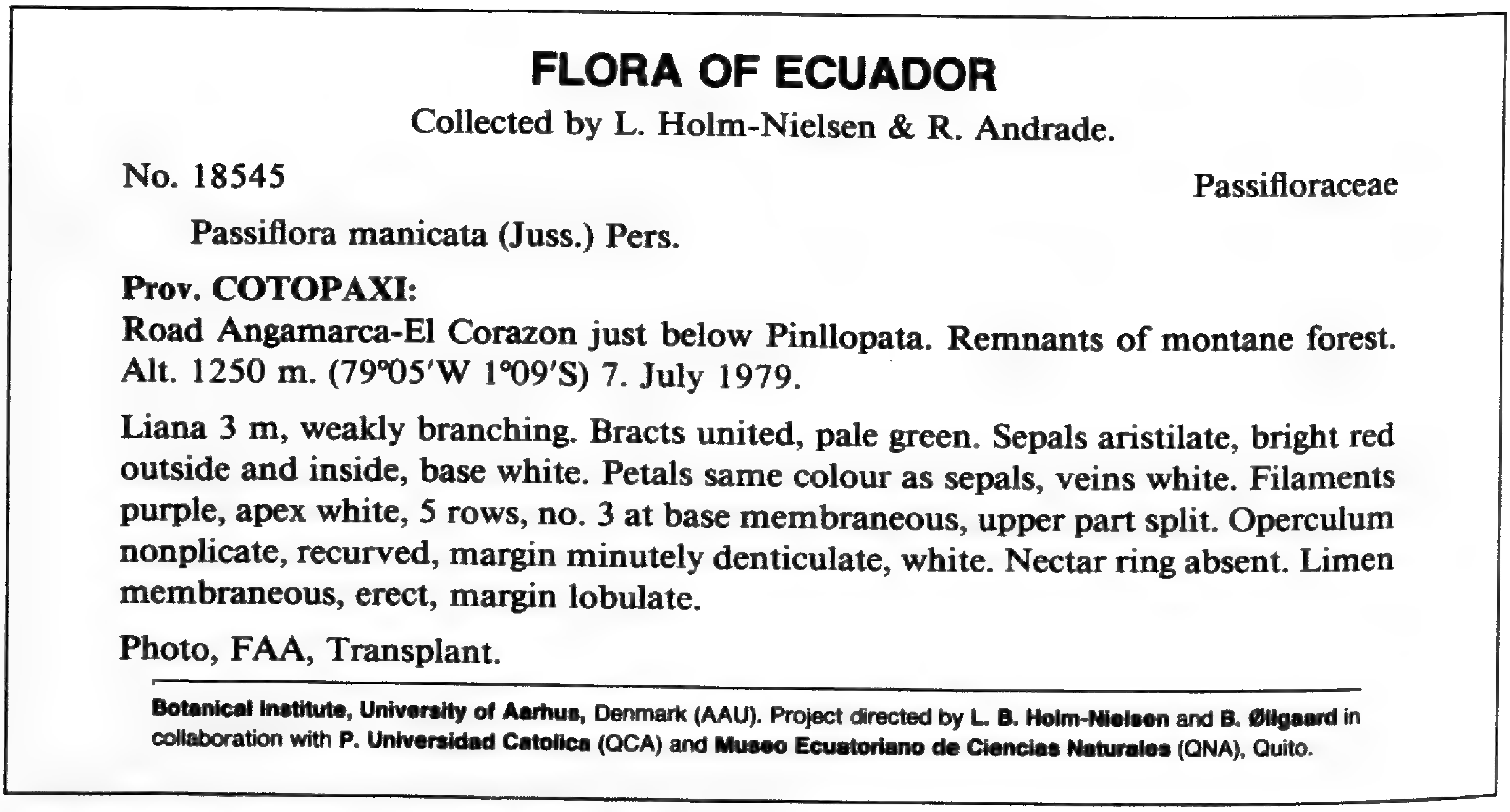
TABLE 1. Checklist for notes of passifloras.

A. General data. (Fig. 2)
  1. Collector and collection number.
  2. Locality: province, closest village/city, latitude, longitude.
  3. Habitat: vegetation, substrate.
  4. Elevation in meters.
  5. Date.
  6. Common name and use.

B. Specimen data. (Fig. 2)
  1. Habit: herb, shrub, tree, liana; and height in meters.
  2. Stem: maximum diameter, smooth, striate, winged, terete, spiny, branching pattern.
  3. Bracts: present, absent, united/free, color.
  4. Sepals: aristilation, color outside and inside.
  5. Petals: color outside and inside.
  6. Corona: color, form (filiform, liguliform, spathulate, falcate, terete, angled), number of rows.
  7. Operculum: present/absent, plicate/nonplicate, curved, recurved, horizontal. Margin of operculum (entire, crenulate, serrulate, filiform).
  8. Nectar ring: present/absent.
  9. Limen: present/absent, margin (entire, crenulate, denticulate).
  10. Androgynophore: color of stamens, anthers, ovary, styles, stigma.
  11. Fruits: mature size, shape, color, seed color.

C. Special data.
  1. Transplant: seeds, cuttings.
  2. Preservation in FAA: stems, leaves, flowers, or fruits.
  3. Photographs: flowers, fruits, etc., picture number.
  4. Pollinators observed.



FLORA OF ECUADOR

Collected by L. Holm-Nielsen & R. Andrade.

No. 18545 Passifloraceae

Passiflora manicata (Juss.) Pers.

Prov. COTOPAXI:

Road Angamarca-El Corazon just below Pinllopata. Remnants of montane forest. Alt. 1250 m. (79°05′W 1°09′S) 7. July 1979.

Liana 3 m, weakly branching. Bracts united, pale green. Sepals aristilate, bright red outside and inside, base white. Petals same colour as sepals, veins white. Filaments purple, apex white, 5 rows, no. 3 at base membraneous, upper part split. Operculum nonplicate, recurved, margin minutely denticulate, white. Nectar ring absent. Limen membraneous, erect, margin lobulate.

Photo, FAA, Transplant.

Botanical Institute, University of Aarhus, Denmark (AAU). Project directed by **L. B. Holm-Nielsen** and **B. Øllgaard** in collaboration with **P. Universidad Catolica** (QCA) and **Museo Ecuatoriano de Ciencias Naturales** (QNA), Quito.

FIGURE 2. Voucher label for a *Passiflora* collection.

NEW RUBIACEAE FROM VENEZUELA

JULIAN A. STEYERMARK[1]

ABSTRACT

Four new species of Rubiaceae are described from Venezuela: three from Territorio Federal Amazonas (*Guettarda leiantha, Psychotria davidsae, Psychotria plowmanii*), and one from Estado Zulia (*Hillia zuliaensis*). One variety is described from Estado Yaracuy (*Psychotria aubletiana* var. *villipila*). These new taxa have resulted from a joint project of exploration in Venezuela under a grant to the Missouri Botanical Garden by the National Science Foundation and to the Division of Biological Investigations, National Park Institute, Herbario Nacional of Caracas, Venezuela by CONICIT (Consejo Nacional de Investigaciones Cientificas y Tecnológicas).

