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Walter Hepworth Lewis
7 October 1990
(Photograph taken by Yutaka Suda.)

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A TRIBUTE TO WALTER H. LEWIS

On Sunday, 7 October 1990, students, colleagues, friends, and family paid tribute to the ongoing career of Walter Hepworth Lewis. Although it is long before Walter's retirement, the organizers of this tribute felt that the passage of his 60th birthday was sufficient reason to celebrate Walter's many-faceted and illustrious career and to recognize his enduring influence on those who have been fortunate enough to know him during the past 35 years.

The tribute to Walter Lewis was held at the Missouri Botanical Garden. It was a day of scientific and social activity attended by over a hundred colleagues and friends. The afternoon symposium was presented by former graduate students and long-time colleagues, and the following 10 papers are the written versions. The diversity of topics indicates the multifarious research interests of Walter Lewis. The social program included a dinner, and the addresses by Peter H. Raven, Director of the Garden, Barbara A. Schaal, Professor of Biology at Washington University, and tributes by John C. Semple, Thomas B. Croat, Yutaka Suda, and others pointed out the many contributions made by Walter and his wife, Memory.

Walter Lewis was born on 26 June 1930 in Ontario and grew up in British Columbia. He attended Victoria University (British Columbia) and the University of British Columbia, where he obtained his undergraduate and master's degrees. Then he studied at the Blandy Experimental Farm of the University of Virginia, where he obtained his doctorate under the guidance of Walter S. Flory, Jr.

Walter's professional career began with a four-year teaching stint at Stephen F. Austin State University at Nacagdoches, Texas. When he was awarded a Guggenheim Fellowship and a grant from the National Science Foundation for study in Europe and Africa, he took a leave of absence. During the next two years he worked in the herbarium at the Royal Botanic Gardens, Kew, and at the University of Leeds, studied at the Swedish Academy of Sciences in Stockholm with Professor Gunnar Erdtman, and took a six-month Land Rover tour of Africa to collect cytological materials for studies of Rubiaceae.

Upon his return to North America he accepted a position in St. Louis with the Missouri Botanical Garden and Washington University. Walter acted as curator and director of the Garden's herbarium from 1964 to 1972 and continues to date as Senior Botanist and as Professor of Biology at the university. It is the St. Louis period for which most tribute participants know Walter, but Alfred Traverse honors an earlier association from days when each used the herbarium of Southern Methodist University.

MISSOURI BOTANICAL GARDEN

Walter arrived in 1964, when activities at the Garden were quite stagnant following the death of

Robert Woodson, former director of the herbarium, and short tenures for Garden directors Hugh Cutler, Edgar Anderson, and Fritz Went. At this time the Garden's outlook was bleak. Walter was determined to change these trends, and he made many significant contributions to the Garden's future.

Fieldwork and exchanges were reactivated to add to herbarium holdings, and the two millionth specimen was added to the herbarium on 1 July 1970. A collections management staff was established for the herbarium, with the hiring of Susan Voerhoek followed by Sheri Davis (now Murphy), and the first professional plant mounters were also hired. Substantial financial support for curatorial activities was obtained from botanist B. A. Krukoff in New York. An agreement was reached with other major herbaria in America and Europe that the Missouri Botanical Garden would act as a primary repository for African collections in North America. This stemmed in part from Walter's earlier travels in Africa and immediately led to a large inflow of African specimens that helped establish the groundwork for the Garden's present African programs. A project was begun to print photographic negatives of African type specimens at Kew.

The *Flora of Panama* project, which had lapsed with Woodson's death in 1963, was resumed by Walter Lewis, who attracted funds from the U. S. Air Force and the National Science Foundation. Walter also obtained support from the Smithsonian Institution and Washington University for a collecting program in Panama, and many students, post-doctoral fellows, and other staff had the opportunity to participate in this program. By 1970, activities revolved around a resident field station where botanists could stay and specimens could be processed. This involved the purchase of a house trailer as a residence and an approach to a bemused Board of Trustees for permission to undertake such an extension of the Garden's activities. These *Flora of Panama* activities resulted in greatly increased acquisition of scientifically interesting specimens, the training of many future tropical botanists, and, ultimately, completion of the *Flora of Panama* itself. The new botanical collections made through the *Flora of Panama* project formed the basis for many scientific careers in other institutions, both in the United States and abroad.

A cooperative program was initiated among four local universities—Washington University, St. Louis University, Southern Illinois University at Edwardsville, and the University of Missouri–St. Louis—to divide and share specializations among them so that students, using the Garden as a focal institution, could obtain the best possible botanical training. One feature of this training begun by Walter was a weekly seminar where staff and students reviewed the systematics of one or more plant families, a series that continues today. Through this consortium of institutions Walter was able to influence Southern Illinois University at Edwardsville to hire a plant morphologist, Richard Keating, and the University of Missouri–St. Louis a phytochemist, John Averett.

Other significant activities for the Garden included revitalizing the *Annals of the Missouri Botanical Garden* in 1964. Will H. Blackwell was selected as Walter's first post-doctoral fellow, followed by Yutaka Suda, Richard Maxwell and Laverne Durkee. He also hired professionals Thomas B. Croat, Marshall R. Crosby, and Duncan M. Porter. Walter, together with then Director of the Garden David Gates, was instrumental in planning the Lehmann Building, where the herbarium and library have been housed since 1972.

Graduate students directed by Walter Lewis include: Daniel F. Austin, R. Kendall Baker, William G. D'Arcy, Robert B. Faden, Cathy Ferris, Alwyn H. Gentry, Joan W. Nowicke, Royce L. Oliver, Kenneth R. Robertson, John C. Semple and Frederick H. Utech. He also acted as advisor to students whose major professors had left the Garden or died: Raymond Altevogt (working with Edgar Anderson), T. C. Huang (Robert Woodson), and Bruce A. MacBryde (Derek Burch).

WASHINGTON UNIVERSITY

Walter Lewis has been an active, cordial, and integral member of the Biology Department at Washington University since the fall of 1964. Dynamic, gifted, stimulating, and popular, he has been an outstanding teacher of undergraduate students. Walter's medicinal plants course, Biology 326, Medical Plants, has had the highest enrollment of all undergraduate upper-level courses offered by the university, and he makes botany an interesting, relevant, and even fun subject. He is always willing to design a seminar or lecture for any of the other courses in the department, and these are superb. When the topic concerns the Jívaro Indians, as is often the case, the lectures are tremendously effective in conveying the importance of the tropics. After one of these presentations, students have even been known to say that they wanted to stop going to medical school and go to work in the tropics!

Walter has also been a prolific researcher, with almost 200 publications of original research. He is the author or coauthor of four texts, *Airborne and Allergenic Pollen of North America* (1983), *Ecology Field Glossary: A Naturalist's Vocabulary* (1977), *Rare and Endangered Species of Missouri* (1974), and *Medical Botany: Plants Affecting Man's Health* (1977); the last is already a classic and in its tenth printing. He also edited *Polyploidy: Biological Relevance* (1980).

Walter's academic success has brought the biology department and Washington University much recognition and honors. In addition to being a Guggenheim Fellow, he was elected to the Linnean Society of London, is a fellow of the Royal Geographical Society (London), has served as president of the International Association for Aerobiology, and currently serves as president of the Society for Economic Botany. In addition, he has served on the editorial boards of *Brittonia, Grana, Journal of Ethnopharmacology, World Pollen and Spore Flora,* and *Economic Botany.*

He has served on the Executive Committee for the Department of Biology, the Committee for the Plant Biology Program in the Division of Biology and Biological Sciences, and as chairman of the Greenhouse Committee. This administrative work has been a tremendous service within and outside of the department, making good use of Walter's tact, diplomacy, and renowned graciousness.

All of Walter's students and colleagues, not only those present at the tribute, have benefited from the richness in Walter's own background. A master of techniques in cytology, palynology, and classical taxonomy, he has been able to provide examples from the many plant families and genera he worked with and knew well—Rosaceae (*Rosa,* his doctoral subject), Rubiaceae, Portulacaceae, Convolvulaceae, Polygalaceae, Iridaceae, Leguminosae (*Erythrina*), Commelinaceae, Linaceae, Verbenaceae, and Araliaceae (*Panax*). His current work on the ethnobotany of the Jívaro Indians of the upper Amazonian basin has been the subject of a television segment on "National Geographic Explorer."

With an awareness that not many graduate students have an opportunity to honor their major professor in the way undertaken here, we reiterate our gratitude for the care and effort that Walter Lewis gave each of us. WGD, JWN, KRR

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RARE CONVOLVULACEAE IN THE SOUTHWESTERN UNITED STATES[1]

Daniel F. Austin[2]

ABSTRACT

Field and herbarium studies of the Convolvulaceae in the southwestern United States indicate that 17 species are rare in all or part of their ranges. Degree of rarity varies. A few show temperate affinities, while most show tropical relationships. Rare Convolvulaceae vary from being exotics introduced in the area to United States endemics. Those species that are globally endangered to threatened are *Bonamia ovalifolia, Calystegia longipes, Ipomoea cardiophylla, I. tenuiloba,* and *I. thurberi.* Species that are uncommon throughout their ranges, but not in peril are *Bonamia repens* and *I. lindheimeri.* Taxa on the margins of their American ranges are *Calystegia macounii, Cressa nudicaulis, Cressa truxillensis, Dichondra argentea, I. dumetorum, I.* × *leucantha, I. longifolia, I. pubescens,* and *Jacquemontia agrestis.*

RESUMEN

Estudios de los campos y los herbarios de las Convolvuláceas en el sudoeste de los Estados Unidos indican que hay 17 especies raras. Todas de las especies no están raras en toda de su distribución, y algunas están más raras que las otras. Algunas especies tienen afinidades a las zonas temperadas, pero la mayoría tienen afinidades a las zonas tropicas. Estas especies varían de especies exóticas y introducidas en la región hasta especies endémicas. Las Convolvuláceas raras que se consideran en peligro mundial son *Bonamia ovalifolia, Calystegia longipes, Ipomoea cardiophylla, I. tenuiloba,* y *I. thurberi.* Las especies que no son comúnes en todos sus distribuciónes, pero no están en peligro son *Bonamia repens,* y *I. lindheimeri.* Las especies en las márgenes de sus distribuciónes son *Calystegia macounii, Cressa nudicaulis, Cressa truxillensis, Dichondra argentea, I. dumetorum, I* × *leucantha, I. longifolia, I. pubescens,* y *Jacquemontia agrestis.*

While a few of the most familiar species of the Convolvulaceae are considered weeds and pests, most of the 1,000 or more species in the family are not this common, nor weedy. Indeed, throughout the range of the family there are numerous rare species. During my recent studies of the Convolvulaceae in the southwestern United States (Austin, 1990a, b, 1991, in press), it became obvious that there were 17 rare and poorly known species in the area. For comparison with the total floras of the states, 30 Convolvulaceae species are now known in Arizona (Austin, in press 1991), 23 species in New Mexico (Austin, 1990b), and 58 species in Texas (Correll & Johnston, 1970). California has 22 species (Munz & Keck, 1959) and Colorado, Nevada, and Utah have up to eight species. For the following discussion, species are considered rare if they were found in less than ten of the previously recorded sites for the species.

Field observations of several species are given, while other species, where little is still known, are pointed out for future students of the region. The information given should draw attention to and give some documentation for those that are potential candidates for endangered and threatened status. Not all of these species are rare throughout their range in the United States, and the specimen citation reflects this. Those species that are known

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from just a few specimens are cited with locality data, when available.

GLOBALLY ENDANGERED OR THREATENED SPECIES

BONAMIA OVALIFOLIA (TORREY) H. HALLIER

This Mexican species is restricted in the United States to a single canyon (Fig. 1) in Big Bend National Park, Texas, and has been discussed elsewhere (Austin, 1988). Specimens serving as the United States' documentation of its rarity are from one locality covering a few square meters. When I studied the plants there were no pollinators seen and no fruits. A single flood or landfall could eliminate the species from the United States. The northern Mexican population apparently has not been relocated since the middle 1800s.

Representative specimens examined. U.S.A. TEXAS: Brewster Co., Big Bend National Park, near Boquillas, *Webster s.n.* (TEX). MEXICO. COAHUILA: Río Grande below San Carlos, *Parry s.n.* (GH, NY).

CALYSTEGIA LONGIPES (S. WATSON) BRUMMITT

This species is endemic to the southwestern United States. Its range includes southern and southeastern California, southern Nevada, southwestern Utah, and central Arizona (Fig. 2). It will be discussed more fully elsewhere (Austin, in prep.). The species does not seem to be common in any part of its range.

In Arizona this rare species has been collected few times since the 1930s and 1940s. Arizona plants have most recently been found in the Bradshaw Mountains (1985), Mazatzal Mountains (1980, 1990), Sierra Ancha Mountains (1986, 1990), and Weaver Mountains (1980, 1990). (Specimens cited below.)

In my own study of this species in two 20-mile road transects made where the species was known to occur, I found only 13 plants, eight in the Sierra Ancha Mountains and five in the Mazatzal Mountains. Along 11 miles in the Weaver Mountains, I found only one plant. Pase & Johnson (1968) did not find the species in their survey of the entire Sierra Ancha Experimental Forest, nor did Wendy Hodgson (pers. comm.) find new populations in her extensive field survey in the Tonto Basin–Mazatzal Mountains during the spring and early summer of 1990. This low frequency, usually noted on herbarium labels, suggests a rare species with exacting ecological requirements. Except for an herbarium label statement that the plants are most common two years after a burn in chaparral, nothing is known of their growth requirements. Chaparral is the preferred habitat.

Most United States species of Convolvulaceae open as the sun strikes them or they open later in the day. *Calystegia longipes* is unusual in that it is matinal, the flowers opening before the sun strikes them, between 5:00 and 5:30 A.M. On 4 May the flowers closed between 3:30 and 4:00 P.M. in the Sierra Ancha site, but by 31 May they were closing by 2:30–3:00 P.M. Temperatures were near 15°C when the flowers first opened on 5 May in the Sierra Ancha site. The population was visited during the first few hours mostly by the exotic honeybee (*Apis mellifera* L.: Apidae). As the temperatures rose toward 21°C there was a shift in flower visitors from the honeybee to the native bees *Osmia brevis* Cresson (females) and *O. texana* Cresson (males) (Megachilidae).

Flowers were almost absent and fruits were uncommon on the eight plants at the Sierra Ancha site on 31 May 1990 on all the plants. About one fruit had been produced per 30–50 flowers in the population. The flowering season had nearly ended, and one plant studied had four open flowers and one bud to open the following day. This contrasts with the early flowering period when there were 45 flowers open on the same plant (morning of 5 May). During the 1990 season, the flowering period was about four weeks. Thirty-five fruits were examined from the plants, and these had 0–4 seeds each (mean = 3.3; standard deviation = 0.9). Several of the fruits had 2–4 aborted seeds. This low fruit set and the number of aborted seeds may indicate genetic aberrations due to small population size and high degree of self-pollination.

Representative specimens examined. U.S.A. ARIZONA: Coconino Co., Mormon Lake, *Collom s.n.* (ASU); Gila Co., near Pine, *McDougal s.n.* (US); Sierra Ancha Mountains, S Pueblo Canyon, *Delamater et al. 4192* (DES), *Austin & Austin 7657* (ASU); Mazatzal Mountains, Pigeon Spring Road to El Oso road jct., *Mittleman & Hodgson 695* (DES), *Austin & Austin 7659* (ASU); Maricopa Co., N of Sunflower, *Earle s.n.* (DES); Mohave Co., along road to Cottonwood Spring, *Mason & Phillips 2887* (ARIZ, ASU, NY, UC); Yavapai Co., Stanton–Yarnell road, *Butterwick & Hillyard 6567* (ARIZ, ASU); Bradshaw Mountains, along jeep trail T.9N, R.1E, NW¼ of NW¼ of Sect. 26, *Ramsden, Delamater & Hodgson 3597* (DES, NY).

IPOMOEA CARDIOPHYLLA GRAY

Originally thought to be restricted to Texas and New Mexico (U.S.A.), the plants are now known also from Arizona and Mexico (Fig. 5) (Chihuahua, Coahuila, Durango, Oaxaca, Queretaro, and Sonora). The type was collected in Texas (Hudspeth

County: Hueco Mountains, E of El Paso, 13 Oct. 1849, *Wright 1314*, GH) where a population was rediscovered by McDonald (1982).

The species was reported from near Tombstone in Arizona by Mason et al. (1986) and was relocated in 1989 (*Austin & Austin 7608*, ASU). This site is at an altitude of 3,700 ft. in mesquite-creosote bush scrub (Chihuahuan desert scrub sensu Brown & Lowe, 1980), and here the population consists of scattered plants extending along a road for about 0.8 miles. No fruits were present on 7 September 1989; some mature fruits were found on 26 September, but these were heavily parasitized by insects.

Flowers open at 6 A.M. and are mostly wilted by 11 A.M. Neither McDonald (1982) nor I found pollinators on the plants. McDonald found a 90% seed set on cultivated plants. The species may be autogamous.

Widening of the highway could eliminate the species from Arizona. Texas and New Mexico plants may be as rare.

Representative specimens studied. U.S.A. ARIZONA: Cochise Co., S Tombstone, *Walker s.n.* (ARIZ); SW of Mule Mountains N hwy. between Huachuca Terrace and Palominas, *Goodding 206-61* (ARIZ). NEW MEXICO: Doña Ana Co., Organ Mountains, 28 Sep. 1902, *Wooton s.n.* (NMC); 28 Sep. 1980, *Worthington 6655* (TEX); 11 Oct. 1980, *6746* (TEX); 23 Oct. 1975, *Von Loh 687* (UNM); Grant Co., N of Silver City, *Zimmerman & Zimmerman 2006* (SNM fide McDonald, 1982). TEXAS: Brewster Co., W of Study Butte, *Warnock 13184-A* (SRSC fide McDonald, 1982).

IPOMOEA TENUILOBA TORREY

With a narrow range (Fig. 8) in Arizona, New Mexico, the trans-Pecos Mountains in Texas, and also in Chihuahua, Mexico, this species seems to be uncommon throughout its range. This impression of rarity is enhanced because of the matinal flowers (opening after 1:00 A.M. and closing between 7:00 and 8:00 A.M.). Because the flowers close early, the plants are difficult to find. Although the morphology of the flowers indicates adaptation for moth pollination, no moth scales on the stigmas or other evidence of visitation by moths was found in 1989. Perhaps the plants in Arizona are autogamous.

This is a rare species that should be considered threatened throughout its range. Plants grow in the pine–juniper–oak zone in Santa Catalina Mountains and Huachuca Mountains. They are restricted to quartzite in the Huachuca Mountains (F. Reichenbacher, pers. comm.). Both varieties and their intermediates have been discussed by Yatskievych & Mason (1984).

Representative specimens examined. U.S.A. ARIZONA: Cochise Co., Ramsey Canyon, at Bledsoe Cabins, Huachuca Mountains, Nature Conservancy Property, *Tulin 1153* (ARIZ); Natural Bridge Trail, Chiricahua Natl. Monument, *Duramos s.n.* (ARIZ); SE Turkey Creek Ranger Station, *Holler et al. 1170* (ASU, DES); Mule Mountains, Mule Pass, *Reichenbacher 811* (ARIZ); Pima Co., Santa Catalina Mountains, Finger Rock Canyon, *Bertolsen s.n.* (ARIZ); Rincon Mountains, along Rincon Beak Trail, *Bowers & McLaughlin R-538* (ARIZ); Santa Catalina Mountains, Bear Canyon, *Van Devender & Eiber s.n.* (ARIZ); Santa Cruz Co., Sycamore Canyon, *Windam & Yatskievych 81–332* (ARIZ, ASU); Santa Rita Mountains, Madera Canyon, *Reeves 1045* (ASU). NEW MEXICO: Eddy Co., 2 Aug. 1909, *Wooton s.n.* (NMC); Grant Co., *Wagner 3444* (UNM); Hidalgo Co., 15 Sep. 1980, *Todsen s.n.* (NMC). TEXAS: Jeff Davis Co., nr. Davis Mountains Resort Headquarters, *Worthington 5020* (UTEP fide Yatskievych & Mason, 1984).

IPOMOEA THURBERI GRAY

For some time the species was thought to be restricted to the United States. Although not included under this name for Mexico by Matuda (1963–1965), this species occurs (Fig. 8) in Chihuahua, Durango, and Sonora, where it has been passed under the name *I. gentryi* Standley [Field Mus. Nat. Hist. 22: 46. 1940. TYPE: Mexico. Chihuahua: Río Mayo, Sierra Canelo, 30 Aug. 1936, *H. S. Gentry 2497* (holotype, F)].

In the United States the species is presently known from Santa Cruz County. It was found in Cochise (Huachuca Mountains, 1882 to 1894) and Pima counties (Santa Rita Mountains, 1927) in the past, but has not been relocated in either area recently.

Kearney & Peebles (1951) reported corollas of this species to be purple. In fact, the corollas have a pink limb and green throat; they wilt and dry with a green tube and purple limb. Flowers, opening around 6:30 P.M., are visited by sphinx moths (probably *Hyles lineata*). All flowers examined had moth scales on the stigmas, indicating moth pollination. Only 30–50 plants constitute the population studied (Santa Cruz. County: *Austin & Austin 7603*, ASU). The species is rare in the United States and in Mexico (J. A. McDonald, pers. comm.) and should be placed on Arizona's endangered plant list.

Representative specimens examined. U.S.A. ARIZONA: Santa Cruz Co., Peña Blanca Lake, *Johnson 95* (ASC); Patagonia Mountains, Washington, *Kearney & Peebles 10142* (ARIZ); Nogales, *Harrison & Fulton 8163* (ARIZ); Canelo Hills, O'Donnell Canyon, just N of Canipe Cienega, Nature Conservancy Property, *Yatskie-*

vych 80-347 (ARIZ); Nogales–Ruby road at jct. of the Summit Motorway, *Kaiser 49–261* (ARIZ); Santa Rita Mountains, Madera Canyon, *Peebles et al. 4560* (ARIZ).

Species Uncommon throughout Their Ranges

BONAMIA REPENS (I. M. JOHNSTON) AUSTIN & STAPLES

The species is restricted to Brewster and Terrell Counties, Texas (Fig. 1), where it is rare. Specimen citation has been given earlier (Austin & Staples, 1985). In Mexico it is similarly uncommon (Austin & Pedraza, 1983).

CALYSTEGIA MACOUNII (GREENE) BRUMMITT

The taxonomy of our North American *Calystegia* is complex, and the group has been discussed by Brummitt (1980). Shinners (1970) may have confused *C. macounii* with *C. sepium*, and the range of the genus within Texas is uncertain. I have not studied herbarium specimens from Texas. Rare in Arizona and New Mexico, this basically Great Plains (Austin, 1986b) species extends into the Southwest (Fig. 2). The plants were first found in Arizona at Flagstaff (17 June 1887, *Mearns 158*, NY) and were recollected there as recently as 1970 (*Smith s.n.*, ASC). The species was collected in Walnut Canyon east of Flagstaff in 1969 (*Burrall s.n.*, MNA) but does not appear in a checklist of the area (Joyce, 1985). The species had not been collected in Arizona since 1971, when I found it again in the early summer of 1990 (*Austin & Austin 7661*, ASU). I have seen only 10 collections from Arizona and New Mexico.

Plants grow in drainages where prairies are adjacent to wetlands, such as near Lake Rogers southwest of Flagstaff. Plants are scattered among *Iris*, *Lupinus*, *Geranium*, and *Achillea* in depressions. Flowers open near dawn and begin to close by 9:30 A.M., especially during the drought of 1990, which caused stress. Bees (genera not determined) were visiting the flowers. The species is notable for its saccate bracts.

Representative specimens examined. U.S.A. ARIZONA: Apache Co., Canyon de Chelly Natl. Monument, upper Canyon Del Muerto, 12 July 1971, *Halse 485* (ARIZ); Coconino Co., SE Flagstaff, 13 July 1966, N shore of Mormon Lake, *Niles 835*, *Reese 164* (ARIZ); Navajo Co., White Mountains, Lakeside, 10 June 1928, *Harrison 5506* (ARIZ, US). NEW MEXICO: San Miguel Co., Las Vegas, Soldier's Camp, 14 June 1927, *Bro. Arsene 18720* (US).

IPOMOEA LINDHEIMERI GRAY

This species occurs (Fig. 6) in Arizona, New Mexico, Texas, and adjacent Mexico. In Arizona this is an extremely rare species, and its continued existence there is problematical. Moreover, the specimens cited for Arizona are intermediate between the typical material from Texas and New Mexico and the allied *I. pubescens*.

Representative specimens examined. U.S.A. ARIZONA: Cochise Co., Gleeson, 25 Aug. 1927, *Thornber s.n.* (ARIZ); Bisbee, 30 Sep. 1930, *Thornber s.n.* (ARIZ); Pima Co., reportedly (see Kearney & Peebles, 1951; Kearney et al., 1960), not verified. NEW MEXICO: Doña Ana Co., 19 Sep. 1976, *Todsen s.n.* (NMC); Eddy Co., Carlsbad Caverns, *Degener 5042* (NY); Otero Co., *Gordon & Norris 552* (UNM); County unknown, *Wright 1612* (NY). TEXAS: Brewster Co., *Marsh 214b* (TEX) (in part); Burnett Co., *Lundell 13489* (TEX); Crockett Co., *Warnock & McBryde 15215* (TEX); Culbertson Co., *Correll & Johnston 19189* (TEX); Jeff Davis Co., *Lundell & Lundell 13126* (TEX); Kenny Co., *Correll 30431* (TEX); Llano Co., *Whitehouse s.n.* (TEX); Pecos Co., *Gould 7220* (TEX); Sutton Co., *Cory 37305* (TEX); Terrell Co., *Johnston 6458* (TEX); Travis Co., *Webster 97* (TEX); Uvalde Co., *Smith & Butterwick 67* (TEX); Val Verde Co., *Flyr 795* (TEX).

Species on the Margins of Their Ranges

CRESSA NUDICAULIS GRISEB.

The species is restricted to the coastal part of southern Texas and adjacent Mexico (Fig. 3). Because it requires coastal saline habitats, its distribution is limited. The wide range but low number of collections from Mexico suggests that the species is also rare there.

Representative specimens examined. U.S.A. TEXAS: Cameron Co., Loma de la Grulla Sur, *Johnston 249-5* (MSC); Kleberg Co., Riviera Beach, *Correll & Correll 38892* (UC), *Correll & Johnston 17838* (UC); Nueces Co., Corpus Cristi, *Heller 1811* (MSC); Willacy Co., nr. Redfish Bay, *Lundell & Lundell 8775* (UC). MEXICO. TAMAULIPAS: Mesquite, Lag. Madre, *LeSueur 630* (ARIZ, F).

CRESSA TRUXILLENSIS HBK

Perhaps my view of the distribution of this species was distorted by the drought of 1989–1990. Actually, one colleague told me that "thousands and thousands of plants" may be found on certain sites. My limited experience was different. In places where it has been previously considered a common weed (e.g., Yuma, Arizona), the plants were rare (*Austin & Austin 7586*, ASU), and no plants could be found at other localities where the species had formerly been collected in Arizona. No field study was made in other states, although the plants were hunted in New Mexico. Plants may be locally common, but populations are infrequent to rare throughout their range in the southwestern United

States (Fig. 3). Indeed, there are patches of suitable habitat for the species throughout the West as may be seen by the distribution map (Fig. 3). Why the species occurs in some of these islands of habitat and not others that seem equally suitable is unknown.

The herbaceous tips arise from a deep root system. Upper parts of the plants die and disappear during the drought, and when rain falls again, they reappear from the roots.

Representative specimens examined. U.S.A. ARIZONA: Maricopa Co., Komatke, floodplain, *Rea s.n.* (ASU-27419); Tempe, S Stitt's home, *Stitt & McClellan 1208* (ASU); Mohave Co., Chemehuevi Valley, *Jepson 5206* (ARIZ); Navajo Co., SW of Joseph City, SE of Winslow, Hugo Meadows, *Pinkava et al. 13836* (ASU), *13839* (ASU); Pinal Co., E Gila Crossing, *Peebles 13233* (ARIZ); Sacaton Agency, *Gilman 234* (ARIZ); Yuma Co., Roll, *Hamilton s.n.* (ASU- 46383, DES-6563); near Yuma, *Gibby s.n.* (DES-1670), *Thornber s.n.* (ARIZ); 40 mi. E Yuma in Mohawk Valley, *Moody s.n.* (ARIZ). NEW MEXICO: Bernalillo Co., *Dittmer & Clark 7361* (UNM); Chaves Co., *Waterfall 4313* (ARIZ); Doña Ana Co., 12 June 1892, *Wooton s.n.* (NMC); Eddy Co., *Castetter 10683* (UNM); Otero Co., 16 May 1936, *Hershey s.n.* (NMC); Soccoro Co., *Castetter s.n.* (UNM 10619). TEXAS: Culberson Co., N Van Horn, *Peck & Peck 15380* (UC), *Correll & Johnston 18457* (UC); El Paso Co., San Antonio, along Rio Grande, at Fenton Road bridge, *Worthington 14132* (DES); Gonzales Co., *Tharp 249* (UC); Howard Co., Big Springs, *Eggert s.n.* (UC); Kleberg Co., Riviera Beach, *Correll & Correll 38892* (UC); Pecos Co., Fort Stockton, *Cory 51953* (UC); Starr Co., E of El Sauz, *Correll 32310* (UC); Ward Co., Barstow, *Tracy & Earle 23a* (MSC, UC). NEVADA: Washoe Co., N side Peavine Mt., *Heller & Kennedy 8663a* (UC? n.v.); County unknown, Virginia River, *Goodding 726* (UC). UTAH: Juab Co., Fish Springs, *Maguire & Holmgren 21854* (UC); Salt Lake Co., nr. Beck's Hot Springs, *Garrett 870f*(NY), *Clements s.n.* (UC), *Garrett 5005* (UC). Also recorded from Box Elder, Davis, Garfield, Millard, Tooele, Utah, Washington, and Weber counties (Welsh et al., 1987). CALIFORNIA: Riverside Co., N Lakeview, *Jacoby 430-4* (DES); San Bernadino Co., Death Valley Natl. Monument, Saratoga Springs, *Moore s.n.* (DES). Also recorded from Alameda, Colusa, Contra Costa, Glenn, Imperial, Inyo, Kern, Lassen, Los Angeles, Merced, Modoc, Orange, San Benito, San Bernadino, San Diego, Santa Barbara, Santa Clara, Santa Cruz, San Joachin, Sonoma, and Yolo counties (Austin & Staples, unpublished).

DICHONDRA ARGENTEA WILLDENOW

This is a widely distributed species (Fig. 4) in New Mexico, the Trans-Pecos Mountains of Texas, and the Chihuahuan Desert region. The plants are very rare in Arizona and uncommon in New Mexico and Texas. The Arizona collection may have represented a western limit to the range of the species or been introduced into Bisbee during the mining operations. The former is suggested by the similarly disjunct species *I. cardiophylla* and *I. lindheimeri.*

Dichondra argentea often grow on southwestern-facing rocky ridges in Doña Ana and Luna counties, New Mexico. Plants may be locally common.

Representative specimens examined. U.S.A. ARIZONA: Cochise Co., Bisbee, *Harrison 8256* (ARIZ). NEW MEXICO: De Baca Co., 23 Oct. 1904, *Wooton s.n.* (NMC); 25 June 1894, *Wooton s.n.* (NMC); Doña Ana Co., Organ Mountains, *Austin & Austin 7637* (ASU); Grant Co., *Knight 2725* (UNM); Harding Co., *Wooton s.n.* (UNM 18050); Luna Co., *Goodding 3189* (NMC).

DICHONDRA SERICEA SWARTZ

This is a widespread tropical American species, although it is known from only one location in Arizona (Fig. 4). The single Arizona location is Sycamore Canyon, near the Mexican border. It was collected several times between 1936 and 1962 and was relocated in 1989 after a long hiatus (*Austin & Austin 7604*, ASU). Population size has declined from that recorded previously on herbarium labels, being restricted to a strip only a few meters long. The plants could be eliminated from the state by one flood, rockfall, or similar event.

There are few flowers and fruits included in the few collections of this population. Study over several months in 1989–1990 indicated that flowering is uncommon and fruiting may be equally rare. This rarity and apparent decline may be related to shading of these heliophylic plants.

Representative specimens examined. U.S.A. ARIZONA: Santa Cruz Co., Sycamore Canyon, about 200 yds. S of Piñasco Canyon, on E bank, 2–10 ft. above stream, near base of rock face, *Barr 62-863* (ARIZ), *Darrow & Haskell 2217* (ARIZ), *Goodding 6620* (ARIZ), *Keiser s.n.* (ARIZ).

IPOMOEA DUMETORUM WILLD. EX ROEM. & SCHULT.

Martin & Hutchins (1981) do not include this species in their flora of New Mexico. This Mexican, Mesoamerican, and South American (Fig. 5) species was identified and relocated by McDonald (1982, 1984) in New Mexico and Texas. McDonald (1984) cited specimens in addition to those listed here.

Representative specimens examined. U.S.A. NEW MEXICO: Doña Ana Co., Organ Mountains, *McDonald 140* (TEX, fide McDonald, 1982); Lincoln Co., White Mountains, alt. 7,400 ft., 25 Aug. 1907, *Wooton & Standley s.n.* (NMC, US); White Mountains, alt. 2,500 m, *Wooton 630* (MO, fide McDonald, 1982). TEXAS: Jeff Davis Co., Mt. Livermore, alt. 2,700 m, *Warnock 23068*

(SRSC, fide McDonald, 1982); Davis Mountains, Madeira Canyon, near Livermore, *Hinckley s.n.* (ARIZ).

IPOMOEA ×LEUCANTHA JACQUIN

This hybrid originated in the southeastern United States (Austin, 1978; Abel & Austin, 1981). From there it has been introduced into various parts of the Americas by seeds (Fig. 5). It was first reported in Arizona under an erroneous identification as *I. triloba* (Kearney & Peebles, 1951) and then as *I. lacunosa* (Shinners, 1965). In Arizona it is known from only six collections. These weeds of agricultural fields are probably not as rare as collections seem to indicate.

This autogamous taxon, known from few collections in the southwest, should not be considered a threatened species but a weed. In the southeastern United States the taxon is occasional and widespread.

Specimens examined. U.S.A. ARIZONA: Maricopa Co., 4 Oct. 1979, *Heathman s.n.* (ARIZ, ASU); Santa Cruz Co., 1884, *Pringle* (ARIZ); Pima Co., 1912, *Thornber s.n.* (ARIZ); 1945, *Goodding & Lusher 128-45* (NY); Yuma Co., 7 Nov. 1985, *Tuttle s.n.* (ARIZ); County unknown, *LeRoy s.n.* (NY).

IPOMOEA LONGIFOLIA BENTHAM

This species is known from Mexico in Sonora south to Durango, Guanajuato, Zacatecas, San Luis Potosí, Aguascalientes, Queretaro, and Jalisco (Fig. 6). In the United States it is restricted to Arizona. These plants, although not rare in their range, are restricted to a small area in southeastern Arizona between the Dragoon (Cochise County) and Pajarito Mountains (Santa Cruz County). Flowers, which open between 3:30 and 4:00 P.M., are pollinated by moths (Austin, 1986a).

The range given by Martin & Hutchins (1981: 1,562) includes the range of *I. shumardiana* (Torrey) Shinners, a distinct Great Plains species. The presence of *I. longifolia* has not been verified for any part of the United States except southeastern Arizona (cf. Austin, 1986a, 1990b).

Representative specimens examined. U.S.A. ARIZONA: Cochise Co., Lochiel, *Cazier & Davidson s.n.* (ASC); NW Bisbee, alt. 5,500 ft., *Deaver 6639* (ARIZ, ASC); NE Coronado Natl. Monument, *Johnson 72-77* (ARIZ, ASC); Whetstone Mountains, Whetstone, *Yatskievych 80-258a* (ARIZ); Santa Cruz Co., Patagonia Mountains, W Sycamore Canyon and Italian Canyon intersection, *Morris et al. 4641* (DES); near jct. of Keno Springs and Duquesne roads, *Delamater et al. 4390* (DES); Arrivaca–Florida Canyon, *Marshall & Blakeley s.n.* (DES-40).

IPOMOEA PUBESCENS LAMARCK

This widespread species has a disjunct distribution from South America to New Mexico, Texas, and adjacent Mexico (south to Durango and San Luis Potosí). It is one of several examples of amphitropical distributions in the family (McDonald, 1984), this reaching its northern limit in the southwestern United States (Fig. 7).

This species was not included by Martin & Hutchins (1981), although they had specimens of it misidentified as *I. lindheimeri* in the UNM herbarium. The species is now extremely rare in Arizona. Of the sites where it was formerly collected (Cochise, Pima, and Santa Cruz counties), plants were relocated in only one (Santa Cruz County: Sycamore Canyon, *Austin & Austin 7605*, ASU). The plants are not common in adjacent Mexico and should be considered endangered in Arizona.

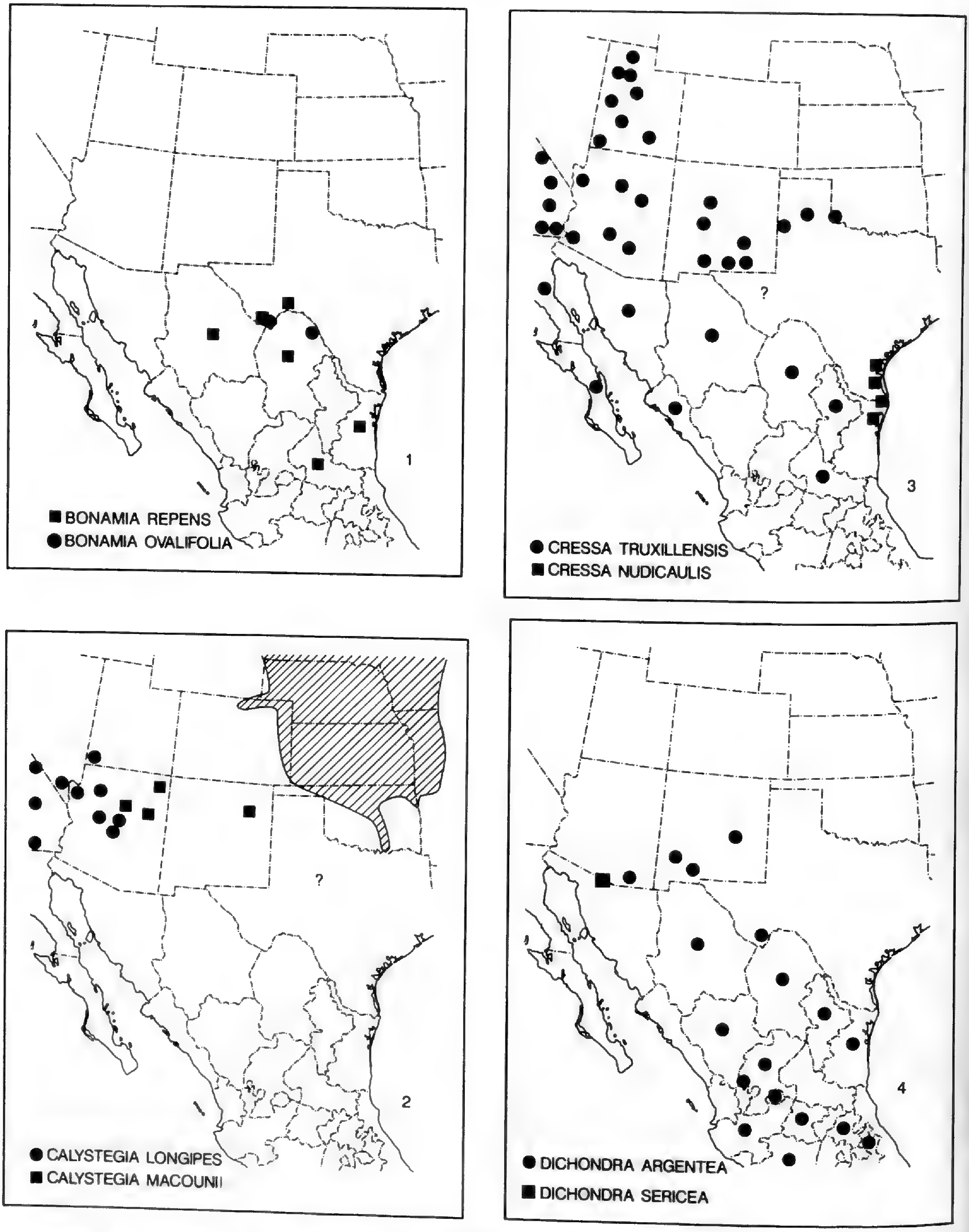
Representative sepcimens examined. U.S.A. ARIZONA: Cochise Co., Huachuca Mountains, Glance Canyon, *Goodding 868-49* (ARIZ); Bisbee, *Thornber s.n.* (ARIZ); Dragoon Mountains, Sala Ranch, *Goodding 72-54* (ARIZ); Tombstone, *Goodding 9506* (ARIZ); Gleeson, *Thornber s.n.* (ARIZ); near Herford, *Harrison 8269* (ARIZ); Bisbee, *Thornber s.n.* (ARIZ); Pima Co., Baboquivari Mountains, Fresnal Canyon, *Gilman B109* (ARIZ); Baboquivari Mountains, Toro Canyon, *Kearny & Peebles 10438* (ARIZ); Santa Cruz Co., Pajarito Mountains, Sycamore Canyon, *Toolin & Kaiser 030* (ARIZ). NEW MEXICO: Doña Ana Co., *Knight 3415* (UNM); Eddy Co., *Bailey 721* (US); Hidalgo Co., Big Hatchet Mountains, Thompson Canyon, *collector unknown 7367* (UNM); Luna Co., Florida Mountains, *Spellenberg & Spellenberg 6626* (NMC). TEXAS: Hudspeth Co., Sierra Diablos, head of Victoria Canyon, *Warnock 11431* (TEX).

JACQUEMONTIA AGRESTIS (CHOISY) MEISNER IN MARTIUS

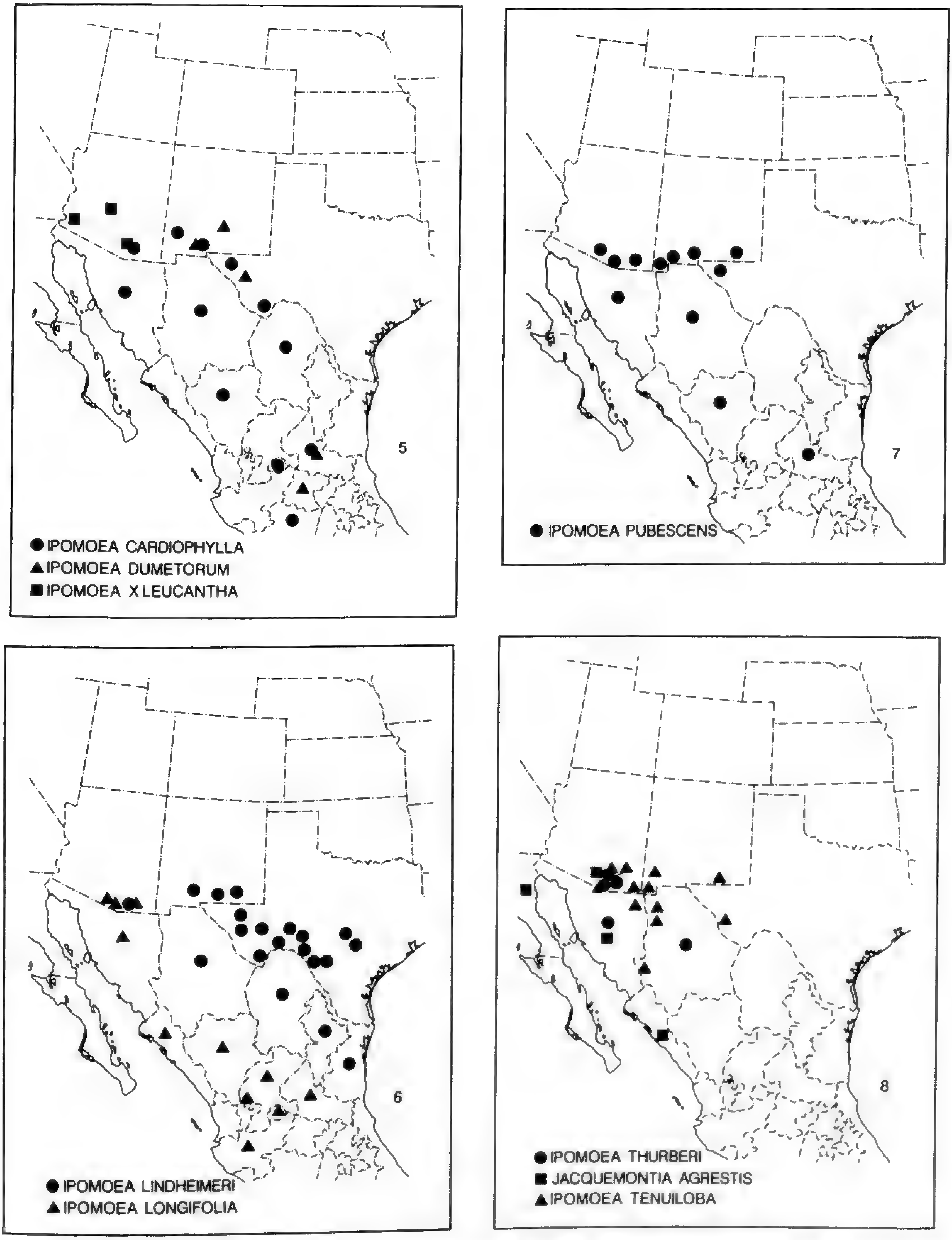
This weedy annual was collected in the Baboquivari Mountains, Arizona, several times between the 1920s and 1940s, but it has not been collected since. It also occurs (Fig. 8) in Mexico (Baja California, Sinaloa, Sonora, south to Yucatan), and continues into Argentina.

The current status of the species in Arizona is uncertain. It may be native, or it may have been brought into the state from Mexico as a weed with plants cultivated by the Tohono O'odham. In Mexico and elsewhere the species is commonly a weed in maize fields and other cultivated crops.

Representative specimens examined. U.S.A. ARIZONA: Pima Co., Baboquivari Mountains, Toro Canyon, *Kearney & Peebles 10389* (ARIZ); Baboquivari Peak, along trail, *Goodding 273-45* (ARIZ); Baboquivari Mountains, Fresnal Canyon, *Gilman B113* (ARIZ).



FIGURES 1–4. Distribution maps.—1. *Bonamia ovalifolia* (circle) and *Bonamia repens* (square).—2. *Calystegia longipes* (circle) and *C. macounii* (square and shading). Range in the Great Plains is based on Great Plains Flora Association (1977) and Austin (1986b). The question mark indicates uncertainty about the range and the species in Texas.—3. *Cressa truxillensis* (circle) and *C. nudicaulis* (square). The question mark indicates uncertainty about the range and the species in Texas.—4. *Dichondra argentea* (circle) and *D. sericea* (square). The extensive range of *D. sericea* in tropical America is not indicated.



FIGURES 5–8. Distribution maps.—5. *Ipomoea cardiophylla* (circle), *I. dumetorum* (triangle), and *I.* × *leucantha* (square).—6. *Ipomoea lindheimeri* (circle) and *I. longifolia* (triangle).—7. *Ipomoea pubescens* in North America.—8. *Ipomoea tenuiloba* (triangle), *I. thurberi* (circle), and *Jacquemontia agrestis* (square) in North America.

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SPECIES DIVERSITY OF ARACEAE IN COLOMBIA: A PRELIMINARY SURVEY[1]

Thomas B. Croat[2]

ABSTRACT

Species diversity of neotropical Araceae is greatest in northwestern South America along the Pacific slopes of the Andes in Colombia and adjacent regions of northern Ecuador. This region is the wettest part of the continent and has some of the largest tracts of relatively undisturbed forests. Colombia is the most species-rich area for Araceae. The family occurs virtually throughout the country, but is much more diverse from sea level to about 1,500 m in the Cordillera Occidental. Of the 15 study sites in Colombia, containing eight different Holdridge Life Zones, the most species-rich was the wettest life zone (premontane rainforest transition to tropical wet forest) at near sea level. Species diversity diminishes substantially at higher elevations even in very wet forests, but is moderately rich to at least 1,100 m. The Cordillera Central of Colombia is substantially drier, particularly during a certain part of the year, and has fewer, more widespread species. It is also the area most heavily disturbed. The Cordillera Oriental is the most poorly collected, but appears to be much less diverse in Araceae than the Cordillera Occidental. The one site studied on the eastern side of the Cordillera Oriental showed the presence of an Amazonian element in the flora. This, coupled with its complement of endemic species at higher and middle elevations, may be an indication that the eastern range will prove to be more species-rich than the central range of the Andes in Colombia.

MATERIALS AND METHODS

This study is based on a series of 15 one- or two-day single site surveys of different areas in Colombia between 1980 and 1990. Although the Araceae are poorly known in their totality, aroid species are generally easy to distinguish by aroid workers on a local basis. This familiarity enables species counts to be made on a site-by-site basis as a means of comparing species diversity between areas. This paper deals with such a study. The purpose of the study is to compare different parts of Colombia both in a general way for a variety of sites throughout the country and in a more specific way for two principal sites on the Pacific slope of the Cordillera Occidental. Voucher specimens are on deposit at the Missouri Botanical Garden. A list of the specific voucher numbers and their dates of collection may be obtained by contacting the author.

INTRODUCTION

The Araceae, a family of 106 genera (Croat, 1988), are taxonomically one of the most poorly known families of flowering plants in the Neotropics. The family has two major centers of diversity, with 32 genera in New World tropics and subtropics and 41 genera in the Old World tropics and subtropics. The total number of species is unknown, but is believed to exceed 3,500. About two-thirds of the species are believed to occur in tropical South America (Croat, 1979), and Colombia may have as many species as all the remaining parts of South America combined. The greatest uncertainty in species count is attributed to the poorly known status of the two largest genera in the family, *Anthurium* and *Philodendron*. The former is believed to have about 1,000 species and the latter approximately 700.

The Central American aroid flora is reasonably well known (Croat, 1981, 1983, 1986a, 1991) and comprises over 500 species. Species diversity in Central America increases as one approaches South America (Croat, 1986b). Using *Anthurium* as an example, Mexico has approximately 50 species, Guatemala 25, Honduras 20, Nicaragua 35, Costa Rica more than 80, and Panama about 160. No approximation is yet possible for Colombia, but certainly it has more species than all of Central America.

In contrast to Central America, many South American countries are poorly known floristically.

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[1] This study was completed with support from National Geographic Society grant 4116-89 as well as National Science Foundation grants DEB80-11649, BSR83-06297, and BSR89-05890 and is based on field observations in Colombia between 1980 and 1990. Voucher specimens are in cultivation at the Missouri Botanical Garden for future extensive observations.