Since 1977 the Missouri Botanical Garden, recipient of a grant from the National Science Foundation of the United States, and the Herbario Nacional of Venezuela, recipient of a similar grant from the equivalent organization of Venezuela (CONICIT), have been conducting joint botanical explorations into various portions of Venezuela to make inventories of the flora in those areas previously unexplored, especially where changes might be forthcoming due to the construction of dams, drainage projects, or agricultural and lumbering activities.

These explorations have resulted in a large number of additions to the known flora of Venezuela, as well as a considerable assemblage of undescribed taxa.

In the present paper a few taxa of undescribed Rubiaceae are presented.

Guettarda leiantha Steyerm., sp. nov. TYPE: Venezuela. Amazonas: along road between Paso El Diablo and Caño de Culebra, 25–30 km SE of Puerto Ayacucho, 100 m, 12 May 1980, *Steyermark, Davidse & Guanchez 122318* (holotype, VEN; isotype, MO).

Arbor 5-metralis, ramis glabris; foliis petiolatis, petiolis 1–2 cm longis modice crispato-pilosis; laminis elliptico-ovatis apice acuminatis basi acutis 12–17 cm longis, 5.5–7.5 cm latis, subtus praeter axillas barbellatas atque nervos breviter crispato-villosulos glabris, supra costa media sparse vel modice adpresso-pilosula aliter glabris, nervis lateralibus utroque latere ca. 7 tenuibus adscendentibus ante marginem 3–4 mm anastomosantibus; inflorescentia semel dichotoma, quoque ramulo inflorescentiae 8–15-flora semel vel non nihil dichotoma; pedunculo tenui 4–5 cm longo, 0.5 mm lato modice minute crispato-pilosulo; floribus tetrameris; calyce hypanthioque 1.5 mm longis, hypanthio 1 mm longo, 0.8 mm lato glabro, lobis calycis paullo inaequalibus suborbiculari-ovatis obtusis 0.3–0.4 mm longis, 0.3–0.4 mm latis sparsim ciliolatis; corolla tenuiter hypocraterimorpha 10 mm longa, tubo 8 mm longo, 1 mm lato extus glabro intus basi annulo denso piloso instructo inde 5 mm sparsim piloso, lobis ovali-oblongis apice rotundatis 1.5 mm longis, 1.5 mm latis, uno vel duobus lobis parce crenulatis intus marginibus papillatis extus glabris; antheris linearibus 2.7 mm longis in parte tertia superiore insertis; stylo 9 mm longo glabro.

Tree 5 m tall, branches glabrous. Leaves petiolate, petioles 1–2 cm long, moderately crisp-pilose; leaf-blades elliptic-ovate, acuminate at apex, acute at base, 12–17 cm long, 5.5–7.5 cm wide, sparsely to moderately appressed-pilosulous above on midnerve, elsewhere glabrous, leaf axils beneath slightly barbellate, shortly crisp-villosulous on main and secondary nerves, glabrous on surface, lateral nerves ca. 7 each side, slender. Inflorescence with 2 primary axes either not forked or once-forked, each fork bearing 8–15 flowers; peduncle slender, 4–5 cm long, 0.5 mm thick, moderately minutely crisp-pilosulous; flowers tetramerous; calyx and hypanthium 1.5 mm long, hypanthium 1 mm long, 0.8 mm wide; calyx lobes slightly unequal, suborbicular-ovate, obtuse, 0.3–0.4 mm by 0.3–0.4 mm, sparsely ciliolate; corolla slenderly hypocrateriform, 10 mm long, the tube 8 mm long, 1 mm broad, glabrous without, sparsely pilose in the basal 5 mm within with a dense pilose ring at the very base, lobes oval-oblong, rounded at apex, 1.5 mm by 1.5 mm, glabrous without, papillate within on margins, 1 or 2 of the lobes inconspicuously crenulate; anthers linear, included, 2.7 mm long, inserted in the uppermost ⅓ of tube; filaments 0.5 mm long; style filiform, 9 mm long, glabrous; fruit not seen.

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ANN. MISSOURI BOT. GARD. 71: 1175–1179. 1984.

This taxon is allied to *G. acreana* Krause and *G. ulei* Krause, from which it may be distinguished by the completely glabrous exterior of the corolla, glabrous hypanthium, inflorescence with only two slender primary axes either once or not at all forked, and glabrous lower surface of the leaf blade.

Hillia zuliaensis Steyerm., sp. nov. TYPE: Venezuela. Zulia: Mara, vicinity of Río Guasare, between Rancho 505 and Cerro Yolanda, 10°53–56'N, 72°26–28'W, 200–270 m, 29 May 1980, *Steyermark, Davidse & Stoddart 122876* (holotype, VEN; isotype, MO). PARATYPE: Venezuela. Zulia: Cerro Los Manantiales, forested uppermost slopes and ridges, E of Río Guasare, W of Hacienda Los Manantiales on property of Professor Morales, 12 km W of Corpozulia Campamento Carichuano, 11°1'N, 72°20'30"W, 600 m, 3 June 1980, *Steyermark, Davidse & Stoddart 123255* (MO, VEN).

Planta epiphytica lignosa omnino glabra; stipulis caducis late obovatis acutis striatis 15 mm longis, 7 mm latis; foliis breviter petiolatis, petiolis 1–5 mm longis; laminis coriaceis late ovatis vel oblongo-ovatis apice abrupte acutis basi rotundatis vel late obtusis 9–12 cm longis, 5–7 cm latis pinnati-nerviis, nervis lateralibus utroque latere 7–8 prominulis adscendentibus ante marginem 1–3 mm anastomosantibus, venulis tertiariis laxe subreticulatis; floribus solitariis terminalibus sessilibus; calyce gamosepalo profunde campanulato inaequaliter 6-fisso, lobis lanceolatis vel triangulari-lanceolatis acutis 3–15 mm longis, 3–8 mm latis, tubo intus squamellis dentiformibus numerosis munito; corolla (immatura) subcampanulato-infundibuliformi 20 mm longa glabra (tubo 12 mm longo basi 3 mm lato orificio 9.5 mm lato, lobis quinque ligulatis apice rotundatis 9 mm longis, 4 mm latis); antheris quinque 10 mm longis, filamentis 2 mm longis; stylo 21 mm longo glabro; ovario subcylindrico anguste obconico 10–12 mm longo, 3–5 mm lato glabro.