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Exceptions are Venezuela (Bunting, 1979; Croat & Lambert, 1986), Argentina (Crisci, 1971), and Paraguay (Croat & Mount, 1988). The Guianas (Guayana, Suriname, and French Guiana) and the lowland Amazonian basin are reasonably well known and contain moderately few new species (probably less than 5–10% of the total). In the case of the latter region, a large portion of the species are widespread, extending throughout the upper Amazonian drainage in Brazil and into the lowlands of Colombia, Ecuador, Peru, and Bolivia. Some species, such as *Philodendron melinonii* Brongn. and *Anthurium bonplandii* Bunting, even extend from the Guiana highlands into the northern Amazon basin. Because of the widespread nature of many of the species in the Amazon basin, the majority of the species occurring there were collected years ago by early explorers, including Spruce, Ule, Poeppig, and others, and were described by the early monographers of the family, H. W. Schott and A. Engler.

Considering its vast extent, the Amazonian basin is comparatively low in species diversity of Araceae. This is perhaps owing to the vast extent of tropical moist forest life zones in the region, which are seasonally too dry for good epiphyte development, and also because much of the area along rivers is annually flooded, sometimes for long periods of time. Madison (1979) reported that the Brazilian state of Amazonas, which encompasses 15% of the Amazon basin, for example, had only about 70 species. I believe that the entire lowland Amazonian basin has probably fewer than 150 species for areas under 150 m elevation.

Southeastern South America was also botanized early and extensively, especially by Glaziou, and many species were described. However, owing to the complex taxonomy of *Anthurium* sect. *Urospadix*, which makes up a large portion of the species in this region, the number of species there is still poorly known. In Brazil, Simon Mayo has made a detailed listing of the species of Araceae from Bahia (Mayo, pers. comm.), and though less species-rich, there is a treatment of the Araceae of Santa Catarina do Sul (Reitz, 1957). However, many portions of southeastern Brazil are still poorly known. The region is also among the most disturbed of all South America, with the state of São Paulo, for example, having only a small percentage of its land surface still forested. Most of the species from southeastern and eastern Brazil are endemic to the region, and relatively few occur also in the Amazonian basin. Species diversity in the Amazon basin increases dramatically to the west, especially as one approaches the Andes.

The highly dissected nature of the Andes has apparently led to great speciation there. Even relatively low elevations, such as the state of Acre in Brazil in the western perimeter of the Amazon basin are (perhaps owing to a rich layer of alluvium washed down from the Andes) richer in species than areas further to the east.

Endemism for Araceae is high in the Andean region, especially at middle elevations on both slopes of the Andes. This is generally true of all elevated regions of Central and South America. Endemism in *Anthurium* was discussed in detail for Central America (Croat, 1983, 1986a, and for *Anthurium* sect. *Pachyneurium*, Croat, 1991). Though the number of endemic species is greatest in the Andes of western South America, endemism is also high for the now much older, eroded mountains of eastern South America, including the Guiana highlands and the remnants in eastern and southeastern Brazil, south of the Amazon River (as was discussed above for *Anthurium* sect. *Urospadix*).

Species diversity in *Araceae* is comparatively high on both slopes of the Andes in northern South America, but diminishes dramatically south of Esmeraldas Province in Ecuador, especially in areas near the coast, owing to the effect of the Humboldt currents and the desertification created by the cool, dry air above it. No species of Araceae occur in Chile or in southern Argentina, despite the fact that some species occur at much higher latitudes in the Northern Hemisphere. Relatively few species occur in Peru west of the Andes, and these are represented either high in the mountains or at lower elevations only near the northern border of the country. The same is true for much of the southern part of Ecuador on the Pacific slope.

GEOGRAPHICAL DIVERSITY OF COLOMBIA

Colombia, with 1,138,914 km^2 (439,737 mi.^{2}), is both large and geographically diverse. Though the Andes begin in southern Colombia as an apparently single massif, they split into three chains in Colombia, with the Cordillera Oriental and the Cordillera Central somewhat separated from the Cordillera Occidental and deflected to the east. The Cordillera Occidental extends northward relatively near the coast until it diminishes in northern Antioquia before reaching the Caribbean Sea. The Cordillera Central extends for about the same distance northward, somewhat parallel to the western range, and is delimited by the Río Cauca valley to the west and the Río Magdalena valley to the east. The Cordillera Oriental is deflected markedly to the northeast, includes a series of vast tablelands, and extends all the way to the Venezuelan border. There it branches into the Cordillera de Mérida, which extends northeast into Venezuela, and the Serranía de Perijá, which extends north along the western Venezuelan border almost to the Caribbean.

The extensive modifications of the topography of Colombia by the elevation of the Andes have resulted in dramatically different climatic regions throughout the country. A total of 29 life zones in the Holdridge Life Zone System (Inst. Geogr. "Agustín Codazzi," 1977) exist in Colombia, and at least 15 of these contain Araceae. The Chocó Department contains eight life zones (Forero, 1982; Forero & Gentry, 1989), and all are rich in Araceae. These include tropical rainforest (bp-T, henceforth referred to as pluvial forest), premontane rainforest (bp-PM), tropical wet forest (bmh-T), premontane wet forest (bmh-PM), tropical moist forest (bh-T), lower montane rainforest (bp-MB), lower montane wet forest (bmh-MB) and montane rainforest (bp-M). Symbols are those used on the Holdridge Life Zone map published by Instituto Geográfico Agustín Codazzi (1977).

Forests along the Pacific slopes of the Andes receive the greatest rainfall, with up to 11,700 mm for various years at Tutunendo (Gentry, 1982). This village lies at ca. 90 m elevation between Quibdó and Bolívar in a region of premontane rainforest. The higher slopes are subject to afternoon fog resulting from the buildup of clouds as moisture accumulates in the atmosphere. Both the rainfall and the moisture-laden clouds increase atmospheric humidity to the extent that epiphytism is greatly enhanced.

Many areas of the Central Cordillera lie to some extent in rain shadows of moisture-laden air arriving off the Pacific Ocean to the west. The same is true for the eastern slopes of the Cordillera Occidental, which are much drier than the opposite slopes of the same mountain chain. These rain shadows affect not only the total amount of rainfall in the central mountain chain, but also the length of the dry season, which greatly diminishes the number of aroid species capable of surviving in the region. The Cordillera Central is much more degraded than the western range because of the drier conditions caused by rain-shadowing and also due to its close proximity to many of the country's larger population centers.

The Cordillera Oriental is more complex climatologically. Portions of the south and central part of the range are affected by rain-shadowing from blockage by the western and central range of mountains. Yet at the same time, the eastern range is affected by moisture-laden air from the Amazon basin. The lower, western slopes of the Cordillera Oriental are relatively dry, whereas the eastern slopes of the same chain are much wetter. To the north, however, the mountains of the eastern chain are affected by the moisture arriving from Lake Maracaibo as well as from the Caribbean Sea. Much of the Cordillera Oriental is degraded, especially in the central portions of the range near the large population centers, such as Bogotá and Bucaramanga. It was the focus of some of the earliest collecting in Colombia, but still remains the most poorly known area for Araceae. Parts of the range to the northeast of Bogotá are so cold and high as to develop true páramo, from which aroids are excluded.

AROID DIVERSITY IN COLOMBIA

With the possible exception of eastern Brazil, the region most poorly known floristically in South America is the slopes of the Andes in western South America. Species diversity is greatest in the wet tropical areas on both sides of the equator in Colombia, Ecuador, and Peru. The aroids are effectively eliminated from the Pacific slope of Peru and southern Ecuador owing to the Humboldt Current desertification, whereas Colombia is exceedingly rich on the very wet Pacific slope, leading to a much greater overall species diversity. This fact, coupled with the high rate of endemism in the family and the much more complex mountain system in Colombia, has created a situation where the aroid flora of this country is the highest of any region in the world. Parts of Ecuador are certainly as species-rich per unit area, but the country is much smaller and geographically less complex.

The South American Andes are poorly known owing to the large number of species occurring in the region and their taxonomic complexity. The genus *Philodendron* and some sections of *Anthurium* are particularly poorly known. Since these two genera may constitute 70–80% of the aroid flora, any given local flora may be very poorly known to the species level. Other complex and poorly known genera, especially at lower elevations, include *Dieffenbachia*, *Monstera*, *Rhodospatha*, and *Spathiphyllum*. *Stenospermation*, rich in species and even more poorly known, is particularly diverse at middle to high elevations in the Andes.

In all, 15 sites were studied throughout Colombia (Fig. 1). The sites included eight along or in the western range, five in the central range, and two in the eastern range. Both major study areas were

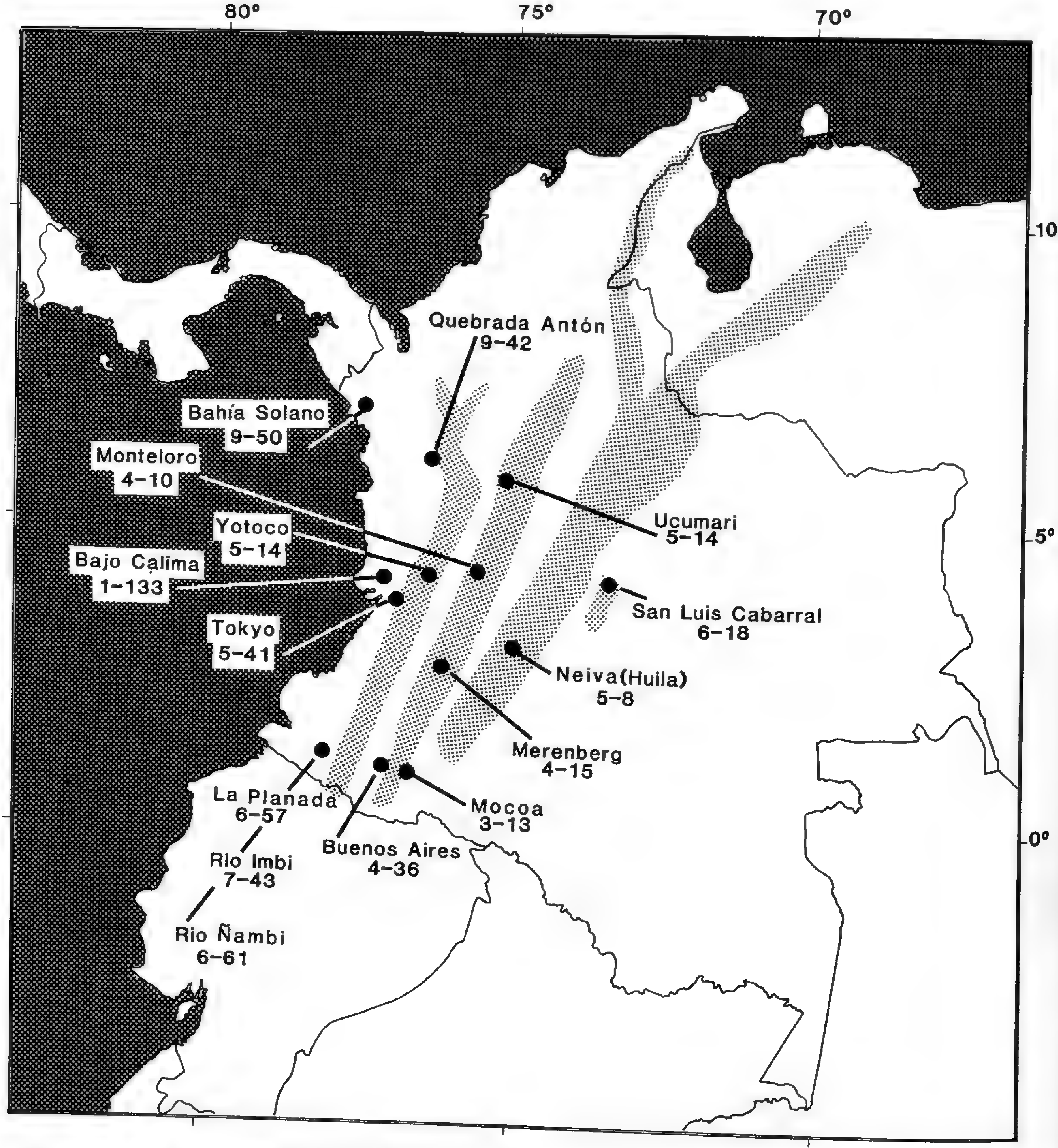

FIG. 1. Fifteen study sites in Colombia with number of genera and species collected. (Map prepared by J. Myers.)

in the Cordillera Occidental. Additional sites have been visited in the eastern range, but they were excluded either because it was deemed that they were not sufficiently natural or not enough time was spent in them to ensure a complete survey.

The study sites were diverse ecologically, ranging from very wet to moderately dry. The life zones included were: premontane rainforest transition to pluvial forest (1); tropical wet forest (2 sites); premontane wet forest (4); premontane rainforest (2); lower montane wet forest (1); lower montane rainforest (1); premontane moist forest (3); lower montane moist forest (1). The only major life zones with large numbers of Araceae that were not studied were tropical moist forest and pluvial rainforest.

Though the two major sites were extensively collected and the results probably come close to representing the total number of species for the sites, the remaining sites were collected for shorter periods of time, and in most cases these results would not be expected to represent the total count of species in the areas. Though the latter surveys are invalid statistically because the sites were not measured nor even deemed to be of equal size, they are believed to reflect accurately the species richness of the relative areas. The results of the survey, I believe, show a true picture of the difference in species diversity in different parts of Colombia. Despite the presumed inaccuracy of the counts for total species in each area, they do reflect, in general terms, the trends for species diversity that are postulated.

Collecting sites were concentrated in the Cordillera Occidental owing to the greater diversity and the greater ease of access to undisturbed sites. In each case a serious attempt was made to collect every species present at each site, whether fertile or sterile. This was essential since at any one time only a small percentage of the flora is fertile. Because live material was collected in most cases for cultivation, future fertile parts will provide ultimate identification.

Discussion of the Study Sites

GENERAL SITES

Cordillera Occidental

(Low Elevations)

Bahía Solano. This is the northernmost site studied, situated at 6°14′N, 77°24′W near sea level in an area of tropical wet forest near the Pacific coast in Chocó Department. The survey netted nine genera and 50 species, but the forest near Bahía Solano is somewhat degraded and perhaps does not properly reflect the richness of the area.

Determined species from the area include *Anthurium formosum* Schott, *A. lancifolium* Schott, *A. obtusilobum* Schott, *A. ramonense* Engl. ex K. Krause, and *Rhodospatha moritziana* Schott.

Quebrada Antón. The site is situated at 5°20′30″N, 76°13′45″W in an area of premontane rainforest at about 240–250 m in the Department of Chocó near the border of Risaralda, along the road between Pueblo Rico, Risaralda, and Istmina, Chocó. Nine genera and 42 species were collected.

The taxa definitely determined to species from the site include *Anthurium formosum, A. ravenii* Croat & Baker, *A. warocqueanum* J. Moore, *Philodendron verrucosum* Mathieu ex Schott, *Rhodospatha moritziana, Stenospermation multiovulatum* (Engl.) N. E. Br., *Syngonium foreroanum* Croat, and *S. macrophyllum* Engl.

(Middle Elevations of Western Slope)

Microondas Tokyo. The site is at 3°30′N, 76°44′W in a region of premontane rainforest around a microwave station at 2,000 m in Valle Department, above the town of Queremal along the old road between Cali and Buenaventura. The study site yielded five genera and 41 species.

Identified species include *Anthurium panduriforme* Schott, *A. obtusilobum*, and *A. tenerum* Engl.

Río Imbi. This study site is located at 1°18′N, 78°04′W along the Río Imbi in the Department of Nariño near Ricaurte, in a somewhat degraded region of premontane wet forest at 1,100 m. It yielded seven genera and 43 species. Only a few of the species located here also occur at the La Planada study site, even though it is only 700 m lower in elevation and barely 7 km away from that latter site.

Known species include *Anthurium panduriforme, A. draconopterum* Sodiro, *A. obscurinervium* Croat, *A. myosuroides* (HBK) Endl., *A. scandens* (Aubl.) Engl., subsp. *pusillum* Sheffer, *Philodendron ecuadoriense* Engl., *P. inequilaterum* Liebm., and *P. verrucosum.*

Río Ñambí. This area is along the Río Ñambí in Nariño Department at 1°18′N, 78°04′W in a region of premontane wet forest at 1,100 m, west of Altaquer. Six genera and 61 species were collected. The region consists of virgin forest and showed surprisingly little floristic relationship to the Río Imbi site located only about 20 km to the northwest, at the same elevation and in the same life zone.

Identified species included *Anthurium draconopterum, Philodendron inequilaterum, P. verrucosum,* and *Xanthosoma daguense* Engl.

(Higher Elevations of Eastern Slope)

Parque Yotoco. This area is a reserve and one of the few remaining tracts of natural vegetation on the eastern slopes of the western massif. It is located in the Department of Valle in a region of premontane moist forest life zone at an elevation of about 1,500 m. The reserve is located along the main highway between Dapa and Loboguerrero at 3°52′N, 76°22′W.

The site contained five genera and 14 species; those identified are *Anthurium myosuroides* and *Xanthosoma daguense* Engl.

Cordillera Central

Five sites were studied in the central massif. The intermountain valleys to the east and west of the Cordillera Central are unknown, since most portions have been completely denuded for a long time. All of the sites studied were at moderately high elevations.

Parque Ucumarí. This is a preserve that lies at 4°02′N, 75°30′W, southeast of the city of Pereira in the drainage of the Río Otun in the Department of Risaralda at 1,900–2,200 m elevation. It lies in a region of lower montane moist forest life zone and is relatively species-poor, owing to the high elevation, with only five genera and 14 species encountered. One of the species common at the site was *Anthurium longegeniculatum* Engl.

Monteloro. The study site is located at 3°55′N, 76°04′W, near the village of Monteloro in eastern Valle Department, in a region of premontane moist forest at 2,080–2,100 m elevation. The general region is much denuded, but the study site remains relatively undisturbed. It yielded only four genera and 10 species.

Anthurium myosuroides was common at the site. Another common, unknown, but distinctive *Anthurium* with cordate blades, a large red spathe, and a yellow-green spadix was also found at the next site, Reserva Merenberg.

Merenberg. The study site known as the Reserva Natural Finca Merenberg is located at 2°16′N, 76°12′W on the eastern slope of the Cordillera Central in the Department of Huila, in a region of lower montane wet forest at 2,300 m. The preserve was established by the owner, Gunter Buch, and the World Wildlife Fund. It was virtually the only remaining natural vegetation left in the region and netted only four genera and 15 species of Araceae.

Known species collected here included *Anthurium corrugatum* Sodiro, *A. longegeniculatum*, *A. microspadix* Schott, *A. scandens* (Aubl.) Engl., and *Chlorospatha longipodum* (K. Krause) Madison.

Buenos Aires. The area studied lies at 1°04′N, 76°48′W on the eastern side of the Cordillera Central in the Department of Putumayo, near the village of Buenos Aires, west of Mocoa, in a region of lower montane rainforest at about 2,500 m. Relatively large tracts of vegetation still exist in this area, but they are becoming rapidly disturbed. The vegetation consists of small trees and shrubs. Four genera and 36 species were found here; the only known species are *Anthurium longegeniculatum* and *A. scandens.*

Mocoa. The area studied lies along the Río Mocoa, near the town of Mocoa at 1°10′N, 76°33′W in Putumayo Department. It lies on the eastern side of the Cordillera Central in an area of premontane wet forest transition zone to tropical wet forest life zone at about 1,800 m. The site was relatively disturbed and yielded only three genera and 13 species.

The species known from the study site are *Anthurium alienatum* Schott, *A. harlingianum* Croat, *A. trinerve* Miq., *Philodendron inequilaterum, P. megalophyllum* Schott, and *P. panduriforme* Schott. All of these are widespread species in the Amazon basin.

Cordillera Oriental

Only two sites are included for the Cordillera Oriental, one located on the western slopes of the massif and one in the Cordillera de la Macarena, which is appropriately a part of the eastern range, though it rises substantially above all the surrounding terrain and is somewhat segregated from the rest of the Cordillera.

Neiva. The study site is located at 2°56–57′N, 75°0–7′W in the Department of Huila in the mountains to the east of the city of Neiva, in a region of premontane moist forest at 745–870 m. The region is somewhat disturbed and has a relatively marked dry season. It yielded only five genera and eight species.

Among the species were the widespread Amazonian species *Philodendron barrosoanum* Bunting and the even more widespread *Xanthosoma mexicanum* Liebm. Also occurring there were *Anthurium glaucospadix* Croat, which occurs on both sides of the Cordillera Central, and *A. nymphaeifolium* K. Koch & Bouché, a species with a generally more northern distribution in the eastern range, as well as the Cordillera de Mérida and Cordillera de la Costa in Venezuela.

San Luis de Cabarral. The study site was located at 3°45′N, 73°45′W, east of the village of Cabarral near the base of the Serranía de la Macarena in an area of tropical wet forest life zone at 530 m elevation. Six genera and 18 species were collected here. These included many widespread Amazonian species, but with some endemics as well. Species with an Amazonian distribution included *Anthurium acrobates* Sodiro, *A. fendleri* Schott, *A. pentaphyllum* (Aubl.) G. Don var. *pentaphyllum, Monstera gracilis* Engl., *M. lechleriana* Schott, *Philodendron acutatum* Schott, *P. barrosoanum, P. fragrantissimum* (Hook.) Kunth, *P. inequilaterum, P. ornatum* Schott, *P. wurdackii* Bunting, *Rhodospatha oblongata* Poeppig, *Spathiphyllum cannifolium* (Dryand.) Schott, and *Syngonium yurimaguense* Engl.

The forest was a remnant, and probably the low numbers do not properly reflect the total potential flora for the region.

SPECIFIC SITES

Two sites will be discussed separately because they represent areas now reasonably well known in comparison to the general sites mentioned above. Both were in the Cordillera Occidental, so for the purposes of general conclusions regarding species diversity in Colombia their data will be incorporated with the general sites.

Bajo Calima. "Bajo Calima" refers generally to the lower Río Calima valley in the Department of Valle. More specifically, as defined here, it refers to the area south of the Río Calima near the Pacific Ocean. The study site is located at 3°57′–4°10′N and 77°01–12′W and is within the forestry concession of Cartón de Colombia. The assistance of the lumber company has been instrumental in the success of the survey. The forestry concession lies largely on a peninsula of land jutting out into the Pacific Ocean and separating the Bahía de Málaga to the north from the Bahía de Buenaventura to the south. It is just north of the coastal city of Buenaventura in Valle Department.

The region consists of a premontane rainforest in transition to pluvial forest. Elevations range from sea level to about 200 m, and drainage is to the north into the Río Calima, to the west into the Bahía de Málaga and to the south into the Bahía de Buenaventura. The overlying forest is dense, with most trees less than 60 cm in girth and less than 30 m in height. The understory vegetation is dense and light conditions are low. Most of the aroid species occur as epiphytes, but only rarely are they very high in the trees. Rainfall at Bajo Calima is usually late in the day or at night and usually begins as a light mist, often as early as 3:00 P.M. Heavier rains usually occur at night. Periods of rain are also common in the early morning. Total rainfall is recorded as 7,470 mm (Gentry, 1991). Rainfall is lowest from December to March (200–300 mm), with the lowest recorded monthly rainfall in January 1963 when only 139 mm fell. Annual temperatures average 27.3°C with a daily minimum of 21.4°C and a maximum of 30.3°C (Faber-Langendoen, 1989).

Species characteristic of the flora are *Anthurium brownei* Masters, *A. chlorocardium* Sodiro, *A. coclense* Croat, *A. insigne* Masters, *A. paludosum* Engl., *A. pluviaticum* R. E. Schultes, *A. trinerve, A. trisectum* Sodiro, *Philodendron grandipes* K. Krause, *P. inequilaterum, P. verrucosum, P. senatocarpium* Madison, *P. tripartitum* (Jacq.) Schott, *Spathiphyllum friedrichsthalii* Schott, *Stenospermation andreanum* Engl., and *Syngonium macrophyllum* Engl.

La Planada. The region is located at 1°08′N, 77°04′W at the Reserva Natural La Planada, a 3,200-ha biological reserve in the Municipio of Ricaurte in Nariño Department. It was established with the assistance of the World Wildlife Fund and operated by the Fundación para Educación Superior. Elevations range from 1,300 to 2,100 m, but most of the collections were made between 1,700 and 1,850 m. The area is classified as premontane wet forest on the Holdridge Life Zone map of Colombia. Its forest canopy is also relatively short, with trees mostly less than 20 m tall. The understory vegetation is even denser than at Bajo Calima, and a much larger percentage of the species occur in partly rotted debris that has accumulated on the ground. In contrast to Bajo Calima, which is generally quite hot, the temperature at La Planada is substantially cooler, with average temperatures ranging from 12° to 22° Celsius. Though mornings are usually clear, rains generally begin by late afternoon, as at Bajo Calima, and continue into the night. Average annual precipitation is more than 4,430 mm. Though rainfall is rarely heavy, the region is often beset with cloudy and rainy conditions that may persist for weeks at a time. The soil perhaps never dries out.

Species characteristic of the flora are *Anthurium carchiense* Croat, *A. microspadix, A. mindense* Sodiro, *A. ovatifolium* Engl., *A. scandens* subsp. *pusillum, Monstera adansonii* Schott, *M. lechleriana, Philodendron lehmannii* Engl., *Rhodospatha densinervia* Engl. & K. Krause, and *Xanthosoma sagittifolium* Schott.

FLORISTIC COMPARISON OF PRINCIPAL STUDY SITES AT BAJO CALIMA AND LA PLANADA

Differences at the generic level

Dramatic differences abound between the two major study sites, the most apparent being the much higher species diversity and generic diversity in the lowland site. With 133 species known, Bajo Calima has more than twice as many species as La Planada, with 57. Moreover, continued studies are likely to increase this difference even further since each succeeding trip to the lower site has added greater numbers of known species. Because of the dramatic difference in elevation, it is not surprising that not a single species is common to the two areas. Since both areas are very wet and lack any significant dry season, temperature is probably the primary reason for differences in species composition between the two sites.

The difference in temperature between the two areas is also likely to be the principal reason for the unequal generic composition (Table 1). Generic diversity is much less at the upland site, with five genera lacking altogether at La Planada. The genera present at Bajo Calima but lacking at La Plana-

TABLE 1. Species diversity in Colombia.

	Anthurium	*Caladium*	*Chlorospatha*	*Dieffenbachia*	*Dracontium*	*Heteropsis*	*Homalomena*	*Monstera*	*Philodendron*	*Rhodospatha*	*Spathiphyllum*	*Stenospermation*	*Syngonium*	*Xanthosoma*	Total
Western Cordillera															
Bahía Solano	26			3			1	1	13	2		2	1	1	50
Quebrada Antón	18		1	2	1				11	2		2	2	3	42
Bajo Calima	63	1	1	4				2	40	3	2	12	3	2	133
Microondas Tokyo	27							2	6			3		3	41
Parque Yotoco	5							1	6	1				1	14
La Planada	32							2	12	1		7		3	57
Río Imbi	19		2	1					17		1	2		1	43
Río Ñambí	26		1						23	3		6		2	61
Central Cordillera															
Ucumarí	10		1						1	1				1	14
Monteloro	7								1	1				1	10
Merenberg	11		1							2				1	15
Buenos Aires	17								12			1		6	36
Mocoa	4								8			1			13
Eastern Cordillera															
San Luis Cabarral	3							3	9	1	1		1		18
Neiva	2			1				1	3					1	8

da include *Caladium, Chlorospatha, Dieffenbachia, Spathiphyllum,* and *Syngonium.* These genera are all characteristically more abundant and diverse at lower than at higher elevations. Three of the genera (*Chlorospatha, Dieffenbachia,* and *Spathiphyllum*) lacking at the 1,800 m site of La Planada are common at the Río Imbi site, only a few kilometers away but at an elevation of 1,100 m.

Dracontium is widespread in Central America, with four species ranging from Mexico to Panama. It is moderately common in some areas of northern Venezuela, and at least one species, *D. loretense* K. Krause, is common in the upper Amazon basin in Peru and Ecuador. It has not been found at either of the principal study sites on the Pacific slope of Colombia. Although rare on the Pacific slope of South America, it is to be expected at Bajo Calima, since it has been collected in premontane rainforest at Quebrada Antón, one of the other study sites. *Dracontium* has also been found on the Pacific slope of Ecuador.

Another genus almost certain to turn up at Bajo Calima is *Homalomena.* It has been collected nearby at a similar elevation southwest of Buenaventura. Three species are known from Chocó, *H. wendlandii* Schott, *H. peltatum* Masters, and one new species.

The genus *Heteropsis* is rare on the Pacific coast of Colombia and was not found at any of the study sites. It is most common in the Amazon basin and in eastern Brazil. While it occurs in Central America in tropical moist forest as far north as Nicaragua, and in northern Colombia at low elevations, it is known on the Pacific slope of South America only in the region of San José Palmar at 930 m elevation in montane wet forest life zones, and in Ecuador in Esmeraldas and Los Ríos Departments in premontane rainforest. No collection has been seen from the central or eastern ranges of the country.

Other genera not found in the surveys that might have been expected were *Montrichardia* and *Urospatha.* Both of these genera occur normally at low elevations. *Montrichardia* has been collected only in northern Chocó Department in the Río Atrato basin, in the Atlantic watershed. Collections have been seen from the Río Atrato near Bojaya at 6°35′N, 76°52′W, ca. 100 km north of Quibdó, but it is not expected to be found in any of the study sites reported here.

Urospatha is most abundant in the Amazon basin. It is restricted to the Caribbean slope in Central America and has been collected in northeastern Venezuela (Monagas and Delta Amacuro). While the genus is common in southeastern Colombia in Vichada, Meta, and Vaupés, no collections have been made in northern Colombia or on the Pacific slope of Colombia.

The genus *Stenospermation* is common at Bajo Calima and La Planada, but its high diversity at Bajo Calima was not expected. In Central America the genus is not very abundant at elevations below 400 m, and then only in tropical wet forest. However, the Bajo Calima area, with 12 species already known, is surprisingly rich. *Stenopermation* species are generally true epiphytes and require very humid sites.

Another surprising feature of the Bajo Calima site is the number of species of typically epiphytic genera of Araceae that occur terrestrially there. This is particularly true in *Anthurium* sect. *Porphyrochitonium*, which only rarely occurs terrestrially in Central America.

The genus *Philodendron* is typically most diverse at lower elevations, and this difference is apparent in the comparison of the two major study sites. *Philodendron* was notably more diverse at Bajo Calima, with 40 species versus only 12 at La Planada. Since the flora of La Planada is less than half as rich in Araceae as Bajo Calima, *Anthurium* species at La Planada were relatively numerous, with a total of 32 species versus 62 at Bajo Calima.

The only genus at La Planada with more species than at Bajo Calima was *Xanthosoma*, with three versus two species, respectively.

Differences at the infrageneric level

In addition to the differences so evident in the generic composition of Bajo Calima and La Planada, differences are also apparent within genera. *Anthurium*, for example, which can be easily separated into taxonomic sections, shows unequal representation in the two areas (Table 2).

The sectional system of classification used here is a slightly modified version of that of Engler (1905). Modifications of Engler's system have been discussed by Croat & Sheffer (1983), which includes the definitions of the 19 sections and illustrations of most.

Anthurium sect. *Tetraspermium* is represented at Bajo Calima by *A. trinerve* and at La Planada by *A. scandens* subsp. *pusillum*, but so far as is known, the most common taxon in the section, *A. scandens* subsp. *scandens*, does not occur at either site. This is unusual, since it is one of the most widespread and common taxa in the family.

TABLE 2. Comparison of *Anthurium* sections at Bajo Calima and La Planada.

Sections of *Anthurium*	Number of species per section	
	Bajo Calima	La Planada
Belolonchium	0	4
Calomystrium	4	2
Cardiolonchium	1	0
Digittinervium	2	1
Pachyneurium	0	1
Polyneurium	11	8
Porphyrochitonium	27	6
Semaeophyllium	1	0
Tetraspermum	1	1
Xialophyllium	6	6
Section unknown (oblong blades)	4	1
Section unknown (cordate blades)	4	5

One of the most remarkable differences in the sectional distribution of *Anthurium* between the two sites was exhibited by section *Porphyrochitonium*, which has 27 species at Bajo Calima and only six at La Planada. This section has a wide distribution, but is concentrated largely at lower elevations along the Pacific slope of South America.

Not surprisingly, section *Pachyneurium* is absent from Bajo Calima. The section is absent from the entire wet Pacific slope, with the exception of one species of series *Multinervia* that occurs at La Planada and two species of series *Pachyneurium* that occur on the highest dry slopes, entering from the Cauca River valley to the east.

Section *Xialophyllium* is generally most well represented at higher elevations, but perhaps owing to the larger size of the area studied at Bajo Calima, the number of species at the two sites is equal, with six species at each site.

Section *Polyneurium* is well represented at both sites, the number of species being more or less proportional to the sizes of the respective floras, with 11 represented at Bajo Calima and eight at La Planada.

Anthurium sect. *Digittinervium* is generally more common at higher elevations, but two species were found at Bajo Calima versus one at La Planada.

Section *Cardiolonchium* occurs at both lower and middle elevations, but the section was found only at Bajo Calima, with one species, *Anthurium splendidum* W. Bull, having been discovered there recently. This was the first herbarium collection of this species since the type was prepared in 1883.

Section *Calomystrium* was represented at both sites, but was not particularly rich at either, with four species at Bajo Calima and two at La Planada.

Anthurium sect. *Belolonchium,* typically occurring at high elevations, would not have been expected at Bajo Calima. Four species of this section occur at La Planada.

Section *Semaeophyllium,* with *Anthurium insigne,* was represented only at Bajo Calima. Both areas still have a share of species whose sectional classifications are not yet known. One group with oblong, epunctate blades, which does not fit into any of the currently described sections, has four species at Bajo Calima and one species at La Planada. Another unknown group with cordate, epunctate leaf blades has four species at Bajo Calima and five species at La Planada.

While it is not yet possible to separate the *Philodendron* species in the two study sites into infrageneric taxonomic groups (with the exception of members of subg. *Pteromischum*), it is possible to separate them into scandent or appressed-climbing plants. Both groups are hemiepiphytic. No truly epiphytic *Philodendron* species occur at either site. At Bajo Calima there are 22 appressed climbers versus 14 vines. Two of the scandent plants were members of subgenus *Pteromischum.*

At La Planada five of the species were appressed epiphytes and six were vines. Only one of the latter group was in subgenus *Pteromischum.*

COMPARISON OF MAJOR MOUNTAIN SYSTEMS IN COLOMBIA

Though there are obvious differences in the quality of the sites in the different ranges (western, central, and eastern) owing to differences in size of the sites and their state of preservation, a general trend is clear. The wetter sites of the Cordillera Occidental yield much higher species totals than do the more mesic sites of the Cordillera Central and Cordillera Oriental. The eight sites in the western range averaged 55 species, whereas all sites in the central and eastern ranges averaged about 14 species. The number of species ranged from 14 to 133 species in the western ranges versus eight to 36 in the combined central and eastern ranges.

Philodendron averaged about 16 species per site for the eight study sites in the western range (ranging from six to 40 species per site) versus about five species per site (ranging from zero to 12) for the seven in the combined central and eastern ranges.

Anthurium averages about 27 species (ranging from five to 63) per site for the study sites in the western ranges versus an average of about eight (ranging from two to 17) in the central and eastern ranges.

Four genera were not represented at all in any of the sites of the central and eastern ranges. These were *Caladium, Chlorospatha, Dracontium,* and *Homalomena.* In addition, *Dieffenbachia* was rare, having been collected only at Neiva on the western slopes of the Cordillera Oriental.

Dracontium occurs on the wet Pacific slope of Colombia and Ecuador, in Venezuela, and throughout much of the Amazon basin, but I have seen no collections from the intermountain valleys in the Cordillera Central or Cordillera Oriental. Since it often occurs in seasonal habits, it is curious that it appears not to have been collected in these regions where numerous appropriate habitats occur. Probably the elevations in these regions are too high. Elsewhere the genus occurs mostly below 600 m elevation.

COMPARISONS OF STUDY SITES WITHIN THE CORDILLERA OCCIDENTAL

Because the study sites in the western range were more numerous and more diverse, some comparisons can be made among them. Although the detailed comparisons of the premontane pluvial forest lowland site at Bajo Calima and the premontane wet forest highland site at La Planada have shown conclusively that species diversity is much greater in the low, warmer site than in the higher, cool site, a comparison of the general lowland and middle elevation sites of the Pacific slope does not conclusively show where species diversity is greatest. Generally, the middle elevation sites were about as species-rich or more so than the sites at lowest elevations.

At the highest elevation sites *Philodendron* was usually dramatically less diverse than *Anthurium,* usually much less than one-half as diverse. At 1,800 m elevation at La Planada, there were 32 species of *Anthurium* versus only 12 species of *Philodendron,* and the Microondas Tokyo site at 2,000 m had 27 versus six species. In contrast, the low elevation sites of Bajo Calima, with 63 *Anthurium* versus 40 *Philodendron,* Bahía Solano (26 vs. 23 species), and Quebrada Antón (18 vs. 11 species) showed that *Philodendron* had one-half to three-quarters the total number of species as *Anthurium.*

In contrast, the middle elevations of 1,100 m at the Río Imbi and the Río Ñambí yielded almost as many *Philodendron* species as *Anthurium*, with 19 *Anthurium* versus 17 *Philodendron* and 26 *Anthurium* versus 23 *Philodendron*, respectively. The Yotoco site at 1,500 m showed even more *Philodendron* than *Anthurium* species, with six versus five species, respectively.

The Yotoco site, the only collecting area on the eastern slope of the western range, was enlightening in another respect. The eastern slopes of the western range of the Andes have a severe dry season and also suffer diminished rainfall as the result of rain-shadowing. The Yotoco site is located near the summit on the eastern slope in premontane moist forest and is substantially drier than the other sites on the Pacific slope of the western range. The study area at Yotoco yielded only 14 species, far fewer than any of those sites on the western slope. It also had only five species of *Anthurium*.

The generally higher number of *Anthurium* versus *Philodendron* species at the highest elevations usually also holds in the central and eastern ranges, where most of the sites were above 2,000 m. For example, the number of *Anthurium* versus *Philodendron* species was 10 versus one at Ucumarí, seven versus one at Monteloro, 11 versus two at Merenberg, and three versus none at Neiva. However, the Buenos Aires site has 17 *Anthurium* versus 12 *Philodendron*. Mocoa, located nearby, had four *Anthurium* versus eight *Philodendron*. The lowland site on the eastern slope of the eastern range at the margin of the Amazonian lowlands had twice as many *Philodendron* as *Anthurium*.

CONCLUSIONS

These preliminary studies of species diversity in Colombia have shown interesting phytogeographic patterns. Remarkable differences are shown between different sites in different life zones and at different elevations. Though the surveys were inadequate to show conclusively which life zones might be richest in Araceae, evidence seems to point clearly to the wettest sites at low elevations. These sites were more diverse than those at high elevations. Study sites in the Cordillera Occidental also appear to be more species-rich than those in the central and eastern ranges.

Perhaps the most surprising finding in the study was the degree to which some sites in close proximity showed little overlap in species composition. For example, the Río Imbi site only a few kilometers away from La Planada and also in premontane wet forest shared few species with La Planada. Even more surprising, the Río Ñambí site, located relatively near Río Imbi in the same life zone and at the same elevation, shared few species with Río Imbi.

Future studies will involve more sites in the Cordillera Central and the Cordillera Oriental to confirm that they are less species-rich. More importantly, lowland sites in pluvial forest will be studied, since I believe that these will prove to be even richer than those of the premontane rainforest with transition to pluvial forest. Plans have been made to make a series of collections at different sites encompassing tropical wet forest, pluvial forest, premontane rainforest, and premontane wet forest in the Department of Nariño. The same will be done in the Department of Valle, where there is a series of reserves between the Pacific Ocean and the Continental Divide. Future studies will also be carried out at a number of sites in the Department of Cauca. These studies should indicate in which life zones species diversity is greatest and the extent of overlap in species composition at different sites. It is hoped that by means of these studies a better picture will emerge of the nature of speciation of the Araceae in this, the richest area on earth for aroid diversity.

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SOLANACEAE OF MADAGASCAR: FORM AND GEOGRAPHY[1]

William G. D'Arcy[2]

ABSTRACT

About half of the small representation of Solanaceae on Madagascar is introduced. The largely endemic representation of native species displays unusual features in hair type, floral egress, anthers, and fruits, which may relate to unusual pollinators and dispersal agents present on the island. Affinities are noted with plants in Africa, South America, and Australia, suggesting that various ancestral stocks probably arrived at different times and have undergone different degrees and kinds of specialization. The Mozambique Channel is a barrier crossed by only one species that can germinate after marine flotation.

Madagascar has a long history of isolation, and its biota has evolved many unusual adaptations that are of general evolutionary interest. This paper results from studies made for a recent floristic treatment of the Solanaceae for Madagascar and the Comoro Islands. Some unusual features of the Solanaceae of Madagascar are discussed, and speculations are offered on relationships and biogeography of these plants.

Solanaceae are not well represented on Madagascar. Fourteen genera and about 60 species are present, of which only two genera and about 30 species are clearly native (Table 1). Of the species native to the flora area, all except six shared with Africa are endemic. Although few in number, the Solanaceae of Madagascar display interesting diversity in both form and presumed source area.

In the present century, the Solanaceae of Madagascar were studied by Bitter (1913, 1917, 1921, 1923), Whalen (1984), Jaeger (1985), and Jaeger & Hepper (1986), each of whom considered the elements from Madagascar in the context of an African or larger sphere. The new treatment (D'Arcy & Rakotozafy, in press) covers Madagascar and the Comoro Islands.

THE FLORISTIC STUDY

My study of the Solanaceae for the flora spanned more than a decade and included examination of specimens at several European institutions, borrowed specimens, and two trips to Madagascar. During the first trip, in 1983, I visited the south of the country, the wet forest and coast east of Tananarive, and Nosi Be and Anivorano Nord at the north end of the island.

In 1987, I went to the Comoro Islands of Grande Comore, Anjouan, and Moheli and revisited places east of Tananarive and in the north of Madagascar. I also studied the wet northeast coast near Mt. Marojejy. A valuable part of the study was observation in the Missouri Botanical Garden research greenhouses of living plants, which were grown from seed obtained personally in Madagascar or

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[1] Grateful acknowledgment is made to the National Geographic Society for help with the underlying floristic treatment (D'Arcy & Rakotozafy, in press), and to the following, not only for specific assistance, but also for generally helpful dialogue: Richard C. Keating, Southern Illinois University at Edwardsville; Alwyn H. Gentry and George Schatz, Missouri Botanical Garden, David E. Symon, State Herbarium of South Australia, Botanic Garden, Adelaide, South Australia; Sandra D. Knapp, Mississippi State University; and Joan Nowicke, Smithsonian Institution. Laboratory, technical, and photographic assistance was provided by Richard C. Keating and his technician, Sue Eder, and photographic assistance was also provided by Michael Vieth, Washington University. K. Kathleen Pickett, Missouri Botanical Garden, helped in cultivation of plants and observations of their characters. Photos that were helpful in assessing characteristics of plants from Madagascar were provided by George Schatz and James Miller, and seeds were provided by these two and by Peter Phillipson and Sigrid Liede, all associated with the Missouri Botanical Garden. Seeds, pickled plant material, and microscope slides were provided by Joseph E. Armstrong, Illinois State University. Information on bees was provided by: L. Anders Nilsson, Department of Systematic Botany, Uppsala University; Steven L. Buchmann, Carl Hayden Bee Research Center, Tucson, Arizona; and Charles D. Michener and Robert W. Brooks, Department of Entomology, University of Kansas. Information relating to the new genus *Tsoala* was provided by J. Bosser, Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris.

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TABLE 1. Numbers of species of Solanaceae on Madagascar.

Genera	Total species	Native species		Introduced species		Doubtful species[b]
		Endemics	Also Africa	Total	Cultivated/ Naturalized[a]	
Brugmansia	2			2	2/0	
Brunfelsia	3			3	3/0	
Capsicum	1			1	1/0	
Cestrum	3			3	3/0	
Cyphomandra	1			1	1/0	
Datura	3			3	3/0	1
Lycium	1		1			
Lycopersicon	1			1	1/0	
Nicandra	1			1	?/1	
Nicotiana	1			1	1/0	
Petunia	1			1	1/0	
Physalis	4			4	0/4	
Tsoala	1	1				
Solanum	39	23	5	11	8/7	2
Totals	62	24	6	32	21/12	3

[a] Includes species that are cultivated, naturalized, or both.

[b] *Datura metel, Solanum aphananthum, Solanum virginianum.*

provided by helpful coworkers. In the notes that follow, observations and speculations are my own unless identified otherwise.

THE SOLANACEAE

Worldwide, the Solanaceae include about 2,300 species arranged in about 95 genera (D'Arcy, 1991). The family comprises two major subfamilies, the Solanoideae, which are cosmopolitan, and the Cestroideae, which have more restricted distribution, occurring mainly in the Americas and Australia.

The greatest diversity of Solanaceae, at both generic and species levels, occurs in western South America, and the extension of this solanaceous flora across Central America into southern Mexico has an elaboration of species but little development at higher taxonomic levels. Other centers of solanaceous diversity are northern Mexico, where a group of endemic genera and infrageneric taxa ranges into the southwestern United States. Southwestern Australia hosts a group of isolated genera, and a group of distinctive but species-poor temperate genera ranges from Japan westward to Gibraltar. The large genera, *Lycianthes* and *Solanum*, have secondary centers in New Guinea with species ranging westward into China and India.

The genus *Solanum* comprises about half the species in the family and is currently (D'Arcy, 1972) arranged in five subgenera and about 55 sections, many of which are more distinctive than genera in other families. *Solanum* is best developed in the New World, but two subgenera, *Leptostemonum* and *Solanum*, are native in the Old World. Subgenus *Leptostemonum*, one of the few large groups of Solanaceae with adaptations to hot and xeric conditions, is well elaborated in Africa and Australia. Subgenus *Solanum* is more widely distributed but has fewer species in the Old World.

Although there is significant development of Solanaceae in Africa, with many species and some development at higher taxonomic levels, there is a notable decrease in the diversity to the east of Africa and Madagascar. Peninsular India and southeast Asia have notably low representation of Solanaceae.

THE ISLAND SETTING

Madagascar is an island continent some 1,000 miles (1,600 km) long with a central uplands, a wet eastern escarpment and lowlands, and drier shelving on the west. The southern part (about as far from the equator as southern Florida) has vegetation distinct from the northern part of the island. Along the island's central core there are several peaks and massifs between 2,000 and almost 3,000 m elevation.

Madagascar was once part of the ancient, southern Gondwanaland continent. It separated from Africa 180–170 mya and reached its present position, somewhat south of its place of origin, about 120 mya (Rabinowitz et al., 1983; Philip Rabinowitz, pers. comm.). Madagascar is now separated from Africa by the Mozambique Channel, which is about 250 mi. (400 km) wide at its narrowest point. The separation occurred before flowering plants are known in the fossil record and long before the South American and African continents separated and began to move apart ca. 130 mya (Pitman, in press). Most texts assume that Madagascar has been at least partly emergent since its separation from Africa. Barron (1987) has suggested that a strike-slip motion between India and Madagascar prior to 120 mya resulted in the linear nature of the continental eastern margin of Madagascar. Although Madagascar drifted away from Africa too early to have carried along any flowering plants, land has been present for colonization by flowering plants since an early date in their evolutionary development.

Introductions of plants and animals across the incipient and actual Mozambique Channel are believed to have led to a more or less continuous flora in the past, but extinction episodes in Africa that were not shared by Madagascar have extirpated African ranges of many taxa (Coetzee, in press). During past aeons, Africa received taxa from Asia or Europe to the north that apparently did not disperse across the Mozambique Channel to Madagascar. Today, Madagascar has a different suite of animal and plant taxa from those of Africa and other regions. For example, there are few mammals—no marsupials, no lagomorphs, one ungulate (extinct), few rodents, and few carnivores—except for a conspicuous elaboration of insectivores and lemurs (Eisenberg, 1981). Bees are apparently not numerous, either in numbers or species, and they relate mostly to African bees (Brooks & Michener, 1988). The bird fauna is unexpectedly small (Jenkins, 1987). Nevertheless, reptiles (Duellman, in press) and hawkmoths (George Schatz, pers. comm.) are well represented.

Human settlement began 1,500–1,000 years ago, with immigrants coming mostly from Indonesia and Africa (Verin, 1986). There was also early contact with Arabia via the Comoro Islands, and Portuguese ships reached Madagascar in 1500. Most of the interior uplands were deforested before 1950. With economic improvement that began about 1983, deforestation has accelerated, as supplies and machinery associated with removal of natural growth have become more plentiful. Today the original vegetation is mainly represented by remnants that are being rapidly replaced by fire-maintained grasslands.

The Comoro Islands are a four-island group about halfway between northern Madagascar and the African mainland. The recent volcanic nature and succession of island ages from east to west is striking. The surface of Grande Comore, the youngest and westernmost, consists of lava rock and boulders and contains little soil. Anjouan and Mayotte, older islands, have well-developed agriculture. Moheli, the smallest island, has less relief, soil, agriculture, and rainfall. The main affinity of the native flora is with Madagascar, although this is now almost entirely replaced by introduced, pantropical species. The Comoro Islands have long been part of the African–Arabic coastal trading province.

THE INTRODUCED SOLANACEAE

On Madagascar, 12 of the 14 Solanaceae genera and more than half the species are introduced, some of them known only in cultivation. Most of the cultivated/introduced flora is now cosmopolitan in tropical cultivation or disturbance. More will be said below of Solanaceae of uncertain origin.

Two introduced species, *Solandra grandiflora* Sw. and *Solanum seaforthianum* Andrews, are known in the Comoro Islands but have not been collected on Madagascar. The first is cultivated in Moroni, Grande Comore, and there are sight records (George Schatz, pers. comm.) from Tananarive, Madagascar. The second is naturalized in woodlands of Grande Comore and Anjouan. Both are widely used as tropical ornamentals.

LYCIUM

Lycium acutifolium is common in southeastern Madagascar, especially near the south coast, but it ranges at least as far north as Betroka and to within 25 km of Tulear on the west. This species displays remarkable variation in growth form, occurring as a free-standing or near-prostrate shrub, and also as a vinelike plant hanging from coastal cliffs. It also occurs in the east Cape region of southern Africa (Fig. 1), according to Prof. H. J. T. Venter, who is revising the South African species of *Lycium*. Because there are other species of *Lycium* in southern Africa, *Lycium acutifolium* is assumed to have been brought, perhaps by natural vectors, to Madagascar from Africa.