Glabrous epiphyte. Stipules caducous, apical, broadly obovate, acute, 15 mm by 7 mm, striate. Leaves shortly petiolate, petioles 1–5 mm long; leaf blades coriaceous, broadly ovate to oblong-ovate, abruptly acute at apex, rounded to broadly obtuse at base, 9–12 cm long, 5–7 cm wide, pinnately nerved with 7–8 prominulous, ascending nerves on each side, anastomosing 1–3 mm from margin, tertiary venation loosely reticulate as seen through transmitted light. Flowers solitary, terminal, sessile. Calyx gamosepalous, 4 cm long, tube 2.6–3.2 cm long, deeply campanulate, unequally split into 6 lanceolate or triangular-lanceolate, acute lobes 3–15 mm long, 3–8 mm wide; squamellae numerous within at base of tube, dentiform, 0.5 mm long. Corolla (immature) subcampanulate-infundibuliform, 20 mm long, the tube 12 mm long, 9.5 mm wide at summit, 3 mm wide below; lobes 5, ligulate-rounded and cucullate at apex, 9 mm long, 4 mm wide; stamens 5, included, attached halfway up tube; anthers 10 mm long; filaments 2 mm long; style 21 mm long, glabrous; ovary subcylindric, narrowly obconic, 10–12 mm long, 5 mm wide at apex, glabrous.

The new species differs from *H. costanensis* Steyerm., heretofore the single species of the group with spathiform calyx, in having a shorter calyx tube with longer calyx lobes.

Psychotria aubletiana Steyerm. var. **villipila** Steyerm., var. nov. TYPE: Venezuela. Yaracuy: Sierra de Aroa, 15–20 km NW of Cocorote on road to Aroa, from 1 km SE of Los Cruceros to El Refugio, ca. 11 km W of San Felipe, 10°24'N, 68°51'W, 1,200–1,600 m, 5 Apr. 1980, *Liesner & Gonzalez 10107* (holotype, VEN; isotype, MO). PARATYPE: Venezuela. Yaracuy: Sierra de Aroa, Cerro Negro, primary forest 8 km SW of San Felipe, 10°17'N, 69°01'W, 1,200–1,800 m, 1–2 Apr. 1980, *Liesner & Gonzalez 9939* (MO, VEN).

Suffrutex 1–1.5-metralis, ramulis superne villosis pilis laxis munitis; stipulis in vaginis extus tomentosis connatis, vaginis dentibus lanceolatis acutis vel acuminatis 2.5–3.5 mm longis glabris ornatis; foliorum laminis costa media subtus laxe pilosa pilis laxe adscendentibus; inflorescentiis axillaribus terminalibusque; inflorescentiae bracteis involucralibus dimidio parte inferiore hirtello-villosis pilis patentibus 1–1.5 mm longis praeditis.

Suffruticose, 1–1.5 m tall, stems shortly appressed between nodes, hirtellous to villosulous below the inflorescences, stipules, and petiolar attachment, villous apically and on uppermost nodes. Stipular sheath 0.5–1 mm long, tomentose without, the teeth lanceolate, acute to acuminate, 2.5–3.5 mm long, 0.5–1 mm wide, glabrous. Leaves petiolate, petiole 3–10 mm long, densely hirtellous-pilosulous with loosely ascending hairs; leaf-blades lance-elliptic or elliptic-lanceolate, acuminate at apex, acute at base, 4.5–8.5 cm long, 1–2.7 cm wide, glabrous above, midrib below loosely pilose with ascending hairs, glabrous elsewhere; lateral nerves 8–9 each side, with finer intermediate nerves. Heads terminal and axillary, subhemispheric, 8–10 mm high, 13–

15 mm wide; involucre hirtellous-villous at base and in lower half with spreading hairs 1–1.5 mm long; floral bracts cucullate, pilosulous near apex and upper half, elsewhere glabrous; corolla tube and lobes glabrous.

This variety differs from *P. aubletiana* Steyerm. var. *aubletiana* in the lanceolate, acute to acuminate stipular teeth, the loose pubescence of the upper portion of the stems, exterior portion of the involucre, similarly loose pubescence of the lower midrib, and in the terminal as well as axillary inflorescences. From *P. aubletiana* var. *producta* Steyerm. it differs in the shorter stipular teeth and villous pubescence of the lower midrib, while from var. *andina* Steyerm. f. *pubescens* Steyerm. it is differentiated by the acute to acuminate stipular teeth and villous spreading pubescence. Because of the terminal as well as axillary inflorescences, future collections may well indicate specific status for this taxon.

Psychotria davidsae Steyerm., sp. nov. TYPE: Venezuela. Amazonas: Atures, virgin rainforest along Río Cataniapo, on N side of river at dam site, 48 km SE of Puerto Ayacucho, 5°35′N, 67°15′W, 200–300 m, 10 May 1980, *Steyermark, Davidse & Guanchez 122197* (holotype, VEN; isotype, MO). PARATYPES: Venezuela. Amazonas: selva húmeda, a lo largo de la carretera, 10–30 km al este de Puerto Ayacucho hacia Gavilán, 5°35′N, 67°22′W, 120 m, 11 June 1977, *Steyermark, Berry, Huber & Redmond 113893* (VEN). Bolívar: Sierra Pakaraima, frontera no. 10, 4°7′N, 65°43′W, 1,200 m, 2 May 1973, *Steyermark, Gil, Quintero & F. José García 107206* (VEN).

Suffrutex 0.5-metralis, ramulis juvenilibus modice vel dense puberulis pilis brunneis brevibus munitis; stipulis in vaginam 1.5 mm longam, 3 mm latam modice puberulam connatis, utroque latere in dentes duos lanceolatos acuminatos 2–2.5 mm longos, 0.5–0.7 mm latos desinentibus; foliis oppositis petiolatis, petiolis 4–12 mm longis dense puberulis pilis brunneis munitis; laminis late ovatis vel elliptico-ovatis vel oblongo-ellipticis apice acutis basi cuneatim acutis 6–15(–26) cm longis, 4–7.5(–13) cm latis, supra praeter costam mediam puberulam glabris, subtus sparsim vel modice subadpresso-puberulis, costa media nerviis lateralibusque modice puberulis pilis patentibus vel crispatis instructis, marginibus ciliatis; nerviis lateralibus utroque latere 6–10 arcuato-adscendentibus in margines desinentibus; inflorescentia terminali axibus principalibus vel saltem inferioribus umbellatim ramosis 2–3 cm longa (pedunculo incluso), 2.5–5 cm lata pedunculata, peduncullo 5–25 mm longo, 1.5 mm diam. dense tomentoso pilis patentibus 0.2–0.4 mm longis munito; inflorescentiae axibus 4–5 patentibus 7–12 mm longis dense brunneo-tomentosis; floribus subcapitatis in extremitatibus axium dispositis, floribus in quoque capitulo plurumque 10–13; capitulis a bracteis 4–7 lingulatis vel subspathulatis cucullatis apice rotundatis vel lato obtusis 4–5 mm × 1.5–2 mm carinatis extus modice puberulis cinctis; bractea principali sub quoque capitulo ligulata apice rotundata carinata 10 mm × 4 mm utrinque modice puberula; calyce hypanthioque 1.8–2 mm longo, hypanthio subgloboso hirsutulo pilis patentibus munito, calyce lobis quinque ovato-lanceolatis acutis 1–1.5 mm longis, 0.7–1 mm latis extus ad apicem hirsutulis, marginibus valde ciliatis intus glabris, basi sinu inter lobos 1-glanduliferis; corolla breviter infundibuliformi 6–6.5 mm longa extus puberula, tubo 3–3.5 mm longo basi 1.5–2 mm lato orificio 3 mm lato, lobis 5–6 lanceolatis, apice cucullato-incurvato attenuato 3 mm × 1–1.5 mm intus glabris, orificio intus dense villoso; antheris 5–6 linearibus 2 mm longis vix exsertis medio tubi insertis; florum longistylorum stylis 6.5–7 mm longis; disco exserto.