TSOALA TUBIFLORA

Tsoala is a new genus discovered among undetermined collections at the Laboratoire de Phanérogamie (Paris) by Jean Bosser. It was collected at several sites in western Madagascar, where most of the forest has been turned into grassland.

The flower has a long tube (8–15 cm), indicative

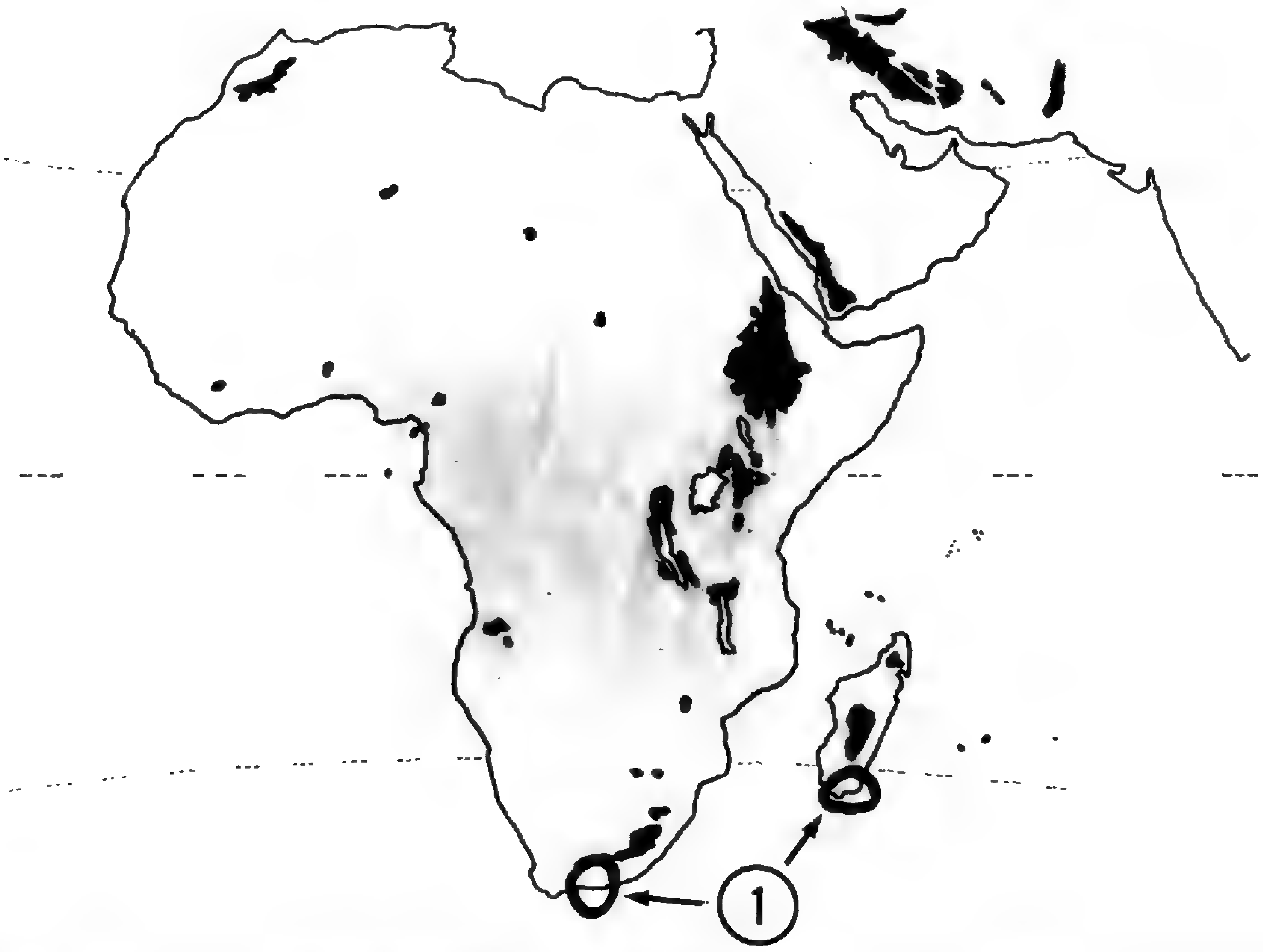

FIGURE 1. Distribution of *Lycium acutifolium* (at 1). Elevations above 2,700–3,000 m are darkened. Data from collections at P and MO.

of hawkmoth pollination, which is especially well developed on Madagascar (George Schatz, pers. comm.). This remarkable species is a shrub with simple leaves and pubescence of simple hairs. The fruit is a woody capsule with large seeds that have nearly straight embryos. We have been unable to detect included phloem, which is diagnostic for Solanaceae, in our material, but this tissue is difficult to detect in dried leaves. The ovary is one-locular except at the base, and there is no sign of an expanded placenta as is common in Solanaceae. All other characters argue for placement in the Solanaceae. A nuclear magnetic resonance spectrum analysis (Soren Jensen, pers. comm.) revealed

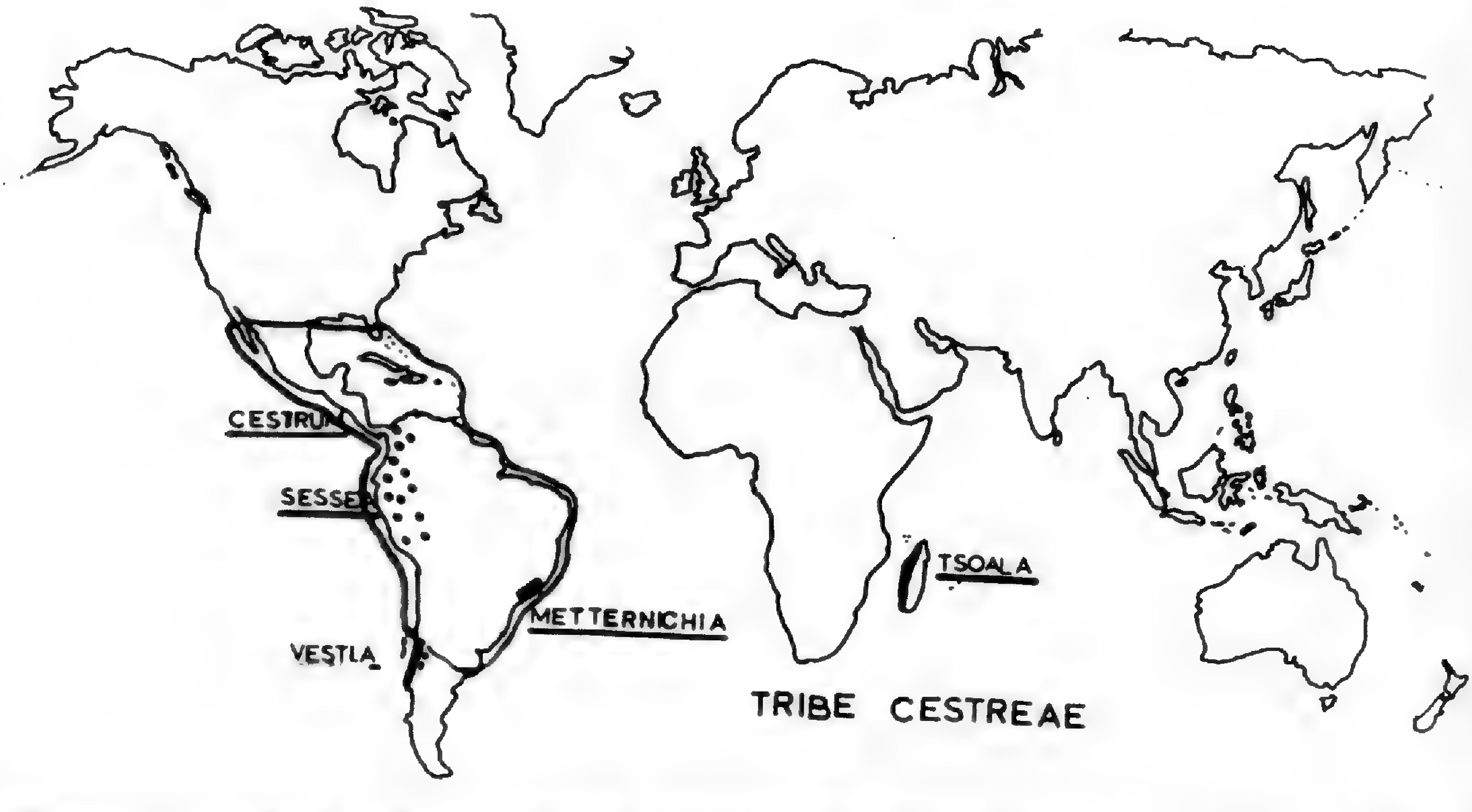

FIGURE 2. Distribution of genera comprising Solanaceae tribe Cestreae. Data from collections at MO and from various literature references.

no iridoid alkaloids. The Solanaceae lack such compounds, while similar-appearing families in the Scrophulariales/Lamiales often have them.

These features place *Tsoala* in tribe Cestreae of subfamily Cestroideae, neither of which was hitherto known from the Africa/Asia region. Tribe Cestreae (Fig. 2) includes four other poorly known genera: *Cestrum* (widespread, tropical America), *Vestia* (Chile), *Sessea* (Andes), and *Metternichia* (Rio de Janeiro). The last two have woody capsules not unlike those of *Tsoala*, but the corollas are of quite different shapes. The occurrence of a member of the Cestreae on Madagascar supports the views that the Solanaceae have a southern or Gondwanaland origin (Raven & Axelrod, 1974; D'Arcy, 1975, 1991).

SOLANUM: THE INTRODUCED SPECIES

About half the species of *Solanum* occurring on Madagascar and the Comoro Islands today are introduced species, including species that occur only in cultivation. Some of the introduced species are so well established and integrated into the present environment of Madagascar that they are commonly considered to be part of the flora. The presumed status of species and groups of *Solanum* is indicated in Table 2.

TABLE 2. Taxonomic arrangement of solanums on Madagascar.

- Subgenus *Solanum*
  - Section *Lemurisolanum* (8 species, all endemic) *S. antalaha*[*], *S. apocynifolium*, *S. ivohibe*[*], *S. madagascariense*, *S. macrothrysum*, *S. marojejy*[*], *S. myrsinoides*[*], *S. trichopetiolum*[*]
  - Section *Macronesiotes* (5 species, all endemic) *S. ankazobe*[*], *S. betroka*[*], *S. humblotii*, *S. imamense*, *S. sambiranense*[*]
  - Section *Afrosolanum* (1 Comoros and Africa) *S. terminale*
- Other groups (introduced: cultivated and/or naturalized) *S. americanum*, *S. pseudocapsicum*, *S. scabrum*, *S. seaforthianum*
- Subgenus *Leptostemonum*
  - Section *Melongena* (*Andromonoecum*) (3 species, 1 Madagascar and Africa, 2 introduced, cultivated) *S. incanum*, *S. macrocarpon*, *S. melongena*
  - Section *Croatianum* (3 species, all endemic) *S. bumeliaeifolium*, *S. croatii*, *S. heinianum*
  - Section *Oliganthes* (plentiful in Africa)
    - Series *Afroindica* (3 species, also in Asia, 1 perhaps native) *S. aethiopicum*, *S. anguivi*, *S. violaceum*
    - Series *Eoafra* (3 species, all endemic) *S. batoides*[*], *S. erythracanthum*, *S. myoxotrichum*
    - Series *Acanthocalyx* (1 species, Africa, Comoros, Madagascar, Mauritius) *S. richardii*
    - Series *Pyracanthum* (1 species, endemic) *S. pyracanthos*
  - Section *Cryptocarpum* (1, endemic) *S. mahoriensis*
- Isolated species (1, endemic) *S. toliaraea*
- Other groups (introduced: cultivated and/or naturalized) *S. torvum*
- Other subgenera (introduced: cultivated and/or naturalized) *S. mauritianum*, *S. tuberosum*

[*] Species to be described in the *Flore de Madagascar et des Comores* (D'Arcy & Rakotozafy, in press).

Solanum americanum Miller, the tropical black nightshade, is one of the most common table vegetables in Madagascar: its aboveground parts are served boiled on rice in most country restaurants and homes throughout the land. The species occurs widely in warm countries, and plants on Madagascar are indistinguishable from those of the Caribbean region. The similar *Solanum scabrum* Miller is cultivated for its berries, and it is sparingly naturalized. This species is commonly cultivated in upland areas of west Africa. Most species of this section, *Solanum*, are found in South America, which is its presumed region of origin, but some Old World elements (*S. nigrum* L., *S. villosum* Miller, *S. scabrum*) seem to have no counterparts in South America, and their presence in the Old World is presumed to be of long standing.

Two other New World species have become pervasive, shrubby weeds in the tropical Africa/Asia region and are common in Madagascar except in the south. These are *Solanum mauritianum* Scop. and *S. torvum* Sw. The fruits of *S. torvum* are commonly eaten in India but perhaps not in Madagascar.

Solanum incanum L., the presumed ancestor of *S. melongena* L., the eggplant, is widespread around the island near villages and along roads, and populations were found whose individuals (in flower) could not be distinguished from *S. melongena*. *Solanum incanum* is widespread in Africa, India, and China. Fruits of both *Solanum incanum* and *S. melongena* float, and seeds of the first can survive a period in sea water of at least five weeks (D'Arcy & Pickett, 1991). Because of its uniform appearance on Madagascar and the great variety of related species in Africa, this group is assumed to have arrived on the island in relatively recent times.

Solanum anguivi Lam. (*S. indicum*) is common around homes in many parts of the island, and it seems to intergrade and perhaps to be interfertile with *S. aethiopicum* L. (*S. integrifolium*). Fruits of *Solanum aethiopicum* will float in sea water (not in fresh water), but those of *S. anguivi* do not. These plants were domesticated in west Africa (Lester & Niakan, 1986), and many forms and related wild "species" exist across the African continent, including the ribbed-fruited forms seen on Madagascar. As there appears to be no series of wild associates in Madagascar, these species are presumed to have been introduced from Africa, where many similar forms are found. Both species are used medicinally and sometimes as food. In Africa, fruits and leaves are eaten, and many wild stocks are used for medicines.

The earliest name for what was formerly called *S. indicum* L. is *S. anguivi*, described from a Commerson collection from Madagascar. The common name for this species in Madagascar is "angivi." Several explanations are available for the presence of a presumed ancestor for a west African cultigen in Madagascar. That the species was introduced to Madagascar well before 1769 when the species was collected by Commerson seems most likely. The species need not have been taken by sea travelers from west Africa to Madagascar. It may occur or have occurred in this form widely across Africa and been present in the wild on the east coast for transport to Madagascar or further east. Or it may have been carried by Islamic pilgrims into their Ethiopian villages on the several-year journey from west Africa to Mecca (Bunting, 1990). From there, it would have been a candidate for transport to the Comoro Islands by coastal traders and thence to Madagascar.

Solanum aethiopicum may have entered Madagascar in the same way as *S. anguivi*, but as the fruit and plants seem identical to some forms cultivated in the United States, it may have been introduced more recently, perhaps by French agriculturists.

To the east of Madagascar, in India and southeast Asia, *S. anguivi* appears to be replaced by *S. violaceum* Ortega. Both species occur on Madagascar, but *S. violaceum* is known by only a few records. As differences between these two extremely similar species have only recently been elucidated, investigation will be necessary to determine more precisely the range of *S. violaceum* and its likely region of origin.

SOLANUM: THE NATIVE SPECIES

Except for the newly discovered endemic genus *Tsoala* noted above, all native Solanaceae on Madagascar are of genus *Solanum*. There are about 25 species of *Solanum* in the flora area, all but two of these endemic. The two largest subgenera, *Solanum* and *Leoptostemonum*, are well represented. Subgenus *Leptostemonum* includes species often having slender anthers with small pores, spines, and stellate pubescence. Subgenus *Solanum* includes species with stout anthers, no spines, and simple or dendritic rather than stellate hairs. The taxonomic arrangement of native species is presented in Table 2. This generally follows the arrangements of Bitter (1913, 1917, 1921, 1923) and Jaeger (1985), and for *Leptostemonum*, Whalen (1984), with a few adjustments made in the current study. Infrageneric names and their authors are as presented in D'Arcy (1972).

UNARMED *SOLANUM* GROUPS (SUBGENUS *SOLANUM*)

SECTION *AFROSOLANUM*

Section *Afrosolanum*, which, unlike the other species treated below, is not strictly native to the flora area, includes many named species, but recent works recognize three (Jaeger, 1985), or only one (Heine, 1960) species, *Solanum terminale* Forsskal. *Solanum terminale* ranges across tropical Africa and the Arabian Peninsula (Fig. 3), mostly at elevations above 2,500 m. It occurs in moist forests as a shrub, scrambler, or climber. The inflorescences are purplish or white flowers in terminal paniculate clusters, the base of the rachis often bearing a series of leaves or bracts that diminish in size upwards.

A noteworthy feature in section *Afrosolanum* and some other African sections is the type of anther dehiscence. The terminal pores, which occur in all species of *Solanum*, soon elongate into longitudinal slits that run to the base of the anther and open to expose the pollen (Fig. 4A).

In contrast, spiny solanums and most New World groups of spineless solanums either lack longitudinal dehiscence, or they develop longitudinal slits from separate sites below the anther apex, and the slits are not continuous with the terminal pore, at least before late anthesis. They seldom or never open below the pore wide enough to expose much pollen. The type of anther dehiscence in section *Afrosolanum* is also found in section *Quadrangulare* and in subgenus *Lyciosolanum*, both groups of southern Africa and in section *Archaeosolanum* of Australia. Bitter (1917) considered subgenus *Lyciosolanum* (*Solanum quineense* L. = *S. aggregatum* Jacq.) to be intermediate between *Lycium* and *Solanum* and "another primitive species among the numerous other ancient types in the Cape Flora." He may also, to judge from the appellation chosen for it, have considered section

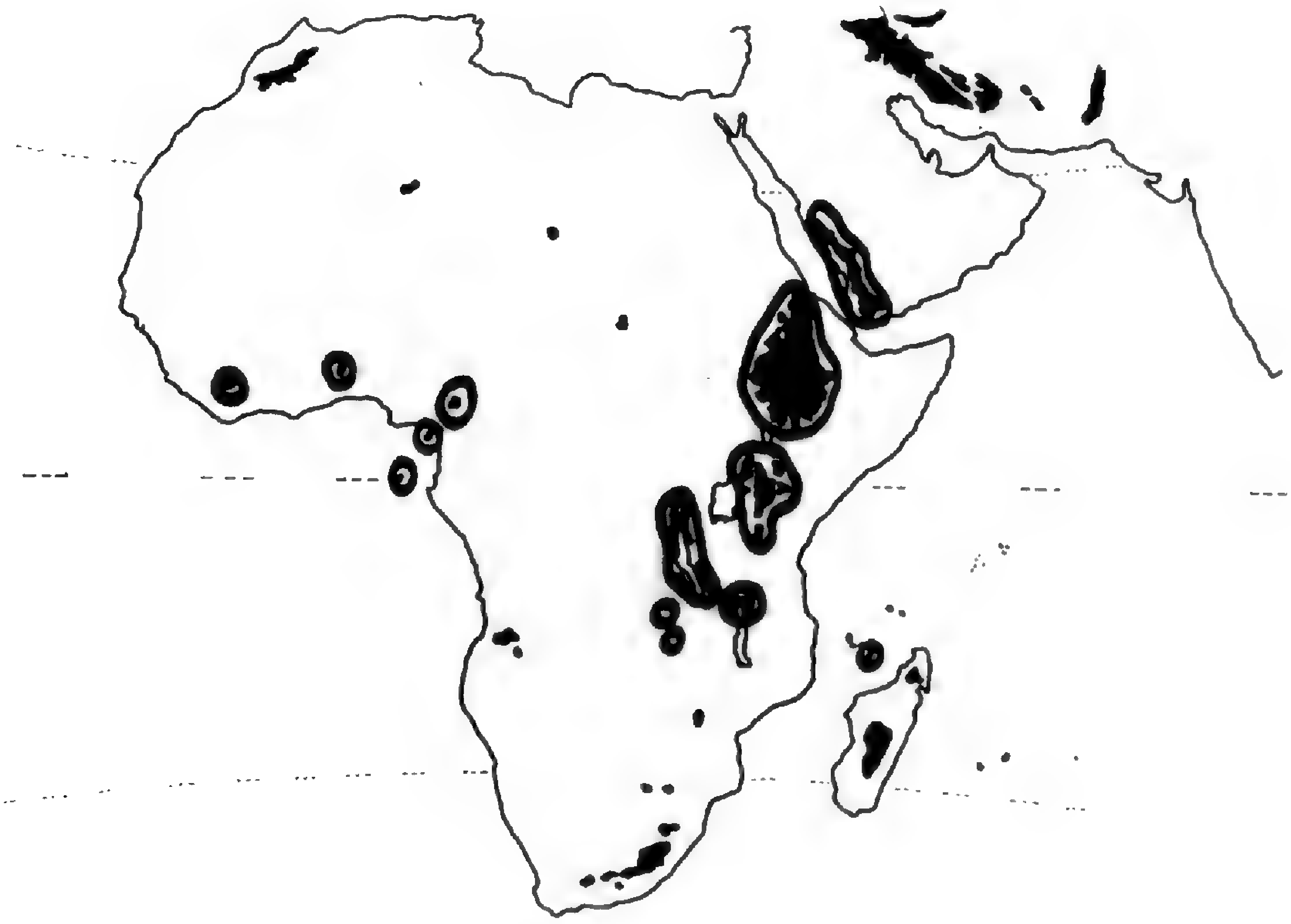

FIGURE 3. Distribution of *Solanum terminale* Forsskal in circled areas. Elevations above 2,700–3,000 m are darkened. Data from Bitter (1913, 1923) and from collections at MO.

Archaeosolanum to be archetypal in the genus. The rapid longitudinal dehiscence may be considered a primitive feature in the genus, if one assumes that *Solanum* evolved from taxa having longitudinally dehiscent anthers as in most other genera of Solanaceae.

The perhaps monotypic section *Afrosolanum* has been collected only once in the flora area, on Mayotte in the Comoro Islands, in 1884. This collection of *S. terminale* became the type collection of *S. comorense* Dammer, a name now relegated to synonymy. Because the species is found on widely isolated mountains, including sites on land masses (Africa and Arabia) that have not been united for many millions of years, it seems to be capable of dispersal over considerable distances. However, it has not been found on Madagascar; this enigma will be discussed later.

SECTIONS *LEMURISOLANUM* AND *MACRONESIOTES*

Two other nonspiny *Solanum* groups, sections *Lemurisolanum* and *Macronesiotes*, occur in the flora area, each represented by several species on Madagascar and the Comoros. Both are similar in many respects and also similar to section *Afrosolanum*, often developing dendritic hairs, sarmentose to epiphytic growth habits, plurifoliate inflorescences, leafing and flowering on short shoots, purplish or bluish flowers, and often conical ovaries. However, they differ from section *Afrosolanum* in their anthers, calyces, and other features. The anthers are sometimes laterally connate, and the presence and degree of this connation seems to vary considerably within species. Dehiscence is by distinctly margined terminal pores with no tendency to longitudinal dehiscence (Fig. 5A). Both groups occur widely in the flora area in all original forests except in southern Madagascar, and both are endemic to the flora area.

FLORAL EGRESS

In species in section *Lemurisolanum*, calyx prefloration is nearly perfect (fused to the top), the only signs of lobes being minute apical tufts of trichomes where the primary veins terminate (Fig. 4B), and floral egress is by stretching (Fig. 4C) with no sign of splitting. See D'Arcy (1986) for an explanation of egress modes in solanaceous calyces. This mode of egress is almost unknown in *Solanum*, which typically opens the calyx by splitting at the sinuses, sometimes with some stretching before splitting. One such case is known in *Solanum* sect. *Geminata*, *S. leucocarpon* Dunal (*S. surinamense* Steudel) in South America, and other examples may be found in this section. Egress by stretching occurs in several other genera of Solanaceae, e.g., *Lycianthes*, *Capsicum*, *Witheringia*. See D'Arcy (1991) for a more complete list. This also occurs in other families, e.g., Melastomataceae (*Medinilla*, Madagascar). Such groups are characteristic of

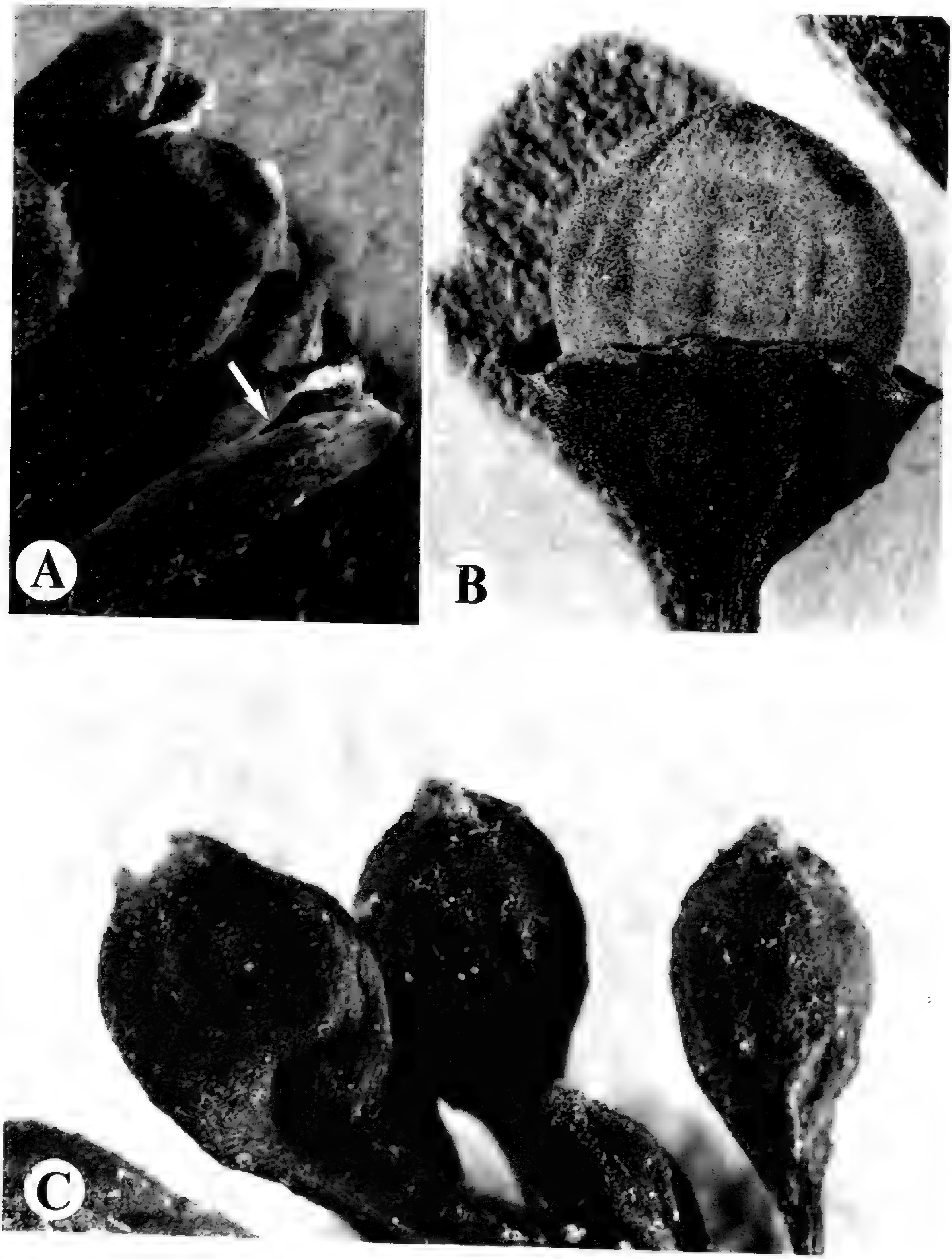

FIGURE 4. Features of *Solanum* species.—A. *Solanum terminale* showing extention of terminal pores into longitudinal slits (at arrow). (After *Humblot 284* (P), type collection of *Solanum comorense* Dammer.)—B. Floral egress of *Solanum madagascariense.* Bud with emerging corolla and fertile parts. The calyx has stretched thin at the apex to permit egress, and there is no sign of splitting or of calyx teeth. (After *Cours 2807* (P).)—C. Floral egress of *Solanum madagascariense* Dunal. Early buds with the calyx fused to the top and minute tufts of trichomes marking the five rudimentary teeth. (After *Cours 2807* (P).)

wet tropical forests, so it is speculated that this mode of egress has evolved independently in several groups under selection by unknown features of wet forests. It is postulated that this feature is one of high specialization, which took considerable time to develop.

ANTHER EMERGENCES

Another interesting feature of section *Lemurisolanum* is the unusual emergences or sculpturing on the anthers (Fig. 5), which Dunal (1852) referred to as hirsute. These are most striking on

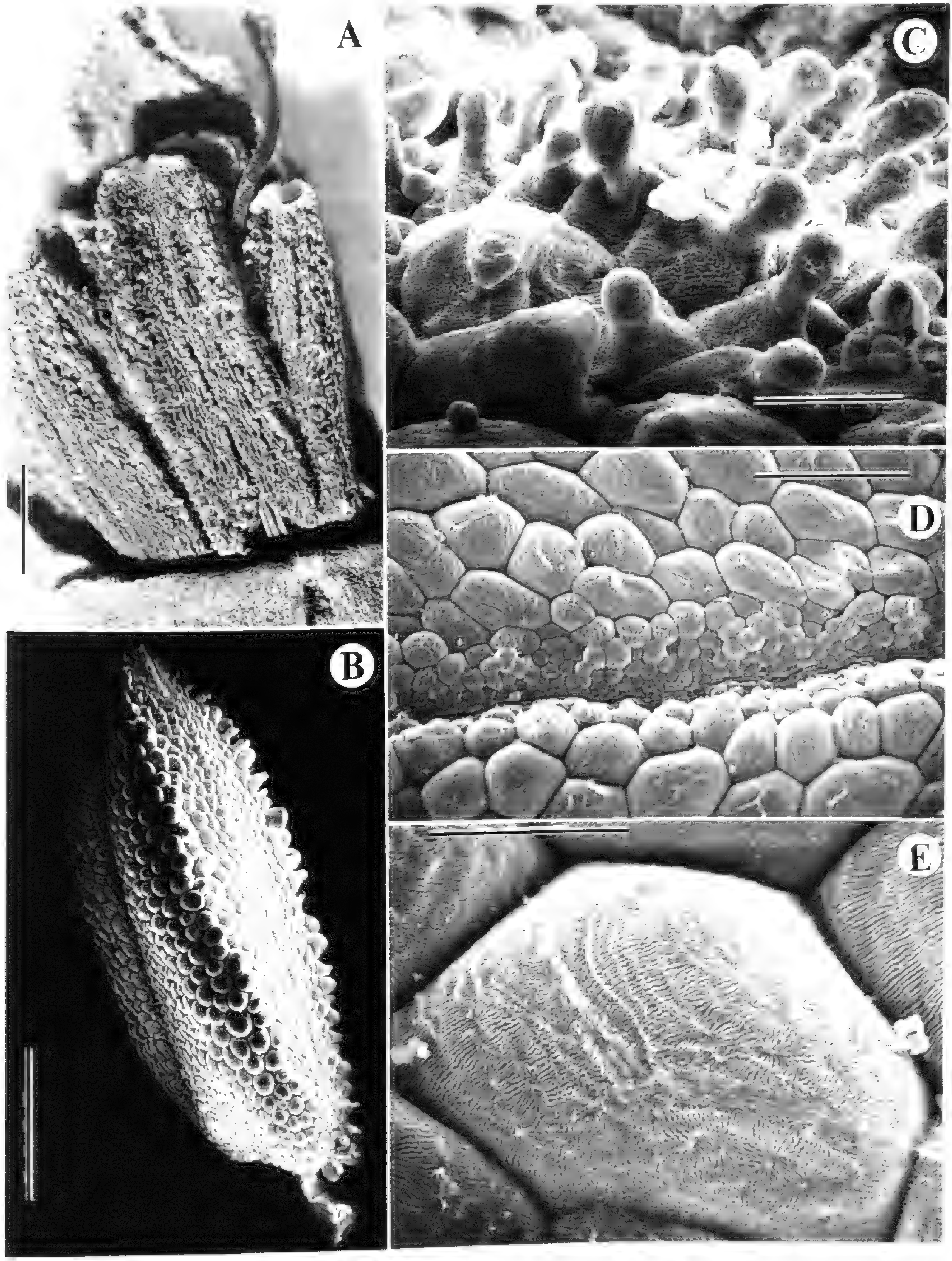

FIGURE 5. Emergences on anthers of *Solanum madagascariense* Dunal. A. Photo of herbarium specimen. Scale = 1 mm.—B. SEM of material preserved in 50% FAA. Material rinsed in a graded ethanol series and critical point dried from liquid CO_2. Specimen was sputter-coated with 200 Å of gold, then photographed with I.S.I. Super IIIA scanning electron microscope. Scale = 1 mm.—C. SEM of restored material. Dried herbarium material treated overnight in concentrated ammonium hydroxide at 60°C in a sealed container under pressure. Preparation as in B. Scale 50 = µm.—D. SEM of liquid preserved material. Preparation as in B. Scale = 200 µm. —E. SEM of liquid preserved material. Preparation as in B. Scale = 50 µm. (All after *Miller 3413* (MO).)

specimens of the north and east coast of Madagascar, but they are also seen in material from other areas of the country and to a slight degree on anthers of the similar sections *Afrosolanum* and *Quadrangulare* on the African continent. I have not seen anything like these in plants from other parts of the world. Such emergences are not to be confused with the trichomes that Bitter (1917: 437–438) noted near the pores of *S. apocynifolium* Baker, which are minute, granular material localized on the contrasting yellow rim of the pores of a few specimens.

The anther emergences are probably pollinator related, and at least three suggestions come to mind on the nature of this relationship. Flowers of *Solanum* and other plants with anther dehiscence by terminal pores are usually pollinated by bees that buzz the anthers to extract the pollen (Buchmann, 1983a, b). One possibility is that the emergences restrict access to pollen by nonpollinating visitors. As noted above, sections *Lemurisolanum* and *Macronesiotes* differ notably from the African *Afrosolanum, Quadrangulare,* and *Lyciosolanum* species in their lack of longitudinal dehiscence, presenting pollen to only those visitors able to access it via the pores or by chewing their way to it. In the Americas, trigonid bees are known to rob pollen regularly from anthers without affecting pollination (Renner, 1983), and they may actually restrict some taxa of flowering plants to sites where these bees are not numerous. If these emergences act as deterrents to chewing through the anther to obtain pollen, they may, in addition to completing closure of the anther wall, help to restrict pollen dispersal to those visitors that can buzz the flowers, the means by which pollinators avail themselves of pollen from terminal-pored anthers. A second possibility is that the emergences provide grasping holds for pollinating bees, enabling them to hold the anther while they "buzz" the stamens. The third possibility is that the emergences are ultraviolet absorptive and provide an orientation cue to pollinating insects. Similar papillate emergences on patches of corolla tissue in some species of the scrophulariaceous genus *Diascia* were illustrated by Steiner (1990) and were demonstrated to affect orientation behavior of at least one pollinator.

It has not been possible to test these hypotheses either by observing bees in their visits to flowers or by testing the nature or contents of the emergences for a chewing-deterrent role or by testing the light reflectance of the anthers and the surrounding corolla tissue. Because these features are restricted to, or best displayed on, plants of Madagascar, they may relate to organisms restricted to this faunal area. Anders Nilsson (pers. comm.) relates that on Madagascar several genera of anthophorid bees hover and grasp anthers of *Solanum* to buzz them and obtain pollen, and at least two genera of halictid bees, and endemic genus *Spegocephala*, with about six species, and *Thrinchostoma*, which is restricted to Madagascar and Africa, also buzz anthers but must land on the anthers to do so. Possibly one or more of these halictids benefits from the availability of the emergences as holdfasts, and perhaps all classes of pollinators are attracted by light contrast between the anthers and corollas.

The contrast between the pollen presentation of otherwise similar plants in Africa and Madagascar is striking. In the African groups the pollen is exposed through an open longitudinal slit and is readily available for any pollen predators. In contrast, in the groups on Madagascar, the pollen is hidden beneath an intact anther wall and elaborate emergences, and the area presented to the outside is reduced by the frequent connation of adjacent anthers, seemingly offering a complicated system of deterrents to pollen predation. The African taxa are distributed across the continent and in the Arabian Peninsula, but they are restricted mainly to cool areas: above 2,500–3,000 m in the tropics or to the south at lower elevations, while the species of Madagascar occur at all elevations below 3,000 m in the tropics. Trigonid and apid bees, both pollen-scavenging groups, are present in Africa and Madagascar and seem likely to be pollen predators in both places. Further findings are needed to suggest how possible differences in pollinator capabilities or pollen predation levels may justify the contrasting pollen presentation systems. The differences in pollen-predation environments may explain why the Mozambique Channel has been such a formidable barrier to migration and establishment of these *Solanum* groups on neighboring continents, especially of the African groups that have well-demonstrated capability for long-distance range extension.

The occurrence of emergences on anthers and of anther connation in section *Lemurisolanum* does not appear to be entirely species specific, varying from completely absent to well developed on similar-looking specimens from neighboring sites. The biological interaction leading to development of these phenomena appears to have acted on a spectrum of taxa and populations in varying degrees, so that anther connation and emergences are of limited value as taxonomic markers. Similar anther emergences, somewhat different in detail, occur on species of *Exacum* (Gentianaceae), which are numer-

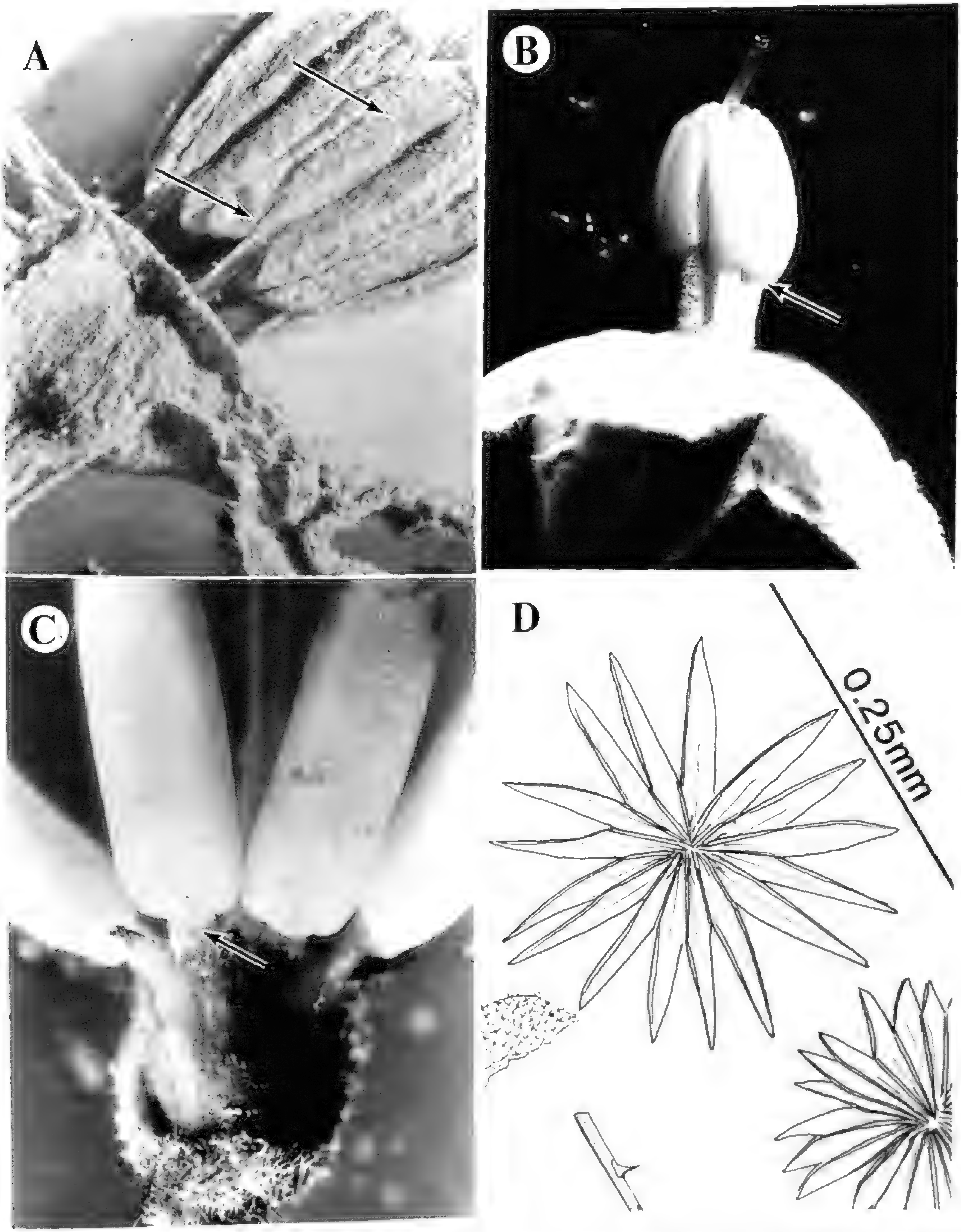

FIGURE 6. Features of some *Solanum* species. A–D Views of abaxial (dorsal) sides of anthers illustrating anther insertion.—A. *Solanum madagascariense* Dunal. Arrows show continuous dorsal position of filament–connective up the length of the anther.—B. *Solanum americanum* Miller. The basal, dorsal overhanging tissue is shown at arrow. In this species, this tissue recedes greatly on drying but still shields the point of anther insertion on the filament from view.—C. *Solanum pyracanthos* Jacq. The basal, dorsal overhanging tissue is shown at arrow.—D. Scutellate hair of *S. croatii*. (After *D'Arcy & Rakotozafy 15341* (MO).)

ous in the same forests on Madagascar (pers. obs.; Klackenberg, 1985). Collections from near Marojejy, the high (2,137 m) mountain near the wet-forested northeast coast of the island, seem to have the best development of emergences, but there are also species in this area with none at all. This is the part of Madagascar where the greatest development of wet forest solanums occurs. To judge from collection dates, blooming or occurrence of at least some of these *Solanum* species is restricted seasonally and in elevation range, which suggests that varied means of reproductive isolation are affecting similar plants within this relatively small area.

ANTHER INSERTION

In most species of *Solanum*, anthers are basifixed, and the filament enters a kind of socket in the anther where a flange of dorsal anther tissue shields the top of the filament and the point of insertion from abaxial view (Fig. 6A, B). When dried, this flange sometimes recedes up the back of the anther, but the point where the filament joins the anther is still within an anther socket. However, in *Solanum madagascariense* Dunal, the insertion of the anther is dorsal, the filament running up the abaxial side to the apex without interruption (Fig. 6C). Sometimes (Fig. 5A) the dorsal sides of the locule walls converge over the back of the filament, but these are not connate or coherent, and the filament can be viewed at least partly exposed all along the dorsal side. The type of anther insertion was verified as *Solanum madagascariense* and a range of other species by histological preparations (floral cross sections).

Similar dorsifixed anthers were not seen in African *S. terminale* or the related section *Quadrangulare* (*S. africanum* Miller). In the Australian section *Archaesolanum*, which is suggested by Bitter's name for it as a primitive group in the genus, anthers sometimes appear be dorsifixed, but histological sections have not yet been made to verify this. However, truly dorsal fixation occurs in solanums belonging to at least two other groups: *Solanum dulcamara* L. (sect. *Dulcamara*) from northern Asia and Europe and *Solanum pensile* Ruíz Lopez & Pavón (sect. *Andropedas*), widespread in tropical lowland South America. Each of these and section *Lemurisolanum* are woody vines or climbers with purple or violet flowers, often with a contrasting eye, borne in lax, many-flowered paniculate inflorescences. In both sections *Dulcamara* and *Lemurisolanum* there may be connation of the anthers. Specimens of *Solanum pensile* look very much like those of *S. madagascariense* in section *Lemurisolanum*, but the androecia differ: one stamen has a longer filament that places its anther well in advance of the others; and the anther dehiscence is by terminal pores and tardily forming longitudinal slits. Each of these groups has been divided into numerous species by various taxonomists, attesting to a considerable variability that has evolved in each group on its respective continent. Because dorsifixed anthers occur in many related genera and basifixed anthers are hardly found, and because these other genera have longitudinal anther dehiscence, which is generally considered to be less specialized than dehiscence by terminal pores as in *Solanum*, dorsifixed anthers are presumed, a priori, to be a character state primitive to basifixed anthers. The widespread taxa of *Solanum* with this feature would appear to represent isolated relict elements in the genus. Michael Nee (pers. comm.) may be correct that these vines are a distinct phylad within *Solanum*.

FRUIT SHAPE

Several species of section *Lemurisolanum* have conical ovaries and fruits, in contrast to the usual rounded ovaries and globose fruits in *Solanum*. One species from Marojejy has fusiform fruits to 4 cm long, which may indicate a shift from bird dispersal to mammal dispersal on an island where bird diversity is low.

SECTION *MACRONESIOTES*

The second group of forest climbers and epiphytes is section *Macronesiotes*. These have many of the features of section *Lemurisolanum*, but the calyx lobes, instead of being nearly obsolete, are well defined, and there is sometimes splitting at the sutures. Plants in this section are of two kinds. The group including the typical *S. imamense* Dunal comprises plants with membranaceous, pubescent leaves, lanceolate or deltoid calyx lobes, which sometimes elongate by splitting at the sinuses, and terrestrial habit. Species in this group closely resemble the American section *Pseudocapsicum*, from which they differ mainly in the small anther pores and lack of longitudinal dehiscence. Also placed in section *Macronesiotes*, as *S. humblotii* Dammer, are some specimens with coriaceous, glabrate leaves, linear calyx lobes, and epiphytic tendencies. In *S. humblotii*, the lobes and pedicels are recorded as red or violet, perhaps acting as part of pollinator attractant. In this section, ovaries are rounded or conical, and at least one large, turbinoid fruit is known resembling the unusual one referred to above in section *Lemurisolanum*.

SPINY *SOLANUM* GROUPS (SUBGENUS *LEPTOSTEMONUM*)

Whalen (1984) estimated that there are about 450 species of subgenus *Leptostemonum*, the spiny solanums, worldwide. He recognized them as forming 33 groups, of which only nine occur in the Africa/Asia sphere of distribution. Only three sections and two isolated species occur on Madagascar (Table 2).

Section *Croatianum* displays a distinctive, scutellate hair type (Fig. 6D). The section was described with three species from southern Madagascar. These are trees or large shrubs bearing sturdy, mostly straight spines as juveniles but usually lacking armature as mature plants. Morphological changes across the group seem to follow a gradient of diminishing rainfall from east to west. *Solanum croatii* D'Arcy & Keating has many-flowered branched inflorescences, ovaries that are basally 4-locular and apically 2-locular, and hairs that are mostly slightly stipitate. *Solanum heinianum* D'Arcy & Keating has leaves and flowers in fascicles or on short shoots (brachyblasts), the hairs resemble those of *S. croatii,* and the ovaries are 4-locular to the top. *Solanum bumeliaefolium* Dunal, apparently the most advanced species in the group, has leaves and flowers in fascicles, the flowers are in short, unbranched racemes, the ovaries are 4-locular, and the trichomes are sessile, scutellate hairs that form lepidote scales that give the leaves a somewhat silvery appearance. Occasional intermediates are found between *S. croatii* and *S. bumeliaefolium*.

The scutellate hair type of section *Croatianum* is highly distinctive in *Solanum*. It is otherwise known in this form only in section *Lepidotum* of South America (Carvalho et al., 1991). Although their hairs are apparently identical, the two sections are not thought to be closely related, so this unusual hair is assumed to have arisen independently in each group. However, in dry parts of western and interior Australia, several species, e.g., *S. sturtianum* F. Muell., *S. nummularium* S. Moore, *S. tumulicolum* Symon, have stellate hairs, the rays of which are fused basally, suggesting an incipient development of the scutellate hair. Use of this hair type as a taxonomic marker may have been overdone in section *Croatianum*; *S. heinianum* differs from the other two species in the section in its brachyblastic growth and other features, and its relationship may actually be elsewhere.

Solanum croatii seems to have no African relationship, but it resembles and seems closely related to *S. sturtianum* from arid western and interior Australia (Symon, 1982). That species has similar leaves, pubescence, flowers, fruits, and overall appearance but has smaller stature (0.5–3 m), smaller leaves, acicular rather than broad-based spines, larger corolla (3–4 cm diam.), dark-colored seeds, and rays of the stellate trichomes are fused only at the bases or not at all. Symon (1981: 206) stated: "*S. sturtianum* does not appear to have close relatives amongst the Australian species of *Solanum*." Both species occur at similar latitudes. In spite of the differences noted, there are enough similarities (synapomorphies?) to suggest that they are sister species.

Section *Oliganthes* is represented on Madagascar by two series and by isolated species (Whalen, 1984; Jaeger, 1985). Series *Afroindica* includes *S. anguivi* and *S. aethiopicum*, which were discussed above under introduced solanums. In this group, flowers are all perfect, and fruits are moist and mostly reddish.

Series *Eoafra*, which was divided into subseries by Bitter (1923), is well represented in eastern Africa with several xeric-tolerant species. The group is well developed and troublesome on Madagascar, both taxonomically and ecologically. Members of the group are found everywhere on the island, and at least one species, *S. erythracanthum* Bojer, is highly resistant to human disturbance. Plants on Madagascar have sessile inflorescences and frequently 4-parted flowers, as do some of the African species. The group appears to be an intergrading series of plants with strikingly different morphologies at the extremes.

One noteworthy species is *S. myoxotrichum* Baker. This appears to intergrade with *S. erythracanthum,* from which it differs in few details other than the echinoid appearance of its setose stems, vining habit, and copious, reddish pubescence. *Solanum myoxotrichum* seems to occupy regions of greater moisture than *S. erythracanthum*.

Similar echinoid stems appear on species of subgenus *Leptostemonum* on other continents. These are generally wetter habitat members of species pairs in which the other member, occupying drier but still mesophytic sites, lacks the density of spines or bristles that gives an echinoid appearance. Such wet/mesophytic species pairs are *S. aturense* Dunal/*S. lanceifolium* Jacq. (sect. *Micracantha*, tropical America); *S. sessilistellatum* Bitter/*S. incanum* (sect. *Melongena*, Africa), *S. densiaculeatum* Symon/*S. turraeafolium* S. Moore (sect. *Graciliflora*, New Guinea); *S. semiarmatum* F. Muell./*S. stelligerum* Smith (sect. *Graciliflora*, Australia).

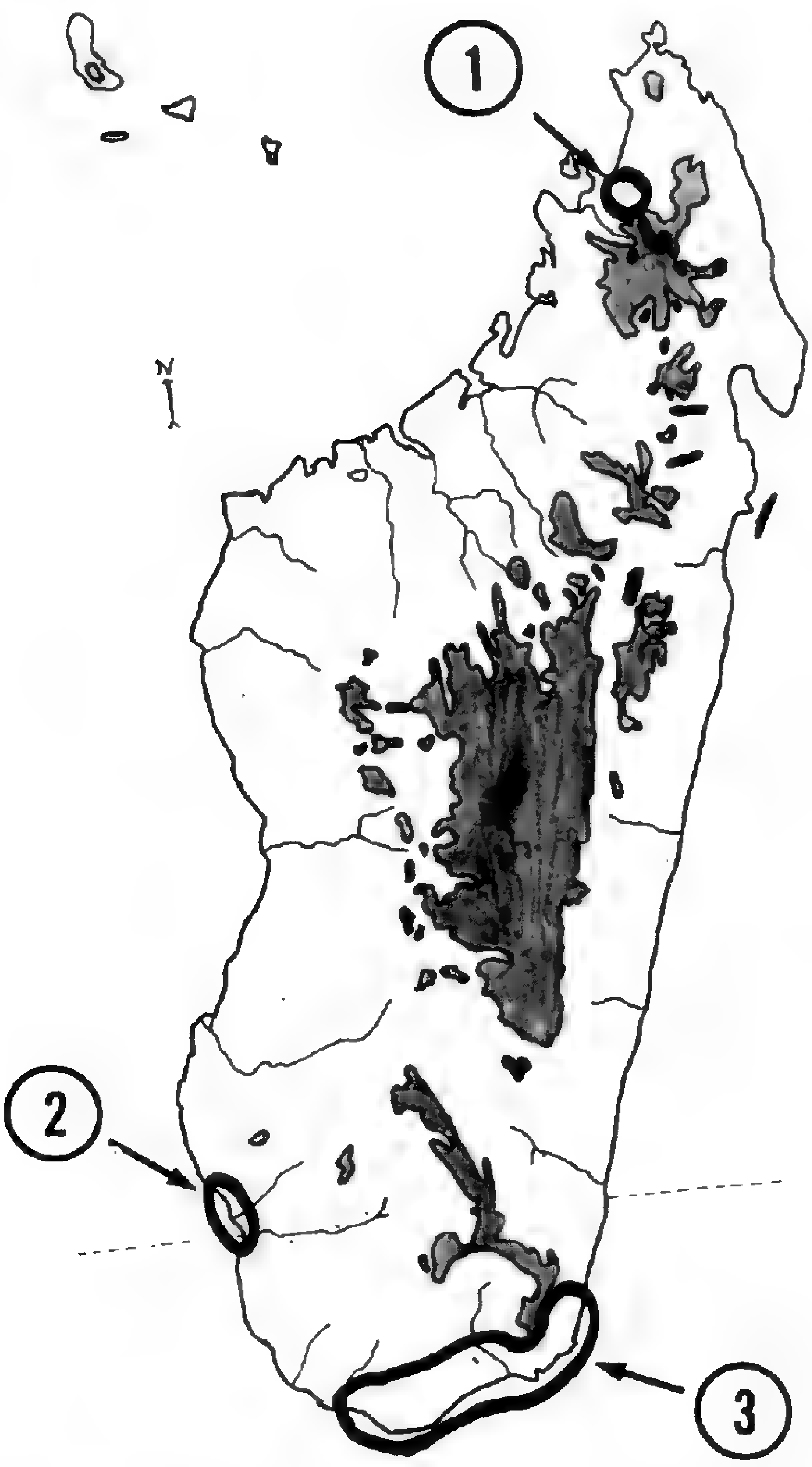

FIGURE 7. Distribution of three *Solanum* species that are isolated taxonomically. 1. *Solanum mahoriense* D'Arcy & Rakotozafy. 2. *Solanum tolearaea* D'Arcy & Rakotozafy. 3. *Solanum pyracanthos* Jacq. Elevations above 2,700–3,000 m are darkened. Data from collections at P and MO.

One extreme in development of this group on Madagascar is an unnamed, small-leaved species from the south that forms bramblelike thickets in the south of the island. Similar-appearing herbarium specimens with slightly larger leaves from eastern Africa, the Arabian Peninsula, Sri Lanka, tropical Asia, Australia, and the Antilles are usually determined as different species, e.g., *S. procumbens* Lour., *S. trilobatum* L. If these are not a result of recent dispersals, there has been convergence on this gross morphology in diverse regions.

Section *Andromonoecum* on Madagascar includes both native species and the two introduced species, *S. incanum* and *S. melongena*. The group is characterized by having andromonoecious sexual expression, felty leaves, calyces slightly accrescent in flower and just after (not in fruit), and mostly yellow fruits with seeds that can germinate after lengthy flotation in sea water (D'Arcy & Pickett, 1991).

TABLE 3. Postulated affinities of *Solanum* groups of Madagascar.

Subgenus *Solanum*	
Section *Afrosolanum*	High African mountains
Section *Lemurisolanum*	Endemic—relictual climbers
Section *Macronesiotes*	Endemic—South America
Subgenus *Leptostemonum*	
Section *Croatianum*	*Solanum sturtianum*, Australia
Section Oliganthes	Widespread, Africa, Tropical Asia
Series *Afroindica*	Widespread, Africa, Tropical Asia
Series *Eoafra*	Eastern Africa and eastern Asia
Section *Andromonoecum*	Widespread, Old World
Series *Pyracanthum*	Madagascar, reentered Africa?
Isolated species	
Solanum mahoriense	*Solanum sisymbriifolium*? South America
Solanum tolearaea	Australian groups?

Andromonoecy in *Solanum* subg. *Leptostemonum* was discussed by Whalen (1984) and Whalen & Costich (1986), who considered plants with this character to be a monophyletic group. In these plants, usually the first flowers in an inflorescence are perfect, while others are staminate. The perfect, or pistillate, flowers tend to have spinier calyces, while the staminate flowers have reduced gynoecia, the styles often not exceeding the filaments. Andromonoecy is sometimes difficult to determine from herbarium material. On Madagascar, it occurs in section *Andromonoecum* and also in all three species of section *Croatianum*.

Solanum pyracanthos Jacq. and *S. richardii* Lam., formerly considered to be isolates and placed in different sections, may actually have a closer relationship. Greenhouse plants of these species were both found to be andromonoecious. A cross (two successful tries) of *S. richardii* pollen onto the stigma of an emasculated flower of *S. pyracanthos* produced a fruit that contained a few developed but sterile seeds. Further testing is needed for verification of the cross. Juvenile leaves of the two species are similar, but mature plants and especially the fruits are quite different. In the golf-ball-sized fruits of *S. richardii* the mesocarp is

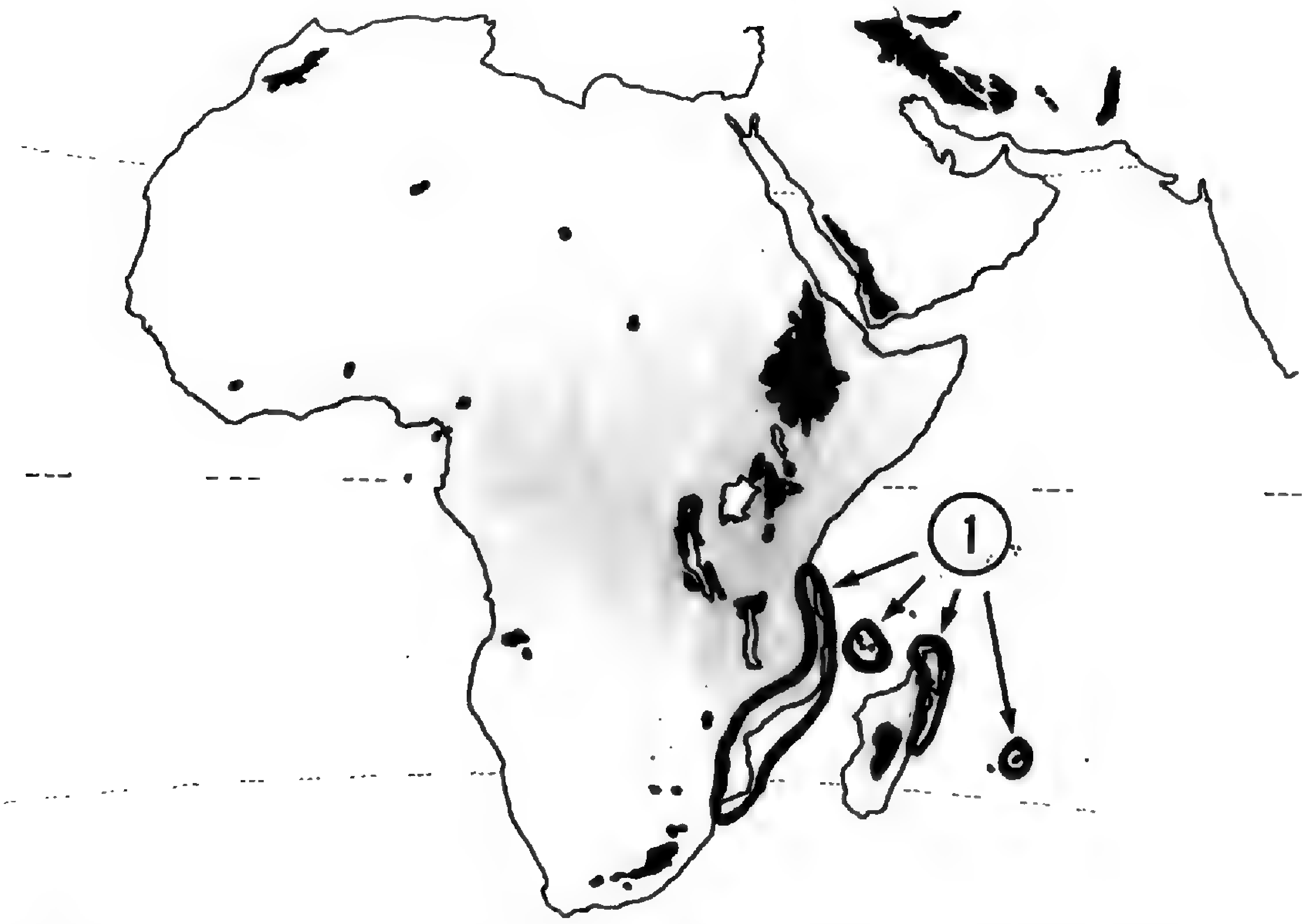

FIGURE 8. Distribution of *Solanum richardii* Dunal (at 1). Elevations above 2,700–3,000 m are darkened. Data from Bitter (1923) and from collections at MO.

thick, spongy, and white, typical of section *Andromonoecum*, and the exocarp is bright orange and opaque. Fruits of *S. pyracanthos* are grape-sized, the mesocarp is thick, hard, and juicy, and the exocarp is green or pale yellow and translucent.

Solanum pyracanthos, which has been grown as an ornamental in European gardens, is endemic to southeastern Madagascar (Fig. 7). *Solanum richardii* occurs in northern coastal Madagascar and the Comoros and has been reported from the island of Mauritius and from coastal Africa (Fig. 8). The ability of seeds to germinate after more than a month in the sea (D'Arcy & Pickett, 1991) may account for this distribution. Because all recent workers have considered these to be isolated species, and no similar plants have been noted by workers studying African relatives (Richard Lester, pers. comm.), they are perhaps an autochthonous group on Madagascar that has dispersed by sea to eastern Africa.

In addition to the groups discussed above, two isolated species are noteworthy in having quite narrow ranges, berries enclosed by accrescent, spiny, bladdery calyces, and andromonoecious sexual expression, but few other similarities. The fruiting calyces are quite different in size but are otherwise alike. *Solanum mahoriense* D'Arcy & Rakotozafy (Fig. 7) occurs in the tropical north of the island, a low sprawling shrub with dissected leaves, purple flowers, and sticky green berries. Some of these features are shared with *S. sisymbriifolium* Lam. of Argentina, which, however, is herbaceous and has white flowers and red fruits. *Solanum toliaraea* D'Arcy & Rakotozafy (Fig. 7) occurs in the temperate southwest of the island and is a small, erect tree. Its relatives are unknown within subgenus *Leptostemonum*.

RELATIONSHIPS OF SOLANACEAE OF MADAGASCAR

The Solanace on Madagascar display interesting features suggestive of both recent and ancient relationships. *Tsoala tubiflora* Bosser & D'Arcy appears to be related to South American genera, suggesting a southern or Gondwanan history for tribe Cestreae, which would reflect an ancient, probably pre-Tertiary distribution.

Postulated affinities of the *Solanum* taxa found on Madagascar are indicated in Table 3. Section *Afrosolanum* clearly relates to the African continent where there is a diverse array of relatives and plants with similar morphology (sects. *Quadrangulare* and *Lyciosolanum*). Its sole record on the Comoro Islands does not suggest antiquity in the flora area. Section *Lemurisolanum*, which displays unusual features, both primitive and advanced, may have evolved from stocks that are represented today by similar, relict groups in temperate Asia and South America. Differing mainly in its elongated calyces, section *Macronesiotes* may have originated from ancestors similar to those of section *Lemurisolanum*.

Section *Croatianum* appears to have its closest relative in Australia, and because of the differentiation in the group on Madagascar, its presence there may be quite old. Species of series *Eoafra* are much like those on adjacent African land areas, and they may have come from Africa more recently, but long enough ago to have evolved a number of distinctive elements. It likely that ancestral stocks arrived more than once, and it is also possible that taxa differentiated on Madagascar migrated back to Africa, although this cannot be determined from present information.

The Mozambique Channel has been a limit for most groups and for most species in the Solanaceae until the arrival of humans. Only one clearly indigenous species, *S. richardii*, which has sea-dispersal capability, is known to straddle this water barrier, occurring in Africa and also the Mascarene Islands.

Those groups that appear to share affinities with Africa and Madagascar, both spiny and spineless, have anthers with small pores. African species with longitudinally dehiscent, relatively open anthers are not found among the *Solanum* groups native to Madagascar. Nonpollinating pollen feeders may prevent colonization by these species on Madagascar. To counter this speculation, three New World species are naturalized and abundant on parts or all of Madagascar. *Solanum mauritianum* has large pores and tardily appearing longitudinal slits, and *S. torvum* and *S. americanum* have small (in absolute size) pores and longtitudinal slits. These species occur mainly in disturbed sites and might not be subject to elimination by pollen predators that are perhaps restricted to natural areas. However, this explanation seems unlikely.

Thus, the Solanaceae of Madagascar display a variety of patterns that may be postulated as both primitive and advanced, and the different stocks may have arrived in Madagascar at different times and from different places. The history of their geography and evolution in relation to their closest relatives is conjectural but must be viewed in light of the observations outlined above.

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FLORAL ATTRACTION AND FLORAL HAIRS IN THE COMMELINACEAE[1]

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ABSTRACT

Commelinaceae flowers are visited mainly by a great variety of bees and syrphid flies. A buzz mechanism associated with poricidal anthers is the most specialized pollination system reported. From a distance, inflorescences and associated structures may attract pollinators visually. At close range, the corolla is almost always showy, and sometimes the calyx is also conspicuous. The androecium is attractive because it produces pollen, the only reward supplied by the flower. Yellow, nearly pollenless anthers, antherodes, hairs, and broad connectives may deceptively attract insects. Floral odors may also attract pollinators. They are taxonomically widespread but uncommon in the family. None have been investigated chemically and a role in pollination has not been demonstrated. Floral hairs related to pollination are largely confined to the androecium and occur widely in the family. Their function may include attracting insects to the flowers (either toward or away from the main source of pollen), providing footholds, retaining fallen pollen, and determining how insects behave on the flower, including how they collect pollen.

The Commelinaceae are a family of herbaceous monocots consisting of 40 genera and approximately 640 species (Faden & Hunt, 1991). The two outstanding features of Commelinaceae flowers that affect their reproductive biology are the lack of nectar and brief flowering times (generally a few hours, always less than a day). The lack of nectar has two important consequences: (1) the flowers rarely attract whole classes of pollinators, notably butterflies, moths, birds, and bats; and (2) the pollen must serve two functions, pollination and rewarding the pollinator. The short anthesis limits certain reproductive strategies, such as the temporal separation or sequential development of the male and female sexual organs or functions in the flower.

The purpose of this paper is to present and discuss two aspects of floral biology within the Commelinaceae: how plants attract pollinators, both visually and with floral scents, and the possible reproductive functions of floral hairs. The literature on floral biology in the family is limited, so much of what will be presented is anecdotal or inferential. It is hoped that bringing together what is known will stimulate further research on pollination and floral biology in Commelinaceae.

POLLINATION OF COMMELINACEAE

Commelinaceae flowers are chiefly entomophilous or autogamous. The main insect visitors are social and solitary bees and syrphid flies. Additional insects that I have recorded on Commelinaceae flowers include other Diptera, various families of Coleoptera, Hemiptera, Homoptera, Orthoptera, Thysanoptera, and occasional ants (Hymenoptera: Formicidae) (Faden, unpublished). Rare butterfly visits have been recorded (Knuth, 1909: 476; Schuster & Schuster, 1971), although I have never observed any. In addition to bees and syrphid flies, potential pollinators include bee flies (Bombyliidae) and some beetles (Melyridae, Buprestidae, Mordellidae, and possibly other families).

The flowers of Commelinaceae species that have been studied in some detail are recorded as being visited by a variety of insects. At the low end is *Tinantia anomala* (Torrey) C. B. Clarke, from which only four bee species plus unidentified syrphid flies were noted (Simpson et al., 1986). At the other extreme are *Tripogandra serrulata* (Vahl) Handlos, on which no fewer than 14 species of bees, six of syrphid flies, and six of other insect

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orders were recorded (Schuster & Schuster, 1971), and *Commelina erecta* L., from the flowers of which 42 species of insects were collected, including nine species of bees and four of syrphid fly (Faden, unpublished). Even some mainly autogamous species may be visited by numerous insects, e.g., annual species of *Tripogandra* (Handlos, 1970). My field research on *Commelina erecta* in Texas (Faden, unpublished) and on numerous African *Aneilema* species (Faden, 1991 and unpublished) suggested that for many Commelinaceae, the longer that a species is observed, the greater the diversity of insects that will be found visiting its flowers.

The only specialized pollination system to have been documented in the family is a buzz mechanism, which has been reported in two unnamed species of *Dichorisandra* (Sigrist & Sazima, 1991). Such a mechanism had been predicted for *Cochliostema* (Vogel, 1978), and it is also likely to be found in species of the several genera, e.g., *Porandra*, that have apical poricidal anther dehiscence. The unusual floral odor in *Palisota hirsuta* (Thunb.) Schumann suggests an unusual pollinator (see below), but there are insufficient field observations.

The behavior of insects on the flowers has been described for several Commelinaceae, e.g., *Tinantia anomala* (Simpson et al., 1986) and *Tripogandra serrulata* (Schuster & Schuster, 1971), but behavioral descriptions generally have not indicated the probable effectiveness of the insect as a pollinator. *Callisia repens* L. is the only—or certainly one of the very few—Commelinaceae that is probably anemophilous.

Commelinaceae for which there are recent data about flower visitors and pollination are: *Aneilema* species (Faden, 1983, 1991, and unpublished), *Commelina erecta* L. (McCollum et al., 1984; Faden, unpublished), *Commelina tuberosa* L. (as *C. communis*) (Brantjes, 1980), *Dichorisandra* species (Sigrist & Sazima, 1991), *Tinantia anomala* (Torrey) C. B. Clarke (Castro, 1978 (as *Commelinantia anomala*); Simpson et al., 1986), *Tradescantia* species (Sinclair, 1967, 1968), *Tripogandra serrulata* (Vahl) Handlos (as *T. cumanensis*) (Schuster & Schuster, 1971), and *Tripogandra* species (Handlos, 1970).

VISUAL ATTRACTION OF POLLINATORS

Commelinaceae attract pollinators mainly visually. Their flowers are usually brightly colored. Commonly, however, the flowers are quite small, and, in such cases, it may be the inflorescences and/or associated structures that attract pollinators, especially from a distance. The most extreme example of this occurs in *Coleotrype madagascarica* C. B. Clarke of Madagascar, in which the upper leaves on the flowering shoot are bright pink basally, with similarly colored sheaths, matching the color of the corollas of the flowers that are borne in sessile, sheath-perforating inflorescences at the bases of these leaves. In *Spatholirion longifolium* (Gagnepain) Dunn the inflorescence axis and cincinni are bright purple and would seem to be much more conspicuous from afar than the tiny flowers. Even in *Cochliostema*, which has among the largest flowers in the Commelinaceae, the long, pink bracts (on the peduncle and at the bases of the cincinni) and pink peduncle and axes may enhance the conspicuousness of the flowers.

Inflorescences may be more striking than the individual flowers when the calyces are colored and accrescent, as in species of *Amischotolype* (e.g., *A. philippensis* (Merrill) ined.) and some populations of *Tinantia leiocalyx* C. B. Clarke. In *Floscopa*, the faded flowers, which typically have colored, long-haired sepals, persist even when they fail to set fruit. In that genus, as well as others with small-flowered species, e.g., *Aneilema*, *Callisia*, *Palisota* and *Tripogandra*, the dense inflorescences with numerous flowers create a visual impact that the same-sized flowers more loosely arrayed would fail to impart.

At close range the individual flowers and their parts are conspicuous. With the exception of a few species of *Callisia*, e.g., *C. repens*, the petals are always obvious, even when small, ranging from white through various shades of pink, blue or violet or, rarely, yellow to orange. In zygomorphic flowers one petal may be reduced and inconspicuous, as in species of *Aneilema* and *Commelina*. All three petals have strikingly fringed margins in *Cochliostema*, *Geogenanthus*, and a related, undescribed, neotropical genus.

The sepals are most commonly green and inconspicuous, but sometimes they are tinged or suffused with red or purple, e.g., species of *Aneilema* and *Tradescantia*; colorfully streaked or striped, e.g., *Aneilema hockii* De Wild.; entirely brightly colored and contrasting with the corolla, e.g., species of *Amischotolype*; or similar in size and color to the petals (petaloid), e.g., *Palisota* and *Streptolirion*. Colored, accrescent and persistent sepals have been mentioned above. In any of these cases the sepals would be expected to play a role in attracting pollinators.

The androecium attracts insects because it produces pollen, the only reward supplied by the flower. The common differentiation of the androecium into two morphologically distinct sets of stamens, or stamens and staminodes, reflects the duality of function: attracting insects yet limiting the amount of pollen they collect. The parts of the androecium that specifically may attract potential pollen vectors are anthers, connectives, filament hairs, pollen, and anther- or pollenlike structures (staminodes, hairs, and connectives).

As the source of pollen, the anthers should be the focus of an insect's attention. This should be true whether the pollen is exposed, as in most genera; is enclosed within apically poricidal anthers (species of *Cartonema, Amischotolype, Coleotrype, Dichorisandra,* and *Porandra*); or is more elaborately sequestered, as in *Cochliostema.* Structures that resemble pollen or create the impression of more pollen than is actually present may also attract (or distract) insects, particularly when the true anthers are less conspicuously colored, e.g., concolorous with the petals (Vogel, 1978; Brantjes, 1980). Thus, yellow antherodes or nearly pollenless anthers, e.g., *Aneilema, Murdannia* and *Commelina,* yellow-bearded stamen filaments, e.g., *Tinantia, Geogenanthus,* and *Cochliostema,* and broad, yellow anther connectives, e.g., *Tradescantia,* may deceptively attract pollinators (Vogel, 1978).

Filament hairs (discussed below) and connectives may also be attractive to insects, aside from mimicking pollen. In *Callisia fragrans* (Lindley) Woodson, the corolla is inconspicuous, but the anther connectives are broad and white and resemble six tiny flags in each flower, probably providing the visual attraction generally furnished by the corolla in other Commelinaceae. In some *Aneilema* species, e.g., *A. rendlei* C. B. Clarke, bees visiting the flowers generally first alight on the greatly expanded, colorful connective of the middle stamen (Faden, 1991, and unpublished). Similarly, in many species of *Commelina,* e.g., *C. hockii* De Wild. and *C. forskaolii* Vahl, the medial stamen anther is more striking than the laterals because of contrasting markings on its broad connective (Faden, unpublished).

Ultra violet (UV) light absorption and reflectance have been little investigated in the Commelinaceae. Handlos (1970: 62) reported the flowers of *Cochliostema odoratissimum* Lemaire and *Tradescantia pallida* (Rose) D. H. Hunt (as *Setcreasea pallida*) to reflect UV light. Simpson et al. (1986) showed that the upper anthers and surrounding hairs in *Tinantia anomala* absorb UV light, in contrast with the UV-reflecting petals behind them.

FLORAL ODORS

Floral odors as attractants of pollinators have not been discussed previously for the Commelinaceae as a whole. They are taxonomically widespread but uncommon in the family. Strong odors have been reported in *Callisia fragrans* (as *Spironema fragrans*) (Lindley, 1840), *Cochliostema odoratissimum* (Lemaire, 1859), *Tradescantia subacaulis* Bush and *T. roseolens* Small (Anderson & Woodson, 1935), and *Tripogandra grandiflora* (Donnell-Smith) Woodson (Handlos, 1970). The strongest odors that I have noted were in *Callisia fragrans* (cultivated plant of unknown provenance), *Callisia multiflora* (Martens & Galeotti) Standley (cultivated plant originally from Mexico), *Cochliostema odoratissimum* (cultivated plant originally from Ecuador), *Palisota alopecurus* Pellegrin (population in Cameroon), *P. bracteosa* C. B. Clarke (cultivated plants of unknown provenance), and *P. hirsuta* (cultivated plants originally from Ghana and Nigeria, and one plant in Cameroon). The reported fragrance by Read (1965) in *Cochliostema velutinum* Read was not characterized as strong or weak, but it is likely to have been relatively strong because the original collector had noted it.

Weak floral scents are more common than strong ones, but they too seem to be infrequent in the family. Handlos (1970) reported very faint scents in *Tripogandra amplexicaulis* (C. B. Clarke) Woodson, *T. purpurascens* (Schauer) Handlos, and *T. saxicola* (Greenman) Woodson, all from Mexico. I have recorded weak odors in populations of the eastern North American *Tradescantia ernestiana* Anderson & Woodson (in Arkansas), *T. gigantea* Rose (Louisiana), *T. hirsuticaulis* Small (Arkansas), *T. hirsutiflora* Bush (Arkansas), and *T. ozarkana* Anderson & Woodson (Arkansas); eight (all African) out of approximately 33 species of *Aneilema* (the others were odorless) (Faden, 1991); *Tinantia erecta* (Jacq.) Schldl. in Mexico (also cultivated plants from Bolivia); and greenhouse-cultivated plants of *Commelina stefaniniana* Chiov. (from Somalia), *Dichorisandra thyrsiflora* Mikan (from a plant originally cultivated in Peru), *Palisota barteri* Hook. (from Ghana), and *Stanfieldiella brachycarpa* (Mildbr.) Brenan (from Gabon). Peace Corps volunteer Bruce Kahn (in litt.) recently reported a slight scent in the flowers of a Cameroonian population of *Pollia condensata* C. B. Clarke, the only record of a floral odor in this genus.

Interspecific variation in floral odor production or strength has been noted in several species. In *Aneilema johnstonii* Schumann some populations were recorded as having weakly fragrant flowers and other populations as odorless (Faden, 1991). Among research plants of *Tinantia erecta* from many populations cultivated in 1988 at the Botanic Garden of the University of Copenhagen I noted some with slight fragrances and others with no odor. Some individual plants in a population of *Tradescantia hirsutiflora* had scented flowers and other plants unscented ones (Faden, unpublished). I consider *Palisota hirsuta* flowers to be strongly scented, but Peace Corps volunteer Bill Keating records (in sched.) only a "slight smell" in a Cameroonian population. This reported difference is, I suspect, a matter of judgment or definition of "strong" and "weak" odors. However, it could also be due to genetic variation among populations, differences in the observer's perception (olfactory sensitivity), the number and density of open flowers in the area, the temperature (higher temperature causing greater volatility and stronger scent), and the conditions under which the flowers are smelled (e.g., in the field vs. a closed greenhouse).

No floral scent in the Commelinaceae has been investigated chemically. Nearly all odors have been characterized merely as "pleasant" or "fragrant," but flowers of *Tradescantia subacaulis* have been described more precisely as violet-scented, and those of *T. roseolens* as having the fragrance of tea-roses (Anderson & Woodson, 1935). I have recorded the weaker odor of *T. hirsuticaulis* as violet-scented and those of *T. ernestiana, T. gigantea,* and *T. ozarkana* as rose-scented. The odor in *Pollia condensata,* mentioned above, was recorded as lemon-scented. The only convincingly recorded nonfragrant scented flowers occur in *Palisota hirsuta.* They are mushroom-scented.

The source of the odor within the flower has been little investigated. When several flowers of *Aneilema somaliense* C. B. Clarke were dissected into sepals, petals, staminodes, stamens, and gynoecium, the staminodes seemed to be at least one source of the scent, but the results were inconclusive (Faden, 1991: 26). In *Palisota hirsuta* the copious but sterile pollen of the upper two stamens is the chief or sole source of the mushroom scent (Faden, unpublished). In *Cochliostema odoratissimum* the fragrance is produced by the petals (Faden, unpublished).

FLORAL HAIRS

Hairs may occur on all floral parts. Their functions probably include defense against insect feeding, protection from desiccation, and pollination. Only their role in pollination will be discussed here. Pollination-related hairs may be present on all floral whorls, but they occur mainly on the androecium. The only sepaline hairs showy enough possibly to be involved in pollination are found in *Floscopa.* The fringing, petaline hairs in *Cochliostema, Geogenanthus,* and a related, undescribed genus may contribute to the attractiveness of these flowers. Gynoecial hairs are usually confined to the ovary and are probably protective, but some species of *Cyanotis* have bearded styles, with colorful, moniliform hairs similar to those of the stamen filaments in the same flowers. Very likely they have the same functions as the staminal hairs (discussed below).

Although absent in many genera, such as *Commelina,* androecial hairs are common in the Commelinaceae (Table 1), and their function is probably related to pollination in nearly all cases. They may function in several ways, including attracting insects to the flower and either to or away from the main source of pollen. They may affect how and where insects move within the flower and how they collect pollen. Finally, the presence or absence of staminal hairs may determine, in part, the kinds of insects that visit a flower.

Hairs may be present and similar on all filaments, as in most actinomorphic flowers, e.g., *Tradescantia* and *Cyanotis.* In many zygomorphic flowers, however, they occur only on specific filaments, e.g., the two lateral stamens in *Aneilema* or the three upper stamens in *Geogenanthus.* In *Tinantia* flowers the filament hairs vary in length, color, abundance, and position on the filament among the five bearded filaments (the sixth is glabrous). In genera having the antesepalous androecial whorl differentiated from the antepetalous whorl, e.g., *Murdannia, Palisota,* and *Tripogandra,* the differences commonly include filament pubescence (Table 1).

Filament hairs differ in structure and conspicuousness. They are most commonly moniliform, i.e., composed of beadlike cells, but in *Aneilema* they are never moniliform (Faden, 1991), and in *Tripogandra* the hairs may be moniliform or not, depending on the species (Handlos, 1970, 1975). Some unusual filament hair types, e.g., glandular hairs, hook-hairs, and branched hairs, are apparently confined to *Aneilema* and are described by Faden (1991). The hairs may be minute (< 0.5 mm) and inconspicuous (e.g., all species of *Aneilema* sect. *Brevibarbata*), but usually they are long and evident.

TABLE 1. Filament hairs in the Commelinaceae (generic circumscription and arrangement follow Faden & Hunt, 1991).

All filaments bearded		All filaments glabrous		Some filaments bearded, some glabrous
Triceratellateae		Cartonemateae		
Triceratella		*Cartonema*		
Tradescantieae		Tradescantieae		Tradescantieae
Streptolirion	*Thyrsanthemum*	*Coleotrype*[1]		*Palisota*
Spatholirion	*Gibasoides*	*Dichorisandra*		*Aethiolirion*[2]
Aethiolirion[3]	*Matudanthus*	*Siderasis*		*Geogenanthus*[4]
Cyanotis	*Elasis*	*Geogenanthus*[5]		*Tinantia*
Belosynapsis	*Gibasis*	*Weldenia*		*Tripogandra*
Coleotrype	*Tradescantia*	*Tradescantia*[6]		
Porandra	*Callisia*	*Callisia*		
Amischotolype	*Tripogandra*[7]			
Cochliostema[8]	*Sauvallea*			
Commelineae		Commelineae		Commelineae
Murdannia		*Stanfieldiella*	*Polyspatha*	*Murdannia*
		Floscopa	*Dictyospermum*	*Aneilema*
		Buforrestia	*Pollia*	*Tricarpelema*[9]
		Murdannia	*Aneilema*	
		Anthericopsis	*Rhopalephora*	
		Tricarpelema	*Commelina*	
		Pseudoparis		

[1] *Coleotrype lutea* H. Perrier only.
[2] Staminate flowers only.
[3] Perfect flowers only.
[4] Rarely all filaments bearded.
[5] *Geogenanthus ciliatus* Brueckner only.
[6] Few species only.
[7] Occasionally both sets of stamens bearded.
[8] A small glabrous staminode sometimes present.
[9] *Tricarpelema glanduliferum* (Joseph & R. Rao) Faden only.

When staminal hairs contribute to the general showiness of the flower, some role in attracting pollinators may be inferred. This is particularly likely where the filaments are densely bearded with long, colored hairs that extend well beyond the corolla, e.g., *Aneilema* sect. *Pedunculosa*, *Cyanotis* and *Tradescantia*, and where the hairs contrast in color with the petals, e.g., some species of *Cyanotis* and *Aneilema*. In species of *Cyanotis*, *Tradescantia*, and *Tripogandra* the pink to blue or violet (sometimes partly white) hairs often closely surround the yellow anthers, seemingly drawing attention to them. In *Streptolirion volubile* Edgew. and *Aneilema chrysopogon* Brenan the hairs below the anthers are yellow, which may draw attention to the anthers either because of the color contrast with the corollas, or because there may appear to be more pollen present than the flowers actually provide.

Vogel (1978) cited *Tinantia* and *Cochliostema* as genera in which yellow hairs mimic pollen and deceptively draw pollinators to them. To this list can be added *Geogenanthus*. In *Tinantia* the upper three stamens have small anthers surrounded by yellow hairs. Vogel terms them "advertising stamens." The lower stamens, with longer filaments, have larger, more polliniferous anthers that are more cryptically colored. Bees should focus on the upper anthers and brush against the lower ones and the style. The pattern in *Geogenanthus rhizanthus* (Ule) Brueckner, as determined from herbarium specimens, appears to be similar to *Tinantia*, except that the upper filaments are more densely bearded and there is less of a size difference between the upper and lower anthers.

The only yellow color in *Cochliostema* flowers is a tuft of hairs on the upper surface of the central, columnlike structure that is composed of the upper three stamens whose greatly expanded connectives completely enclose their anthers. Vogel (1978) suggested that insects trying to collect pollen from the yellow hairs probably cause pollen to be shed from the anthers by vibration.

Simpson et al. (1986) have made the only detailed study in Commelinaceae that tests Vogel's deception hypothesis. Working with *Tinantia anomala* in Texas, they found that the upper stamens are more obvious to insects than to humans and the lower stamens less so, owing to differences in UV absorption/reflectance in different parts of the flower. They discovered that the upper stamens produced about half as much pollen as the lower, that pollen grains from the upper anthers were about 8% shorter than the lower anther pollen, and that pollen from both sets of anthers was equally fertile.

The main visitors to the flowers were syrphid flies and bees. Syrphid flies focused on the upper anthers but did not contact the stigma. Large native bees, such as *Bombus pennsylvanicus,* landed on the upper stamens and contacted the stigma with their abdomen, but their visits were infrequent. Smaller bees were more common, and *Agapostemon texanus* visited both sets of stamens, but the authors do not consider these bees significant pollinators. The most abundant visitor was the introduced honeybee, *Apis mellifera,* which, unlike the native bees, first foraged on the lower anthers, then the upper, while regularly contacting the stigma.

Simpson et al. (1986) concluded that *Tinantia anomala* does not support Vogel's hypothesis because few native insects of the proper size to effect pollination behave in the predicted manner, and because the upper anther pollen is fertile and the plant autogamous. However, Simpson et al. do confirm that native insects focus on the upper stamens, as predicted, and that at least the larger native bees are effective pollinators. Because *T. anomala* is autogamous, it requires out-crossing only to maintain genetic diversity, not for seed production. Therefore, although there seems to be a great waste of pollen in this species, it is still possible that native bees provide the necessary level of out-crossing.

There is little direct evidence that filament hairs affect how insects "work" flowers. In species of *Aneilema* sect. *Brevibarbata* the stamen filament hairs are inconspicuous because they are minute (sometimes < 0.5 mm long), usually colorless, and are attached on the lower surface of the sigmoid lateral stamen filaments (Faden, 1991). In flowers of *A. umbrosum* (Vahl) Kunth subsp. *umbrosum* in Ghana I observed small bees (probably *Lasioglossum* sp., Halictidae) hanging upside down from the bearded portion of the stamen filament, head facing the base of the flower, while the rear legs collected pollen from the anther (Faden, unpublished). Thus, these tiny hairs may serve as footholds for insects.

Staminal hairs may serve to retain pollen that falls or is dislodged from the anthers, maintaining it in a position where it is both accessible to insects for collection and can also contact them ventrally (Renner, pers. comm.). In *Cyanotis* the staminal hairs would appear to be essential because anther dehiscence is functionally by basal pores. The pollen is squeezed out into the tangle of filament and (when present) stylar hairs and could otherwise be lost but for them.

The hairs of the densely bearded filaments in species of *Tradescantia* and *Cyanotis* may function further by interfering with pollen collection. Medium- to large-sized bees have been observed sometimes to draw together the anthers of a flower before collecting pollen (honeybees on *Aneilema johnstonii* in Zambia; *Amegilla* sp. (Anthophoridae) on *Aneilema hockii* in Kenya; Faden, unpublished), which might increase the efficiency of pollen collection (over sequential collection from individual anthers). These Commelinaceae have glabrous, divergent stamen filaments. The density of the filament hairs and their proximity to the anthers in *Tradescantia* and *Cyanotis* flowers may interfere both with the anthers being pulled together and with pollen being scraped or combed off them. The bearded style in many *Cyanotis* species may further keep the stamens apart. Pollen caught in the dense staminal (or stylar) hairs could not be collected rapidly. Thus, while the filament hairs in *Tradescantia, Cyanotis,* and probably other genera, may attract pollinators by being colorful and contrasting with the anthers, they may also reduce the efficiency of pollen collection by closely surrounding the anthers. Sinclair (1967, 1968) mentioned (and I can confirm from garden observations) that honeybees visiting *Tradescantia* flowers often pull all of the anthers together and then collect pollen from them. Whether native bees also do this is unknown.

The presence or absence of staminal hairs may relate to the types of pollinators that visit flowers. Because hairs provide more surface area and more footholds, they may tend to favor insects that must land in order to feed, such as smaller bees and syrphid flies. Knuth (1906: 106) recorded the filament hairs in *Tradescantia* as providing support and footholds for insects, noting that such flowers were especially favored by bees. In *Aneilema* I have recorded more species of flies (mostly syrphid flies) than bees visiting the flowers of all three species of section *Pedunculosa*—characterized by long, colorful stamen filament hairs—from which flower visitors were collected. In contrast, all seven species of section *Lamprodithyros*—characterized by glabrous filaments—had more bee than fly species visiting their flowers. Within section *Amelina*, which may have either glabrous or bearded filaments, the two species sampled with glabrous filaments were visited by more bee species, and the one with long-bearded filaments by more diptera (Faden, 1991). The correlation between long-bearded filaments and fly visitation in *Aneilema* should be considered tentative because the data for most of the *Aneilema* species were derived from casual collecting, not long-term studies. In any event, the diversity of insects visiting the flowers of a species is less important than the number of individuals and the effectiveness of the insect species in bringing about pollination, and these were not recorded.

DISCUSSION

The selected topics discussed in this paper, how Commelinaceae flowers attract pollinators and how floral hairs may function in pollination, may serve as an introduction to the larger subject of reproductive biology in the family. Clearly, our knowledge even of the topics discussed is quite limited. With regard to other aspects of reproductive biology, even such basic information as daily flowering times is unknown for the majority of Commelinaceae. What are most needed are more long-term field observations and experimental investigations. Studies of pollination and reproductive biology require little or no technology, and therefore they are especially well suited for students or researchers at small institutions and in developing countries. It is hoped that this paper will stimulate biologists to look more closely at the reproductive biology of locally occurring species of this nearly cosmopolitan family.

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A SYNOPSIS OF BIGNONIACEAE ETHNOBOTANY AND ECONOMIC BOTANY[1]

A. H. Gentry[2]

ABSTRACT

Bignoniaceae include attractive ornamental flowering trees and lianas and produce hard and durable timbers, many pharmacologically active chemicals, various products used in local handicrafts, and even a few edible seeds and fruits. These uses are summarized here.

When I came to Washington University as a graduate student to work with Walter Lewis, I was aware that my specific interests in large woody tropical plants were rather different from his focus at that time on largely herbaceous and temperate taxa (e.g., Lewis 1962, 1976; Lewis & Oliver, 1961; Lewis & Semple, 1977). Worse, a major theme of Lewis's research has been change in chromosome number (e.g., Lewis, 1976, 1980; Lewis & Terrell, 1962), but nearly all Bignoniaceae have 40 chromosomes (Goldblatt & Gentry, 1979), making studies of chromosome number of minimal interest. As a graduate student, I was grateful that Walter Lewis gave me the freedom and support to go to the tropics and study Bignoniaceae, even though my proposed research impinged little on his own interests. Today I am delighted to report that we have come full circle: ethnobotany of the Bignoniaceae, one of the families that the Lewises (Lewis et al., 1987, 1988) have found to be the most significant in their studies of Jivaro ethnomedicine, is a most fitting contribution to a symposium dedicated to Walter.

Contrary to van Steenis (1978), who stated, "There are no outstanding qualities marking Bignoniaceae as useful plants," the Bignoniaceae do indeed have ethnobotanical significance. The utility of Bignoniaceae spans a broad gamut of human endeavor. Here I will summarize some of the uses of Bignoniaceae for horticulture, food, handicrafts, timber, dyes, rituals, and medicine.

HORTICULTURE AND ORNAMENTALS

This family is of paramount horticultural importance because of its often spectacular flowers. For example, Menninger (1960), widely known as "The Flowering Tree Man," has stated that *Tabebuia* contains "the most satisfactory flowering trees for parkway and yard planting in southern Florida." At least seven neotropical countries have chosen a species of Bignoniaceae as their national flower or tree (Table 1). *Jacaranda mimosifolia* D. Don is perhaps the world's most widely planted ornamental tropical tree (Gentry, 1984; Fig. 1). Perhaps its closest competition for such a designation is *Spathodea campanulata* Beauv., also a Bignoniaceae (e.g., Gentry, 1982; Fig. 1). In some eastern African and tropical Asian cities, *Millingtonia hortensis* L.f., with its fragrant hawkmoth-pollinated flowers, fills a similar role, at least locally. Menninger (1970) listed 34 different Bignoniaceae vine species of horticultural importance (second only to Leguminosae): *Podranea ricasoliana* (Tanfani) Sprague and *Pyrostegia venusta* (Ker Gawler) Miers are among the most attractive and widely cultivated of all tropical ornamental vines, while *Campsis radicans* enjoys a similar distinction in the temperate zone. Even the currently burgeoning artificial flower industry appreciates Bignoniaceae, with recognizable plastic versions of *Tecoma capensis* (Thunb.) Lindley and *Millingtonia hortensis*, currently available in the Bangkok market (Santisuk, pers. comm.).

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[1] Dedicated to Walter Lewis on the occasion of his 60th birthday with thanks for his role in helping me develop my career as a student of Bignoniaceae and of tropical forests in general. I thank the National Science Foundation for the series of grants (most recently BSR-8607113) that has supported my study of Bignoniaceae over the years during which the ethnobotanical data reported here were assembled. As a result, Bignoniaceae are now one of the few tropical forest families well enough known to make possible accurate identification of the often miserable, nearly always sterile, vouchers on which ethnobotanical studies are mostly based.

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ANN. MISSOURI BOT. GARD. 79: 53–64. 1992.

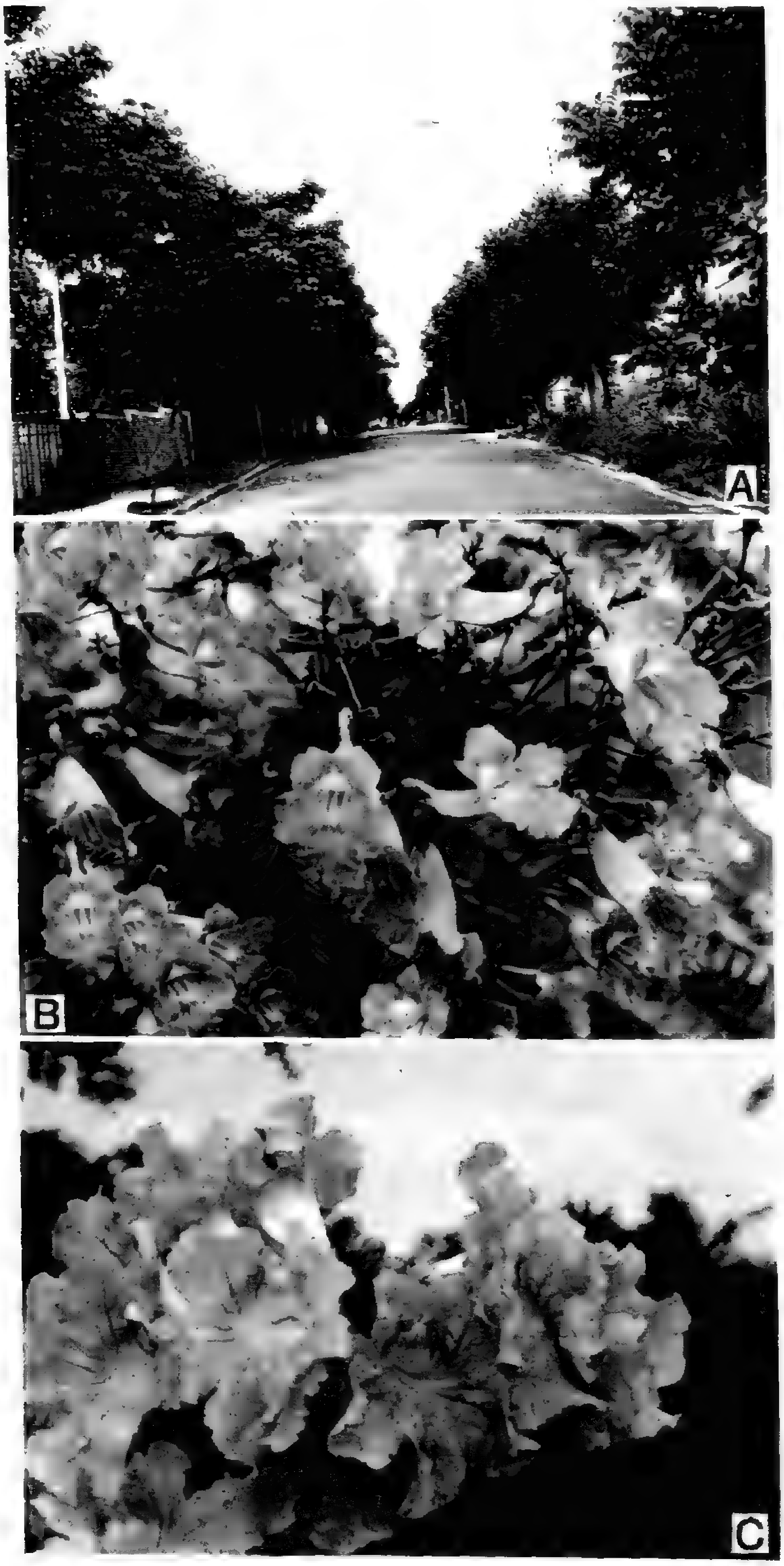

FIGURE 1. Bignoniaceae used in horticulture.—A. Street in Campinas, São Paulo, Brazil, lined entirely with *Spathodea campanulata.*—B. *Jacaranda mimosifolia,* perhaps the most widely cultivated flowering subtropical tree in the world.—C. *Tabebuia rosea,* national tree of El Salvador, widely cultivated throughout the world's tropics.

FOOD

Bignoniaceae also have more utilitarian attributes, although only a few species are used for food, and none are a major food crop. Nevertheless, *Parmentiera aculeata* (HBK) Seemann (Fig. 2) is a significant cultivated fruit tree in the Mayan region (Gentry, 1980). *Parmentiera stenocarpa* Dugand & L. B. Smith, endemic to the Colombian Chocó, produces an edible fruit that has been promoted as having commercial potential because of a flavor apt for desserts or fruit juices (Romero-Castañeda, 1985). In pre-Colombian Panama, the pulp of the tree calabash (*Crescentia cujete* L.) was eaten (Wafer, 1699). Today its seeds are used to make a refresco called "semilla de jícaro," which is locally popular in Nicaragua (Fig. 2), almost constituting a kind of national drink, although this use seems not to have spread to other countries. The waxy fruit of *Parmentiera cereifera* Seemann has occasionally been eaten in Panama (Gentry, 1980) and was formerly an important cattle food (Seemann, 1851). In Africa the ripe fruit of *Kigelia africana* (Lam.) Benth. is baked and added to beer, where it aids fermentation but may cause headaches (Lovett, 1990); its seeds are also roasted in time of famine. The garlic-smelling species of *Mansoa* and clove-smelling *Tynanthus* are frequently used as condiments.

HANDICRAFTS

More significant may be the use of Bignoniaceae fruits for various utensils and in local handicrafts. By far the most important such use is of the exocarp of *Crescentia cujete* (Fig. 2). As early as 13 October 1492, on the very day he discovered the New World, Columbus reported in his journal on the use of *Crescentia* exocarp to bail native canoes (Sauer, 1969). Even today, nearly every dugout canoe in out-of-the-way parts of the Neotropics carries its piece of *Crescentia* exocarp for use as

TABLE 1. Bignoniaceae national symbols (national tree or national flower).