Subligneous plant 0.5 m tall, the young stems moderately to densely short brown-puberulous. Stipules moderately pubescent with short brown, ascending hairs, the sheath shorter than the teeth, 1.5 mm long, 3 mm wide, teeth lanceolate, acuminate, 2–2.5 mm long, 0.5–0.7 mm wide. Leaves broadly ovate or elliptic-ovate, acute at apex, cuneately acute at base, 6–15(–26) cm long, 4–7.5(–13) cm wide, glabrous above except the midrib puberulent, midrib and lateral nerves below moderately puberulous with spreading or crisp brown pubescence, elsewhere sparsely to moderately puberulous on surface with subappressed hairs, margins ciliolate; lateral nerves 6–10 each side, arcuately ascending, ending at margins. Inflorescence terminal, pedunculate, including peduncle 2–3 cm long, 2.5–5 cm wide, the main or lower axes umbellately branched; peduncle 5–25 mm long, 1.5 mm thick, densely tomentose with spreading hairs 0.2–0.4 mm long, axes of inflorescence 4–5, spreading, 7–12 cm long, densely brown-tomentose; flowers subcapitate at the ends of each axis, in groups mainly of 3 heads with 10–13 flowers in each group; heads subtended by 4–7 lingulate to subspathulate, rounded to broadly obtuse, cucullate bracts 4–5 mm long, 1.5–2 mm wide, carinate, moderately puberulous without, subglabrous within or sometimes puberulous; larger bract subtending the 3 groups ligulate, rounded at apex, carinate, 10 mm long, 4 mm wide, moderately puberulous both sides. Calyx and hypanthium 1.8–2 mm long; hypanthium subglobose-depressed, hirsutulous with spreading brown hairs, 0.5–1 mm high; calyx lobes 5, ovate-lanceolate, acute, 1–1.5 mm long, 0.75–1 mm wide, hirsutulous apically without, glabrous within, strongly ciliate, with 1 or sometimes 2 elliptical squamellae in the sinus between each calyx lobe within; disk exserted, about ½ length of calyx lobes. Corolla white-creamy, short infundibuliform, 6–6.5 mm long, puberulous-pilosulous without, tube 3–3.5 mm long, 1.5–2 mm wide at base, 3 mm wide at orifice, densely villous within at orifice, base of lobes and upper part of tube; lobes 5–6, lanceolate, cucullate-incurved and attenuate at apex, 3 mm long, 1–1.5 mm wide, glabrous within; stamens 5–6, anthers linear, 2 mm long, barely exserted, inserted ½ up tube; filaments 0.5 mm long; style exserted in long-styled flowers, 6.5–7 mm long.

This species is closely related to *P. brazoi* Steyerm., of northernmost Brazil (Serra da Neblina) and southeastern Colombia. From that taxon, *P. davidsae* differs in the following being more densely pubescent: stipules, peduncles, axes of the inflorescence, calyx, and hypanthium, and lower surface of the leaf blades; the petioles are shorter, the calyx lobes more densely ciliolate; the corolla more densely pubescent in the upper half of the interior and orifice. It affords me great pleasure to dedicate this species to Dr. Gerrit Davidse, Coordinator for the Missouri Botanical Garden of the joint exploration project with Venezuela.

Psychotria plowmanii Steyerm., sp. nov. TYPE: Venezuela. Amazonas: Atures, virgin rainforest along Río Cataniapo, 44–45 km SE of Puerto Ayacucho, 3 km downstream from dam site, 5°35'N, 67°15'W, 200–300 m, 9 May 1980, *Steyermark, Davidse & Guanchez 122132* (holotype, VEN; isotype, MO). PARATYPES: Venezuela. Amazonas: Atures, bosque alto denso, a aproximadamente 2 km al suroeste del caserio San Pedro de Cataniapo, al suroeste de Puerto Ayacucho, 5°39'N, 67°11'W, 90–110 m, 1980, *Guanchez 140* (VEN); hillside forest immediately behind "El Tobogán de la selva" camping area, 35 km S of Puerto Ayacucho, 85 m, 21 Feb. 1979, *Plowman 7715* (F).

Frutex 1.5–2-metralis; foliis oppositis petiolatis, petiolis 6–9 mm longis glabris; stipulis in vaginam 2–4 mm longam, 3–6 mm latam extus glabram connatis, supremis late deltoideis obtusis dense albo-ciliatis 1.5 mm longis, vetustioribus apice truncatis; laminis chartaceis oblanceolatis vel elliptico-oblanceolatis apice acutis vel acuminatis basi cuneatim acutis vel acuminatis 13–20 cm × 4–9 cm utrinque glabris, nervis lateralibus utroque latere 9–13 divaricate adscendentibus ante marginem 2–4 mm anastomasantibus utrinque elevatis, venulis tertiariis grosse reticulatis subtus manifeste elevatis; inflorescentia terminali 1.5–3.5 cm longa, 2–4 cm lata pedunculata, pedunculo 2.5–4.5 mm longo, 1 mm lato minute sparsimque papillato-puberulo; inflorescentiae axibus quinque vel sex 6–11 mm longis, infimis patentibus vel reflexis longioribus quam superioribus multifloris; floribus sessilibus aggregatis ad extremitates ramulorum dispositis; bracteis subaxibus suborbiculari-ovatis subacutis 0.8–1.5 mm longis ciliolatis calyce hypanthioque 1.2 mm longo, hypanthio breviter cylindrico 0.9 mm longo dimidia parte inferiore minute puberulenti, calycis tubo lobisque 0.3 mm longis, lobis quinque leviter deltoideis subobtusis minute papillato-ciliolatis, tubo sparsim minute papillato-puberulo; corolla cremosa infundibuliformi 3 mm longa, 0.7–1.3 mm lata extus glabra, tubo intus dimidia parte superiore dense pubescenti, lobis quinque lanceolatis obtusis apice cucullato-inflexis 1 mm × 0.7–0.9 mm; antheris oblongis 0.9 mm longis; pistillo 3 mm longo, stylo dimidio parte superiore sparsim papillato-puberulo.