Country	Species	Source
Argentina	*Jacaranda mimosifolia* D. Don	Fabris, 1965 (runner-up as national tree)
Bahamas	*Tecoma stans* (L.) Juss. ex HBK	
Brazil	*Tabebuia serratifolia* (Vahl) Nicholson	Gentry et al., 1984
Ecuador	*Tabebuia chrysantha* (Jacq.) Nicholson	
El Salvador	*Tabebuia rosea* (Bertol.) DC.	Menninger, 1949
Japan	*Paulownia tomentosa* (Scrophulariaceae?)	Asch, 1968
Paraguay	*Tabebuia heptaphylla* (Vell. Conc.) Toledo	Brunner, pers. comm.
Venezuela	*Tabebuia billbergii* (Bureau & Schumann) Standley	Steyermark, 1973
Virgin Islands	*Tecoma stans* (L.) Juss. ex Kunth	

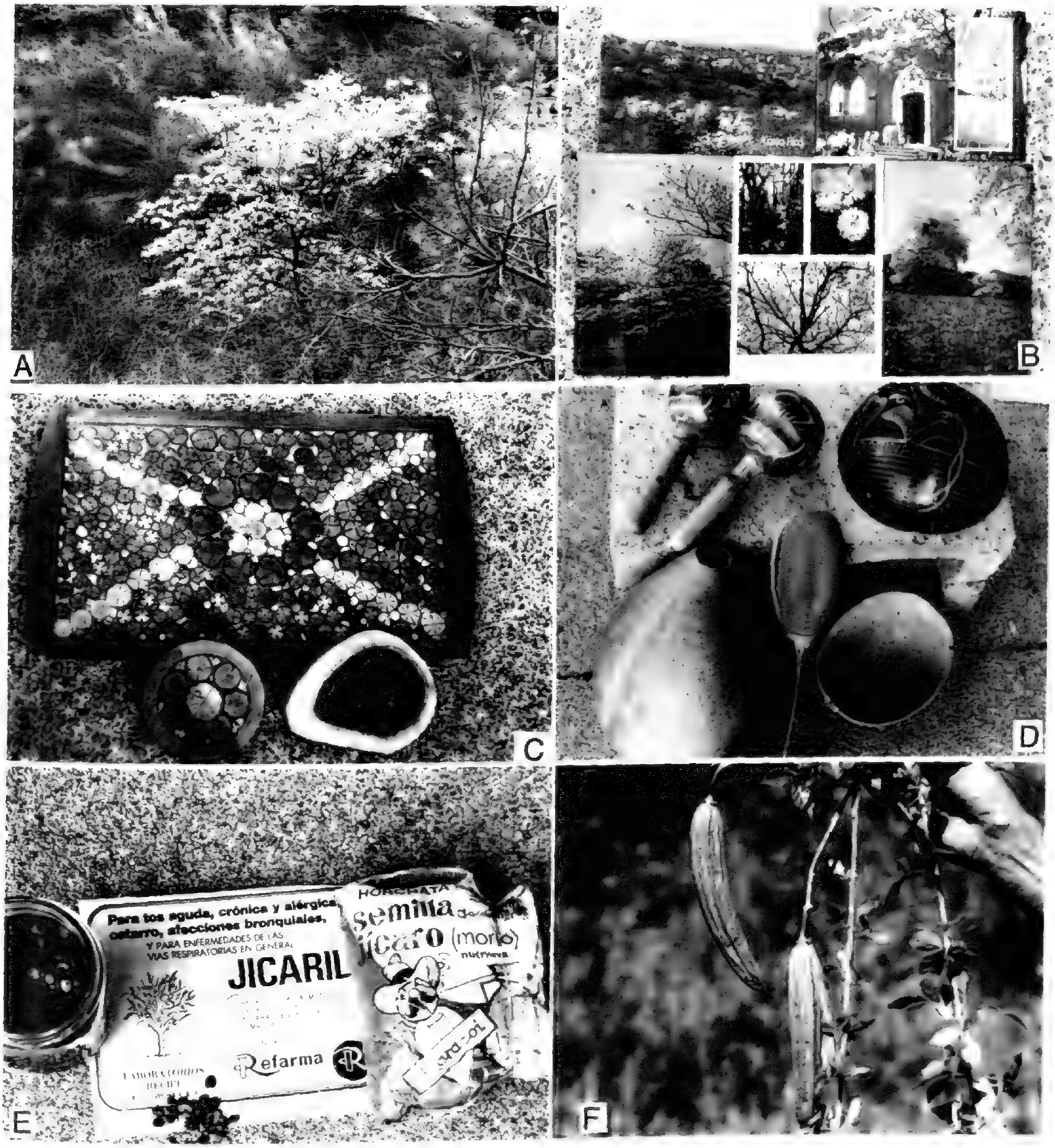

FIGURE 2. Miscellaneous uses of Bignoniaceae.—A. Mass-flowering tree of *Tabebuia ochracea.* B. Mass-flowering trees of *Tabebuia ochracea* subsp. *neochrysantha* as illustrated on Costa Rican postcards. C. Cross sections of Bignoniaceae lianas used in local handicrafts, São Paulo, Brazil.—D. Bignoniaceae fruits used as utensils and in local handicrafts. Upper left = *Crescentia alata* used for maraca rattles; upper right = *Crescentia cujete* decorated for wall-hanging; middle = *Pithecoctenium crucigerum* used as a kind of artificial flower in "floral" arrangements; bottom left and right = *Crescentia cujete* used as household containers. E. "Semilla de jícaro" (*C. cujete*), a favorite Nicaraguan refresco. Left, a container of seeds; right, a packet of powdered seeds; middle, a newspaper clipping advertising *Crescentia* seeds.—F. *Parmentiera aculeata* fruits, cultivated in Guatemala.

a bailer. Engraving of the fruit of *Crescentia* is a significant local artesan industry among various rural groups (Fig. 2; Price, 1982). The smaller fruits of *C. alata* are used as "maraca" rattles (Fig. 2) in much of Mexico and Central America. Maraca manufacture is so important in Mexico's Morelos state that Bye (1992) reports that the entire fruit production of 12,000 trees per year is needed to support the local industry, a figure that gains significance in view of the fact that only 12,381 calabash trees are known to grow in the entire state.

The Siona Indians of Amazonian Ecuador use capsule valves of *Jacaranda copaia* (Aublet) D.

FIGURE 3. Bignoniaceae wood used in construction and cabinetry.—A. Bignoniaceae liana used to tie floating dock together, Mazan, Peru.—B. Interior trim and woodwork of house in Campinas, São Paulo, Brazil, entirely of *Tabebuia heptaphylla*.—C. Truckload of "lapacho" logs (*Tabebuia heptaphylla*) headed for market in eastern Paraguay.

Don as tools to shape pottery (Vickers & Plowman, 1984). In Africa the fruit of *Kigelia* is hollowed out to make a kind of mousetrap using a bait and noose; it is also made into ladles, cups, and dolls (Lovett, 1990). The dried fruit valves of *Pithecoctenium* are frequently placed on a stick (Fig. 2) and used in exotic "floral" arrangements; I once encountered the fruits of the rather rare *Amphilophium pannosum* (DC.) Bureau & K. Schumann similarly displayed in Germany, though how they had arrived there is anybody's guess.

The aesthetic appeal of the contrastingly dark heartwood and light sapwood of many *Tabebuia* species has led to use of the wood in local handicrafts. In western Ecuador, *Tabebuia chrysantha* (Jacq.) Nicholson ("guayacan") is one of the most important timber woods, with much of its lumber being converted into knickknacks, such as salad and sugar bowls and carved statues, and furniture. One indication of the esteem in which "guayacan" (now becoming rare due to overexploitation) is held is the prevalence on the tourist market of items of imitation guayacan made by painting dark brown bands or patches on an article made from a light-colored wood (Gentry, 1980).

The strikingly anomalous cross sections of Bignoniaceae lianas are used in making parquetlike trays and placemats in southern Brazil (Fig. 2). Bignoniaceae lianas are the basis of an important basket-weaving cottage industry of the Guaymi indigenous community at Coto Brus, Costa Rica (Benzecry, pers. comm.). There are also reports from the Yucatán of bignon lianas being used in basketmaking (e.g., *Arrabidaea pubescens* (L.) A. Gentry, fide *Chan et al. 301*, XAL, M). Reputedly (R. Ocampo, pers. comm.), stems of *Cydista* are now being removed in large quantities from the Guatemalan Petén for similar purposes. An *Arrabidaea* species is used in Caqueta, Colombia, to make "balais" or manioc strainers (coladoras) (*Toro et al. 12*, Herbarium of TROPENBOS-Colombia housed at the Corporación Araracuara, abbreviated to ARAR in the rest of this paper).

Bignoniaceae lianas are used frequently in local construction, tying together everything from houses to piers (Fig. 3). In some areas this may be their major use; for example, all four of the Bignoniaceae liana species reported by Boom (1990) to be used by the Panare Indians were used as lashing materials. Elsewhere there are herbarium-label records of at least nine different genera used for this purpose. An interesting special use of bignons for tying is as tourniquets for snakebite (*Duke 10875*, MO), which the Chocó Indians of Darién make out of the thin and flexuous juvenile stems of *Mansoa parvifolia* (A. Gentry) A. Gentry.

TIMBER

In terms of financial return, wood products may be the most important contribution of Bignoniaceae to humanity. Many of the tree taxa are important sources of timber. The large neotropical genus *Tabebuia*, which has many species with unusually strong wood, is especially important in this respect (see Gentry, 1991). *Tabebuia*, along with *Guaiacum*, may have the hardest, heaviest, most durable wood of any neotropical tree (Record & Hess, 1940; Gentry, 1980). For example, *Tabebuia guayacan* (Seemann) Hemsley was among the most resistant to wood-boring organisms of all the Panamanian woods tested by Bultman & Southwell (1976; Southwell & Bultman, 1971), and nearly all the sound trees that remain standing in Gatun Lake, more than 50 years after flooding by construction of the Panama Canal, are that species. Not surprisingly, the timbers of this species in the ruined colonial cathedral at Panamá Viejo are still sturdy after exposure to the elements for 400 years. *Tabebuia serratifolia* (Vahl) Nicholson, closely related to *T. guayacan*, is currently the most highly desirable hardwood in Pará, Brazil, being worth $40 per m³ before sawing (Uhl & Vieira, 1989). Currently efforts are being made to import wood of this species to the United States (source at Amazonex Lumber Co., pers. comm.). In western Ecuador two other related hard-wooded species (*T. chrysantha* and *T. billbergii* subsp. *ampla* A. Gentry) are among the most important timber woods. The furniture and interior trim of many of the finest homes in Guayaquil are made of *Tabebuia* wood. The similar wood of *Tabebuia heptaphylla* is much prized in Paraguay and southern Brazil. In São Paulo State this species is commonly used for floors and interior trim (Fig. 3).

These same wood properties are appreciated by campesinos and indigenous peoples as well. For example, the metates (corn grinders) of the Guajira Indians in northern Colombia are always made of the wood of *T. billbergii* (Bureau & Schumann) Standley (Cuadros, pers. comm.), and *T. serratifolia* is used preferentially for ax handles by the Ka'apor of Brazil (fide W. Balee).

Because most of the good timber trees in southern Brazil have already been cut, the Paraná forests of Paraguay are now the main regional source of *Tabebuia* wood; *T. heptaphylla* is currently the most important timber species in eastern Paraguay, being high-graded from otherwise intact forests, as at Río Jejui-Mí (Fig. 3).

Curiously, other species of *Tabebuia*, especially those growing in swamps, have unusually lightweight woods. The light spongy wood of the roots of *T. cassinoides* (Lam.) DC., for example, has been reportedly used for lifebuoys, razor straps, and inner shoe soles in Brazil (Correa, 1926), and its wood for spoons and ladles, troughs, paper pulp, and even wooden shoes.

There is also a large group of *Tabebuia* species with intermediate-weight woods. One of these, *Tabebuia heterophylla* (DC.) Britton, widespread in the Antilles, is among the most important timber trees on many West Indian islands. This species and closely related *T. angustata* Britton are especially used for wharves and canoes because of their durability in contact with salt water (e.g., Gentry, 1991; Hodge & Taylor, 1957). *Tabebuia rosea*, called "roble" (Spanish for oak) in some countries, is much sought after in Mexico and Central America for general construction and carpentry. In Panama this is the fourth species to be selectively cut by timber cruisers before general lumbering of an area begins (Gentry, 1980). In northwestern South America, *T. rosea* (Bertol.) DC., is also an important timber tree. A relative, *T. roseo-alba* (Ridley) Sandw., is used for "tabua, taco, frigo, e ripas" in Brazil (*Lino 138*, MO). Another relative, *Tabebuia insignis* (Miq.) Sandw., is the main native "additive" to the Jari plantation paper pulp (Fearnside, 1988). *Paratecoma*, a related genus endemic to coastal Brazil but now almost extinct, was once the most important timber tree of the Rio de Janeiro area, being used to finish all the better-class houses and commercial buildings of Rio de Janeiro and for much of the best-quality furniture there (Record & Mell, 1924). In the Peruvian Andes *Tecoma sambucifolia* HBK is an important wood for carpentry (*Lopez & Sagastegui 2779*, LP, MO).

Another Bignoniaceae genus with timber potential is *Jacaranda*. *Jacaranda copaia* subsp. *spectabilis*, for example, is an important second growth species in many moist areas of the lowland Neotropics. It is fast-growing and is currently being promoted in Amazonian Ecuador as one of the most promising lightweight neotropical timbers (Peck, pers. comm.). *Crescentia* wood is used specifically to make wooden saddles in western Mexico (Bye, pers. comm.). In eastern Africa, the International Council for Research in Agroforestry (ICRAF) has selected *Markhamia lutea* (Benth.) Schumann as one of five focal species for agroforestry tree breeding (D. Boland, pers. comm.).

DYES

Several Bignoniaceae are used for dyes. The best known of these is *Arrabidaea chica* (Humb. & Bonpl.) Verlat, the use of which as a body paint was so important to the indigenous cultures along the Orinoco that the local equivalent of "He is so poor that he can't clothe half his body" became "He is so poor he can't paint half his body" (Humboldt & Bonpland, 1808). That species is still used by the Indians of Amazonian Colombia and Ecuador today to paint women's lips as well as faces and bodies (Garcia-Barriga, 1975; Vickers & Plowman, 1984). It is also used by the Chocó Indians to dye basketry fibers black as well as red, depending on the treatment (pers. obs.) and by the Sionas of Amazonian Ecuador to make a dark brown or blackish dye for painting designs on clothing (Vickers & Plowman, 1984).

Another famous bignon dye is "yangua" or *Cybistax antisyphilitica* (C. Martius) C. Martius ex DC., whose use as a blue dye in the Tarapoto region of Peru was reported by Spruce (1859). Less well known is the use of bark of *Sparattosperma leucanthum* (Vell. Conc.) Schumann by the Chacobos of Bolivia to produce a brown dye used to stain cotton thread (Boom, 1987) or the fruit of *Crescentia* to produce a black dye (Hodge & Taylor, 1957).

Ritual Uses

Even Christianity has sometimes climbed on to the Bignoniaceae bandwagon. The cross-shaped, 3-foliolate leaves and winged petiole of *Crescentia alata* HBK led to its cultivation in the Philippines because of the suggested religious symbolism, while the distinct cross seen in stem cross sections of *Bignonia capreolata* (hence the vernacular name "cross vine") has led to similar connotations (Gentry, 1982).

Bignoniaceae also have their place in indigenous religion. For example, a leaf concoction of *Anemopaegma paraense* Bureau & Schumann is used by the Wayapi of French Guiana to exorcise a child whose father has violated a sloth-hunting interdiction (Grenand, 1980). It is not clear whether reports of use of an infusion of *Cydista aequinoctialis* (L.) Miers, *Arrabidaea corallina* (Jacq.) Sandw. or *A. inaequalis* (DC. ex Splitg.) Schumann as eye drops by the Witotos in Amazonian Colombia "to see more" refers to hallucination or religion. Whether to categorize the waving by a Tirio medicine man of *Stizophyllum* branches over sick people to cure fever (Plotkin, pers. comm.) as medicine or religion is equally moot. Another faith-related use of a bignoniaceous "charm" is reported from the Brazilian Xingu (*Balee 2225*, NY), where the Ka'apor tape *Stizophyllum riparium* on children's legs to make them grow taller.

Poisons and Medicines

According to Frank Lloyd Wright, "A doctor can bury his mistakes, but an architect can only advise his clients to plant vines." This dictum takes on new significance when viewed in the context of Bignoniaceae. It is in medical ethnobotany that Bignoniaceae achieve their greatest prominence, and, although a number of Bignoniaceae trees have medicinal uses, it is the lianas that have the greatest array of bioactive constituents (Gentry & Cook, 1984; Phillips, 1991). The doctor, as well as the architect, might be well advised to turn to vines, especially bignon lianas. For example, 10 of the 12 Bignoniaceae genera used medicinally by the Jivaro in Peru were lianas (Lewis et al., 1987), and no fewer than 13 genera of bignon lianas were listed by Phillips (1991) as having specific medicinal uses. Altogether, I now have records for 27 genera of Bignoniaceae lianas and nine genera of trees that are used medicinally.

At the opposite extreme, but no less biologically active, are various Bignoniaceae species reported as toxic, in several cases the same taxa that are medicinal in other contexts. Paramount among poisonous Bignoniaceae is the genus *Tanaecium*. *Tanaecium excitiosum* Dugand of the Magdalena Valley of Colombia is locally famous for its toxicity to cattle (Dugand, 1942) and has been largely eradicated in an attempt to reduce livestock death (pers. obs.). Crushed leaves and stems of almond-smelling *Tanaecium nocturnum* (Barb. Rodr.) Bureau & Schumann are used by the Wayapi of French Guiana to enervate bees while gathering honey (Grenand, 1980), and similarly toxic effects have been reported on humans (Prance et al., 1977). Another well-documented instance of poisonous Bignoniaceae involves two closely related species of *Arrabidaea*, *A. elegans* (Vell.) A. Gentry and *A. bilabiata* (Sprague) Sandw., which have been responsible for numerous livestock poisonings (Tokarnia et al., 1969; Gentry, 1983).

Poisonous properties may also be advantageous in hunting or fishing. For example, *Memora* may have efficacy as a fish poison. *Memora allamandiflora* (Spruce) Bureau reportedly has been used as a fish poison on the Xingu (*Balee 1962*, NY), and *M. cladotricha* Sandw. is sometimes called "barbasco huasca" (= fish-poison vine) in Peru, indicating similar use. There are several reports of Bignoniaceae as curare ingredients in Amazonia, including the roots of *Distictella magnoliifolia* (HBK) Sandw. and *Martinella obovata* (HBK) Bureau & Schumann by the Barasana (Schultes, 1969, 1970), *Schlegelia cauliflora* A. Gentry and *Callichlamys latifolia* (Rich.) Schumann by the Miranas (*La Rotta 379*, ARAR; Garcia-Barriga, 1975), *Arrabidaea* aff. *oligantha* by the Yukuna (*Pabon 800*, ARAR), and *Schlegelia scandens* (Briq. &

FIGURE 4. Bignoniaceae as sources of biologically active chemicals.—A. *Melloa quadrivalvis*, "mata cangrejo," used to trap crabs in northern Colombia.—B. *Melloa* stem sections as stored underground at house of local "cangrejero" prior to use.—C. Crabs caught with bait made of *Melloa* by picking them up outside their holes the next morning. D. Bark of *Tabebuia* for sale in market at Iquitos, Peru (on shelf).—E. *Cariniana* (Lecythidaceae) tree stripped of bark (in forest reserve at Puerto Almendras, near Iquitos, Peru), which resembles *Tabebuia* bark; *Tabebuia* bark has been over-harvested locally so that the morphologically similar, although biologically inactive, bark of *Cariniana* is now being sold instead, as a kind of fake *Tabebuia* bark.

Spruce) Sandw. by the Tikuna (Schultes & Raffauf, 1990).

Another interesting use of a species of Bignoniaceae for its poisonous properties is of *Melloa quadrivalvis* (Jacq.) A. Gentry to immobilize crabs in northern Colombia (Gentry & Cuadros, in prep.; Fig. 4). The plant is locally called "mata cangrejo," and its use is a closely guarded secret among certain families of professional crabbers. A bait is prepared from shavings of *Melloa* stem and banana and is left overnight outside a series of crab holes in an appropriate coastal area. The next morning the crabber merely returns to the crab holes, picks up the crabs, which have been immobilized outside their holes by the *Melloa*, and carries them off to market. Apparently the effect of the *Melloa* is temporary and nontoxic to humans, since the crabs have largely recuperated by the time they reach market, and no adverse effects have been reported from eating them.

Hallucinogens might be classed as either poisons or medicines, depending on one's perspective. Here, too, Bignoniaceae lianas make a significant ethnobotanical contribution. *Tanaecium nocturnum* is used as an hallucinogenic snuff called "kosibo" by the Paumari Indians of Brazil and similarly by the Puinaves of Colombia (Prance et al., 1977). *Mussatia hyacinthina* (Standley) Sandw., or "chamairo" (Quechua for "wick of delight"), is a widely used coca additive in Peru and Bolivia and has an independent euphoric effect (Plowman, 1980). In Bolivia, *Clytostoma sciuripabulum* Bureau & Schumann roots are sometimes mixed with coca as a substitute for "chamairo" by the Chimane (*Davis & Marshall 1187*, MO). Another occasional coca additive is *Distictis pulverulentus* (Sandw.) A. Gentry, the ashes of the burned leaves of which are mixed with their coca by the Makuna (Schultes & Raffauf, 1990).

Perhaps more akin to hallucinations than to medicine are the aphrodisiacal properties attributed to other Bignoniaceae lianas, for example clove-smelling *Tynanthus*, or "clavo huasca," by the Peruvian Jivaros (Lewis et al., 1987). Especially noteworthy in this context, the same *Tanaecium nocturnum* that is used by the Paumari as a hallucinogenic snuff is used by the Panamanian Chocó as an aphrodisiac (Gentry, 1973) and as a bath to repel women by the Peruvian Ese-Eje (Phillips, pers. comm.).

Another Bignoniaceae famous for its reputed aphrodisiacal properties is *Anemopaegma arvense* (Vell. Conc.) Stellf. ex de Sousa, or "catuaba," of the Brazilian cerrado. The vernacular name, Tupi, for "tree of togetherness," reflects its reputation; an herbal tea prepared from "catuaba" is supposed to be especially efficacious for combating male impotence (Sylvester, 1989). Other Bignoniaceae with reported aphrodisiacal uses include a confection of the flowers of *Stereosperma chelonoides* (L.f.) DC. (as *S. suaveolens*) in India (Chopra et al., 1956), and *Macfadyena uncata* (Andrews) Sprague & Sandw. as a love charm in Amazonian Peru (Phillips, pers. comm.).

Although there have been few detailed or systematic investigations of Bignoniaceae phytochemistry, it is obvious from their characteristic vegetative odors that the species of many genera are related by distinctive suites of chemical characters. For example, *Tynanthus* smells like cloves, most *Mansoa* species smell like garlic, *Tanaecium* has either an almond or bitter odor, *Paragonia* a sweetish odor, *Godmania* a rank odor that has been likened to that of horse urine. This kind of chemical signature is also reflected in the similar ethnomedicinal uses for different species of the same genus. One of the most striking examples is *Martinella* (Gentry & Cook, 1984), which is widely used throughout most of South America as a medicine for conjunctivitis. Such medicinal uses are reflected in an abundance of specific epithets like "ophthalmica" (*Bignonia ophthalmica*, a synonym of *Martinella obovata*), "antisyphilitica" (*Cybistax antisyphilitica*), "impetiginosa" (*Tabebuia impetiginosa* (C. Martius ex DC.) Standley), "curialis" (*Tecoma curialis*, a synonym of *Tabebuia heptaphylla* (Vell. Conc.) Toledo), and in the vernacular name "para todo" for *Tabebuia aurea* (Manso) Benth. & Hook. ex S. Moore.

A number of Bignoniaceae taxa have been reported to be active against such major medical scourges as cancer, diabetes, syphilis, malaria, hepatitis, rabies, and leshmaniasis. The most famous of these is the use of the bark of various species of *Tabebuia* as a cancer cure (Fig. 4; see Awang, 1988; Gyllenhaal & Farnsworth, ms. in prep.). Many of the cytotoxic effects of Bignoniaceae extracts on neoplasic cells, as well as their documented effectiveness against trypanosomiasis and various viruses are due to properties of the lapachol and related naphthoquinones that are widespread in, and mostly restricted to, this family (Ferreira et al., 1990).

Additional recent ethnobotanical reports of indigenous uses of *Tabebuia* bark against cancer include that of *T. incana* A. Gentry and *T. impetiginosa* by the Campas in Peru (Reynel et al., 1990), of *T. serratifolia* in Colombia (Garcia-Barriga, 1975), and of *T. rosea* by the Mayas in Mexico (Dominguez & Alcorn, 1985). That almost all such reports are for the genus *Tabebuia*, and that they come from such widely scattered localities and ethnic groups, lends ethnobotanical credence to the postulated medical effectiveness.

Unfortunately, the uncritical tend to interpret such data overzealously, in a manner that often casts doubt on the real, as well as the more fanciful, effectiveness of a plant like *Tabebuia*. For example, "ozone-friendly" *Tabebuia* ("lapacho" or "pau d'arco") was reported in a recent article (Sylvester, 1989) to build immunity, improve vitality, and strengthen cells, as well as being effective against diabetes, leukemia, multiple sclerosis, arthritis, rheumatism, allergies, chronic infections, colds, influenza, boils, snake bites, and AIDS; no doubt the unusual flowers, which "are carnivorous and eat insects, keeping the tree free from parasites and viral growths," contribute to its healing power as does the fact that "it apparently only grows where there is a high ozone content in the air where vital negative ions are also concentrated." Yet these distinctly off-the-wall observations are confusingly interspersed with better documented ones about effectiveness against *Candida albicans* and several kinds of cancer.

There are also several reports of Bignoniaceae with antimalarial properties. These include *Pleonotoma melioides* (S. Moore) A. Gentry (J. Rios Trigosa, pers. comm.), *Macfadyena unguis-cati* (L.) A. Gentry (Garcia-Barriga, 1975), *Tabebuia rosea* (*Steyermark 51372*, F), and *T. ochracea* (Cham.) Standley (Schultes & Raffauf, 1990). Bignoniaceae reported as effective against syphilis include *Arrabidaea chica* (Triana fide Garcia-Barriga, 1975), *Macfadyena unguis-cati* (Garcia-Barriga, 1975), *Tabebuia heptaphylla* (Martius, 1843), *Tecoma stans* (L.) Juss. ex Kunth (Liogier, 1974, fide Duke, pers. comm.), and *Cybistax antisyphilitica* (Martius, 1843); *Jacaranda caucana* Pitt. has also been reported to be effective against venereal disease (*Grant 10711*, WIS; Garcia-Barriga, 1975). Both *Callichlamys latifolia* and *Jacaranda copaia* have been reported to be specifically used by the Peruvian Jivaro against leshmaniasis (Lewis et al., 1987), and *Cybistax antisyphilitica* roots against epilepsy (*Mathias & Taylor 5617*, MO). *Tabebuia rosea* has been reported to be used against rabies in Guatemala (*Ruano 425*, US). *Tecoma stans* is reputed to be effective against diabetes in several countries, apparently because a piperidine derivative lowers blood sugar levels by stimulating insulin production (Lozoya-Meckes & Mellado-Campos, 1985; Perl, 1988; Duke, pers. comm.).

On the other hand, equally specific reports of the use of strongly aromatic genera like *Mansoa* against tuberculosis, *Tynanthus* against hepatitis, and both against rheumatism (e.g., Lewis et al., 1987) may well be more closely related to psychological than physiological effects. Garlic-smelling *Mansoa* is especially instructive in this connection. Most appropriately called "pedo de padre" (= priest's fart) in Central America, it may well serve to repel insects (Lewis et al., 1987)—as well as most other organisms. No doubt burning it where sick chickens roost to prevent an epidemic (Alarcón, 1988) would have as strong a repulsive effect on the potential disease vectors of the chickens as drying it in a closed building does on an unwary plant collector (pers. obs.). However, much of its exceedingly wide medical application against a great variety of ailments, including such difficult-to-treat ones as snakebite, is likely to be due to placebo effect.

Another kind of precautionary note on Bignoniaceae ethnomedicinal uses may also be appropriate. In at least some cases, unreliable or uncooperative informants may have invented uses or misidentified the plant involved. Thus, the dozens of independent reports, including an unpublished one dating from 1791, of use of *Martinella* for eye ailments surely indicates that the plant is an effective medicine (Gentry & Cook, 1984). However, there are also isolated reports of uses of *Spathicalyx xanthophylla* (DC). A. Gentry (Schultes, 1970), *Haplolophium rodriguesii* A. Gentry (*Boom 4688*, NY), *Macfadyena uncata* (Lewis et al., 1987), *Tabebuia insignis* var. *monophylla* Sandw. (*Schultes & Cabrera 19734*), and *Arrabidaea chica* (Schultes & Raffauf, 1990) to treat conjunctivitis. All of these are vegetatively rather similar to *Martinella*, and one wonders whether some kind of mix-up, intentional or otherwise, might be involved. Similar confusion between plants may also apply to the reported use to cure diarrhea of four of the five identified useful bignon lianas (plus another unidentified one) in Boom's (1987) study of Chacobo ethnobotany. This is otherwise a rarely reported use for bignons and has not been reported elsewhere for the same taxa, some of which normally have other very specific uses. Either the Chacobo are inordinately preoccupied with diarrhea, or perhaps more likely, the informants are providing less than precise data. On the other hand, the use of an obscure species like *Memora flavida* (DC.) Bureau & Schumann by three different Surinamese ethnic groups (Tirios, Wayanas, and Akuriyos) for essentially the same purpose (for aching joints, body aches, and to treat aching facial muscles, respectively) (Plotkin, pers. comm.) strongly suggests that a genuine biologically active property of this species is involved.

In summary, while it is difficult to know to what extent the extensive ethnomedicinal literature on Bignoniaceae, and especially bignon lianas, reflects real pharmacological activity, the fact that there are so many such reports strongly suggests that there is a real basis for many of them. Indeed, taken at face value they suggest that Bignoniaceae constitute a kind of one-family rainforest pharmacy, with different taxa curing ailments of the eyes (*Pleonotoma variabilis* (Jacq.) Miers (fide *La Rotta 379* ARAR), *Martinella*), ears (*Arrabidaea florida* DC.: Schultes & Raffauf, 1990), teeth (*Arrabidaea chica* (caries prevention), *Crescentia* leaves (toothaches), *Lundia erionema* DC. (bleeding gums)), nose and throat (e.g., *Mansoa, Crescentia, Stizophyllum, Pyrostegia, Parmentiera, Tanaecium nocturnum*), skin (e.g., *Amphilophium, Callichlamys, Cydista, Jacaranda, Memora, Mussatia, Kigelia, Parmentiera, Tabebuia, Tanaecium*), stomach and intestines (eg., *Arrabidaea, Callichlamys, Crescentia, Jacaranda, Macfadyena, Mussatia, Paragonia, Parmentiera, Pithecoctenium, Pleonotoma, Tabebuia*), kidneys (*Parmentiera*), liver (*Macfadyena: Schinini 4892*, CTES), joints (*Mansoa, Tynanthus, Jacaranda, Macfadyena, Memora, Pitecoctenium, Tabebuia*). In addition to being used against the above-mentioned maladies and against asthma, influenza, and the common cold, they are used to treat fevers (*Arrabidaea candicans* (Rich.) DC., *Callichlamys, Macfadyena, Mansoa, Martinella, Memora, Tanaecium nocturnum, Tynanthus, Xylophragma*), headaches (*Arrabidaea spicata* Bureau & Schumann, *Pithecoctenium*), diarrhea (*Arrabidaea candicans, A. platyphylla* DC., *Callichlamys, Lundia, Mussatia, Tanaecium nocturnum, Tynanthus*), flatulence (*Mussatia, Tabebuia barbata* (E. Meyer) Sandw.: by the Kuripakos specifically to combat excess flatulence from eating tapir meat), hemorrhaging (*Crescentia, Macfadyena*, flowers of *Tabebuia obscura* (Bureau & Schumann) Sandw.), hiccoughs (*Schlegelia macrophylla* Ducke), snakebite (e.g., *Mansoa, Clytostoma sciuripabulum, Tabebuia aurea* (fide *Balick et al. 1395*, MO), *Tecoma stans*), and behavioral disorders (*Macfadyena uncata* against aggressive tendencies in Peru, *Crescentia cujete* as a tranquilizer in Ecuador (*Miller et al. 2397*, MO), *Stereospermum colais* (Buch.-Ham. ex Dillwyn) Mabberley (as *S. tetragonum*) for maniacal cases in India). They are used against baldness (*Tynanthus panurensis* (Bureau) Sandw. in Ecuador (*Marles 113*, F)), to treat broken bones (*Pithecoctenium crucigerum* (L.) A. Gentry by the Peruvian Amuesha (fide *Salick 7198*, MO), as a permanent contraceptive (*Macfadyena uncata* in Peru) and to cause spontaneous abortion (*Crescentia cujete* in Ecuador (*Marles 123*, F; *Miller et al. 2397*, MO), as a cosmetic to keep the skin soft and moist (*Arrabidaea chica, Memora cladotricha*), or to remove pimples (*Amphilophium paniculatum* (L.) HBK (fide *Standley 19719A*, US)), and to eliminate tapeworms (*Macfadyena unguis-cati*) or treat ringworm (*Cydista lilacina* A. Gentry: *Balee 2596*, NY). They are even used in veterinary medicine (e.g., *Tynanthus panurensis* in Colombia to "enfriar el calor de los animales": *La Rotta 379*, ARAR; *Ceratophytum tetragonolobum* (Jacq.) Sprague & Sandw. in Mexico for coughing dogs: *Ucán 752*, XAL, M) (Alarcon, 1988; Boom, 1987, 1990; Chopra et al., 1956; Garcia-Barriga, 1975; Grenand, 1980; Lewis et al., 1987; Phillips, 1991; Plowman, 1980; Reynel et al., 1990; Schultes & Raffauf, 1990; Tournon et al., 1986; Vickers & Plowman, 1984).

Bignoniaceae clearly enrich the lives of the people who share the world's tropical forests with them. Although they are already important to the developed world as well, it seems likely that they can become even more useful. Bignoniaceae would seem clearly to merit additional ethnobotanical, especially pharmacological, investigation, before they, along with the knowledge of their plethora of potential uses and the very rainforests in which they live, disappear from the face of the earth.

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EXINE STRUCTURE OF PANTOPORATE *CAMPANULA* (CAMPANULACEAE) SPECIES[1]

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Abstract

The only species in Campanulaceae known to have pollen with pantoporate apertures are five species of *Campanula*: *C. americana, C. californica, C. exigua, C. griffinii,* and *C. sharsmithiae.* All other species examined of this large genus (ca. 300 species) have 3–4(–7) pores, spaced equidistant on the equator of the grain. The pantoporate species, especially the widely distributed annual or biennial herb *C. americana,* are further distinguished by elongate or well-developed columellae. The larger columellae of this species may be correlated with their lower density. Except for the similarities in pollen, *C. americana* does not appear closely related to the three slender annuals, *C. exigua, C. griffinii,* and *C. sharsmithiae,* each of which has a restricted distribution in California. *Campanula americana* also is not closely related to the pantoporate perennial, *C. californica,* or to the fourth California annual, *C. angustiflora,* which has 4–6-zonoporate pollen with a tectum and exine structure almost identical to *C. sharsmithiae.* The pantoporate grains of *C. californica,* with pores that are not always uniform in size or distribution, and the zonoporate grains of *C. angustiflora,* with unevenly distributed pores and elongate columellae, may represent transition stages between the two pollen types. In this study and previous ones, all species of Campanulaceae with well-developed or elongate columellae have been shown to have a high number (more than five) of apertures. Whether more apertures make the pollen wall more vulnerable to collapse and whether selective pressures have resulted in a more rigid wall by means of elongate columellae are debatable. The highly distinctive pollen-collecting hairs found in the Campanuloideae are illustrated and discussed.

In a systematic study of four closely related annual species of *Campanula,* all endemic to California, Morin (1980) established the existence of pantoporate (pores distributed over the entire surface) pollen in three, *C. exigua* Rattan, *C. griffinii* Morin, and *C. sharsmithiae* Morin, and 4–6-zonoporate pollen in *C. angustiflora* Eastwood. Later, Morin (unpublished) found the pantoporate aperture type in the weakly perennial *C. californica* (Kell. Heller). Prior to her studies only one other species in Campanulaceae, the robust annual or biennial *Campanula americana* L., native to eastern and central North America, was known to have a pantoporate aperture type (Avetisian, 1967; Dunbar, 1973a, b, 1975a, b, 1981, 1984; Shetler, 1982; for life history of *C. americana* see Shetler, 1958, and Baskin & Baskin, 1984). The unusual and very limited occurrence of pantoporate pollen in Campanulaceae prompted this investigation of the exine structure of *Campanula americana* and the California pantoporate species.

Exines subjected to partial degradation by plasma-ashing suggest that the fundamental tectum/sculpture in the subfamily Campanuloideae are rodlike or threadlike structures.

Although not specifically studied here, the pollination biology of *Campanula,* the species of which show pronounced protandry and adaptations to insects, is characterized by a unique and still largely unexplained mechanism. While the flower is still in bud, anthers dehisce and deposit the pollen on the pollen-collecting hairs of the upper style. As anthesis proceeds, both pollen and the unicellular hairs gradually disappear, the former owing to pollinator activity, the latter to retraction/invagination into their expanded bases. The fact that in some cases the retracted hair is observed "to trap" a pollen grain has prompted speculation that the invagination is an adaptation for autogamy (for review, see Shetler, 1979). This does not seem to be the case (Shetler, 1982; Lloyd & Yates, 1982), however; the possible functions of the collecting hairs are presented in the discussion section.

Materials and Methods

For examination of pollen, anthers were removed from herbarium material and routinely acetolyzed (Erdtman, 1966) for all preparations: light microscopy (LM), scanning electron microscopy

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copy (SEM), transmission electron microscopy (TEM), and plasma-ashing.

For SEM, pollen was coated with carbon, then gold-palladium, and examined and photographed with a Cambridge 250 Stereoscan Electron Microscope or a Hitachi 570 SEM.

For TEM, pollen was incorporated into agar, fixed with osmium tetroxide, stained with uranyl acetate, and embedded in Spurrs resin or L. R. White. After sectioning, the pollen was stained in lead citrate and examined in a JEOL 100, 1200EX, or a Philips 200 transmission electron microscope.

For LM, pollen was mounted in glycerin jelly and sealed with paraffin. Measurements (see Table 1) are based on 20 grains in LM.

For examination of collecting hairs, styles were dissected from herbarium flowers and attached to specimen stubs, coated with gold-palladium, and examined and photographed in a Cambridge 250 or an S410 scanning electron microscope. The collections examined are listed in Table 1.

In plasma-ashing an electrical field changes diatomic oxygen into excited oxygen ions to form a highly reactive plasma that causes low temperature combustion of organic molecules. The most common use of plasma-ashing is for removal of organic matter from inorganic structures, e.g., tissue from sponge spicules. For this application, end-point detectors can determine precisely when the organic layers have been removed. In completely organic samples such as exines, however, the only control (available to us) is duration of ashing. Based on an earlier study of pollen from 33 species representing 10 families (Nowicke et al., 1986), the first hour of ashing produces the most profound effect—a reduction in the sculpturing components resulting in skeletonlike exines. For greater detail, see Nowicke et al. (1986).

All LM slides and EM micrographs are deposited at the Palynological Laboratory, National Museum of Natural History, Smithsonian Institution.

RESULTS

In the course of the entire Campanulaceae study, the pollen of 58 collections representing 41 species from nine genera was examined in LM and SEM, and 21 of the 41 were examined in TEM. Twenty-eight species of *Campanula* were examined in LM and SEM, 14 of which were also examined in TEM. For the most part only the species that are cited in the text and/or illustrated are given in Table 1.

All 18 species of *Campanula* cited in Table 1 have oblate-spheroidal or spheroidal pollen with porate apertures and a tectum that consists of spinules and irregularly oriented threadlike or rodlike structures (Figs. 1–41, 54, 55, 57, 58). For porate Campanulaceae, Dunbar (1984: 1) classified surface sculpture types into the following categories: ridges; ridges, with top end bent upwards; fingerlike structures; protrusions; irregular ridges; and reticulum in low relief. With the exception of the last category, applicable only to *Campanula americana* in our study, we believe that these closely related categories are minor variations in the orientation of the rods or threads. Although the term rod, with its implication of a straight or erect linear structure, may be more fitting for some tecta than others, e.g., Figure 41 versus Figures 55 or 58, we will use rod in the remainder of the text to describe the ropelike strands making up the surface of the tectum, often intertwined in spaghettilike fashion. These rods can vary in their size, degree of distinction (e.g., Figs. 15, 31 vs. 9, 41), extent of projection (e.g., Fig. 35 vs. 38, 41), and orientation (e.g., mostly horizontal as in Fig. 35 or with rods more erect/vertical as in Figs. 17, 23, and 46).

In SEM, the relationship between the rods and spinules seems clear—the free tips of rods appear to coalesce to form spinules. In every *Campanula* species examined in SEM, the base of at least some spinules is continuous with three or more rods. This condition is illustrated best in the plasma-ashed samples, Figures 56 and 59, but almost as well in Figures 8, 29, 38, 41, and 58. In the past (Dunbar, 1973a; Morin, 1980), the spinules have been considered as basally rooted or divided, but we now think that the spinules are the result of free tips of rods coalescing and not of rods formed by the basal subdivision of spinules (see discussion below).

In thin section, all species examined have stratified exines with an endexine, foot layer, columellae, and tectum, but these components are variously developed.

Based on the above characteristics the pollen of *Campanula* is a recognizable type: porate with a tectum consisting of spinules and variously oriented rods. But the distribution of the pores defines two distinctive subtypes with very unequal frequencies. Five species are pantoporate (Figs. 1, 7, 13, 21, and 24), with as few as six apertures and as many as 18. All remaining campanulas have three, sometimes four, or more rarely five or six (seven in a few grains of *C. rotundifolia*) pores placed equidistant on the equator of the grain (some grains of *C. angustiflora* excepted).

Our TEM investigation revealed subtle differences in the structure of the exine: in the panto-

TABLE 1. Species examined, voucher data, pollen data, and figure numbers.

Species	Collection[1]	Location	Figure(s)	Grain size[2]	Pore size	Number of pores
Campanula alpina Jacq.	*Bujorean & Nyarady s.n.* 7/1/23	Romania	28–30	P(28) 30 (32) × E(30) 32 (35)	4–5.2	3
C. americana L.	*Demaske 2128*	Wisconsin		(36) 38 (40)	5.2–6.5	12–15
	Shimek s.n. 8/15/27	Iowa	3–6	(35) 38 (40)	5.2–6.5	10–13
	Soper & Dale 4081	Canada	1, 2	(35) 38 (39)	5.2–6.5	10–13
	Hartley 1472	Wisconsin	60, 62–69			
	Ward s.n. 4/7/1878	Maryland	61			
C. angustiflora Eastwood	*Constance et al. 3045*	California	16–20	P(29) 31 (32) × E(31) 34 (36)	4–6.5	(4–)6
C. barbata L.	*Hermann 19483*	France	33–35	P(29) 32 (34) × E(30) 31 (34)	5.2–6.5	3
C. baumgartenii J. Becker	*Hall 3125*	Germany	57–59	P(27) 29 (31) × E(30) 31 (43)	5.2	3–4
C. californica (Kell.) Heller	*McMurphy 22*	California	24–27	(39) 40 (45)	2.6–4	7–11
C. divaricata Michx.	*Allard 2116*	Virginia		P(30) 32 (35) × E(32) 35 (36)	5.2–6.5	3
	Duncan 11925	South Carolina		P(29) 31 (34) × E(32) 34 (36)	5.2	3
C. exigua Rattan	*Sharsmith & Sharsmith 3358*	California	7, 8, 10–12	(36) 40 (42)	5.2	12–14
	Morin 297 (MO)	California	9	(34) 35 (38)	4–5.2	12–15
C. glomerata L.	*Collins & Fernald s.n.* 1904	Canada		P(29) 30 (34) × E(31) 33 (38)	4.5–6.5	(2) 3 (4)
C. griffinii Morin	*Griffin 4120* (MO)	California	13, 14	(30) 31 (34)	5.2–6.5	6–9
	Howell 21813	California	15	(30) 33 (35)	4–5.2	7–12
C. hagielia Boiss.	*Rechinger 3678*	Greece	31, 32	P(21) 23 (25) × E(22) 25 (26)	3.9–5.2	3 (4)
C. lasiocarpa Cham.	*Hulten s.n.* 7/15/61	Alaska		P(30) 32 (35) × E(31) 33 (35)	5.2–6.5	3–4
C. macrorhiza Gay ex A. DC.	*Wilczek & Dutoit* 21-VII-30	France		P(27) 29 (30) × E(29) 31 (33)	4–5.2	(2) 3 (4)
C. medium L.	*Thomas 10926*	Montana	54–56	P(34) 37 (39) × E(36) 39 (40)		3
C. rhomboidalis L.	*Maillefer 37599*	Switzerland	36–38	P(26) 29 (31) × E(28) 29 (34)	4–5.2	3 (4)
C. rotundifolia L.	*Charpin et al. s.n.* 7/15/69	Italy	39	P(32) 37 (40) × E(34) 36 (41)	5.2–6.5	3–4
	Terrell & Brown 3858	Colorado	40, 41	P(30) 33 (38) × E(34) 36 (41)	5.2–6.5	4 (5)
C. sharsmithiae Morin	*Morin 301* (MO)	California	21–23	(35) 38 (40)	4–5.2	12–18
C. sibirica L.	*Csato 2977*	Romania		P(29) 32 (34) × E(31) 33 (36)	5.6–7.1	(2) 3 (4)
Codonopsis bulleyana Forrest ex Diels	*Rock 5444*	China	51–53	P(41) 44 (48) × E(41) 46 (49)	17–36	6–8
C. convolvulacea Kurs	*Rock 6603*	China	42–44	P(38) 42 (48) × E(43) 46 (51)	7.8–13	6
Githopsis pulchella Vatke	*Constance s.n.* 5/19/51	California	45–47	P(36) 40 (45) × E(39) 43 (47)	5.8–7.8	6
Wahlenbergia linarioides DC.	*Schwarz 10877*	Argentina	48–50	P(25) 28 (30) × E(29) 31 (32)	4.5–5.2	3 (4)

[1] All US unless otherwise indicated.

[2] Does not include spinules; P = polar dimension, E = equatorial dimension; numbers in ( ) indicate range.

porate type the prominent or elongate columellae project through the tectum to form the core of most spinules, e.g., Figures 3–5, 10, 11, 19, 20, 27, whereas in the zonoporate type the columellae are reduced (e.g., Figs. 30, 32, and 37) and the spinules are not formed by columellae (see above discussion of SEM data). The zonoporate type usually has a well-developed foot layer (Figs. 32, 34, 37).

A complete description of each pollen type is given below; for pollen size, the range of the mean (Table 1) is given.

PANTOPORATE POLLEN TYPE—FIGURES 1–15, 21–27

Pollen spheroidal, 31–40 μm diam., with 6–18 pores, the pores 4–6.5 μm diam., the tectum consisting of rods and spinules, or microreticulate and spinulate; exine structure consisting of lamellate endexine prominently thickened at the pores; the foot layer mostly thin or sometimes equal in thickness to the nonapertural endexine; the columellae elongate, prominent, at least some of which project through the tectum to form the core of most spinules; the tectum incomplete or nearly complete (*C. griffinii*). Five species: *Campanula americana*, *C. californica*, *C. exigua*, *C. griffinii*, and *C. sharsmithiae*.

Campanula americana (Figs. 1–6) is 12–15-pantoporate with a microreticulate tectum in which horizontal rods are muri or vice versa. No other species of *Campanula* examined in this study or illustrated in others (Dunbar, 1973a, b, 1975a, 1984; Morin, 1980) has a microreticulate tectum or such massive columellae. The rods/muri and spinules are more evident in some grains than in others. In thin section (Figs. 3–5), the exine of *C. americana* consists of a lamellate endexine present throughout the grain but greatly thickened near the pores and with a thin foot layer. Comparison of radial sections of *C. americana* (Fig. 3) with those of other pantoporate species, e.g., *C. exigua* (Fig. 11), *C. sharsmithiae* (Fig. 22), and *C. californica* (Fig. 27), as well as zonoporate species, e.g., *C. alpina* (Fig. 30) and *C. hagiela* (Fig. 32), emphasizes the unusual development of the columellae in *C. americana.* Larger columellae may be a compensation for, or correlation with, fewer columellae The density of columellae in the tangential section of *C. americana* (Fig. 4) is much lower than that in *C. exigua* (Fig. 10): when a grid one centimeter square was variously placed over the area occupied by columellae, the highest number of columellae for *C. americana* was 10, while that for *C. exigua* was 30.

The pollen of the remaining pantoporate species, *C. californica* (Figs. 24–27), *C. exigua* (Figs. 7–12), *C. sharsmithiae* (Figs. 21–23), and *C. griffinii* (Figs. 13–15), was examined in LM and SEM. The first three species were also examined in TEM, as was the zooporate annual, *C. angustiflora.*

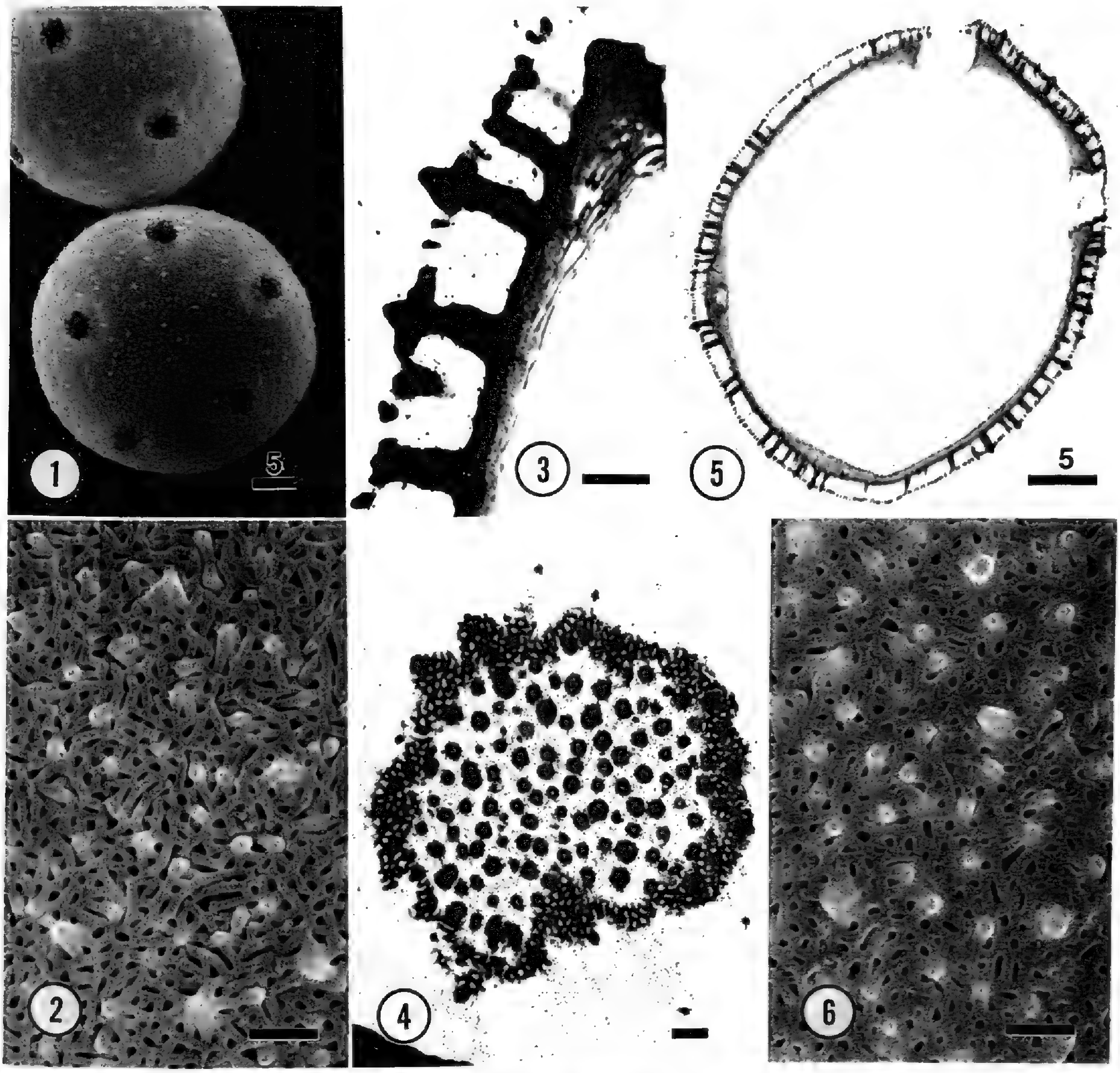
The weakly perennial *Campanula californica* (Figs. 24–27) has the elongate columellae associated with the pantoporate type, but the distribution and size of the pores are not uniform. In LM there are numerous grains that, in optical section, have four to six pores on the "equator"; each hemisphere (top and bottom focus) may have only one pore, or one hemisphere may have none at all; in more rare cases neither hemisphere has a pore; very frequently one of the pores is distinctly smaller. The elongate spinules, obvious even in LM, would distinguish the pollen of *C. californica* from all remaining pantoporate types. These observations suggest that the pollen of *C. californica* is intermediate between the two pollen types, but closer to the pantoporate than to the zonoporate.