Shrub 1.5–2 m tall. Stipular sheath 2–4 mm long, 3–6 mm wide, glabrous without, truncate or nearly so at the summit of older sheaths, uppermost sheath densely white-ciliate on border, uppermost stipule broadly deltoid, obtuse, 1.5 mm high. Leaves petiolate, petiole 6–9 mm long, glabrous; leaf blades oblanceolate to elliptic-oblanceolate, acute to acuminate at apex, cuneately acute to acuminate at base, domatia absent in leaf axils beneath, 13–20 cm by 4–9 cm, glabrous; lateral nerves 9–13 each side, elevated both sides, divaricately ascending, anastomosing 2–4 mm from margin, tertiary venation coarsely reticulate, conspicuous and elevated below, impressed above and less conspicuous. Inflorescence terminal, about as broad as long, 1.5–3.5 cm long, 2–4 cm wide, many-flowered toward the apices of the lateral axes, with 5–6 axes, the lowest pair spreading to reflexed and longer than the upper ones, 9–11 mm long, papillate-puberulent; peduncle 2.5–4.5 mm long, 1 mm thick, slender, minutely and sparsely papillate-puberulent; flowers sessile; bracts subtending axes of inflorescence suborbicular-ovate, subacute, 0.8–1.5 mm long, ciliate. Calyx and hypanthium 1.2 mm long, hypanthium short-cylindric, 0.9 mm long, 0.5 mm wide, sparsely minutely puberulent in lower half; calyx tube and lobes 0.3 mm long, 1 mm wide, sparsely papillate-puberulent on calyx tube to glabrate; calyx lobes 5, shallowly deltoid, subobtuse, minutely papillate-ciliolate, 0.3 mm high, 0.4 mm wide; corolla creamy, infundibuliform, 3 mm long, basally narrowed to 0.7 mm wide, expanded at the limb to 1 mm long and 1.3 mm wide at summit, glabrous without; corolla tube densely pubescent within midway at base of stamens; corolla lobes 5, lanceolate, obtuse at the cucullate inflexed apex, 1 mm long, 0.7–0.9 mm wide. Stamens 5, anthers oblong, attached 1 mm above base of corolla tube; style 0.6 mm long, rounded at apex, sparsely papillate-puberulent in upper half.

This taxon differs from *P. ventuariana* Standl. & Steyerm. in the puberulent hypanthium and shorter inflorescence nearly as broad as long with fewer axes. From *P. coussareoides* Standl. it may be differentiated by the shorter corolla and shorter, differently shaped inflorescence with fewer axes.

NOTES ON NEOTROPICAL LAURACEAE

Henk van der Werff[1]

Abstract

The following notes are based on a study of herbarium specimens of neotropical Lauraceae and are the first results of a long-term project on the American representatives of that family. Unless otherwise stated, all specimens studied are deposited in the herbarium of the Missouri Botanical Garden (MO). When necessary, flowers were softened by boiling for about half an hour. Softening with detergent required much more time (usually about two hours) and this method was discontinued. Lauraceous flowers are trimerous and consist of two (usually equal) whorls of three tepals and four whorls of three stamens, which are numbered from outside to inside with Roman numerals; the anthers of whorl IV, the innermost ones, are reduced to staminodia or lacking.

Aiouea lundelliana Allen, J. Arnold Arbor. 26: 419. 1945. TYPE: Panama. Chiriqui, *White 225* (holotype, MO!).

Allen (1945) cited one flowering collection (the type) and two fruiting collections in her description. Kostermans annotated the type in 1959 as *Aiouea costaricensis* (Mez) Kostermans, a species restricted to Costa Rica and Panama. However, Renner (1982) excluded the species from *Aiouea* and referred it to *Ocotea*. In *Ocotea* it would key to *O. tonduzii* Standley, known from Costa Rica and Panama; indeed, Allen (1945) mentioned in the discussion of *O. tonduzii* that fruiting material is often confused with that of *Aiouea* (which she called *Aniba* by mistake) and that differences are very hard to formulate. *Aiouea lundelliana* and *A. costaricensis* are said to differ in leaf characters: leaves to 16(–18) cm long and 7.5 cm wide with apex obtusely and shortly acuminate and reticulation slightly prominent beneath in *A. lundelliana* and leaves to 12(–13) cm long and 6 cm wide with obtuse or rounded apex (very occasionally shortly acuminate) and reticulation very prominent beneath in *A. costaricensis*. These differences are weak and it is likely that only one species of *Aiouea* occurs in Costa Rica and Panama.

Renner (1982) transferred *A. lundelliana* to *Ocotea* because the type specimen has anthers with four cells, while *Aiouea* has 2-celled anthers. The difference in number of anther cells is the only good character separating *Ocotea* from *Aiouea*; other characters mentioned in literature either do not apply to the Central American *Aiouea* species (*Aiouea* is said to have conspicuous staminodia; in *Ocotea* staminodia are inconspicuous or lacking, but Renner (1982) describes *A. costaricensis* as having minute staminodia, 0.5 mm long, or without staminodia) or are not sufficient for the separation of genera (leaves often drying yellow-green and with a thickened margin in *Aiouea*; in *Ocotea* leaves dry variously and thickened margin is not a rule). The different generic identifications by Allen and Kostermans on one hand and Renner on the other stimulated me to check the number of anther cells in several flowers of the same specimen in order to verify if that number is constant. As controls, I also checked several flowers from collections identified as *Aiouea costaricensis* and *Ocotea tonduzii*. These species were chosen because of their great resemblance to *A. lundelliana*.

Aiouea costaricensis

Hartshorn 1121. Nine flowers checked. Anthers I, II and III all had 2 cells.

Utley 3040. Five flowers checked; all anthers had 2 cells.

Ocotea tonduzii

Poveda 429, 1091 and *Stevens 14131*. Of each collection ten flowers checked. All anthers (I, II, and III) had 4 cells.

Aiouea lundelliana

White 225. Eight flowers checked. Anthers I and II were usually 2-celled, but sometimes only 1 cell was developed. Anthers III were 4-celled in two flowers, 2-celled in one flower, and sometimes rudimentary (no cells visible).

Mori & Kallunki 5680. Six flowers checked. One flower had anthers I and II 4-celled and III rudimentary; three flowers had I and II 2-celled, III not sufficiently developed for counting, and

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one flower was entirely 2-celled with open anther cells (were closed in other flowers).

Lao 333. Two flowers checked. Some anthers were 2-celled, some 4-celled. On the 4-celled anthers the upper two cells were usually much smaller than the lower two.