Campanula exigua (Figs. 7–12) is 12–15-pantoporate with well-defined, short, sometimes erect rods (Figs. 8, 9). In thin section the electron densities of the foot layer and endexine are similar (Fig. 11), making it difficult to characterize them individually, but together they form a well-defined unit that becomes much thicker near the pores. The columellae, although not as large as in *C. americana*, are the predominant layer in mesoporal (nonapertural) areas, and most appear to project through the irregular tectum to form the core of the spinules. Their elongation is underscored in tangential section (Fig. 11) by the proportion of the total area they occupy. In both collections examined, the rods (Figs. 8, 9) are distinct from each other and are short, and some appear vertical.

One collection of *C. griffinii*, *Griffin 4120* (Figs. 13, 14), was 7–9-pantoporate with a typically campanulaceous tectum; the other, *Howell 21813* (Fig. 15), was 8–11-pantoporate with more poorly defined tectal rods.

Campanula sharsmithiae (Figs. 21–23) is 12–18-pantoporate with a tectum that appears to consist of irregularly defined elements as well as rods. In thin section (Fig. 22) the exine of this species consists of a thick, mostly lamellate endexine that is slightly less electron dense than the thin foot layer and well-developed columellae, some of which project through the tectum to form spinules. The exine structures in *C. exigua* and *C. sharsmithiae* are similar.

In contrast to *Campanula americana*, *C. cal-*



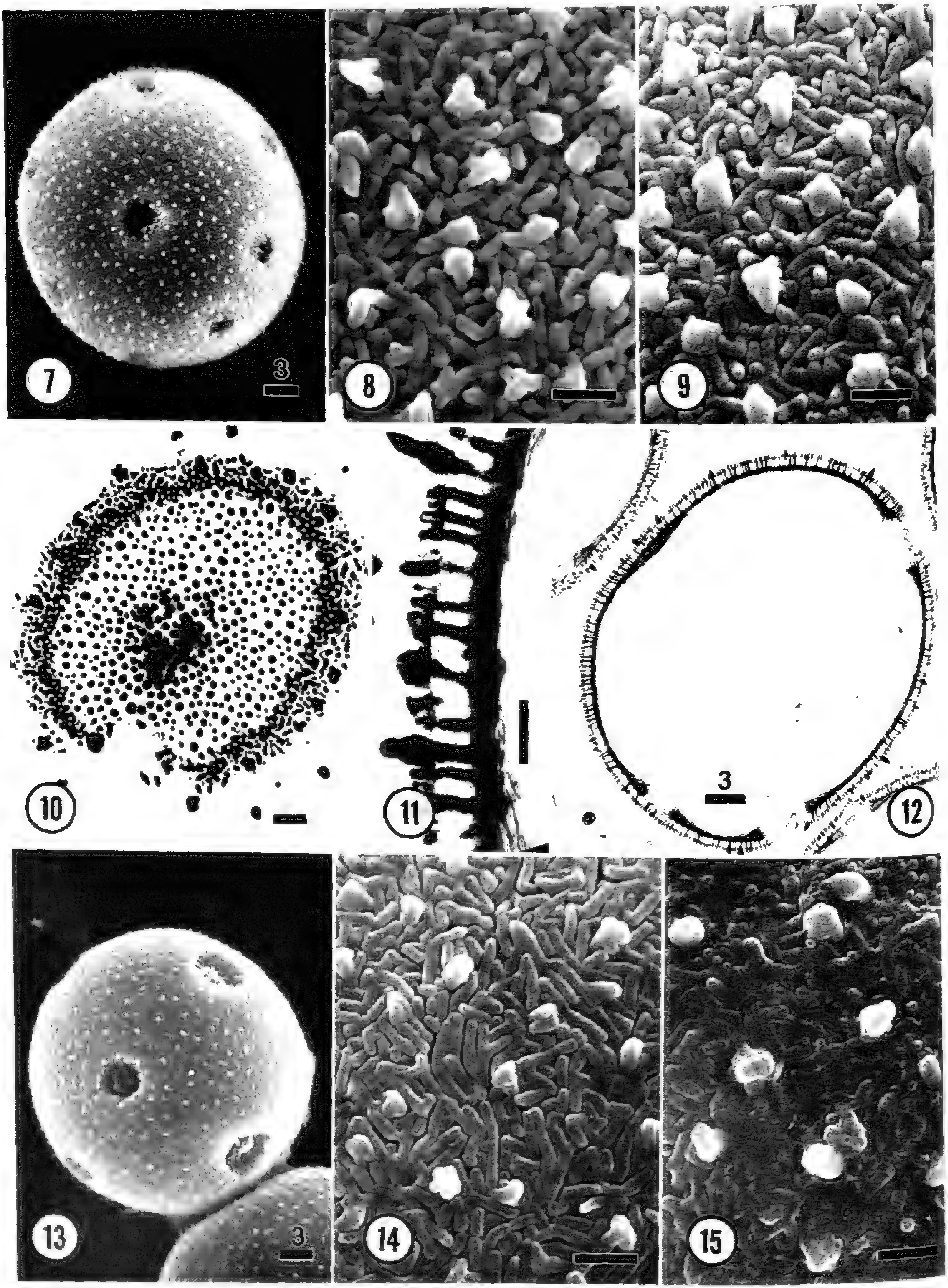
FIGURES 1–6. SEM and TEM of *Campanula americana* pollen.—1. SEM of two pantoporate grains.—2. SEM of tectum.—3. TEM of radial section including part of pore. Note massive columellae, some of which project through the tectum, and thickened, lamellate endexine nearer the pore.—4. TEM of tangential section. Perforated tectum (outer ring) agrees with that portrayed in SEM, Figures 2 and 6.—5. TEM of mostly radial section through whole grain.—6. SEM of tectum. Scale bars = 1 μm unless otherwise indicated.

ifornica, *C. exigua*, *C. griffinii*, and *C. sharsmithiae*, all other campanulas, to our knowledge, have pollen that is 3–4(–7)-zonoporate.

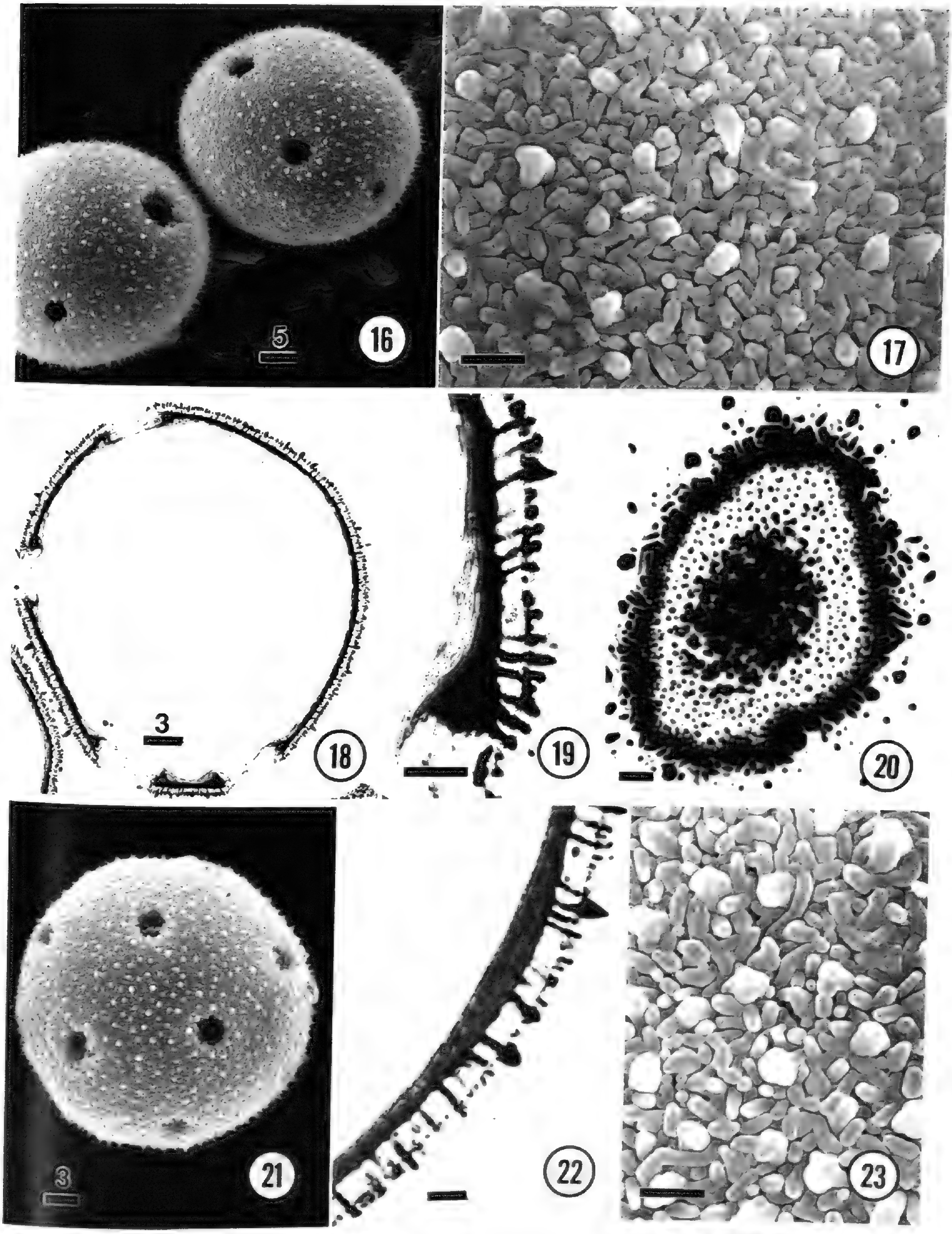
ZONOPORATE POLLEN TYPE—
FIGURES 16–20, 28–41, 54, 55, 57, 58

Pollen mostly oblate-spheroidal, Polar diameter (23–)29–37 μm × Equatorial diameter (25–)31–39 μm, 3–4 pores (rarely 7, *C. rotundifolia*), the pores circular or slightly elongated polarly (= lolongate), the longest dimension 4.0–6.5 μm, the tectum consisting of irregularly oriented rods, frequently with a free tip, some of which coalesce to form spinules; exine structure consists of a lamellate endexine that becomes much thicker near the pores; a well-developed foot layer that is thicker than the nonapertural endexine; reduced or short columellae; and a complete or almost complete tectum, with small to large spinules that are not continuous with columellae.

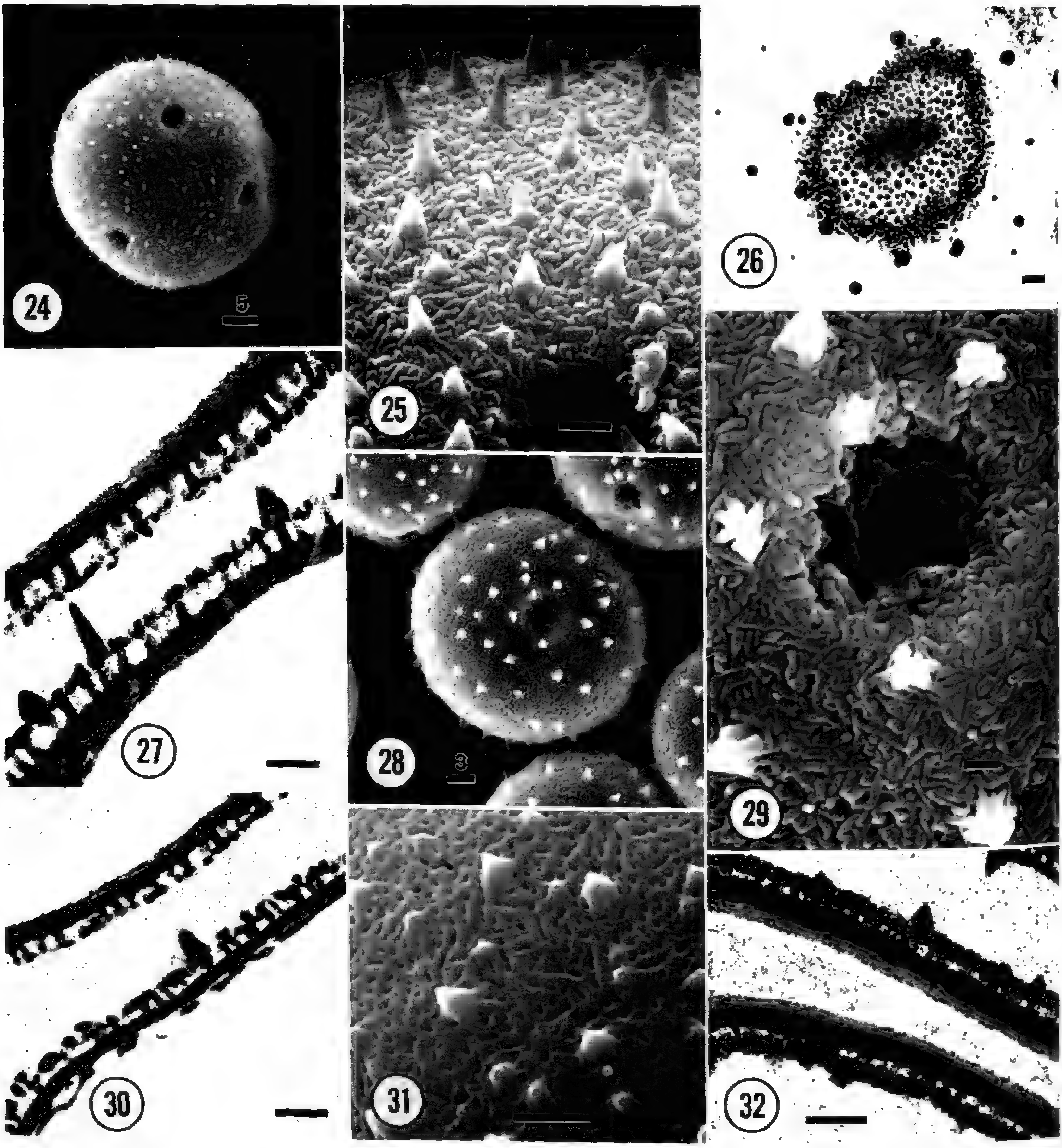
The pollen of seven zonoporate species, *C. alpina* Jacq. (Figs. 28–30), *C. angustiflora* (Figs. 16–20), *C. barbata* L. (Figs. 33–35), *C. baumgartenii* J. Becker (Figs. 57, 58), *C. hagiela* Boiss. (Figs. 31, 32), *C. rhomboidalis* L. (Figs. 36–38), and *C. rotundifolia* L. (Figs. 39–41), is illustrated here in LM, SEM, and TEM. With the exception



FIGURES 7–15. SEM and TEM of *Campanula* pollen. 7-12. *C. exigua.*—7. SEM of pantoporate grain.—8. SEM of tectum.—9. SEM of tectum from another collection (see Table 1).—10. TEM of tangential section. Note tectal perforations and the large area occupied by columellae cut at right angle to their long axes.—11. TEM of radial section. Note prominent columellae, some of which project through tectum.—12. TEM of section of whole grain. Note buildup of endexine near apertures. 13–15. *C. griffinii.*—13. SEM of whole grain. Note larger and fewer apertures than in the remaining pantoporate species.—14. SEM of tectum.—15. SEM of tectum from another collection (see Table 1). Scale bars = 1 μm unless otherwise indicated.



FIGURES 16–23. SEM and TEM of *Campanula* pollen. 16–20. *C. angustiflora*. —16. SEM of zonoporate grains. Note irregularity of pore distribution and size. —17. SEM of tectum. —18. TEM of section of whole grain. The fact that the four visible apertures are similar in size indicates that the section is close to being parallel with the actual equator of the grain. If there are apertures on the right side they are well above or below the equator. —19. TEM of radial section including part of pore. Note that some columellae project through the tectum. —20. TEM of tangential section. Compare columellae size and area occupied with Figures 4 and 10. 21–23. *C. sharsmithiae*. —21. SEM of pantoporate grains. —22. TEM of radial section. The thickened and lamellate endexine indicates proximity to an aperture. —23. SEM of tectum. Compare with tectum of *C. angustiflora*, Figure 17. Scale bars = 1 μm unless otherwise indicated.

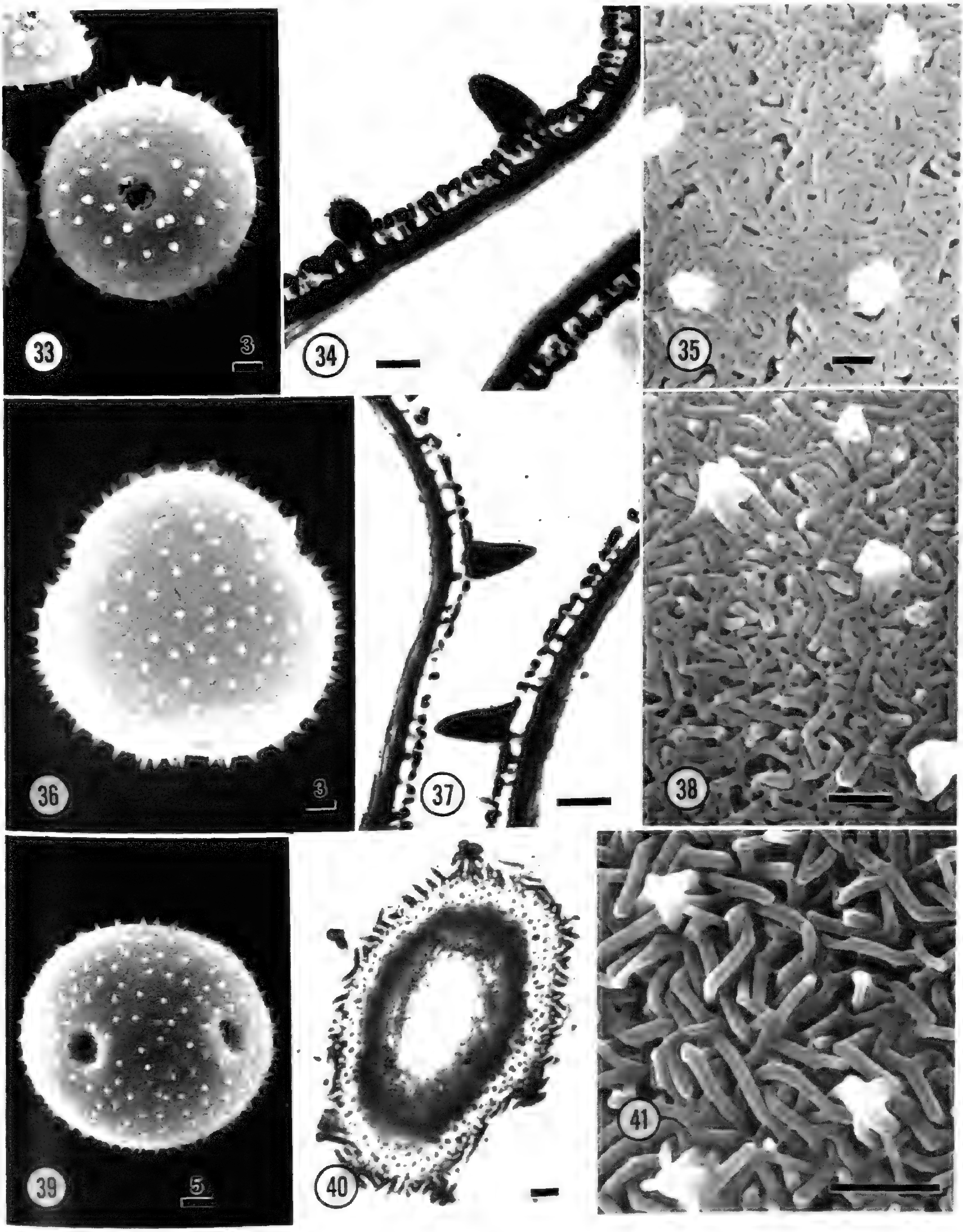


FIGURES 24–32. SEM and TEM of *Campanula* pollen. 24–27. *C. californica*.—24. SEM of pantoporate grain. Note long spines.—25. SEM of tectum with part of pore.—26. TEM of tangential section. Compare the diameter of these columellae with those in Figure 10 of *C. exigua* and in Figure 37 of *C. rotundifolia*.—27. TEM of slightly oblique radial sections of two grains. Note elongate columellae and the direct connection with spinules. 28–30. *C. alpina*.—28. SEM of zonoporate grain in equatorial view.—29. SEM of tectum with pore. Note direct relationship of spines with rods.—30. TEM of oblique sections of two grains. 31, 32. *C. hagiela*.—31. SEM of tectum. Note small irregular-sized spinules and lack of distinction of rods.—32. TEM of radial section of collapsed grain including two walls. Note well-developed foot layer, small columellae, and almost continuous tectum. Scale bars = 1 μm unless otherwise indicated.

of *C. angustiflora*, discussed separately below, the exines of the above species are similar: irregularly oriented rods that are distinct, e.g., Figure 41, or barely visible, e.g., Figure 31, and poorly developed or short columellae with the foot layer/endexine the predominant component (Figs. 30, 32, 34, 37, 40).

Campanula rhomboidalis (Figs. 36–38) has pollen with three pores on the equator of the grain and a tectum (Fig. 38) that is representative of the genus. In TEM (Fig. 37) the most prominent unit is the foot layer/endexine, while the columellae are very short.

Of the zooporate species examined in TEM,



FIGURES 33–41. SEM and TEM of *Campanula* pollen. 33–35. *C. barbata.* —33. SEM of zonoporate grain. —34. TEM of radial section.—35. SEM of tectum. 36–38. *C. rhomboidalis.* —36. SEM of polar view of 3-porate grain. —37. TEM of slightly oblique radial sections of two grains. —38. SEM of tectum. 39–41. *C. rotundifolia.* —39. SEM of equatorial view of (probably) 4-zonoporate grain. —40. TEM of tangential section. The most prominent component is the foot layer.—41. SEM of tectum. Scale bars = 1 μm unless otherwise indicated.

Campanula barbata (Fig. 34) has the most well-defined, albeit short, columellae.

Although the pollen of *Campanula angustiflora* (Figs. 16–20) is zonoporate, the higher number of pores (4–6) and their somewhat irregular distribution—not necessarily equidistant from each other and not all on the equator—distinguishes this pollen from many zonoporate types. Moreover, the tectum and exine structure link this annual to the pantoporate ones. Some grains of *C. angustiflora* (Fig. 17) have a tectum that is almost indistinguishable from some grains of *C. sharsmithiae* (Fig. 23)—both have irregularly shaped elements in addition to rods. Most likely these elements are derivatives of the horizontal rods; perhaps they are only the free tips. Clearly, the exine structure is more similar to that of the pantoporate species than to the zonoporate species: elongate columellae in *C. angustiflora* (Fig. 19) project through the tectum to form spinules like the pantoporate taxa (Fig. 22).

For purposes of comparison, species of three other genera of Campanulaceae are illustrated here: *Codonopsis convolvulacea* Kurs (Figs. 42–44), *Githopsis pulchella* Vatke (Figs. 45–47), and *Wahlenbergia linarioides* DC. (Figs. 48–50).

Codonopsis convolvulacea (Figs. 42–44) is 7-zonocolpate with short colpi and a tectum with densely spaced rods and large spinules. In TEM (Fig. 44), however, it is distinct from most Campanulaceae: a well-defined endexine, no foot layer, and columellae that appear to terminate abruptly, with an outer irregular layer seemingly composed of very short columellae connected to the rods. Some inner columellae narrow at the interface and then become expanded again in the outer layer of columellae. None of the grains examined in TEM had a foot-layer, and the columellae extended as such to the endexine. *Codonopsis bulleyana* Forrest ex Diels, Figures 51 and 52, also examined in TEM but not illustrated here, has a very generalized exine structure with a definite foot layer and simple columellae (Nowicke, unpublished data).

Githopsis pulchella (Figs. 45–47) is 6–7(–8)-zonoporate, as in other species of the genus (Morin, 1983), with a tectum remarkably similar to *Campanula angustiflora* (Fig. 17) and *C. sharsmithiae* (Fig. 23) in which the rods appear more erect. The fact that the radial section in Figure 47 is somewhat oblique has enhanced the thickness of the foot layer/endexine and obscured the continuity of most columellae as spinules. Other sections (Nowicke, unpublished) show most, if not all, columellae projecting through the tectum. Note also the resemblance of the inner surface of the tectum in the lower grain in Figure 47 to *Codonopsis convolvulaceae* (Fig. 44).

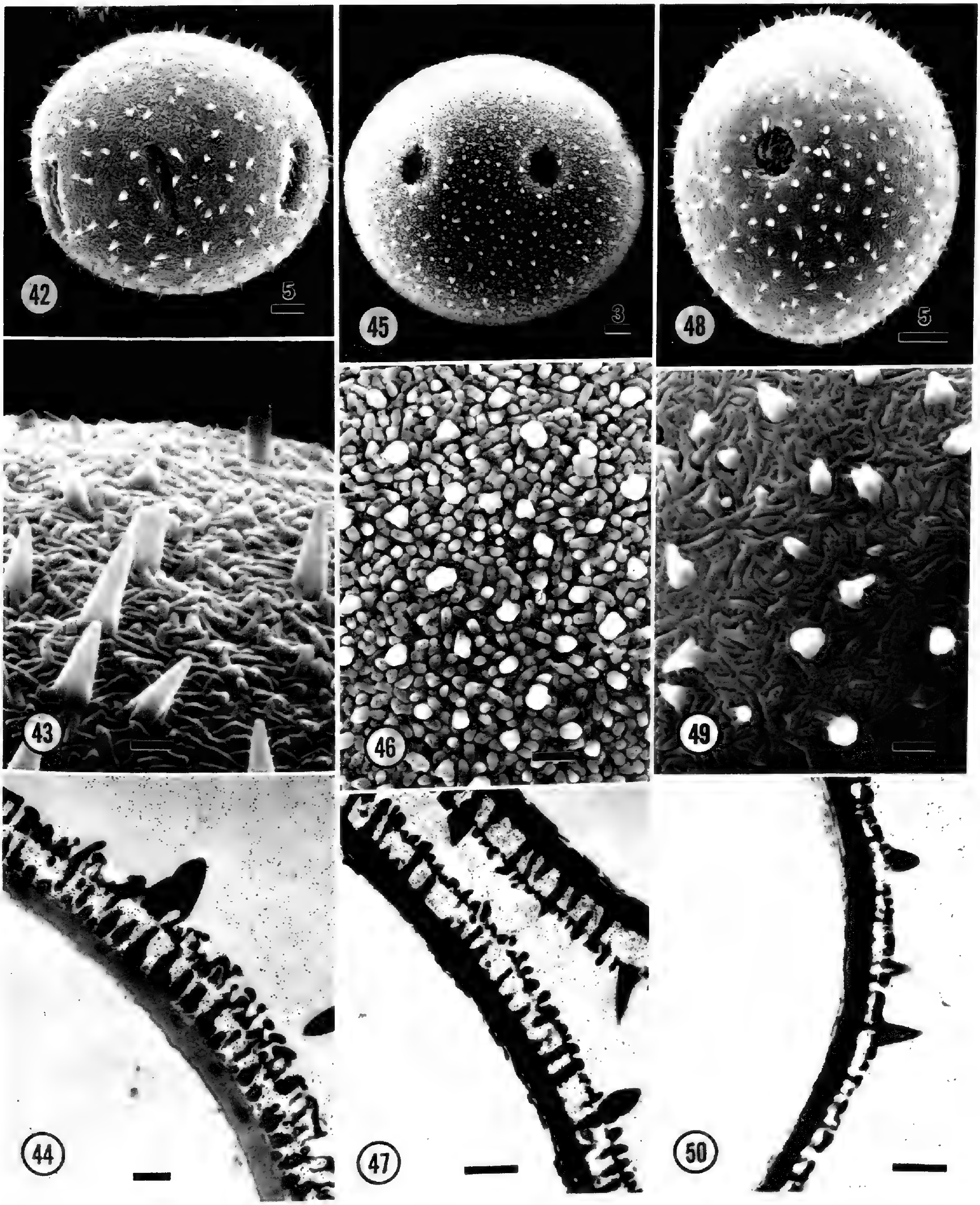
The pollen of *Wahlenbergia linarioides* (Figs. 48–50) is 3-zonoporate with a typically campanulaceous tectum and exine structure.

As part of an earlier study (Nowicke et al., 1986) of substructure of two distinct pollen types (a compound layer of striae [= lirae] and a derived triangular array) that occurred together in a number of families, exines of Berberidaceae, Cistaceae, Euphorbiaceae, and Geraniaceae were partially degraded by plasma-ashing (see Materials and Methods). To better judge the effect of plasma-ashing on these two pollen types, additional exines, including species of Campanulaceae, were ashed and examined in SEM. Control (nonashed) and ashed exines of *Codonopsis bulleyana* (Figs. 51–53), *Campanula medium* (Figs. 54–56), and *C. baumgarteni* (Figs. 57–59) are illustrated in high-magnification SEMs. In the two *Campanula* species, plasma-ashing (Figs. 56, 59) clearly shows the rod-like substructure of the spinules as well as the tectum. In *Codonopsis bulleyana,* however, there are no spinules, and in the control there is no evidence of rods (Figs. 51, 52), unlike in a second species, *Codonopsis convolvulaceae* (Figs. 39–41). After plasma-ashing for 60 minutes, a network (Fig. 53), not unlike the rods in typical campanulaceous tecta, is evident. The small protuberances could be interpreted as vestiges of the free tip of many rods. Thus the tectum of *C. bulleyana* (Fig. 52) may represent a reduced stage in which the identity of the rods (as well as spinules) has, for all intents and purposes, been lost, or it may represent a primitive state in which these elements have not yet become differentiated.

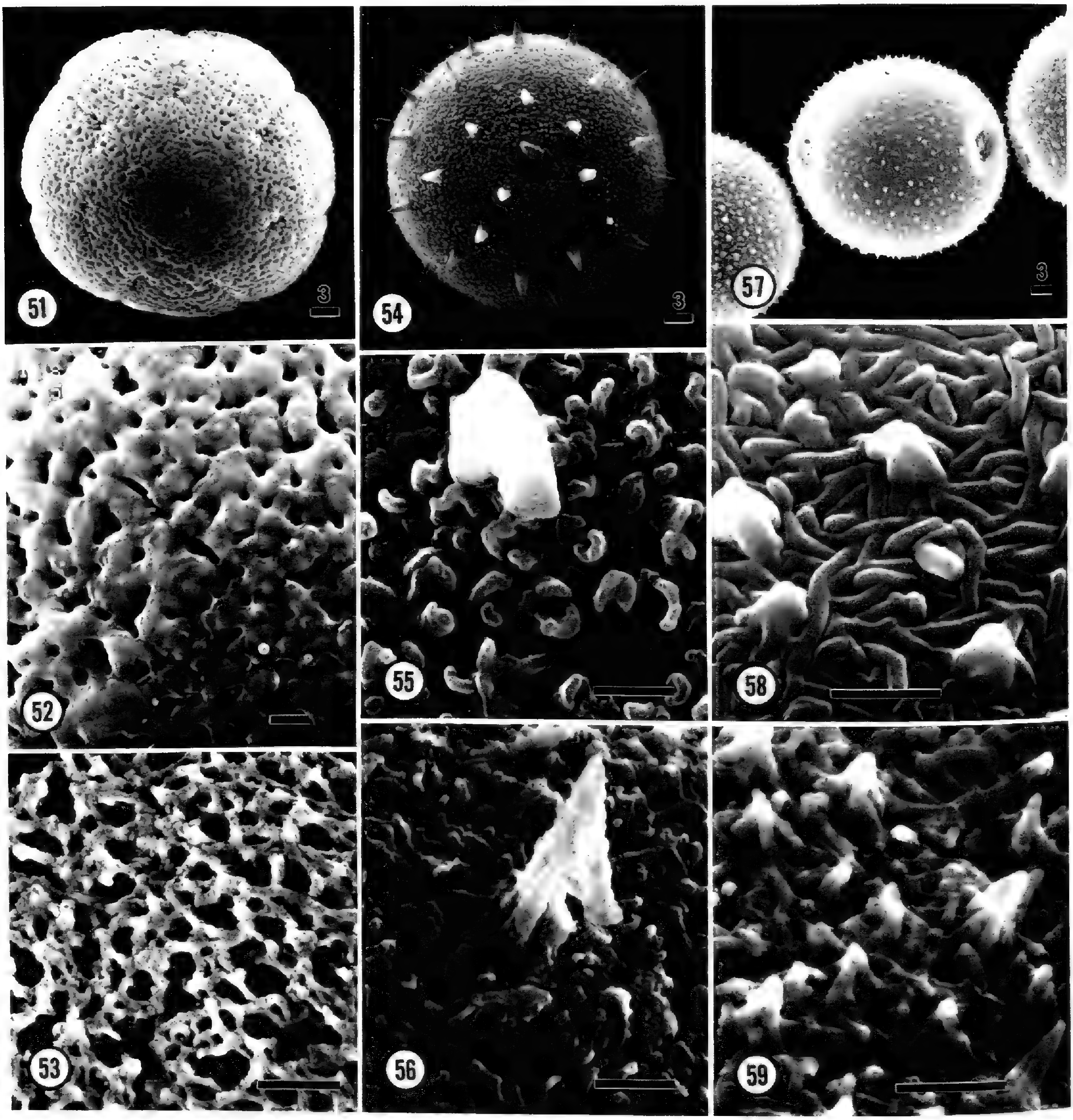
DISCUSSION

For the most part our results agree with those of Dunbar (1984), who characterized the pollen of *Campanula* as having bacula that "are generally short and stubble-like except in one species where they are high." The exception to which she referred is *C. americana.* Dunbar, although aware of the existence of the pantoporate California species, had no opportunity (apparently) to examine them in thin section.

The relationship between *Campanula americana* and the four pantoporate California species is perplexing. Although the "microperforate" tectum of *C. americana* distinguishes it from the California species, all five species share two very restricted, at least in *Campanula,* pollen characters—pantoporate aperture type and elongate col-



FIGURES 42–50. SEM and TEM of Campanulaceae pollen. 42–44. *Codonopsis convolvulacea*.—42. SEM of equatorial view of 7–8-brevicolpate grain.—43. SEM of tectum showing elongate spines and distinct, interwoven rods.—44. TEM of slightly oblique radial section. Note unusual structure of ektexine: the apparent absence of a foot layer, the truncated columellae, and the irregular tectum. Compare this species with *Codonopsis bulleyana* (Figs. 51, 52). 45–47. *Githopsis pulchella*.—45. SEM of slightly oblique view of 5–7-zonoporate grain.—46. SEM of tectum. Compare with *C. angustiflora* (Fig. 17) and *C. sharsmithiae* (Fig. 23).—47. TEM of slightly oblique radial sections of two grains. The electron density of the endexine is so similar to that of the foot layer that their common boundary is difficult to discern, but the endexine is thicker; note that some columellae project through tectum to form core of some spinules. 48–50. *Wahlenbergia linarioides*.—48. SEM of equatorial view of 3-zonoporate grain.—49. SEM of tectum.—50. TEM of radial section. Note thick foot layer, diminutive columellae, and spinules that are not extensions of columellae. Scale bars = 1 μm unless otherwise indicated.



FIGURES 51–59. SEMs of control and plasma-ashed exines of *Codonopsis* and *Campanula*. 51–53. *Codonopsis bulleyana*.—51. Control. Slightly oblique polar view showing seven colpi.—52. Control. Tectum.—53. Exine plasma-ashed for 90 minutes. See legend of Figure 59. 54–56. *Campanula medium*.—54. Control. Whole grain.—55. Control. Tectum including large spinule.—56. Exine plasma-ashed for 180 minutes. Note that at least part of spinule is a continuation of rods. 57–59. *Campanula baumgartenii*.—57. Control. Whole grain plus parts of two others.—58. Control. Tectum. 59. Exine plasma-ashed for 60 minutes. Plasma-ashing produces skeletonlike exines; in Figure 56 the very prominent spinule appears to be the result of at least four rods coalescing, but the remainder of the tectum is very similar to that in *Codonopsis bulleyana* in Figure 53. In fact, the fundamental structure of the tectum in Figure 53 is not very different from that in Figure 56. When Figure 58 of the control of *Campanula baumgartenii* is compared with the plasma-ashed tectum in Figure 59, the spinules are clearly the result of coalescing of several rods. Scale bars = 1 μm unless otherwise indicated.

umellae that project through the tectum to form the core of most spinules.

The most obvious explanation, and the easiest to dismiss for various reasons, is that the five pantoporate species are closely related. The difference in habit is conspicuous: *Campanula americana* grows up to 2 m tall and has leaves 7–15 cm long (Gleason, 1952; Shetler, 1958, 1962, 1963; Baskin & Baskin, 1984); the California species are 2–25(–40) cm tall with leaves < 11 mm long, except for *C. californica*, which has leaves up to 25 mm long (Munz & Keck, 1973). Small (1903), in his *Flora of the Southeastern United States*, elevated *C. americana* to generic status as *Cam-*

panulastrum americanum (L.) Small, based on its rotate corolla, recurved style, and seemingly spicate inflorescence versus the campanulate corolla, erect style, and mostly terminal flowers in the remaining campanulas (the inflorescence of *C. americana* is basically cymose, as in many campanulas, but is divaricately branched, appearing spicate, racemose, or paniculate (Shetler, 1958). Subsequent authors have not followed Small's treatment, although Shetler & Matthews (1967) argued at one point for its recognition.

The five pantoporate species do not group naturally by the chromosome numbers that have been reported: *Campanula americana* is $n = 29$ (Gadella, 1964; Shetler & Matthews, in 1964 unpublished count), unique in the genus (Gadella, 1964); *C. exigua*, *C. griffinii*, and *C. sharsmithiae* are $n = 17$ (Morin, 1980); *C. angustiflora* is $n = 15$; and *C. californica* has, apparently, not been counted. In a cytological study of 77 species of *Campanula* (Gadella, 1964), the range of diploid numbers was 16 to 102, with 45 species having $2n = 34$, six with $2n = 20$, and another six with $2n = 68$. The relatively high haploid number of *C. americana* suggests allopolyploidy, as does the robust habit and high number of pollen apertures. Conversely, the more diminutive habit of the California pantoporate species and the lower number of apertures (*C. sharsmithiae* excepted) suggest that their numbers are diploid.

Polyploidy is frequently correlated with larger pollen, but this is not the case in these five campanulas: the pollen of *C. sharsmithiae* and of one collection of *C. exigua* (*Sharsmith & Sharsmith 3358*) is just as large or slightly larger than that of *C. americana*. In fact, all 11 collections of pantoporate species examined (Table 1) have overlapping size measurements.

It is unlikely that the pantoporate aperture type and the prominent columellae are genetically linked—prominent columellae occur in other genera of the Campanuloidae that have equatorial apertures, e.g., *Githopsis pulchella* (Fig. 47).

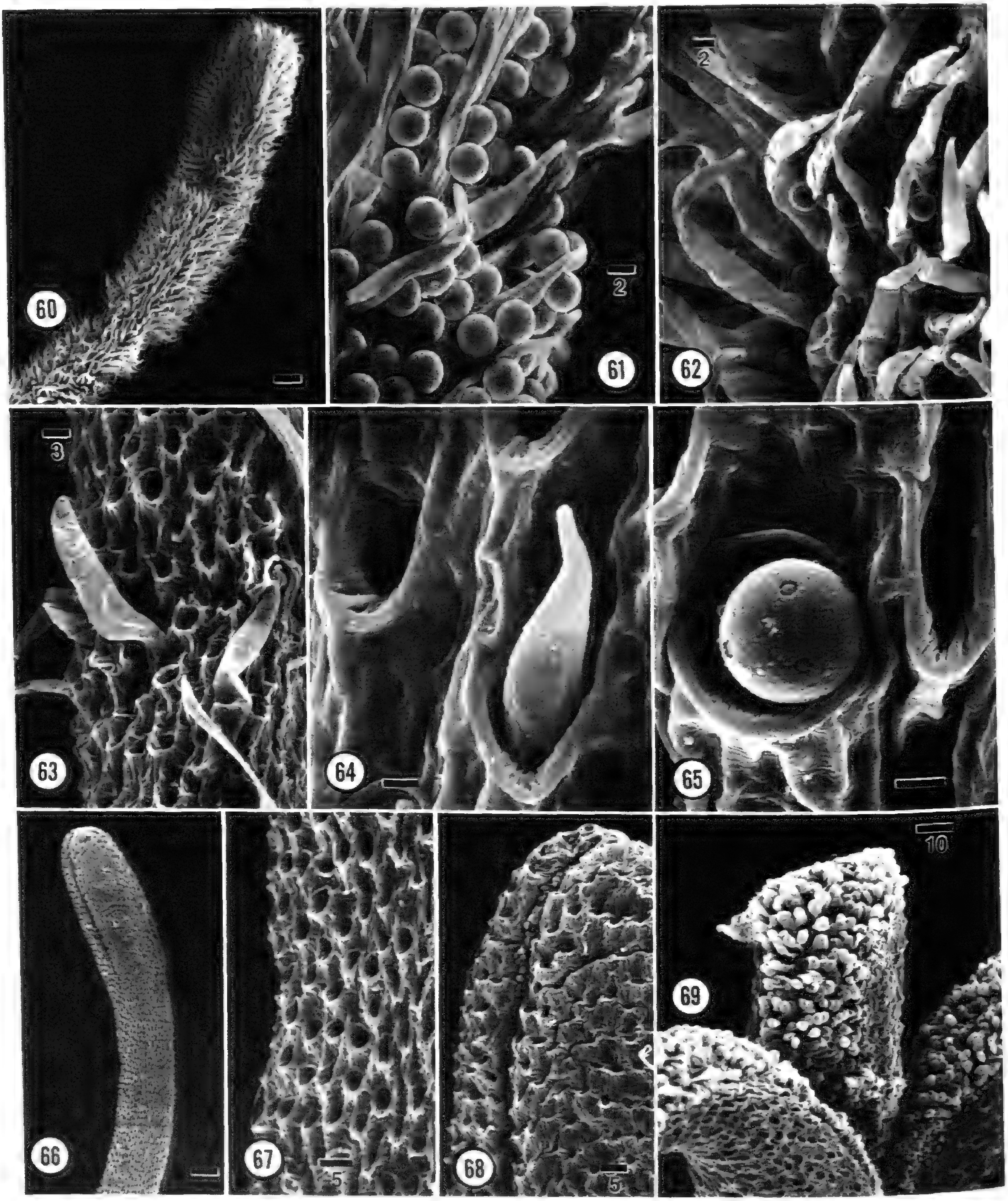
In Campanulaceae, however, all species reported to have relatively high or elongate columellae also have a relatively high number of apertures. Dunbar (1984) reported high columellae for *Githopsis calycina*, *Cyananthus incanus*, and *Codonopsis clematidea*, which are 6-porate, 9-colpate, and 8-colpate, respectively. Perhaps a greater number of apertures makes the exine more vulnerable to collapse, and selective pressures have resulted in a more rigid wall by means of elongate columellae.

We have arrived at much the same conclusion that Morin (1980) did: pantoporate apertures (and well-developed columellae) have evolved independently at least twice in *Campanula*. Admittedly, this explanation only begs the next question—why, in a large family, should pantoporate apertures evolve twice in the North American species of one genus and be absent in all the other taxa, insofar as they are known?

That the Campanuloideae are a closely related assemblage of species is suggested by the unusual and complex pollination mechanism involving retractile pollen-collecting hairs that apparently is common to all genera and species (reviewed by Shetler, 1979; see also Carolin, 1960, and Lloyd & Yates, 1982). Figures 60–69 of *C. americana* document the stages in pollination: Figure 60 shows a mature style just before anther dehiscence; Figure 61 illustrates the condition just after dehiscence when the concomitant elongation of the lower part of the style causes hairs to "sweep up" pollen; Figure 62 shows a later stage in which much of the pollen has been removed; Figure 63 is a low magnification SEM of a style with most of hairs already retracted; Figure 64 shows two hairs, one (upper) completely invaginated, another in the last stage of invagination; in Figure 65 a pollen grain is partially in the basal lumen; Figures 66–68 show the style with all hairs invaginated and stigmas still not spread; finally, in Figure 69 the stigmatic lobes have been spread, exposing stigmatic surfaces. The invagination mechanism and this sequence are common to all species examined thus far in SEM, some 30 species from different genera (Shetler, unpublished), and thus would appear to be common throughout the Campanuloideae. The mechanism is not known to occur in the Lobelioideae or any other plant family.

The adaptive value of the collecting hairs and their retractile mechanism, unique in the plant kingdom (Uphof, 1962), has long been a matter of speculation but remains to be explained satisfactorily (see Shetler, 1979, for historical review). Although the function of the collecting hairs as a mechanism for indirectly presenting pollen to pollinators is long established, and various workers have demonstrated a relationship between insect activity and the pace of hair retraction as well as pollen removal, there has not been agreement on the exact nature of the relationship between insect activity on the one hand and hair retraction and pollen removal on the other hand.

The bellflowers (Campanuloideae) are all protandrous, with the pollen being swept from the introrse anthers onto the style by the collecting hairs as the flower bud opens and the style elon-



FIGURES 60–69. SEM of pollen collecting hairs of *Campanula americana*. —60. Style with hairs before anthers have dehisced. ×20. —61. Style showing numerous collecting hairs and pollen grains. ×260.—62. Style at later stage, from which most pollen has been removed. ×200.—63. Style at still later stage, in which most of collecting hairs have already invaginated. ×175.—64. Collecting hair in last stage of invagination. ×750.—65. Pollen grain partially invaginated. ×1,000. —66. Style with all hairs invaginated, giving a "pitted" look; stigmas still closed. ×20. —67. See legend of Figure 66. ×110. —68. See legend of Figure 66. ×100.—69. Open stigmas. ×75. Scale bars = 0.5 mm for Figures 60, 66; scale bars = 100 μm for Figures 61–65, 67–69.

gates. When the flower opens the pollen appears as a cylinder around the style reaching to the mouth of the tube or projecting beyond in species with rotate corollas, e.g., *C. americana*. The hairs gradually retract from the top of the style downward. In accessing nectar located between the ovary and the expanded filament bases, the pollinators also appear to remove pollen from the top down. Usually, all hairs are invaginated and all pollen removed before the stigmas spread and expose their surfaces to begin the pistillate phase of the flower.

Kirchner (1897) was the first to suggest that insects could only gather pollen *after* the collecting hairs had retracted and released it. More recently, Carolin (1960) came to the same conclusion, indicating that the pollen could be dislodged by the insects much more easily after the hairs collapsed. Previous observations of *C. americana* and *C. rotundifolia* sens. lat. by Shetler (1958, 1962, 1982) indicate, however, that the hairs retract as the pollen is removed, not before it is removed, and that both hair retraction and pollen removal are slowed when insect activity is absent or limited.

In a study of intrasexual selection and the segregation of pollen and stigma in hermaphroditic plants, Lloyd & Yates (1982) used as their example *Wahlenbergia albomarginata* Hooker, an endemic New Zealand species of this large and wide-ranging genus of Southern Hemisphere bellflowers, which have the typical collecting-hair mechanism. They were able to elucidate more precisely the hair-retracting process, showing that it really is a combination of invagination and telescoping or retracting. They also found that pollen was difficult to remove forcibly, with a fine brush, from the style where the hairs had not yet retracted, but in those cases where it came off easily the hairs proved to have been already retracted. They stated (Lloyd & Yates, 1982: 908) that their observations show that in this species ". . . retraction of the hairs normally precedes the removal of the pollen and therefore supports the hypothesis that retraction facilitates pollen removal."

The evidence presented, however, is not altogether convincing when they say, "The pollen-collecting hairs are usually present among the pollen on those parts of the style which are still abundantly clothed with pollen, but they have retracted into the style, on those parts of the style from which pollen has been removed." This begs the question of which disappears first. They then cite their figure 2, where they explain away an SEM micrograph (fig. 2c) that shows extended hairs without pollen present, as having lost the pollen in preparation. They conclude (Lloyd & Yates 1982: 908) that the collecting hairs function only to collect pollen and are actually detrimental to pollen removal by insects and that "the progressive retraction of the hairs down the style allows pollen to be gradually released from one flower in small increments throughout the male phase." In evolutionary terms, they speculate that this gradual-release mechanism and a prolonged male phase, which "have the effect of spreading the presentation of pollen in time" and increasing paternal fitness, may be brought about through intrasexual selection.

Richardson & Stephenson (1989), in their recent, controlled observations and experiments with *Campanula rapunculoides* L., found that the "duration of the staminate phase was related to the rate of pollen removal" (p. 535). In general, their findings with respect to the relative duration of the staminate and pistillate phases were consistent with Shetler's findings for *C. americana*. They concur with Lloyd and Yates, however, on the difficulty of removing pollen before the hairs have invaginated and also with their explanation of the gradual retraction of hairs from the stigmatic end downward as a means of reducing the amount of pollen that can be removed in a single insect visit, thus constituting a mechanism for releasing the pollen load incrementally.