To exclude the possibility that *Aiouea lundelliana* is represented by pistillate specimens of a dioecious *Ocotea* species with poorly developed anthers, I checked seven flowers of an obvious dioecious *Ocotea* species (*Ocotea cernua* (Nees) Mez, represented by *Brigada Doranthes 3015,* Mexico). This species is not similar to the other three species. In all seven flowers, anthers I and II were 4-celled; in three flowers, anthers III were 4-celled; and in four flowers, they were rudimentary. No 2-celled anthers were seen. Thus, *Aiouea lundelliana* cannot be regarded as a pistillate specimen of a dioecious *Ocotea* species.

The number of anther cells is one of the important characters in the generic classification of Lauraceae. It has always been assumed that this number is constant and I have not found any references to examples of flowers with varying numbers of anther cells on the same whorl (*Endlicheria anomala* Nees ex Meissner is unusual in having anthers I and II 2-celled and anthers III 4-celled, but these numbers are constant: I and II are always 2-celled and III always 4-celled. Similar conditions are also reported for *Phoebe* and *Persea* species). The variation in number of anther cells in *Aiouea lundelliana* stands in strong contrast to the constancy of the number of anther cells in the *Aiouea* and *Ocotea* species and suggests that *Aiouea lundelliana* is a hybrid between an *Aiouea* and *Ocotea* species. This putative hybrid is known only from the Cerro Punta area, Chiriqui province, Panama; the collections were made in 1938, 1971, and 1975. The Mori and Kallunki collection has young fruits, so it is likely that the population on Cerro Punta will persist.

Although infrageneric hybrids in Lauraceae have been reported (Kubitzki, 1982), intergeneric hybridization has, to my knowledge, not been reported earlier. The generic boundaries in neotropical Lauraceae were already considered weak without evidence for intergeneric hybridization and this hybridization makes the need for a reassessment of the genera even more urgent.

Nectandra kunthiana (Nees) Kosterm., Meded. Bot. Mus. Herb. Rijks Univ. Utrecht 25: 19. 1936. *Acrodiclidium kunthianum* Nees, Syst. Laur. 269. 1836. TYPE: French Guyana, *Poiteau s.n.* (P, n.v.). *Ocotea kunthiana* (Nees) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 291. 1889.

Ocotea cooperi Allen, J. Arnold Arbor. 26: 335. 1945. TYPE: Panama. Bocas del Toro, *Cooper & Slater 96* (holotype, F; isotypes, GH, Y, n.v.).

Nectandra meyeriana Lasser, Bol. Soc. Venez. Ci. Nat. 11: 184. 1948. TYPE: Venezuela. Aragua: Rancho Grande, *Pittier 15.274* (holotype, VEN, n.v.).

Pleurothyrium cowanianum Allen, Mem. New York Bot. Gard. 10(5): 121. 1963. TYPE: Venezuela. Amazonas, *Maguire, Cowan & Wirdack 29830* (holotype, NY, n.v.).

Nectandra kunthiana, a wide-ranging species, is characterized by its large, oblong leaves with raised reticulation on both surfaces, rounded leafbases, and brown tomentose pubescence on young twigs, inflorescence, and flowers. It does not fit very well in any of the neotropical lauraceous genera. It differs from typical *Nectandra* in being dioecious and from *Ocotea* in the position of the anther cells (not in two superposed rows, but more or less in an arc). Its generic position can be determined only after the neotropical lauraceous genera are much better defined. Differences cited by Allen (1965) between *Nectandra kunthiana* and *N. meyeriana* (leaves more consistently oblong, sharply reticulate throughout, with presumably a narrow, slightly acute cusp) are insufficient to separate these two species. A character given by Allen (1963) for *Pleurothyrium cowanianum,* leaf margins with dense pubescence, applies only to young leaves and occurs also on Peruvian and Ecuadorian material; older leaves, found on fruiting material, are much less pubescent.

Because *Ocotea cooperi, Nectandra meyeriana,* and *Pleurothyrium cowanianum* cannot be separated from *Nectandra kunthiana,* they are here placed in synonymy under the latter species.

Nectandra kunthiana is now known from the Guyanas, Venezuela, Peru, Ecuador, Colombia, Panama, and Costa Rica, and I expect it occurs in Brazil as well.

Nectandra martinicensis Mez, Mitt. Bot. Vereins Kreis Freiburg 47, 48: 421. 1888. TYPE: Trinidad, *Sieber 99* (lectotype, G, n.v.; isolectotype, MO).

Nectandra glandulifolia Lasser, Bol. Técn. Minist. Agric. 3: 16, t. 12. 1942. TYPE: Venezuela. Miranda, *Pittier 8270* (holotype, VEN!). For additional synonymy, see Howard, 1981.

Nectandra martinicensis is an inconspicuous, widespread species that has been described three times from Central America (Bernardi, 1967). Characteristic for this species is the combination of membranaceous leaves, densely gland-dotted above, and the whitish pubescence on inflorescence and buds. *Pittier 8270* is in no way different from *N. martinicensis* and therefore *N. glandifolia* is reduced to synonymy under that species. The known distribution of *N. martinicensis* is Mexico, Belize, El Salvador, Nicaragua, Costa Rica, Panama, Colombia, Ecuador (fide Bernardi, 1967), Venezuela (coastal mountains from Zulia to Miranda), Trinidad, Tobago, and Montserrat.

Ocotea calophylla Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 298. 1889. *Pleurothyrium velutinum* Meissner in DC., Prodr. 15(1): 170. 1864. TYPE: Colombia. Near Antiquia, *Jervise s.n.* (K, n.v.).

Ocotea fulvescens Standley & L. O. Williams, Ceiba 1: 237. 1951. TYPE: Costa Rica. Cordillera de Talamance, 2,800 m, *Leon 2166* (isotype, MO!).

Ocotea calophylla Mez is one of the very few species of *Ocotea* restricted to high montane forests of the Venezuelan and Colombian Andes, usually above 2,500 m. Diagnostic characters are, in addition to its habitat, the sessile leaves with dense, ferruginous pubescence on the lower surface, the recurved base of the leaves, and the two vernation lines on the leaves. When Standley and Williams published *Ocotea fulvescens,* they compared it only with other Central American species, from which they considered it distinct because of its dense and persistent pubescence. Because *Ocotea fulvescens* agrees in all characters with *Ocotea calophylla,* it is here placed in synonymy under the latter species.

Phoebe cinnamomifolia (Kunth) Nees, Linnaea 21: 488. 1848. *Persea cinnamomifolia* Kunth, Nov. Gen. 2: 160. 1815. TYPE: Colombia, *Humboldt & Bonpland s.n.* (P, n.v.).

Phoebe mexicana Meissner in DC., Prodr. 15(1): 31. 1864. SYNTYPES: Mexico. Near Jalapa, *Galeotti 7026* (BR, n.v.); Mirader, *Linden 20* (BR, n.v.).

Phoebe filamentosa Allen, Mem. New York Bot. Gard. 15: 69. 1966. TYPE: Venezuela. Merida: along Río Onia, *Steyermark 56740* (holotype, F!; isotype, MO!).

Phoebe cinnamomifolia is a wide-ranging, rather variable species, characterized by its almost glabrous, tripliveined leaves, lower leaf surfaces pale green due to the densely papillose epidermis, and the erect axillary or terminal inflorescences. Size of the leaves and pubescence of the flowers vary; plants from higher elevation tend to have smaller, more coriaceous leaves and pubescent inflorescences and flowers, whereas material from wet lowland forest (Barro Colorado, Panama; Río Onia, Venezuela) has larger leaves and glabrous inflorescences and flowers. *Phoebe johnstonii* Allen, known only from Panama, was separated by Allen from *P. mexicana* because of its shorter inflorescences (to 15 cm long in *P. mexicana,* usually less than 12 cm in *P. johnstonii*), flowers not white-pubescent, and thinner and narrower leaves. It is doubtful whether it can be maintained as distinct from *P. cinnamomifolia.*

Phoebe cinnamomifolia occurs throughout Central America, where it has been named *P. mexicana,* and in Venezuela, Colombia, and Peru.

Phoebe triplinervis (Ruíz Lopez & Pavon) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 211. 1889. *Laurus triplinervis* Ruíz Lopez & Pavon, Fl. Peruv. 4: 30, t. 363. 1957. TYPE: Peru. Cuchero, *Ruíz Lopez, & Pavon s.n.*

Phoebe pichisensis A. C. Smith, Bull. Torrey Bot. Club 38: 103. 1931. TYPE: Peru. Junin, *Killip & Smith 25430* (holotype, NY!; isotype, F!).

Macbride (1938) separated *P. pichisensis* from *P. triplinervis* by the leaf venation: pinnate in *P. pichisensis,* and tripliveined in *P. triplinervis.* However, venation on the type material of *P. pichisensis* does not differ from the venation of isotypes of *P. triplinervis* (MO!, F!). Since there are not other differences, *P. pichisensis* is reduced to synonymy under *P. triplinervis. Phoebe paraguayensis* Hassler (isotype *Hassler 11305,* F!) is very similar to *P. triplinervis* and may very well prove to be conspecific with it once more material is available.

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NOTES

ALECTRA ASPERA (CHAM. & SCHLECHT.) L. O. WILLIAMS

While writing the account of the genus *Alectra* Thunberg for the forthcoming Flora Mesoamericana, covering the area from Chiapas to Panama (Gentry, 1981), we encountered a problem concerning the correct name for the Central American species.

Pedicularis melampyroides L. C. Rich. (1792) is the first published name for the species. The species was transferred into the genus *Alectra* by Kuntze (1891). Melchior (1941), in his revision of the genus *Alectra,* accepted *A. melampyroides* (L. C. Rich.) O. Kuntze as the valid name. However, this is a later homonym of *Alectra melampyroides* Benth. (1846), which is a synonym of *Alectra sessiliflora* (Vahl) O. Kuntze (1891). The name *A. melampyroides* (L. C. Rich.) O. Kuntze is therefore illegitimate and cannot be used. Bentham (1846) used the name *Alectra brasiliensis* for the Central American species.

Another name, *Scrophularia fluminensis,* was published for the species by Vellozo (1831) in "Florae Fluminensis." Carauta (1973) stated that the effective date of publication of "Florae Fluminensis" was 1829 for the text volume, not 1825 as indicated on the title page. The "Florae Fluminensis Icones" vol. 6, containing the illustration of *S. fluminensis* Vellozo, was not published until 1831, although the title page is dated 1827. Stearn (1971) transferred the species into *Alectra* with the combination *A. fluminensis* (Vellozo) Stearn.

A further name, *Glossostylis aspera* Cham. & Schlecht. (1828), was published for the same species and transferred to the genus *Alectra* by Williams (1972).

The title page of Vellozo's "Florae Fluminensis" would indicate that *Scrophularia fluminensis* was the earliest valid specific epithet. However delay in distribution of this work means that the earliest epithet is from *Glossostylis aspera* and the correct name for the species is *Alectra aspera* (Cham. & Schlecht.) L. O. Williams. The synonyms of this taxon are listed below.

Alectra aspera (Cham. & Schlecht.) L. O. Williams, Fieldiana, Bot. 34: 118. 1972. *Glossostylis aspera* Cham. & Schlecht., Linnaea 3: 23. 1828. TYPE: Brazil. Provincia Rio Janeiro in fossis prope St. Annam, xii, *Beyrich s.n.* (HAL?, not seen).

Alectra brasiliensis Benth. in DC., Prodr. 10: 339. 1846. *Melasma brasiliense* (Benth.) Chodat & Hassler, Bull. Herb. Boissier 4: 291. 1904.

Alectra fluminensis (Vellozo) Stearn, J. Arnold Arbor. 52: 635. 1971. *Scrophularia fluminensis* Vellozo, Florae Fluminensis 263. 1829.

Alectra melampyroides (L. C. Rich.) O. Kuntze, Revis. Gen. Pl. 2: 458. 1891, non Benth. 1846. *Pedicularis melampyroides* L. C. Rich., Actes Soc. Hist. Nat. Paris 1(1): 111. 1792. *Nigrina melampyroides* (L. C. Rich.) O. Kuntze, Revis. Gen. Pl. 3(2): 237. 1898. *Melasma melampyroides* (L. C. Rich.) Pennell ex Britton & Wilson in Sci. Surv. Porto Rico & Virgin Islands 6(2): 188. 1925.

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CIRCAEA ALPINA L. (ONAGRACEAE) IN THAILAND

Craib (1931) included *Circaea alpina* L. in his "Florae Siamensis Enumeratio" on the basis of a collection made by Kerr at Doi Chiengdao. Fifty years later Shimizu et al. (1981), without citing specimens or references, included *C. alpina* in their preliminary list of temperate species in the flora of Thailand. Previously, Gagnepain (Gagnepain in Lecomte, 1921) provided a key to five species of *Circaea* to be expected in "Indo-China," and described and illustrated (p. 983, fig. 107: 17–22) *C. mollis* Sieb. & Zucc., the only species known at the time from the region he was treating.

In my monograph of *Circaea* (Boufford, 1982) I did not attribute any members of the genus to Thailand. Since then, however, I have seen two specimens of the Kerr collection cited by Craib. These specimens are *Circaea alpina* L. subsp. *imaicola* (Asch. & Mag.) Kitamura; they apparently remain as the only collection of the genus made to date in Thailand. Label data of the Kerr specimens are: Thailand, Doi Chiengdao, ca. 2,100 m, on mossy rocks, *A. F. G. Kerr 6607* (ABD, K).