Whether the conclusions and hypotheses of Lloyd & Yates (1982) are directly applicable to *Campanula americana* remains unanswered, but one aspect that neither they nor Richardson & Stephenson (1989) mention is the trapping of pollen grains in the basal cavities left by the invaginated hairs (Fig. 65; and Shetler, 1982: fig. 8). This phenomenon has been documented by Shetler (1979, 1982, and unpublished data) for many bellflower species.

We regard the question of the dependence of pollen removal on hair invagination still open and unresolved. Until the actual triggering mechanism (for hair invagination) is understood, the precise relationship of hair invagination to pollen removal will remain debatable. Preliminary unpublished studies by Shetler of *Campanula rotundifolia* show that pollen is removed while collecting hairs are still fully extended, and that individual pollen grains can be "pulled into" the large basal lumina of retracted hairs. (Styles at three stages of maturation from field collections preserved in FAA were embedded in paraffin and thick-sectioned.) Furthermore, Shetler's (1958, 1962, 1982) observations of *C. americana* and *C. rotundifolia* that collecting hairs disappear more slowly when there is little or no insect activity to remove pollen require explanation, and it would appear that Richardson and Stephenson have made similar observations of *C. rapunculoides*.

The palynological data presented here confirm the rarity of the pantoporate aperture type in Campanulaceae, i.e., 34 of the original total of 39 species examined had apertures placed on the equator of the grain. The distinction between pantoporate and zonoporate aperture types is supported by differences in exine structure: well-developed, projecting columellae in the former versus reduced or short columellae and a thicker foot layer in the latter. The finely perforated tectum and very large columellae of *C. americana* appear to be unique in the genus, if not in the family, and, along with its unique chromosome number ($n = 29$) and morphology, emphasize the distinctiveness of this species. The pantoporate pollen of *C. californica,* in which neither the distribution nor size of the pores is uniform, suggests a transition stage between panto- and zonoporate types. The zonoporate annual *C. angustiflora* is clearly allied to the pantoporate *C. sharsmithiae* in tectum sculpture and exine structure. The irregular distribution and higher number of pores in the former species could also be interpreted as a transition stage between the pantoporate and zonoporate conditions.

ABOUT THE FIGURES

The collections illustrated are given in the Figure(s) column in Table 1. Scales = 1 micron unless indicated otherwise. A number above the scale bar means the length of the bar must be divided by that number in calculating the magnification. For example, in Figure 1, the actual magnification is ×1,200, but it is impossible to cut accurately a bar 1.2 mm long; so a bar was cut 6 mm long and the factor 5 placed above: 6 mm (or 6,000 microns)/5 = 1,200.

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SUMMARY OF LEAVES IN THE GENERA OF MALOIDEAE (ROSACEAE)[1]

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ABSTRACT

The persistence, complexity, lobing, margins, venation, texture, shape, adaxial glands, and heteroblastic nature of leaves are summarized for all 28 genera of Maloideae. The leaves can be simple with entire, toothed, or pinnately lobed margins, or they can be pinnately compound. They can be deciduous to evergreen, thin and membranaceous to very coriaceous; they have either camptodromous or craspedodromous secondary venation and come in a wide variety of shapes. Leaves of mature foliage on short shoots can differ markedly from those on juvenile or long shoots. The amount of variation within a genus is often correlated with the number of species, with the large genera *Malus*, *Pyrus*, *Aria*, and *Crataegus* having the greatest diversity. Within a genus only a limited number of leaf types occur. The diversity of leaves in Maloideae may be due to a multifarious original gene pool that arose with the polychotomous, amphipolyploid origin of the subfamily resulting from hybridization between early members of the Spiraeoideae and Amygdaloideae.

Maloideae are a large subfamily of Rosaceae with 28 genera (Robertson et al., 1991) and approximately 940 species, excluding hybrids and species of uncertain status (Phipps et al., 1990). Many Maloideae are important members of natural plant communities in the North Temperate Zone, and many are also cultivated either as ornamentals or for their edible fruits. Familiar genera include *Malus* (apples), *Pyrus* (pears), *Crataegus* (hawthorns), *Amelanchier* (shadbushes), *Cotoneaster* (cotoneasters), *Pyracantha* (firethorns), *Cydonia* (quince), *Chaenomeles* (Japanese quince), *Eriobotrya* (loquat), *Sorbus* (mountain ashes, Rowan), and *Aria* (whitebeams).

The authors are engaged in the study of generic limits and evolution in Maloideae. In a checklist of Maloideae (Phipps et al., 1990), initiated at the beginning of our studies primarily to serve as a guide to help us select taxa for examination, genera were defined using a conservative and traditional approach that represents a consensus of many mid- to late-twentieth century authors; a total of 23 genera were recognized. The results of our own research on generic limits have subsequently been published in Phipps et al. (1991) and Robertson et al. (1991); a total of 28 genera are recognized in the latter. The generic limits in Robertson et al. (1991) differ in several important aspects from the checklist. *Sorbus* sens. lat. is considered polyphyletic and the species have been reassigned to five genera: *Sorbus* sens. str., *Cormus*, *Chamaemespilus*, *Aria*, and *Torminalis*. In addition, *Eriolobus* and *Docyniopsis* are considered distinct from *Malus*, while *Micromeles* is included in *Aria* and *Stranvaesia* and *Aronia* in *Photinia*.

For our studies on generic delimitation, we have assembled a large data set of morphological characters. The present paper presents a summary of

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leaves; other papers that deal with fruits (Rohrer et al., in press), flowers, and inflorescences are in press or preparation. A more detailed account of leaves, including specimens examined, character states, and data analysis, will be presented in a later publication. This is the first attempt to evaluate leaves of Maloideae at suprageneric levels. Previous work has either been at higher levels of classification (Hickey & Wolfe, 1975) or at the generic level (Dickinson & Phipps, 1984; El-Gazzar, 1980; Merrill, 1978, 1979).

MATERIALS AND METHODS

From the nearly 1,000 species of Maloideae (Phipps et al., 1990), a subset of about 200 species representing all genera and major subgeneric groups was selected for study. Most observations for leaves were from living plants, photographs of living plants, and herbarium specimens made by us from the living collections of the Royal Botanic Gardens, Kew; Royal Botanic Garden, Edinburgh; Ventnor Botanic Garden, Isle of Wight; University of Liverpool Botanic Gardens, Ness; Long Ashton Research Station; and the Morton Arboretum. Many of the plants from these living collections were from wild collected sources, and we have checked the identifications of the plants. Additional observations were made from material examined or borrowed from herbaria, especially K, MO, and F. A summary of this data organized under nine basic characters is presented for all genera in Table 1, and complete data as well as additional characters will appear in a subsequent publication. Leaf terminology principally follows Hickey (1973, 1979). The scanning electron photomicrographs were made on an AMRAY Model 1830. The generic limits used in this summary are those adopted by Robertson et al. (1991).

RESULTS

Leaf types in Maloideae vary greatly (Table 1; Figs. 1, 3), although leaf arrangement is always alternate. Most genera and species have simple leaves, which can be entire, toothed, or pinnately lobed; palmately lobed leaves are essentially absent. The most common leaf type is simple, toothed, with camptodromous venation (Fig. 2B–E), although toothed or lobed leaves with craspedodromous venation are also frequent (Fig. 1A, D). Pinnately compound leaves occur in three genera (Fig. 1B). Variations for the different attributes are discussed in the sections below; descriptions apply to *mature foliage of short shoots*, when present; exceptions for heteroblastic leaves of long shoots and juvenile foliage are noted in the last section. It must be remembered that ecological pressures may play an important role in certain leaf features (Gabrielian, 1978), although these have been little studied.

PERSISTENCE

Because most members of Maloideae are components of the North Temperate Zone, deciduous leaves are by far the most common. However, evergreen or semi-evergreen (persistent during winter but shed as new growth appears in spring) leaves are characteristic of certain genera of Maloideae: *Chamaemeles, Dichotomanthes, Docynia, Hesperomeles, Heteromeles, Eriobotrya, Osteomeles, Pyracantha,* and *Rhaphiolepis.* Both deciduous and evergreen species are found in *Cotoneaster*, and a few species of *Photinia, Crataegus,* and *Malus* are evergreen or semi-evergreen, although most are deciduous. Evergreen leaves in Maloideae are generally found in species from tropical and subtropical regions, high elevations, and areas with a Mediterranean climate or xeric conditions.

COMPLEXITY

All genera except three have simple leaves, which can be variously lobed, toothed, or entire margined. Only *Cormus, Osteomeles,* and *Sorbus* have odd-pinnately compound leaves with a terminal leaflet (Fig. 1B). As discussed in Phipps et al. (1991) and Robertson et al. (1991), *Sorbus* and *Cormus* are closely related, while *Osteomeles* is close to *Hesperomeles* and *Crataegus.* Taxa that arose by hybridization between one parent with pinnately compound leaves and the other parent with simple leaves (i.e., ×*Sorbocotoneaster*, ×*Sorbaronia*, and the numerous hybrids between *Sorbus* and *Aria*) have leaves that are intermediate in complexity (Fig. 1C), usually with several free leaflets below and a variously lobed part above; for a detailed analysis of one such hybrid, see Hull & Smart (1984), and for a comparison of leaf architecture and ontogeny of simple, pinnate, and half-compound leaves see Merrill (1978, 1979). No leaves of Maloideae are palmately compound, such as those found in some Rosoideae.

LOBING

Some kind of lobing occurs in the mature foliage of nine of the 28 genera, although the only genera with consistently lobed leaves are *Torminalis* (Fig. 1A) and *Eriolobus*. The leaves are unlobed in nearly all species of *Pyrus*, but deeply pinnately lobed

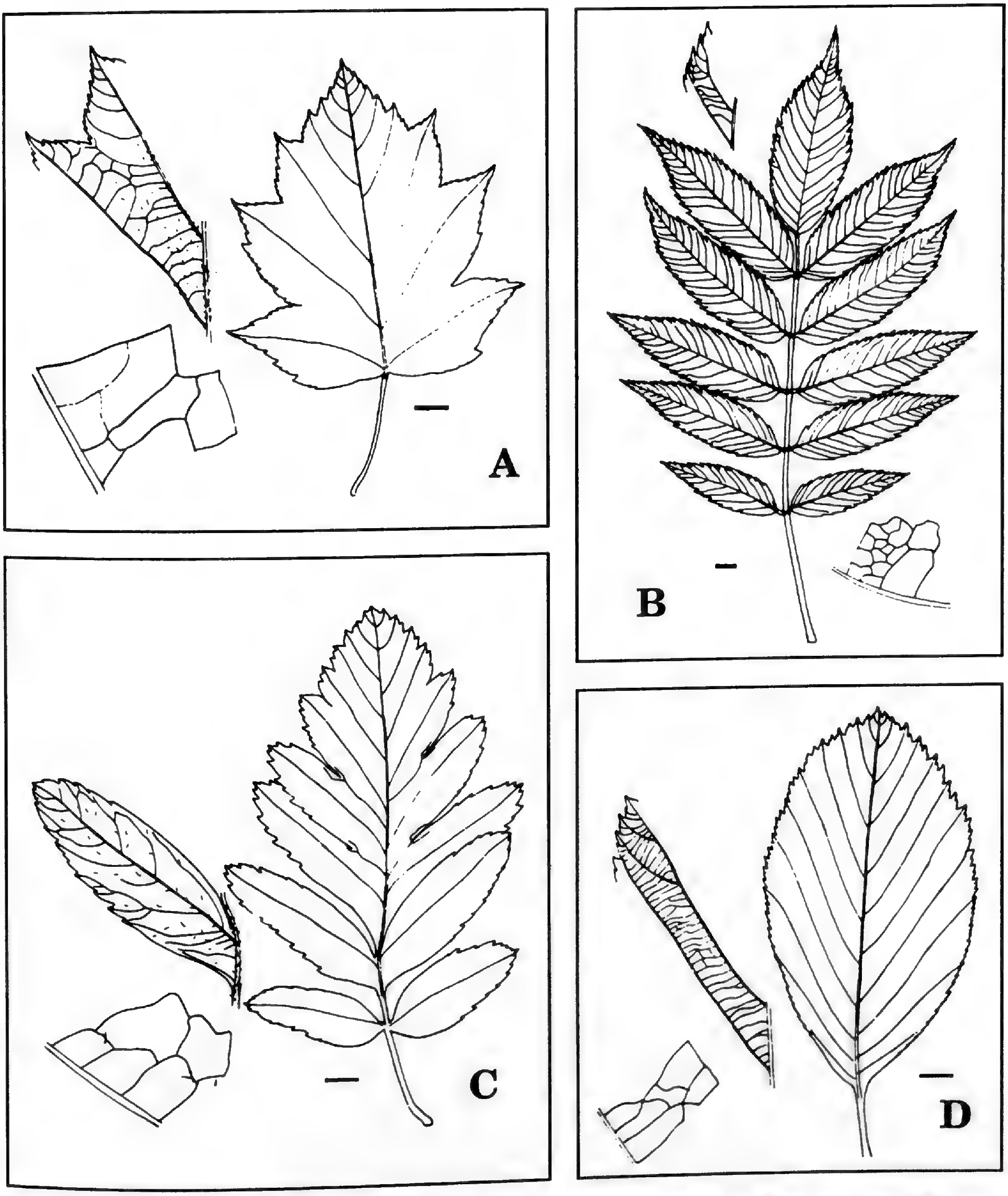

FIGURE 1. Leaf types of Maloideae.—A. Pinnately lobed, craspedodromous leaf of *Torminalis clusii* (Roemer) Robertson & Phipps.—B. Pinnately compound leaf of *Sorbus commixta* Hedlund, mature leaf.—C. Incompletely pinnately compound leaf of *Sorbus* ×*intermedia* (Ehrhart) Persoon (thought to be a hybrid between *Torminalis* or *Sorbus* sens. str. and *Aria*).—D. Toothed, craspedodromous leaf of *Aria nivea* Host. Insets show secondary and tertiary venation. Scale bar = 1 cm on whole leaves.

leaves occur on all or parts of some individuals of *P. regelii* Rehder. Occasionally slightly lobed leaves can be found in *Hesperomeles*, but they are usually unlobed. In *Docynia*, the mature foliage is unlobed with entire or serrulate margins, but the juvenile foliage is deeply pinnately lobed. Slightly lobed mature leaves occasionally occur in *Docyniopsis*, whereas juvenile leaves are prominently lobed.

Lobed leaves in Maloideae are most often associated with groups of species in *Malus*, *Crataegus*, and *Aria*. Within *Malus*, slightly to prominently lobed leaves occur at least on the long shoots

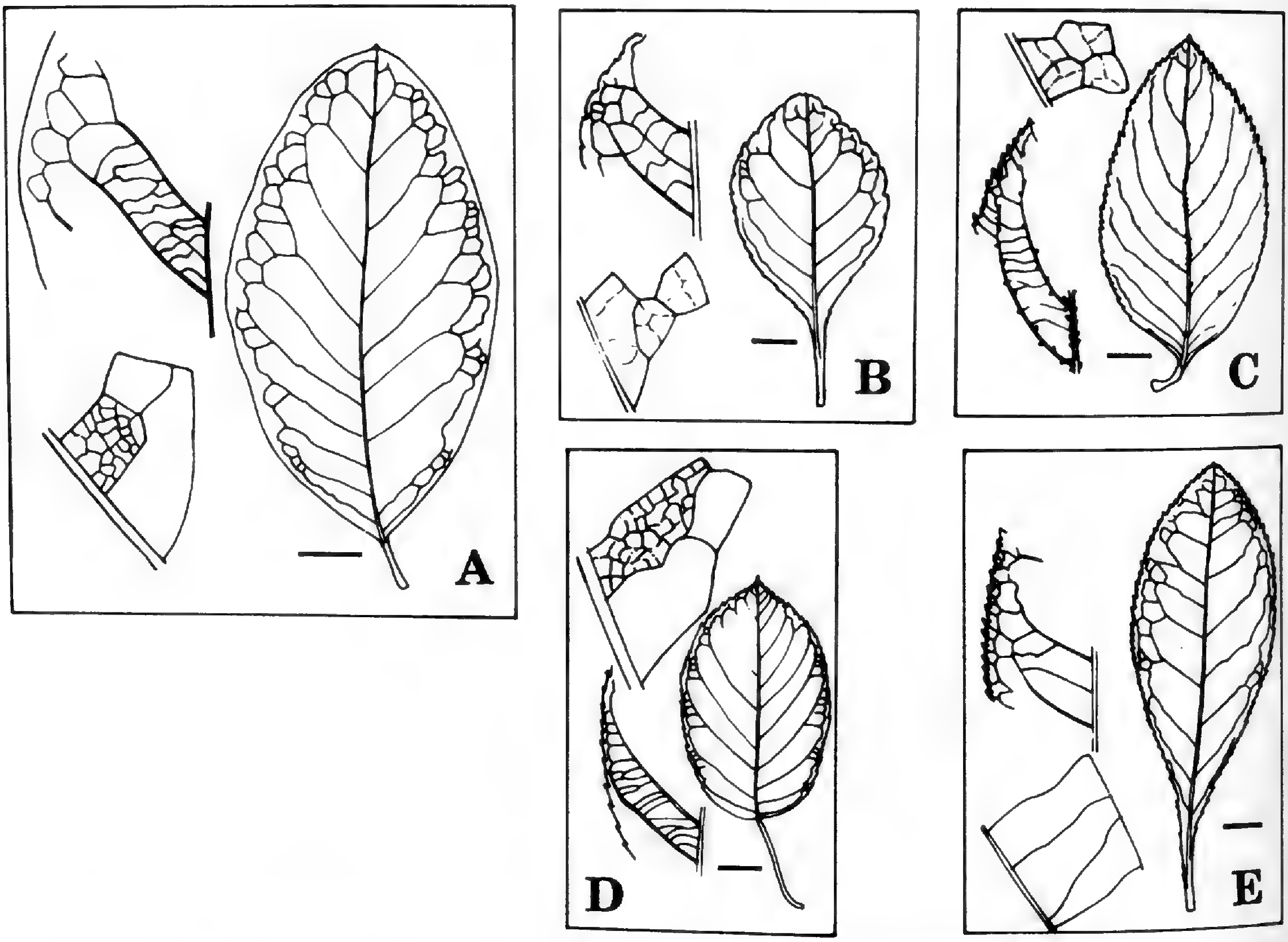

FIGURE 2. Leaves of Maloideae with camptodromous venation.—A. *Cotoneaster frigidus* Wallich ex Lindley.—B. *Chaenomeles japonica* (Thunberg) Lindley.—C. *Chamaemespilus alpina* (Miller) Robertson & Phipps.—D. *Amelanchier arborea* (Michaux f.) Fernald.—E. *Photinia lasiogyna* (Franchet) Schneider. Insets show secondary and tertiary venation. Scale bar = 1 cm on whole leaves.

and sometimes also on the short shoots of subgenus *Malus* sect. *Sieboldianae* (the section as defined in Rehder, 1940; subsections *Sieboldianae* and *Kansuenses* of Huckins, 1972), subgenus *Chloromeles*, and subgenus *Sorbomalus*. Deeply lobed leaves are found in *Crataegus* sect. *Crataegus* (following Phipps et al., 1990), which is confined to the Old World, except for *C. marshallii* Egglest. of the southeastern United States, but shallowly lobed leaves occur in many sections. Unlobed leaves are only found in a few species of *Crataegus*, for example, *C. uniflora*, *C. brachyacantha*, and *C. douglasii* var. *suksdorfii*. Most species of *Aria* have toothed, often doubly serrate or dentate leaves that are unlobed (Fig. 1D). However, slightly lobed leaves are occasionally found, for example, in *Aria nivea* Host (*Sorbus aria* (L.) Crantz) and *A. alnifolia* (Sieb. & Zucc.) Decaisne. The many species often assigned to *Aria* or *Sorbus* sect. *Aria* that have shallowly to deeply lobed leaves (see Gabrielian, 1978) are of alloploid origin between species of *Sorbus* with pinnately compound leaves or *Torminalis* with pinnately lobed leaves and *Aria* with unlobed leaves; the authors are currently working on resolving the nomenclatural problems that result when *Sorbus* is divided into five genera, following Robertson et al. (1991).

Lobing in Maloideae is nearly always pinnate. The leaves of *Eriolobus trilobatus* (Poiret) M. Roemer are deeply 3-lobed and can appear almost palmate. However, the terminal lobe is usually further divided into three lobes, and the overall lobing pattern and the secondary venation are pinnate. Occasionally, some species of *Crataegus* have leaves that are nearly palmate, but the venation is pinnate.

MARGINS

Leaves of most Maloideae are variously lobed or toothed, but *Cotoneaster* (with 264 species listed in Phipps et al., 1990) and *Cydonia* (monotypic) have consistently entire margins (Fig. 2A). *Dichotomanthes* and *Mespilus* normally have entire margins, although teeth can occasionally be found on some leaves. Species with entire margins also occur in *Docynia*, *Eriobotrya*, *Hesperomeles*, *Ma-*

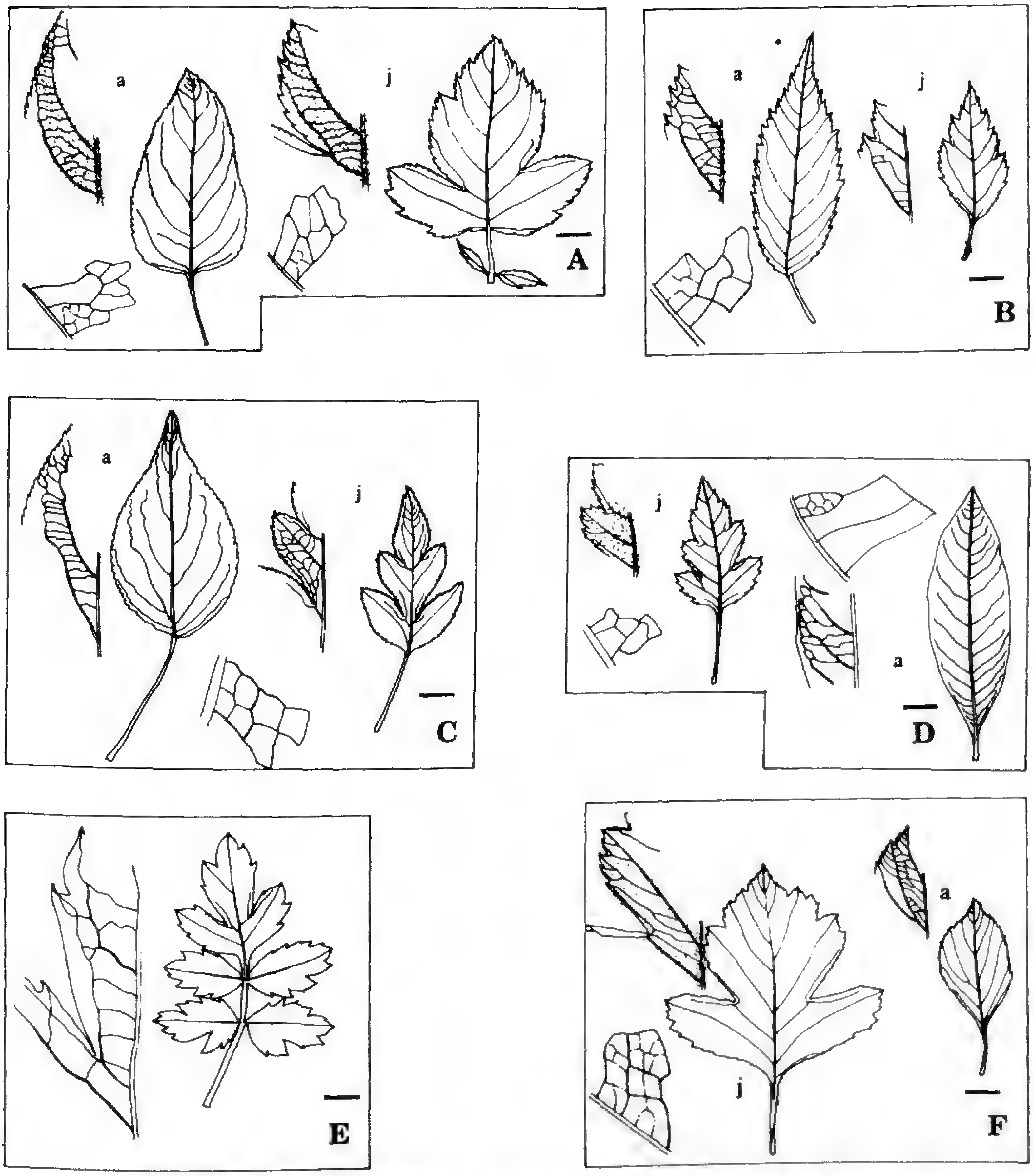

FIGURE 3. Heteroblastic foliage in Maloideae.—A. *Malus fusca* (Raf.) Schneider.—B. *Malus melliana* (Handel-Mazzetti) Rehder (*Docyniopsis*).—C. *Pyrus calleryana* Decaisne.—D. *Docynia delavayi* (Franchet) Schneider.—E. *Sorbus koehneana* Schneider.—F. *Crataegus viridis* L.—a, adult leaves.—j, juvenile leaves. Insets show secondary and tertiary venation. Scale bar = 1 cm on whole leaves.

lacomeles, *Photinia*, and *Rhaphiolepis*. The leaflets of *Osteomeles* are always entire, whereas most species of *Sorbus* have serrate leaflets; entire margins, such as found in *S. harrowiana* (Balf. f. & W. W. Sm.) Rehder, are quite rare.

The teeth of Maloideae are the rosoid type of Hickey (1973, 1979) and Hickey & Wolfe (1975), with a clear glandular apical foramen. Within Maloideae, it is more common for teeth to be more conspicuous toward the apex of the leaves, decreasing in size toward the bases (Fig. 1D), than for the teeth to be uniformly distributed from apex to base (Fig. 2E). Teeth are predominantly serrate, with a trend to crenate in some genera, most notably *Aria*, *Chaenomeles* (Fig. 2B), *Malus* (Fig. 3A-a), *Photinia*, and *Pyrus* (Fig. 3C-a), and to dentate in *Aria* and *Docyniopsis*. The size and density of teeth vary greatly in Maloideae. The

TABLE 1. Selected morphological leaf characters of the genera of Maloideae based primarily on our observations and collections of living and herbarium material. The information in all columns except the last refers to mature foliage on short shoots, when present. The generic limits and sequence of genera are from Robertson et al. (1991).

Genera	Persistence	Complexity	Lobing	Margins
Crataegus	deciduous or rarely semi-evergreen	simple	shallowly to deeply pinnately lobed or unlobed	toothed, usually serrate, rarely crenate
Mespilus	deciduous	simple	unlobed	entire or apically finely serrate
Hesperomeles	evergreen or semi-evergreen	simple	rarely slightly lobed	dentate, finely serrate, or apically crenate
Osteomeles	evergreen	pinnately compound	leaflets unlobed	leaflets entire
Amelanchier	deciduous	simple	unlobed	serrate, especially toward tip, rarely entire
Peraphyllum	deciduous	simple	unlobed	faintly serrate, especially toward tip
Malacomeles	semi-evergreen	simple	unlobed	denticulate or entire
Rhaphiolepis	evergreen	simple	unlobed	entire or serrate at least toward tip
Eriobotrya	evergreen	simple	unlobed	finely to coarsely serrate, especially toward tip, or entire
Pyrus sens. str.	deciduous	simple	unlobed or rarely deeply pinnately lobed	finely to coarsely serrate, crenate or entire
Cydonia	deciduous	simple	unlobed	entire
Pseudocydonia	deciduous or semi-evergreen	simple	unlobed	serrate with cylindrical, glandular teeth
Chaenomeles	deciduous	simple	unlobed	serrate or crenate
Docynia	evergreen or semi-evergreen	simple	unlobed	entire or serrulate
Docyniopsis	deciduous	simple	lobed or unlobed	serrate to dentate
Malus sens. str. (but including *Chloromeles* and *Sinomalus*)	deciduous	simple	lobed or unlobed	crenate or serrate
Eriolobus	deciduous	simple	deeply 3-lobed, center lobe further 3-lobed	serrate
Aria (including *Micromeles*)	deciduous	simple	unlobed to slightly lobed	serrate or crenate
Chamaemespilus	deciduous	simple	unlobed	serrate
Cormus	deciduous	pinnately compound	leaflets unlobed	leaflets serrate

TABLE 1. Extended.

Secondary venation	Texture	Shape	Adaxial glands	Heteroblastic foliage
craspedodromous in lobed leaves, camptodromous in unlobed leaves	chartaceous to coriaceous	basically rhomboid, elliptic, or ovate	absent	juvenile leaves usually deeply lobed, craspedodromous
camptodromous	chartaceous	narrowly obovate to narrowly elliptic	absent	juvenile leaves unlobed or shallowly lobed in *M. canescens*
camptodromous	coriaceous	broadly elliptic to orbicular or broadly obovate	absent	homoblastic
leaflets camptodromous	coriaceous	leaflets elliptic to oblong	present on rachis	homoblastic
camptodromous	chartaceous or coriaceous in spp. from western North America	elliptic, oblong, or ovate, sometimes broad	absent	homoblastic
camptodromous	coriaceous	narrowly obovate	absent	homoblastic
camptodromous	coriaceous	ovate, elliptic, obovate, or orbicular	absent	homoblastic
camptodromous	moderately to extremely coriaceous	narrowly to broadly elliptic or obovate	absent	homoblastic
camptodromous or craspedodromous	coriaceous	narrowly to broadly elliptic or obovate	absent	homoblastic
camptodromous or craspedodromous when lobed	chartaceous	narrowly to broadly ovate, obovate, or elliptic	present	juvenile leaves unlobed or often 1–3-lobed and craspedodromous
camptodromous	chartaceous	ovate or elliptic	absent	homoblastic
camptodromous	chartaceous	elliptic to obovate	absent	homoblastic
camptodromous	chartaceous	ovate, obovate, elliptic, or lanceolate	absent	homoblastic
camptodromous	thick-chartaceous	lanceolate, narrowly ovate or ovate	present	juvenile leaves deeply lobed, craspedodromous
craspedodromous when lobed or unlobed and camptodromous	chartaceous	ovate to broadly ovate	absent	lobed, craspedodromous
craspedodromous when lobed or unlobed and camptodromous	chartaceous	basically ovate or elliptic	present	unlobed or shallowly to deeply lobed and craspedodromous
craspedodromous	chartaceous	broadly ovate to transverse-ovate in outline	present	deeply lobed, craspedodromous
craspedodromous or camptodromous	chartaceous	ovate, elliptic, or obovate	present	homoblastic
camptodromous	chartaceous	ovate or elliptic	present	homoblastic
leaflets camptodromous	chartaceous	leaflets ovate or elliptic	present on rachis	homoblastic

TABLE 1. Continued.

Genera	Persistence	Complexity	Lobing	Margins
Torminalis	deciduous	simple	shallowly to deeply pinnately lobed	serrate or dentate
Heteromeles	evergreen	simple	unlobed	coarsely serrate
Photinia (including *Pourthiaea*, *Stranvaesia*, and *Aronia*)	deciduous, semi-evergreen or evergreen	simple	unlobed	coarsely to finely serrate or rarely crenate or margins entire
Sorbus sens. str.	deciduous or rarely semi-evergreen	pinnately compound	leaflets unlobed	leaflets serrate or rarely entire
Cotoneaster	deciduous, semi-evergreen or evergreen	simple	unlobed	entire
Pyracantha	evergreen or semi-evergreen	simple	unlobed	serrate or crenate, rarely entire
Dichotomanthes	evergreen	simple	unlobed	entire or remotely serrate above
Chamaemeles	evergreen	simple	unlobed	remotely crenate

leaves of *Heteromeles* and some species of *Eriobotrya* and *Rhaphiolepis* are coarsely serrate with large, widely spaced teeth. In *Aria* (Fig. 1D), *Chamaemespilus* (Fig. 2C), *Crataegus*, *Docyniopsis*, and *Malus*, some species have fairly large, sharp, rather closely spaced teeth. Finely serrate or crenate leaves occur in some species of *Amelanchier* (Fig. 2D), *Chaenomeles* (Fig. 2B), *Eriobotrya*, *Rhaphiolepis*, *Malus* (Fig. 3A-a), *Photinia* (Fig. 2E), and *Pyrus*. The leaves of *Chamaemeles*, *Malacomeles*, and some species of *Amelanchier* and *Hesperomeles* generally have only a small number of teeth toward the leaf apices. Differing from those of all other Maloideae are the cylindrical, gland-tipped teeth of *Pseudocydonia*. The teeth can be markedly doubly serrate or dentate in some species of *Aria*, *Crataegus*, *Docyniopsis*, and *Malus*, and a numerical leaf incision index must be used to consistently distinguish between shallowly lobed and coarsely toothed.

SECONDARY VENATION

There is a strong correlation between lobing, toothing, and type of secondary venation. Lobed leaves always have craspedodromous venation, as in *Torminalis* (Fig. 1D), *Eriolobus*, and some species of *Crataegus* and *Malus*. In most taxa, the secondary veins only go to the tips of the lobes, but in some species of *Crataegus*, *Docynia*, and *Malus* the veins also go to the base of the sinuses. The doubly toothed leaves found in some species of *Aria*, *Crataegus*, *Docyniopsis*, and *Malus* are also craspedodromous. Camptodromous venation is characteristic of leaves with simply serrate to entire margins (Fig. 2) and is the only type of venation found in 20 of the 25 genera with simple leaves. Within *Aria* some species are consistently craspedodromous, whereas others are only camptodromous. In *Crataegus* and *Malus*, some groups of species are also consistently either craspedodromous or camptodromous, but other groups have both lobed craspedodromous and unlobed camptodromous leaves on the same plant. This last situation also occurs in *Docyniopsis*. The leaflets of pinnately compound leaves are always camptodromous.

TEXTURE

Texture is somewhat correlated with persistence. Most deciduous leaves are chartaceous, with the thinnest leaves found in some species of *Amelanchier*, *Crataegus*, and *Pyrus*. In genera that have a wide ecological latitude, such as *Amelanchier*, *Crataegus*, *Pyrus*, and *Photinia*, there are trends toward coriaceous leaves in species of dry or subtropical habitats. Evergreen or at least semi-evergreen leaves are thicker and coriaceous to a greater or lesser degree, and coriaceous leaves are characteristic of *Chamaemeles*, *Eriobotrya*, *Hesperomeles*, *Heteromeles*, *Malacomeles*, *Osteomeles*, *Pyracantha*, and *Peraphyllum*.

TABLE 1. Extended, Continued.

Secondary venation	Texture	Shape	Adaxial glands	Heteroblastic foliage
craspedodromous	chartaceous	broadly ovate in outline	absent	juvenile leaves lobed, craspedodromous
camptodromous	coriaceous	narrowly elliptic or narrowly oblong	absent	homoblastic
camptodromous	chartaceous to coriaceous	ovate, elliptic, obovate, or oblong	present	homoblastic
leaflets camptodromous	chartaceous or rarely coriaceous	leaflets elliptic, ovate	present on rachis	homoblastic
camptodromous	chartaceous to coriaceous	elliptic, ovate, or obovate	absent	homoblastic
camptodromous	somewhat coriaceous	elliptic to obovate	absent	homoblastic
camptodromous	somewhat coriaceous	ovate to elliptic	absent	homoblastic
camptodromous	coriaceous	spathulate	absent	homoblastic

SHAPE

Most Maloideae have leaves that are broadly to narrowly elliptic, oblong, ovate, or less often, obovate; linear leaves are absent. A few taxa of *Crataegus* have suborbicular or even depressed ovoid outlines. Few large genera have characteristic leaf shapes, except for *Crataegus*, which tends to have leaves that are basically rhomboid with cuneate bases, although there is much variation within *Crataegus*. Although the leaves of *Cotoneaster* are always unlobed with entire margins, leaf shape shows a very wide range. *Pyrus* is also quite varied, especially in width, from lanceolate to nearly orbicular. Leaf apices are often acute to acuminate, although rounded to obtuse or emarginate tips are frequent; most of the rounded types are also mucronate. Bases are typically rounded to cuneate, with some cordate bases found in *Eriolobus* and truncate to slightly cordate bases found in *Cydonia*, *Torminalis*, and some species of *Crataegus*, *Docyniopsis*, *Malus*, and *Pyrus*. There are subtle differences in leaf shape in Maloideae that are best suited to morphometric analyses, such as those demonstrated by Dickinson (1986) and Dickinson et al. (1987) with *Crataegus*.

Leaf size varies greatly in Maloideae, but because it is generally not related to generic delimitation, size is not included in Table 1. The largest simple leaves are found in *Eriobotrya japonica*, which can be up to 27 cm long and 7 cm wide, while perhaps the smallest leaves are in some species of *Cotoneaster*, *Hesperomeles*, *Malacomeles*, and *Crataegus* series *Lacrimatae*, which are 5–10 mm long and 3–4 mm wide. The vast majority of Maloideae have leaves 3–8 cm long and 2–5 cm wide, which is small for a woody group. The pinnately compound leaves of *Sorbus* vary greatly. Average length of the complete leaf of different species can be 6–30 cm, the number of leaflets can be as few as 5 or as many as 35, and leaflet length varies from 1 to 13 cm. *Osteomeles* usually have 11–17 small leaflets, each 3–5 mm long and 1–2 mm wide.

ADAXIAL GLANDS

These glands are reddish to reddish black, cylindrical, and 0.1–0.5 mm long, and they are found along the midrib on the adaxial surface of leaves; sometimes they occur along secondary veins as well. In most previous works on Maloideae (Decaisne, 1874) or on North American woody plants (Rehder, 1940), the presence of these glands is used as a key or distinctive feature of *Aronia* (Fig. 5). On closer examination, these glands are also found in some species of *Aria*, *Chamaemespilus*, *Docynia*, *Eriolobus*, *Malus*, *Photinia* sens. str., and *Pyrus*. This is one reason why *Aronia* was not considered generically distinct from *Photinia* by Robertson et al. (1991).

Similar glands are found in clusters at the point at which leaflets attach to the rachis of pinnately compound leaves in all species of *Sorbus* and *Osteomeles*; a few small glands can occasionally be found on the midvein of leaflets in some species of *Sorbus*. The pinnately compound leaves of *Sorbaria* (Spiraeoideae) also have these glands, but we have not seen them in any members of the Amygdaloideae or Rosoideae. Intergeneric hybrids between *Aronia* (when recognized as a distinct genus), with simple leaves, and *Sorbus* sens. str., with pinnately compound leaves, always have adaxial glands on the leaves. No petiolar glands such as are common in Amygdaloideae are found in Maloideae.

HETEROBLASTIC FOLIAGE

The foliage of many Maloideae is heteroblastic, varying within individuals between juvenile and adult shoots (Fig. 3), long and short shoots, and leaves within short shoots. The leaves of juvenile and long shoots tend to be rather similar since both usually have neoformed leaves, rather than the regularly preformed leaves of short shoots. Some genera, such as *Amelanchier*, *Cotoneaster*, and *Photinia*, are homoblastic with the leaves of short shoots being the same or sometimes smaller than those of long shoots. It may turn out that some of the genera listed as homoblastic in Table 1 have heteroblastic differences when living material of additional species is examined in greater detail. (We have examined one tree of *Photinia serrulata* Lindley at the Hillier Arboretum (*Robertson 3826*, ILLS) that has sucker shoots with prominently serrately margined leaves while the leaves of normal branches have crenate margins.)

In many species of *Crataegus*, *Malus*, *Docynia*, *Docyniopsis*, and *Pyrus*, there is a fundamental difference between the leaves of short shoots and those of long shoots and/or juvenile plants. A number of species of *Crataegus* (Fig. 3F) and *Malus* (Fig. 3A) have unlobed leaves with camptodromous venation on short shoots and lobed leaves with craspedodromous venation on long shoots. Unlobed leaves are primarily characteristic of the mature foliage of *Docynia* (Fig. 3D), *Docyniopsis* (Fig. 3B), and *Pyrus* (Fig. 3C), but the juvenile foliage of at least some species of these genera is prominently lobed, as is that of some *Malus* and *Crataegus* species with unlobed mature foliage.

Not all heteroblasty in Maloideae is marked by major differences, such as lobed versus unlobed leaves. Dickinson & Phipps (1984) found differences in both size and shape on short shoots from node to node. Some species of *Aria* have leaves more deeply toothed or lobed on long shoots than on short shoots. The seedling leaves of *Sorbus* sens. str. are sometimes incompletely pinnately compound, with the terminal leaflet being deeply lobed and with secondary veins going to the sinuses as well as to the tips of the lobes (Fig. 3E). Although the leaves of *Mespilus germanica* are usually entire on both long and short shoots, occasionally toothed or even slightly lobed leaves can be found on some long shoots.

As a general rule in Maloideae, the leaves on long shoots tend to be larger and have sharper, more prominent teeth and/or deeper lobing than those on short shoots (Fig. 3); also, stipules are often larger and more persistent on long shoots. A good example of the last is *Chaenomeles*, where the long shoots have very large, persistent stipules (Weber, 1964).

DISCUSSION

The genera of Maloideae are delimited by Robertson et al. (1991) as follows: nine are monotypic, seven contain between two and four species, three have between nine and 11 species, seven have between 26 and 98 species, and only *Crataegus* and *Cotoneaster* have more than 100. Although not based primarily on leaf characters, this generic scheme, especially the division of *Sorbus* sens. lat. into five genera, has resulted in greater homogeneity of genera with regard to leaves.

The amount of foliar variation within a genus is associated with the number of species. Within the larger genera, the variation can be thought of in terms of variations on one or two themes per genus, with modifications often the result of ecological adaptations. Species of *Cotoneaster*, without exception, have leaves with entire margins and camptodromous venation, with the species differing in leaf size, shape, texture, and persistence. The leaves of *Pyrus* are generally ovate with finely reticulate veins and trends from medium to broad or narrow and from serrate to crenate to entire margins; see tables 5 and 6 in Challice & Westwood (1973) for the range of variation for some leaf characters in *Pyrus*. Most genera are, with practice, easy to recognize from the leaves alone.

By and large, however, leaves have not been used to make major subdivisions in either the subfamily or genera. Some exceptions at the generic level are *Malus*, *Crataegus*, and *Sorbus* sens. lat. All of the various subgeneric classifications of *Malus*, such as those of Koidzumi (1934), Rehder (1940), Yü & Yen (1956), Langenfeld (1971), and Huckins (1972), use leaves extensively in delimiting subgeneric taxa. The actual categories and their delimitations differ to greater or lesser extents between these authors, but in all classification

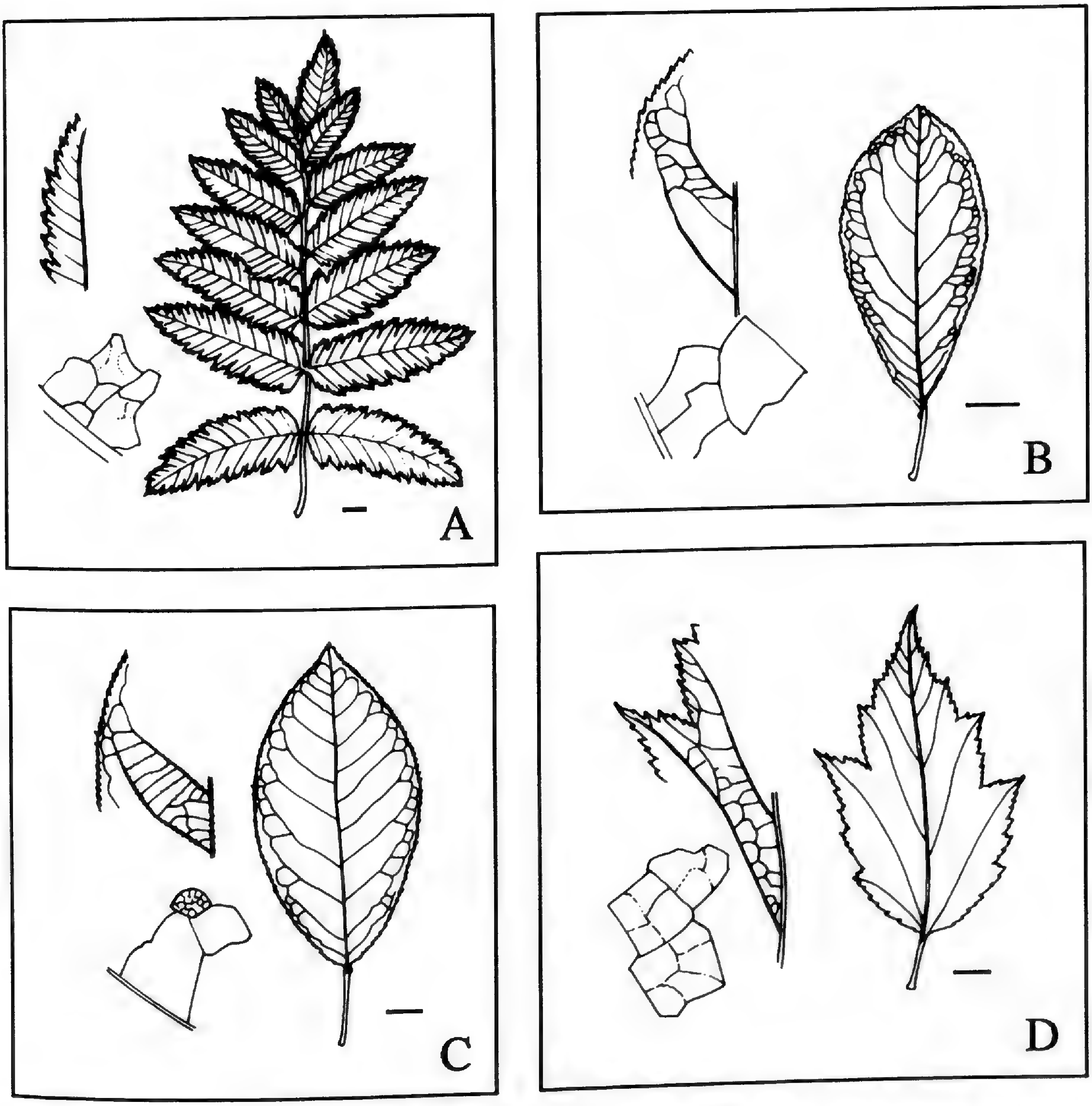

FIGURE 4. Leaves of Spiraeoideae (A, B) and Amygdaloideae (C, D).—A. *Sorbaria sorbifolia* (L.) A. Braun.—B. *Neillia sinensis* Oliver.—C. *Padus virginana* (L.) Borkhausen.—D. *Prunus domestica* L. Insets show secondary and tertiary venation. Scale bar = 1 cm on whole leaves.

schemes some subgeneric taxa only have unlobed leaves with camptodromous venation on both long and short shoots, others have unlobed leaves on short shoots and lobed leaves on long shoots, and yet others only have lobed leaves with craspedodromous venation on both long and short shoots.

Many Old World species of *Crataegus* are characterized by rather small, deeply lobed leaves with veins that extend both to the tips of the lobes and to the sinuses. Using this character, as well as cytology and geography, El-Gazzar (1980) placed these species in subgenus *Crataegus* and established subgenus *Americanae* for species with mostly unlobed leaves of the New World. Phipps (1988) found the suite of characters used by El-Gazzar to be inconsistent, while recognizing that the species from western Eurasia with deeply lobed leaves constitute a valid group, which was later recognized as section *Crataegus* in Phipps et al. (1990). The many other sections and series in *Crataegus* recognized by Phipps et al. (1990) are, at least in part, based on leaf lobing and venation.