Circaea alpina subsp. *imaicola* has been collected in similar situations in north and west Burma and in extreme northwestern Vietnam. Although its occurrence in Thailand at about 20°N latitude is somewhat south of the main range of distribution, it is not as far south as the populations in southern India at about 10°N latitude where the subspecies is found at about the same elevation. Another species, *C. mollis* Sieb. & Zucc. has been collected in northern Burma, northern Laos, and in extreme northwestern Vietnam. Throughout its range *Circaea mollis* occurs at lower elevations and generally at lower latitudes than *C. alpina* subsp. *imaicola*. It is also to be expected in Thailand, and both taxa should be sought wherever temperate elements are found.

I would like to thank P. S. Ashton, H. Koyama, P. H. Raven, T. Shimizu, and T. Smitinand for their help in trying to locate specimens of *Circaea* from Thailand, and the directors of ABD and K for their loan of sepcimens.

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A NEW SPECIES OF *GUATTERIA* (ANNONACEAE) FROM PANAMA

Guatteria jefensis Barringer (Annonaceae) a new species from Cerro Jefe, Panama is distinguished from *G. inuncta* Fries by its smaller, thicker leaves, larger petals, umbonate anthers, and fruits with short thick stipes. It seems to be most closely related to species in section *Tylodiscus* R. E. Fries.

The genus *Guatteria* Ruiz & Pavon consists of about 250 species of neotropical trees and shrubs. Species are found from southern Mexico and the West Indies to Bolivia and southern Brazil, with the greatest density of species in the Amazon basin. The genus is distinguished from other Annonaceae by its axillary flowers with ebracteate pedicels, imbricate petals, anthers with thick, flattened apices, and carpels with solitary basal ovules.

The genus was revised by R. E. Fries (1939), who recognized 212 species. Fries continued to describe new species and by the time he wrote the treatment for the Flora of Panama (Fries, 1962) he recognized nine Panamanian species, only five of which had been included in the revision. After Fries's death, little work was done on the family until Paul Maas and his group at Utrecht began their studies. The difficulty in interpreting Fries's concepts has been a major cause for the decreased interest in the family. Whereas many of Fries's taxa are good, his keys and diagnostic characters are difficult to work with and are sometimes inaccurate. This has caused a buildup of undetermined material in herbaria. The species described here has been in herbaria for over a decade, but has been unrecognized until now.

Guatteria jefensis Barringer, sp. nov. TYPE: Panama. Panama: Cerro Jefe, near radio tower in *Clusia* forest, 3,000 ft., 3 Mar. 1979, *B. Hammel 6302* (holotype, MO!).

Guatteria inuncta R. E. Fries affinis sed foliis minoribus, coriaceis, ad basim rotundatis, petalis majioribus, antheris umbonatis, monocarpis et stipitibus majioribus.

Shrub or small tree, 3–4 m tall; young branches sericeous with adpressed yellow-red hairs, glabrescent. Leaves alternate, often distichous; petiole 3–5 mm long thick, black, caniculate above, sericeous when young; lamina ovate, 7–12 cm long, 3–5 cm wide, coriaceous, stiff, often slightly conduplicate, the base rounded, the apex acute to acuminate, venation pinnate, 10–13 secondary veins per side, secondaries not forming a conspicuous, arching submarginal vein, the tertiary veins obscure, glabrous and sometimes shiny above, sericeous on veins below. Flowers 1–2 per axil on leafless portions of branches or in the axils of older leaves; pedicels 15–18 mm long, articulate 3–5 mm above the base, sericeous, thickened above; sepals 3, rounded-triangulate, densely yellow sericeous outside, often slightly sericeous within, the apex obtuse; petals broadly obovate to ovate, 10–15 mm long, 9–15 mm wide, the apex sometimes serrate on older petals, the outer three densely yellow sericeous below and less so above on outer surface, the inner surface with very fine brownish pubescence, the inner three slightly yellow sericeous on outside, with fine brown pubescence near apex on inner surface and dark brown and glabrous at base within; stamens many, 1.5–2 mm long, the apex expanded and flattened, slightly umbonate, the disk plane to slightly convex, pilose between the stamens and the carpels, the hairs concealed by the dense packing of the stamens and styles; carpels many, 2–2.5 mm long, slightly sunken at the center of the disk, the ovule solitary, basal, erect. Monocarps ovoid, obtuse, 10–12 mm long, green turning purple, borne in dense clusters, the stipes thick, 8–12 mm long, red.

Additional specimens examined. PANAMA. Cerro Jefe, 11 Apr. 1977, *D'Arcy 11376* (MO); 21.7 km from Panamerican Highway, 22 June 1977, *Folsom 3852* (MO, 2); cloud forest, 850–900 m, 1.5 km WNW of weather station, 11 Apr. 1977, *Folsom, Skog & D'Arcy 2510* (MO); thick forest near top of Cerro, 13 Sept. 1970, *Foster & Kennedy 1897* (MO); summit and along road on E slope, low cloud forest, 5 Apr. 1982, *Knapp & Huft 4580* (MO); cloud forest dominated by *Clusia* spp. and *Colpothrinax cookii*, premontane wet forest, along trail on ridge running NE from summit, ca. 100 m, 11 May 1975, *Mori & Kallunki 6078* (MO); 5 June 1975, *Mori & Kallunki 6501* (MO); 800 m, 10 July 1976, *Sullivan 230* (MO); cloud forest, 850–900 m, 1.5 km WNW of weather station, 7 Oct. 1980, *Sytsma 1476* (MO); top of Cerro, 3,140 ft., 7 Apr. 1966, *Tyson 3593* (MO).

Guatteria jefensis is recognized by its shrubby habit, small, coriaceous leaves, large flowers on older portions of the branches, umbonate an-

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thers, and ovoid fruits with short, thick stipes. Also, the leaves are often slightly conduplicate and appear folded on herbarium sheets. It is most easily confused with *G. inuncta* R. E. Fries, the only other shrubby species of *Guatteria* in Panama. *Guatteria inuncta* has larger leaves with cuneate bases, smaller flowers, anthers with flat apices, and fruits on long stipes.

It is often difficult to judge when the flowers have matured. Petals of most *Guatteria* species are never tightly closed in bud. Even when the flowers are quite young, the anthers and stigmas are easily seen. As the flowers mature, the petals enlarge and spread until, at anthesis, the anthers are fully exposed. Flower color changes during the development, gradually turning from green, to yellow and sometimes to a brownish yellow.

According to Fries's (1939) classification, *G. jefensis* should be placed in section *Tylodiscus* R. E. Fries along with *G. dolichopoda* J. D. Smith. *Guatteria jefensis* has the umbonate anthers and the dark, glabrous patches at the base of the petals that mark that section but does not have fruits borne on slender stipes as found in all species of that section.

I thank Gerrit Davidse for allowing me to study the Mesoamerican material of Annonaceae and William Burger for his help and his critical reading of the manuscript. This research was supported by NSF grant DEB-8103184 to William Burger.

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