The traditional generic delimitation of *Sorbus* sens. lat., as used by Rehder (1940), McAllister (1986), and Phipps et al. (1990), includes a wide variety of leaf types: pinnately compound, pin-

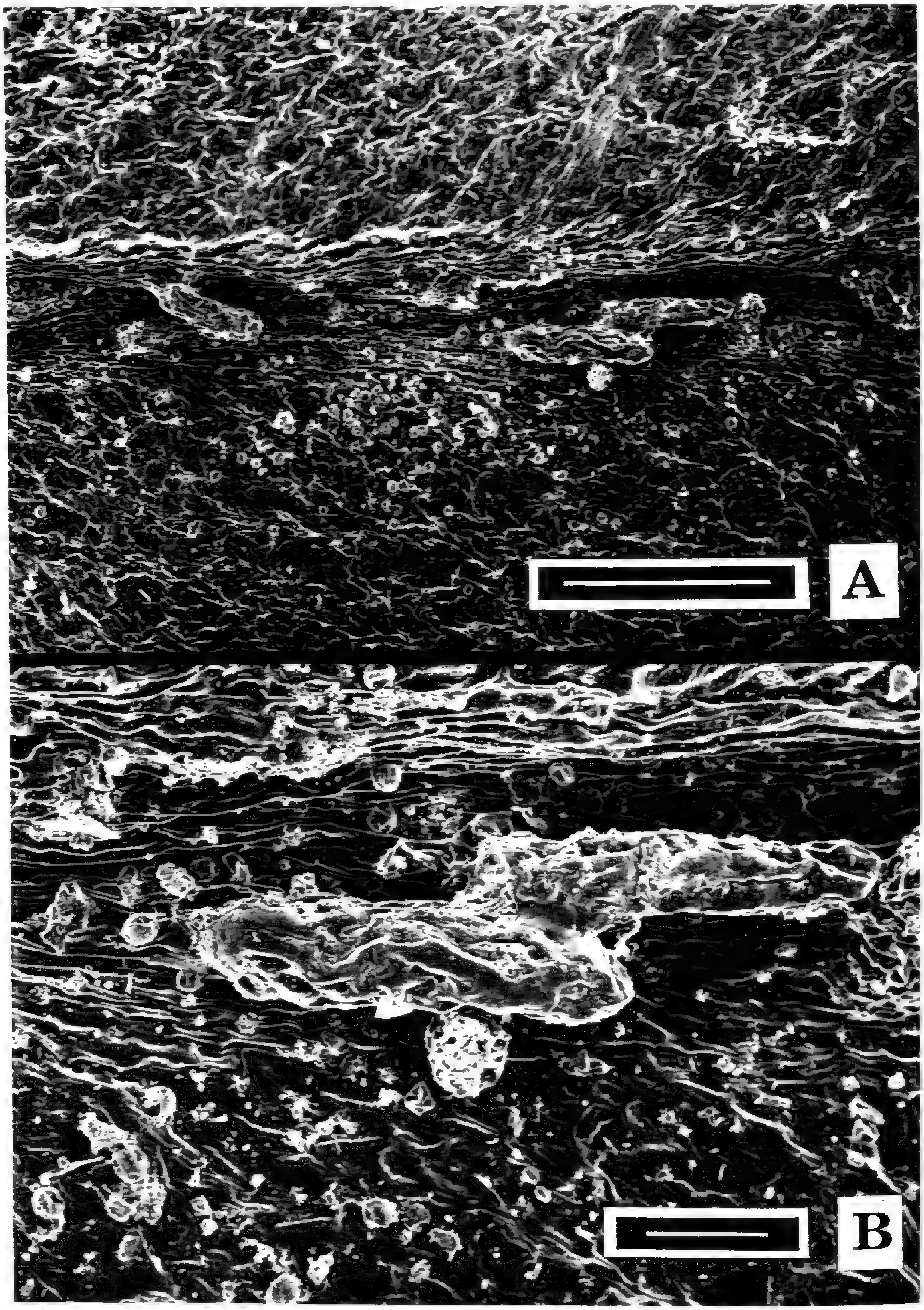

FIGURE 5. Scanning electron photomicrographs of adaxial glandular trichomes in *Photinia melanocarpa* (Michaux) Robertson & Phipps.—A. View of upper leaf surface showing glands in midrib, scale bar = 0.5 cm.—B. Detail of two glands; scale bar = 100 μm.

nately lobed, toothed, and entire, with both craspedodromous and camptodromous venation. Much narrower generic limits were used in Robertson et al. (1991), with *Sorbus* sens. lat. being divided into five genera. These resulting genera have more consistent leaf characteristics: *Sorbus* and *Cormus* are pinnately compound, *Torminalis* is pinnately lobed, and *Chamaemespilus* is simple and toothed with camptodromous venation. Only *Aria* has substantial diversity of leaves. There are two basic types in *Aria*: coarsely toothed and sometimes lobed with craspedodromous venation, and finer toothed with camptodromous venation. Kovanda & Challice (1981) presented a rationale for segregating *Micromeles* from *Aria* based on deciduous calyx lobes. Our studies (Rohrer et al., in press) of maloid fruit

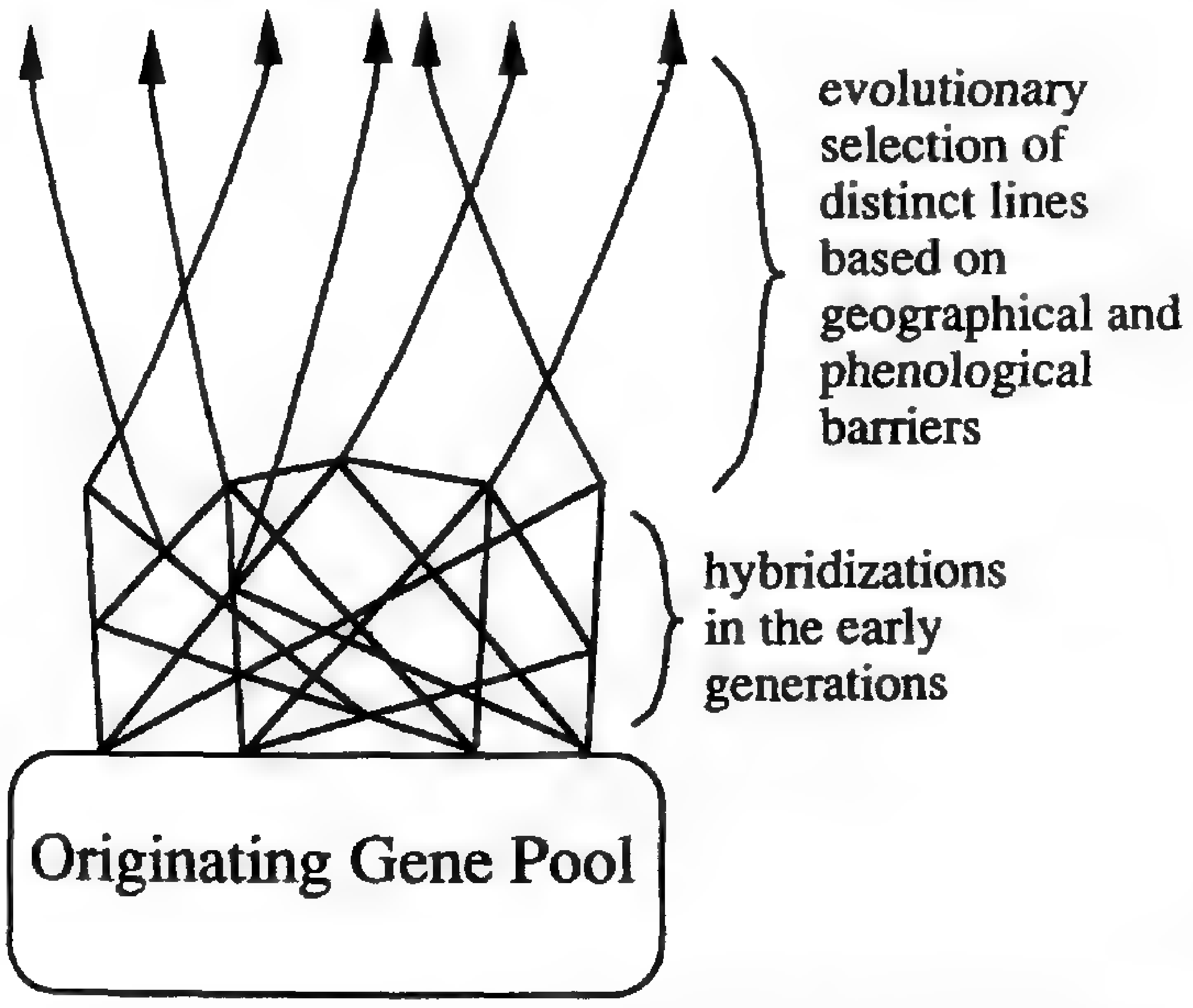

FIGURE 6. Model of polychotomous evolution of Maloideae from alloploid gene pool. Adapted from Phipps et al. (1991).

indicate that this character is inconsistent, but the presence of heterogeneous flesh in the fruits provides strong evidence for including *Micromeles* in *Aria*, and leaf data support this as well.

After examining the large number of taxa used in our data set on leaves, it is possible to postulate a transition series with the following sequence: (1) pinnately lobed with sharp teeth and craspedodromous venation; (2) coarsely doubly serrate or dentate with craspedodromous venation and the secondary veins going to the tips of the largest teeth; (3) unlobed but toothed and craspedodromous with the secondary veins going to the tips of some or all of the teeth; (4) unlobed and toothed with camptodromous venation; (5) unlobed with entire margins and camptodromous venation. Heteroblastic foliage can be found in some taxa in groups 2–5, and the most derived foliage type would be group 5 without heteroblastic foliage.

Although pinnately compound leaves are considered primitive in the Rosales according to Hickey & Wolfe (1975) and Kalkman (1988), they are rare in Maloideae, occurring only in three genera. Two of these genera, *Sorbus* and *Cormus*, are closely related, while *Osteomeles* is in a different clade (Phipps et al., 1991). This suggests either that pinnately compound leaves have arisen twice in Maloideae or, if pinnately compound leaves are primitive in Maloideae, they have been retained in two separate evolutionary lines. Kovanda (1965) suggested that all three genera may represent different evolutionary lines.

Phipps et al. (1991) postulated that Maloideae could have arisen through polychotomous evolution from an allopolyploid gene pool that resulted from hybridizations between early Spiraeoideae and Amygdaloideae (Fig. 6). Even today barriers to hybridization are weak in Maloideae, as shown by the large number of intergeneric hybrids (see fig. 1 in Robertson et al., 1991). Following the generic limits established in Robertson et al. (1991), even trigeneric hybrids are thought to occur in Maloideae. An example is given in a table in McAllister (1986) involving *Sorbus* sens. str., *Aria*, and *Torminalis* (although all taxa in McAllister are included in *Sorbus*, sens. lat.).

Such a polychotomous origin could explain the diversity of leaf types in Maloideae. If this hypothesis is correct, then the presence of compound leaves in two unrelated lines of Maloideae can be explained by their polychotomous origin. The pinnately compound leaves of *Sorbus* (Fig. 1B) are extremely similar to those of *Sorbaria* (Fig. 4A) of the Spiraeoideae, even to adaxial glands on the rachis. Most Spiraeoideae, however, have pinnately lobed and serrate leaves with craspedodromous venation, such as *Neillia sinensis* (Fig. 4B), and these are rather similar to those of many Maloideae. Unlobed, toothed leaves with camptodromous venation, found in many Maloideae, are characteristic of Amygdaloideae, such as *Padus virginica* (Fig. 4C) and *Prunus domestica* (Fig. 4D). The petiolar glands found in Amygdaloideae are never found in Maloideae. Thus, the kinds of leaves found today in Maloideae support the hypothesis that neither pinnately compound nor simple, craspedodromous or camptodromous venation can be considered primitive in Maloideae; rather, they both were involved in the hybrid complex that gave rise to the Maloideae.

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A GEOGRAPHIC SUMMARY OF CHROMOSOME NUMBER REPORTS FOR NORTH AMERICAN ASTERS AND GOLDENRODS (ASTERACEAE: ASTEREAE)[1]

John C. Semple[2]

ABSTRACT

A microcomputer system that facilitates record keeping of text-based nomenclatural and cytotaxonomic files is described. The system was used to maintain records on asters and goldenrods. More than 4,800 chromosome number reports for asters (*Aster, Virgulaster, Virgulus*) and over 2,000 reports for goldenrods (*Solidago* excluding *Euthamia*) were analyzed. By far the greatest number of chromosome number reports (2,110) were for Ontario, Canada. The numbers of counts for each taxon (species, subspecies, or variety) for each province or territory in Canada and state in the United States and for all of Mexico were determined. The total number of chromosome number reports and estimated numbers of taxa (species, subspecies, and varieties) of asters and of goldenrods by province, territory, and state were compared and are presented graphically. Both asters and goldenrods achieve their greatest morphological diversity in the eastern United States, peaking in North Carolina. The numbers of counts for asters and goldenrods in each area were fairly highly correlated ($r = 0.70$ excluding Ontario; $r = 0.97$ including Ontario) as were the numbers of taxa counted including Ontario ($r = 0.73$), but the percentages of taxa counted per area were not strongly correlated ($r = 0.49$). Asters show more diversity in western North America than goldenrods, and 86% of the areas had more aster than goldenrod taxa.

My work on various members of the Astereae began under the tutelage of Walter H. Lewis more than two decades ago. Walter's early guidance and inspiration are gratefully acknowledged, and this cytotaxonomic paper is dedicated to him.

Asters and goldenrods are common in many habitats throughout most of North America north of Mexico. *Aster* L. sens. lat. (*Aster* of Jones, 1980a; *Aster, Virgulus* Raf. (synonym: *Lasallea*) and *Virgulaster* Semple of Semple & Brouillet, 1980a, and Semple et al., 1989) are estimated to include about 145 species and more than 225 subspecies and varieties in Canada, the United States, and Mexico. Numerous studies have reported chromosome numbers for many of these taxa (see Semple & Brouillet, 1980b, and additional references cited below). Base numbers of $x = 9$, 8, and 7 occur in *Aster* sens. str. (Semple & Brouillet, 1980a); base numbers of $x = 21$ and 13 occur in *Virgulaster*; and base numbers of $x = 9$, 5, and 4 occur in *Virgulus*. *Aster* sens. lat. includes all of these base numbers (Jones, 1980a, b). *Solidago* L. (excluding *Euthamia* Nutt.) is estimated to include about 90 species and more than 140 subspecies and varieties in Canada, the United States, and Mexico. Chromosome numbers have been reported for most of these taxa (see Semple et al., 1984, and additional references cited below); all taxa have a chromosomal base number of $x = 9$. Polyploidy is common in both asters and goldenrods. More than 6,900 individual chromosome number reports exist for *Aster* sens. lat. and *Solidago* in North America alone. In order to keep track of these reports and to have convenient access to the data, a system of microcomputer hardware and software was assembled. It is described below. Some geographic generalizations about chromosome number reports for asters and goldenrods in North America were arrived at using the system and are presented below.

MATERIALS AND METHODS

HARDWARE

Programs were run on a Waitronics Esprit 386/25 personal computer (8/25 MHz clock speed)

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with a 387/25 math coprocessor, eight megabytes of memory, a 100 megabyte hard drive (15 msec. access time), and a Zenith VGA color monitor. (Waitronics Ltd. (Waterloo, Ontario N2J 2Y9, Canada) is one of a number of local companies assembling microcomputers (IBM clones) that are sold at reduced prices to the University of Waterloo for research purposes.)

SOFTWARE

All software used to tabulate and analyze the chromosome count data were widely available commercial products. The data and word-processing programs were accessed using *DESQview* (Quarterdeck Office Systems, Santa Monica, California 90405, U.S.A.). This memory management program allows the user to run more than one program at a time and to transfer screen data from one program to another regardless of the compatibility of the individual programs. For example, a personal appointment calendar program can be running in the background, while word processing and data entries are being performed in two additional programs.

Raw data were entered into files using *askSam* Version 4.1b (Access Stored Knowledge via Symbolic Access Method; askSam Systems, 1989). Each report was entered as ASCII text without field designation in the following order: taxon (binomial and subspecies or variety if appropriate); chromosome number reported in standardized format (e.g., “2n=9II” or “2n=18” differentiating meiotic from mitotic reports); country (e.g., “CDN, US, MEXICO”); province, territory, or state (postal code abbreviation, e.g., “ON”); county, regional municipality, parish, or district (e.g., “Waterloo Reg.Mun.”); details of location data (e.g., “Hwy-7 4 km W of Kitchener, rdside ditch”); collector and collection number; location of voucher(s) if not WAT; abbreviated publication data including any synonym used (e.g., “Anderson et al.’74, as A. h., as n=32”; in the original publication the report was listed as $n = 32$ under the name *Aster hesperius*), and any miscellaneous comments (e.g., observations about vouchers or a summary(ies) of published comments about the count or voucher, such as corrected identifications). The following are examples of report entries (in quotes and exactly as entered) with explanatory comments in brackets [=] added here but not included in the data file:

1. └A. alpigenus┘ ssp. └alpigenus┘ 2n=36 US CA. Mono Co.: Tioga Pass, 0.25 mi E of Yosemite Nat’l Pk, └S & Hd 8688┘ (TRIBCNTS-3 [= published by Semple et al., 1989], to sp. [= published to species level only, subspecies identification not determined at the time of publication])
2. └A. glaucodes┘ 2n=9II US WY. Albany Co.: Snowy Range, 3 mi NW of Centennial, └Hartman 3045┘ (RM) (Hartman’77)
3. └A. pilosus┘ var. └pilo.┘ [epithets sometimes abbreviated] 2n=32 US AL. Cleburne-Calhoun count line; SE of Anniston, └S & Ch 6305┘ [= collectors, *Semple & Chmielewski*] (PILOGEO-2 [= published by Semple & Chmielewski, 1985], as var. └priceae┘; corrected S, Ch & Lane 1989 [= Semple et al. 1989 noted that the collection on which the 1985 report was based was reidentified as var. *pilosus*])
4. └Sol. rigida┘ ssp. └glabrata┘ cf. 2n=18 US TN. Coffee Co.: Manchester, └JRB [= *J.R. Beaudry*] & DeSelm 57-472┘ (Beaudry’63, as └Sol. jacksonii┘ var. └hum.┘ [= var. *humilis*, which is not a synonym of *S. rigida* ssp. *glabrata*]) UNMAPPED [= location has not been added to unpublished cytogeography map on species because identification was uncertain at time record was added to file]
5. └Sol. simplex┘ ssp. └randii┘ var. └monticola┘ 2n=36 CDN PQ. Mégantic Co.: Black Lake, └JRB [= J.R. Beaudry] & Cinq-Mars 56-433┘ (Beaudry & Chabot’59, as └S. randii┘; R&S’87, as └S. glut. ran.┘ var. └ran.┘ [= *Solidago glutinosa* subsp. *randii* var. *randii*, which is a synonym of *S. simplex* var. *monticola*])

The symbols “└” and “┘” (keyboard characters alt-192 and alt-217, respectively) were inserted to replace non-ASCII printer codes indicating that the enclosed word(s) should be italicized. These conveniently allow specific letters or words to be converted to italics when shifting text between *askSam* and *Wordperfect*. The two symbols can be used as query characters in searching data bases.

Any of the information in a data file can be retrieved using the Query subroutine in *askSam*, and any individual report can be edited at any time. The Query subroutine also can be used to obtain a tally of the reports containing designated search fields (e.g., “└A. lanceolatus┘ {PRINT}”). Boulean searches can also be made (e.g., “└A. lanceolatus┘ var. └lanceolatus┘ {AND} 2n=48 {NOT} CDN ON {TAL}”). Any or all of the data can be transferred directly or indirectly to a word-processing program file (in this case *Wordperfect* version 5.1; Wordperfect Corp., Orem, Utah 84057, U.S.A.) using either a subroutine in *askSam* by saving the results of a Query operation as a new ASCII text file or by using the screen capture option in *DESQview* and performing a direct transfer to an existing file being edited in *Wordperfect.* It is this convenience in searching files and exchanging information between data base programs and word-processing files that makes the system being discussed useful for systematists.

Totals for the number of reports for each taxon obtained from Query operations in *askSam* were entered into a matrix (taxon by political region) prepared using the spreadsheet program *Quattro* (Borland International, Scotts Valley, California 95066, U.S.A.). The total number of counts for each taxon, the total number of counts per political region (country; province, territory, or state), the number of taxa and the number of counted and uncounted taxa for each political region, and a grand total for all count reports were calculated as part of the matrix of 28,890 data fields. The process of filling and editing the *Quattro* matrix was facilitated using the Video and Switch options available in *DESQview.* A 50-lines-of-text screen allowed *askSam* and *Quattro* to be viewed simultaneously. A compiler program could not be used with *askSam.*

Also frequently consulted were *askSam* files on aster and goldenrod nomenclature (approximately 345 kilobytes (Kb) and 200 Kb, respectively) and a literature file. These were necessary for chromosome numbers reported under infrequently used synonyms. Each nomenclature file includes ASCII text data on basionyms, synonyms, types, phylogenetic relationships, excluded taxa, and miscellaneous comments.

DATA BASE

Data on chromosome number reports were obtained from the literature and nearly 600 unpublished reports from studies on certain species complexes being investigated by my laboratory. Data were taken from 121 publications (see references in Semple & Brouillet, 1980b and Semple et al., 1984; and Morinaga & Fukashima, 1931; Higinbotham, 1936; Smith, 1965; Johnson & Packer, 1968; Packer, 1968; Mulligan & Cody, 1971; Kapoor, 1972; Mulligan et al., 1972; Andreasen & Eshbaugh, 1973; Witherspoon et al., 1974; Keil & Stuessy, 1975; Keil & Pinkava, 1976; Hartman, 1977; Kapoor, 1977; Keil & Pinkava, 1977; Jones, 1978; Powell & Powell, 1978; Dawe & Murray, 1979; Morton, 1979; Keil & Pinkava, 1979; Pringle, 1979; Dawe & Murray, 1980; Semple, 1980; Weedin & Powell, 1980; Brouillet & Semple, 1981; Dawe & Murray, 1981; Keil & Pinkava, 1981; Parfitt & Harriman, 1981; Semple, 1981; Semple et al., 1981; Kapoor & Gervais, 1982; Löve & Löve, 1982a, b; Semple, 1982; Semple & Brammall, 1982; Brouillet, 1983; Chmielewski & Semple, 1983; Dean & Chambers, 1983; Hill, 1983; Sherif et al., 1983; Semple et al., 1983a, b; Strother, 1983; Ward, 1983; Windham & Schaack, 1983; Allen, 1984; Hill, 1984; Jones, 1983; Morton, 1984; Mulligan, 1984; Sanderson et al., 1984; Semple, 1984; Allen, 1985; Houle & Brouillet, 1985; Chmielewski & Semple, 1985a, b; Semple, 1985; Semple & Chmielewski, 1985; Chmielewski, 1986; Sundberg, 1986; Sundberg & Dillon, 1986; Ward & Spellenberg, 1986; Brouillet & Labrecque, 1987; Chinnappa & Chmielewski, 1987; Chmielewski, 1987; Chmielewski et al., 1987; Lamboy, 1987; Ringius & Semple, 1987; Semple & Chmielewski, 1987; Vahidy et al., 1987; Heard & Semple, 1988; Lamboy, 1988; Semple, 1988; Campbell & Medley, 1989; Legault & Brouillet, 1989; Nesom, 1989; Semple et al., 1989; Brammall & Semple, 1990; Chmielewski & Semple, 1990; Semple et al., 1990; Semple & Chmielewski, 1991). These data were entered under the taxon name used in the source publication unless the name was known to be a synonym for another name included in the data files. The file on asters had 4,884 records and was about 553 Kb in size at the time of writing, and the goldenrods file had 2,099 records (including non-North American reports) and was about 257 Kb. In some cases, corrections found in later publications were incorporated into the original data base record. The vouchers for the majority of the reports not published by my laboratory were not seen as part of this study. Therefore, the data base may have some biases due to misidentifications. Also, no vouchers are known for some reports, and the original identifications had to be accepted on faith or the reports rejected as unconfirmable.

For certain taxa, a corrected chromosome count and a comment noting this adjustment were included in the data file record. For example, prior to 1978 reports for all members of *Aster* sect. *Dumosi* subsect. *Heterophylli* were published reflecting an assumed chromosomal base number of $x = 9$. Jones (1978) demonstrated that the chromosomal base number for subsect. *Heterophylli* is $x = 8$. Therefore, older published counts of $n = 9$ were entered as "2n=8II cf." in the data matrix, with "as n=9" appended to the publication data. These corrections did not affect the summaries presented in this paper, but could influence other manipulations of the matrix.

In other cases, an "unusual" chromosome number report for a taxa was entered as published, with a comment that further investigation is required. By "unusual" I mean, for example, the one count out of 40 or more that was not in agreement with the other counts for the taxon.

GRAPHICS AND STATISTICS

Maps were prepared using the graphics program *Coreldraw* Version 1.02 (Corel Systems Corporation, 1600 Carling Ave., Ottawa, Ontario K1Z 8R7, Canada), which must be run under *Windows* Version 2 or higher (Microsoft Inc., Redmond, Washington 98073, U.S.A.). Maps were printed using a QMS-PS 810 postscript laser printer.

Pearson correlations were calculated using *SYSTAT* Version 5.0 (SYSTAT, Inc., 1800 Sherman Ave., Evanston, Illinois 60201, U.S.A.).

RESULTS AND DISCUSSION

A total of 6,908 chromosome number reports for asters and goldenrods from Canada, the United States, and Mexico were included in the study (Table 1). The results of the analyses of the data matrix on chromosome number reports and numbers of taxa per political region are presented pictorially in Figures 1–4. The total numbers of reports for each province and territory in Canada, each state in the United States, and all of Mexico are given in Table 1 and Figures 1 and 3 for *Aster* sens. lat. and *Solidago*, respectively. A total of 4,844 reports was entered into the *askSam* data file on asters. Of these, 1,520 were for plants native to Ontario. The next largest numbers of reports were for Oregon, Québec, and Michigan with 194, 144, and 133 reports, respectively. There were more than 100 reports each for California, Colorado, Florida, New York, North Carolina, and Virginia. The lowest number of counts in the United States was from Delaware with only two reports. No count reports were included in the data files for asters from Newfoundland and Labrador, and there was only one report from Prince Edward Island. Two thousand sixty-four reports were entered into the *askSam* data file on goldenrods. Of these, 590 were for plants native to Ontario. The next largest numbers of reports were from Québec, New York, California, and Colorado with 144, 75, 73, and 58 reports, respectively. No other state in the United States had more than 50 reports. No count reports were included in the data files for goldenrods from Prince Edward Island. Only 30 reports for asters and six for goldenrods from Mexico were entered into the files.

Tentative estimates were made of the total number of taxa down to varietal level for each province and territory in Canada, each state in the United States, and for Mexico (Table 1). These are presented graphically for asters and goldenrods in Figures 2 and 4, respectively. Overall, the number of aster taxa and the number of goldenrod taxa for each area correlate rather highly ($r = 0.7$), but the majority of the regions (86%) have more aster than goldenrod taxa (Table 1). The diversity of taxa for asters and goldenrods is greatest in the eastern United States; previously, Cronquist (1955) noted this to be the case for goldenrods. The greatest numbers of species, subspecies, and varieties for both asters and goldenrods occur in North Carolina (56 and 51 estimated, respectively). The fewest taxa occur in Alaska and the far northern areas across Canada. The western part of North America has far fewer goldenrod taxa than the eastern part. However, the pattern for asters is different because several taxon-rich sections and subsections of asters achieve their greatest diversity in the west, unlike any group of goldenrods. The number of taxa along the Pacific coast is high primarily because of the presence of *Aster* sect. *Eucephalus* and *Aster* sect. *Dumosi* subsect. *Foliacei*. Without these two groups, the general pattern of diversity in asters would be quite similar to that in goldenrods.

There was a great range (0% to 90%) among geopolitical regions in the percentage of taxa for which at least one individual's chromosome number had been determined (Table 1; Figs. 2, 4). The mean percentages of taxa from Canada, the United States, and Mexico sampled cytologically were 49.1% for asters and 45.1% for goldenrods. The highest percentages of taxa that were counted were for Manitoba and Ontario: 90% and 75% in the former, and 80% and 83% in the latter for aster and goldenrod taxa, respectively. Percentages were lower in all other provinces and states. In Canada, the numbers of counts and the percentages of taxa counted were lowest in Newfoundland and Prince Edward Island. Thirty-four out of 62 provinces, territories, states, and Mexico (54.8%) had more aster taxa counted than goldenrod taxa, but on average only 4% more aster than goldenrod taxa were counted per area. Generally, the percentages of aster and goldenrod taxa sampled in an area did not correlate strongly ($r = 0.49$). For example, five of the 23 estimated aster taxa for Nevada (22%) versus five of the seven goldenrod taxa

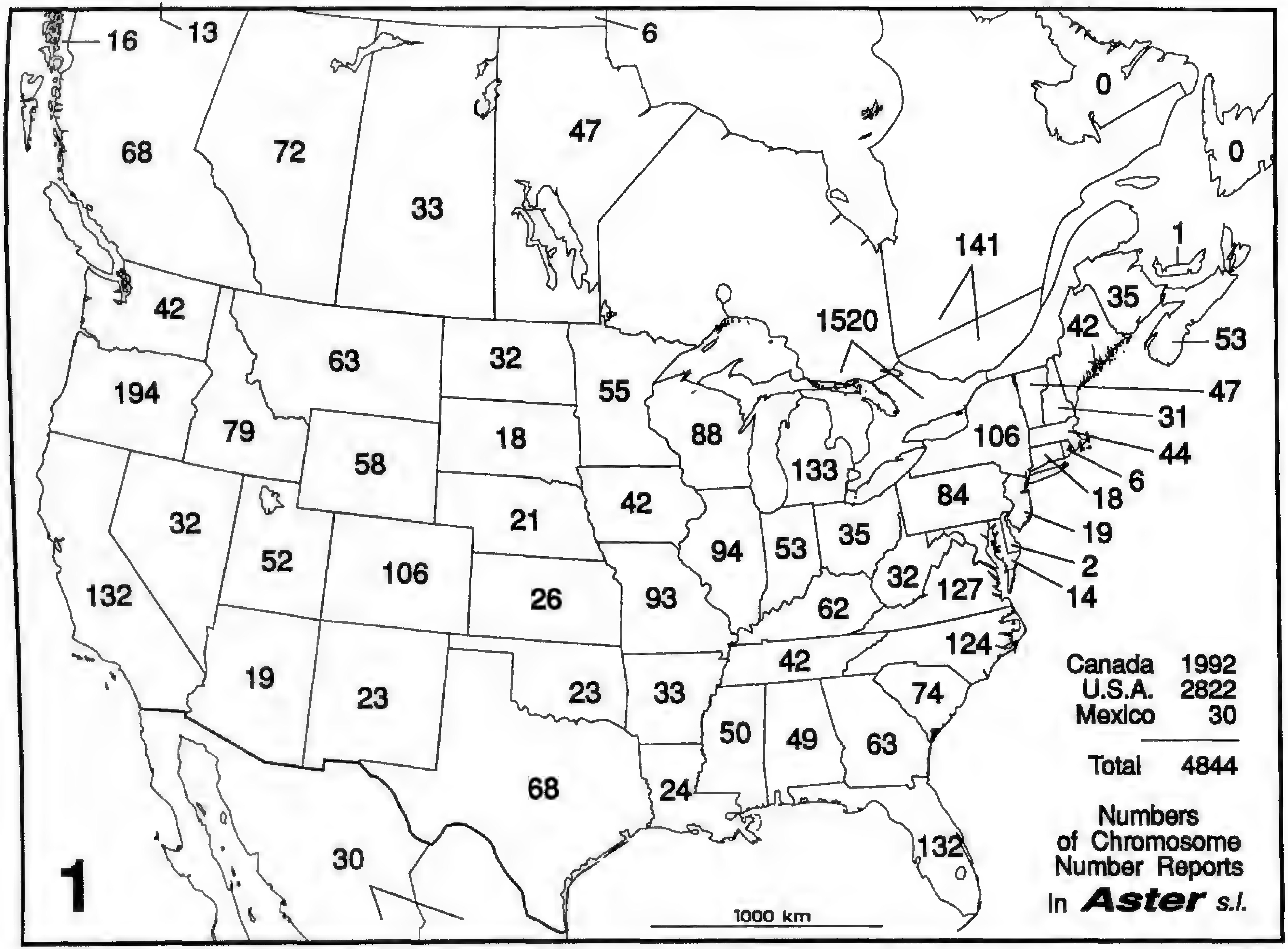

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FIGURE 1. Numbers of chromosome number reports for *Aster* sens. lat. (*Aster*, *Virgulaster*, and *Virgulus*) in Canada, the United States, and Mexico. Only small portions of Alaska and the Northwest Territories are indicated at the top of the map; Yukon Territory is not included in the map. Numbers indicated are for both subregions of Ontario, Québec, and Mexico, respectively.

TABLE 1. Numbers of chromosome number reports, estimated numbers of taxa (species, subspecies, and varieties), numbers of taxa counted, and percentages of taxa counted for the provinces and territories of Canada, states of the United States, and all of Mexico.

Geopolitical area	Total number of reports	Estimated total number of taxa	Asters				Goldenrods				Asters − Goldenrods	
			Number of reports	Number of taxa		% of taxa counted	Number of reports	Number of taxa		% of taxa counted	Number of taxa	% counted
				Estimated	Counted			Estimated	Counted			
						CANADA						
Alberta	95	39	72	26	17	65	23	13	8	62	13	3
British Columbia	95	39	68	29	16	55	27	10	6	60	19	−5
Manitoba	87	40	47	20	18	90	40	20	15	75	0	15
New Brunswick	47	42	35	19	14	74	12	23	8	35	−4	39
Newfoundland	9	20	0	6	0	0	9	14	2	14	−8	−14
Labrador*	0	14	0	0	0	0	0	0	0	0	−8	—
Northwest Territories	14	9	6	5	2	40	8	4	2	50	1	−10
Nova Scotia	78	33	53	12	9	75	25	21	11	52	−9	23
Ontario	2,110	90	1,520	49	39	80	590	41	34	83	8	−3
Prince Edward Is.	1	28	1	10	1	10	0	18	0	0	−8	10
Québec	288	56	144	24	15	63	144	32	24	75	−8	−12
Saskatchewan	48	31	33	18	8	44	15	13	5	38	5	6
Yukon Territories	51	18	13	11	1	9	38	7	2	29	4	−20
Means (subtotals)	(2,923)	35.5	(1,992)	19.1	11.7	50.4	(931)	18	9.8	47.8	2.7	2.7
						U.S.A.						
Alabama	63	75	49	42	21	50	15	33	12	36	9	14
Alaska	47	15	16	8	6	75	31	7	3	43	1	32
Arizona	44	24	19	14	8	57	25	10	7	70	4	−13
Arkansas	63	66	33	33	15	45	30	33	15	45	0	0
California	205	43	132	33	21	64	73	10	7	70	23	−6
Colorado	164	47	106	29	13	45	58	18	12	67	11	−22
Connecticut	26	51	18	27	12	44	8	24	6	25	3	19
Delaware	8	45	2	23	3	13	6	22	4	18	1	−5
Florida	167	56	132	33	25	76	35	23	15	65	10	11
Georgia	79	89	63	45	24	53	16	44	13	30	1	23
Idaho	93	39	79	29	13	45	14	10	5	50	19	−5
Illinois	109	69	94	46	29	63	15	23	7	30	23	33
Indiana	67	57	53	30	17	57	14	27	10	37	3	20
Iowa	51	46	42	27	15	56	9	19	9	47	8	9

TABLE 1. Continued.

			Asters				Goldenrods				Asters − Goldenrods	
				Number of taxa				Number of taxa				
Geopolitical area	Total number of reports	Estimated total number of taxa	Number of reports	Estimated	Counted	% of taxa counted	Number of reports	Estimated	Counted	% of taxa counted	Number of taxa	% counted
Kansas	45	40	26	23	10	43	19	17	12	71	6	−28
Kentucky	74	73	62	40	18	45	12	33	11	33	7	12
Louisiana	30	69	24	37	13	35	6	32	5	16	5	19
Maine	57	49	42	26	14	54	15	23	11	48	3	6
Maryland	24	60	14	30	8	27	10	30	8	27	0	0
Massachusetts	82	59	44	34	20	59	38	25	16	64	9	−5
Michigan	174	59	133	31	22	71	41	28	17	61	3	10
Minnesota	114	52	88	30	21	70	26	22	10	45	8	25
Mississippi	55	64	50	35	15	43	5	29	6	21	6	22
Missouri	117	61	93	31	21	68	24	30	12	40	1	28
Montana	79	41	63	28	16	57	16	13	7	54	15	3
Nebraska	37	34	21	21	11	52	16	13	6	46	8	6
Nevada	39	30	32	23	5	22	7	7	5	71	16	−49
New Hampshire	56	52	31	28	14	50	25	24	13	54	4	−4
New Jersey	46	73	19	43	11	26	27	30	16	53	13	−27
New Mexico	62	40	23	22	13	59	39	18	12	67	4	−8
New York	181	80	106	51	22	43	75	31	20	65	20	−22
North Carolina	171	107	124	56	30	54	47	51	27	53	5	1
North Dakota	51	29	32	16	7	44	19	13	6	46	3	−2
Ohio	49	49	35	27	11	41	12	22	3	14	5	27
Oklahoma	38	55	23	28	17	61	15	27	13	48	1	13
Oregon	209	46	194	33	20	61	15	13	6	46	20	15
Pennsylvania	103	62	84	39	16	41	19	23	12	52	16	−11
Rhode Island	11	46	6	25	5	20	5	21	5	24	4	−4
South Carolina	99	84	74	44	24	55	25	40	15	38	4	17
South Dakota	35	26	18	14	7	50	17	12	8	67	2	−17
Tennessee	92	78	42	40	18	45	50	38	22	58	2	−13
Texas	83	67	68	29	20	69	15	38	12	32	−9	37
Utah	69	35	52	24	9	38	17	11	6	55	13	−17
Vermont	80	51	47	29	17	59	33	22	12	55	7	4
Virginia	154	80	127	38	27	71	27	42	14	33	−4	38

TABLE 1. Continued.

Geopolitical area	Total number of reports	Estimated total number of taxa	Asters				Goldenrods				Asters − Goldenrods	
			Number of reports	Number of taxa: Estimated	Number of taxa: Counted	% of taxa counted	Number of reports	Number of taxa: Estimated	Number of taxa: Counted	% of taxa counted	Number of taxa	% counted
Washington	48	46	42	34	10	29	6	12	5	42	22	−11
West Virginia	42	66	32	34	12	35	10	32	6	19	2	16
Wisconsin	116	68	86	40	27	68	27	28	14	50	12	18
Wyoming	76	54	58	35	15	43	18	19	11	58	16	−15
Means (subtotals)	(3,949)	55.3	(2,822)	31.4	15.7	50.0	(1,127)	23.9	10.4	46.1	7.4	3.9
Canada & U.S.A. Means (subtotals)	(6,872)	51.1	(4,818)	29.8	15.9	50.1	(2,058)	22.8	10.3	46.4	6.2	3.7
MEXICO												
Mexico	36	41	30	14	5	36	6	27	3	11	−13	25
TOTALS	6,908		4,844				2,064					
MEANS	111.4	50.9	78.1	28.7	14.7	49.9	33.3	22.8	10.1	45.9	5.9	4.0

* Labrador is part of the Province of Newfoundland; data on the island and the mainland portions of the province are listed separately for clarity.

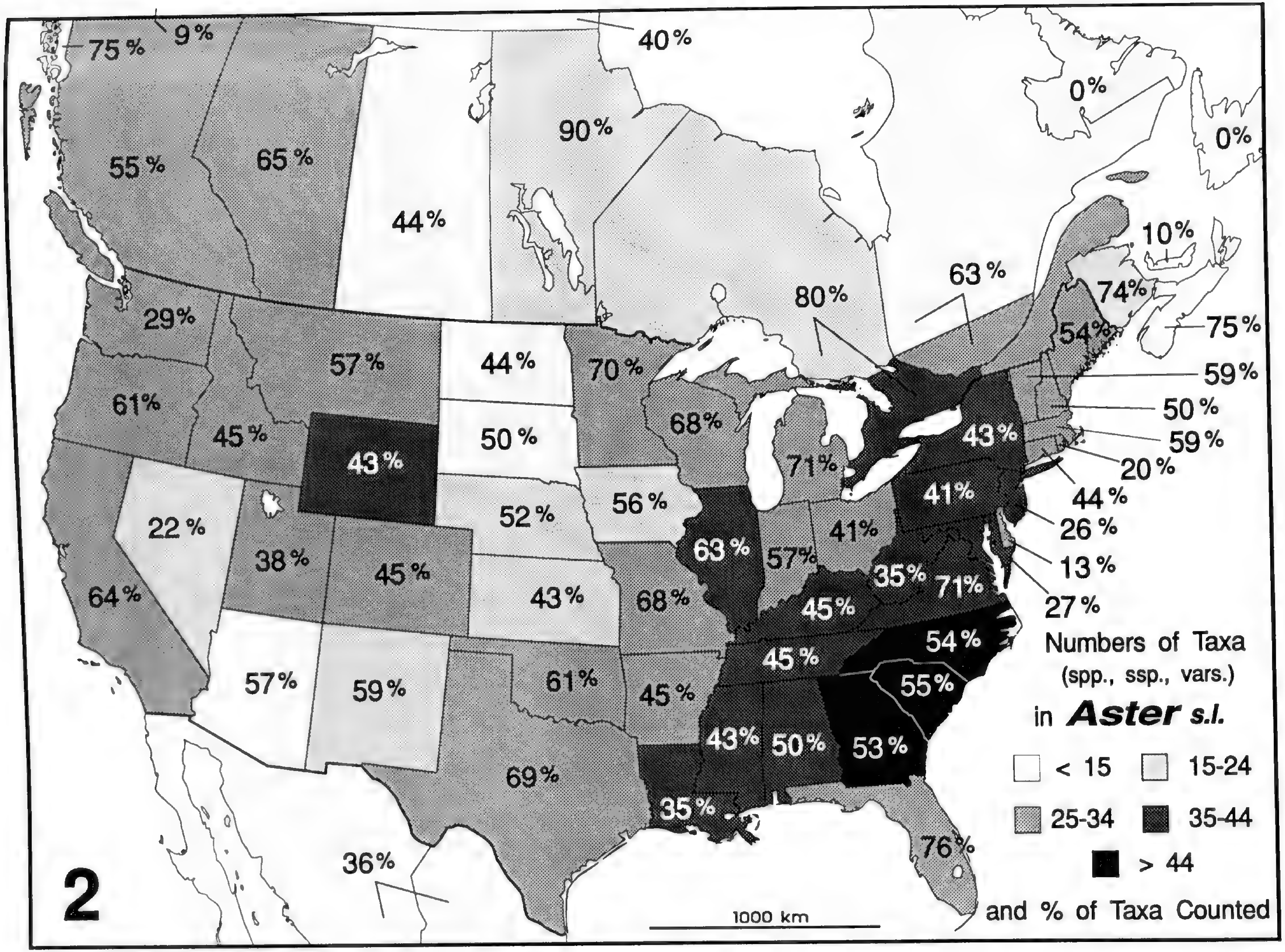

FIGURE 2. Estimated numbers of taxa (species, subspecies, and varieties; shading) in *Aster* sens. lat. (*Aster*, *Virgulaster*, and *Virgulus*) and percentages of taxa for which a chromosome number has been determined (numbers in the regions indicated). Numbers indicated are for both subregions of Ontario, Québec, and Mexico, respectively.

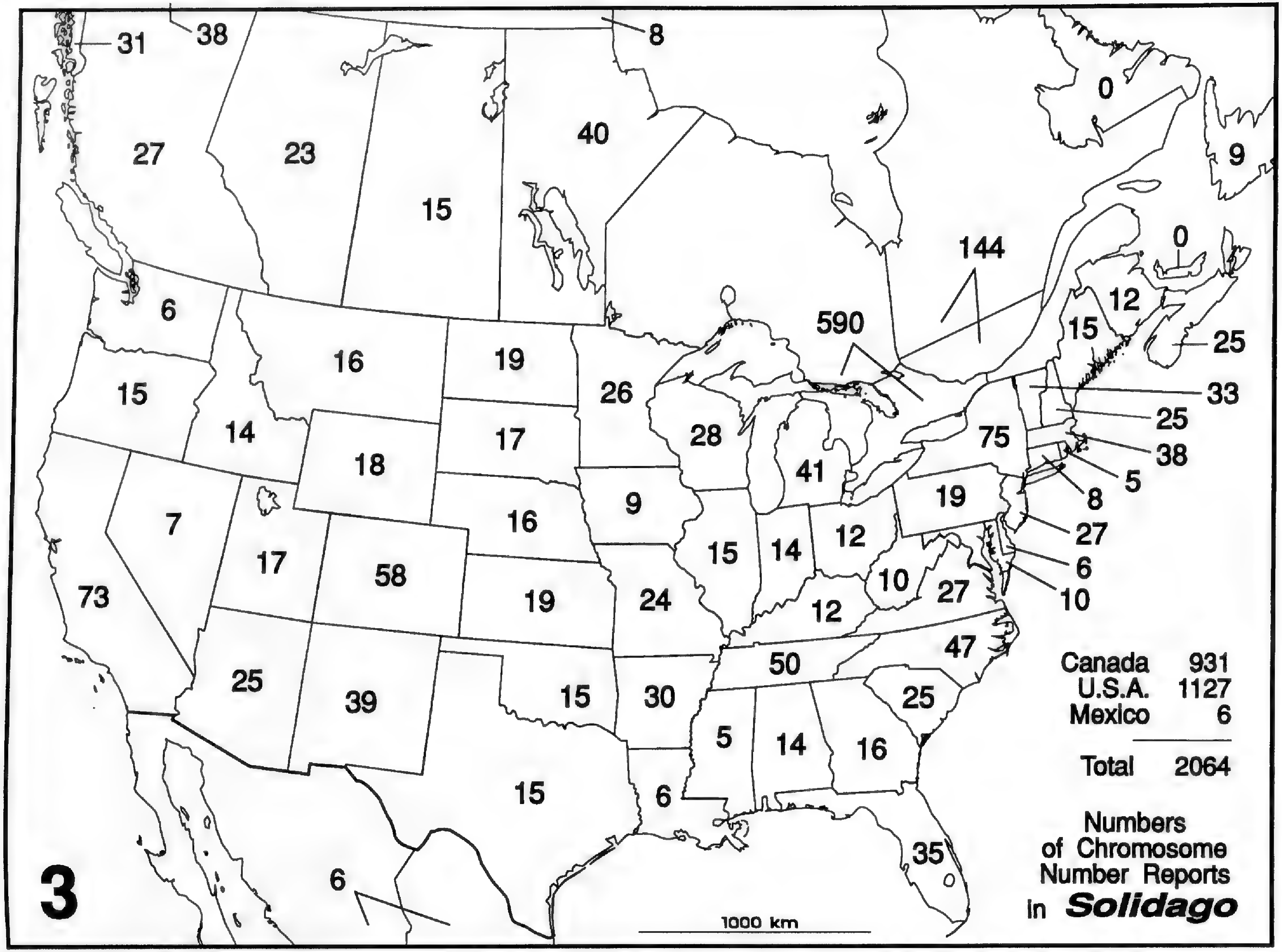

FIGURE 3. Numbers of chromosome number reports for *Solidago* (excluding *Euthamia*) in Canada, the United States, and Mexico. Only small portions of Alaska and the Northwest Territories are indicated; Yukon Territory is not included in the map. Numbers indicated are for both subregions of Ontario, Québec, and Mexico, respectively.

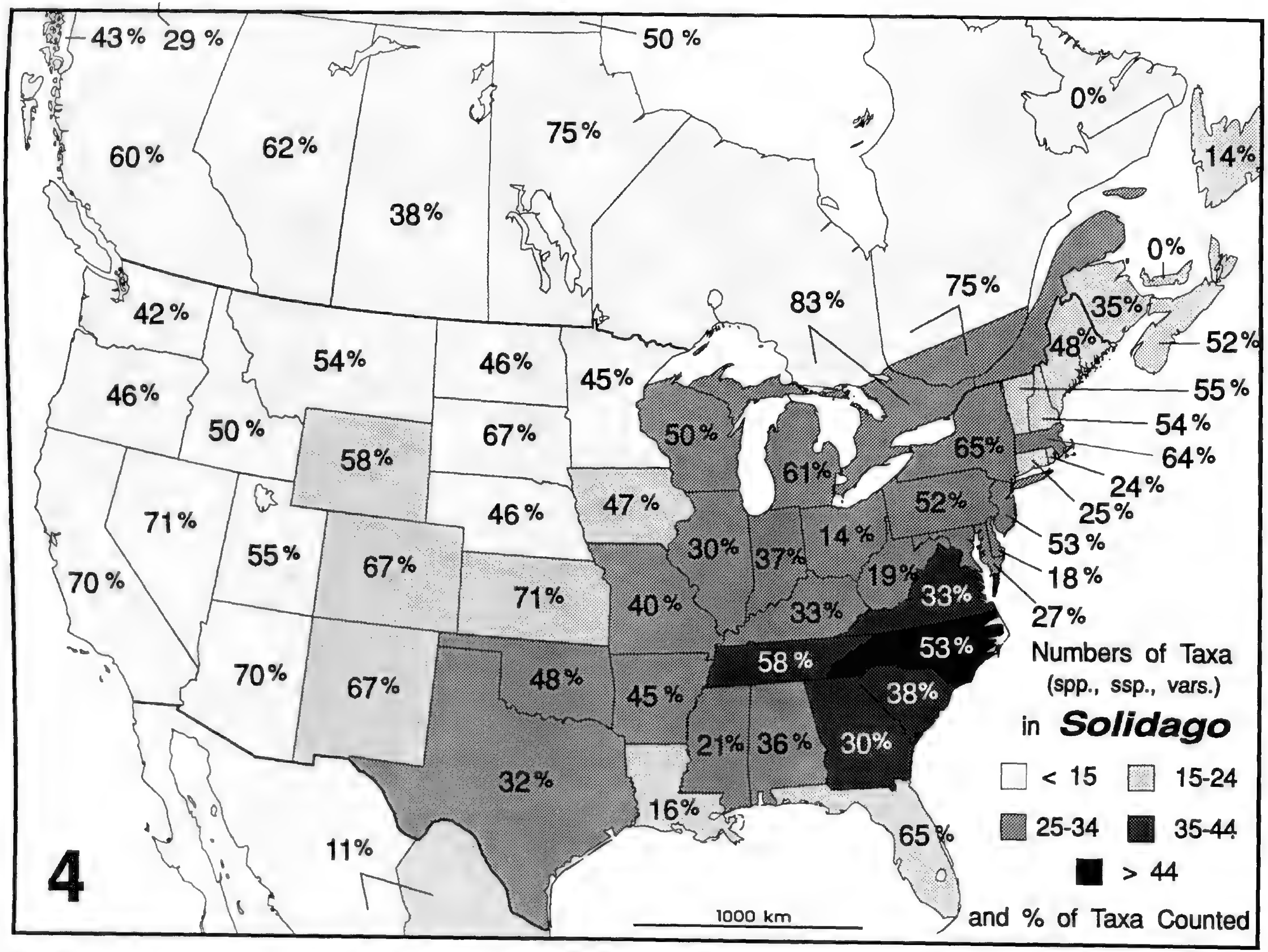

FIGURE 4. Estimated numbers of taxa (species, subspecies, and varieties; shading) in *Solidago* (excluding *Euthamia*) and percentages of taxa for which a chromosome number has been determined (numbers in the regions indicated). Numbers indicated are for both subregions of Ontario, Québec, and Mexico, respectively.

(71%) had been sampled, and 20 of the 29 estimated aster taxa for Texas (69%) versus 12 of the 38 goldenrod taxa (32%) had been sampled.

The numbers of taxa per geopolitical region (Table 1) were my estimates and should be viewed as preliminary. The numbers were based on numerous floras, revisions, and my work. Both over- and underestimates are likely because I have not examined all of the tens of thousands of herbarium specimens that need to be seen to fully document the distributions of the taxa in the aster and goldenrod genera. For this reason, ranges rather than actual numbers of taxa are presented in Figures 2 and 4. Of course, there will always be some disagreement on the number of taxa present in any given area because taxonomists are notorious for disagreeing about such matters. Nonetheless, the general patterns are presented with some confidence.

The size of the data base from Mexico was small relative to the size of the country, and this warrants comment. This low number of reports may be due to an incomplete search of literature not included in the standard chromosome number indices. Of note, no references in Spanish are included in the literature cited in this paper, although there was no deliberate ignoring of non-English publications. The numbers of taxa are in accord with those from neighboring states in the United States. For goldenrods, the sample size in most western states reflects the amount of work done in a particular state by my laboratory; to date we have not undertaken collecting expeditions into Mexico. This alone may account for the low number of reports in comparison to areas further north. Without the work of Scott Sundberg, the number of counts of asters would be much lower for Mexico. A number of collectors in the United States have provided material that allowed my laboratory to make the only chromosome number determination(s) for a number of taxa from the collectors' home territories. The number of collections of Mexican asters and goldenrods with viable achenes sent to my laboratory by more active collectors has been very low, and therefore, any specimens received would be valuable.

Asters and goldenrods have a reputation for frequent hybridization. Reports for 65 and 13 putative wild aster and goldenrod hybrids, respectively, were included in the data base (1.34% and 0.63%); these low values include both inter- and infraspecific crosses. Only eight of the 6,908 reports (0.12%) were triploid. For Ontario, 22 of the 2,110 reports were for interspecific hybrids, and none of the reports was triploid.

The most critical factor determining the total number of reports and the percentage of taxa sampled was the laboratories active in a particular region. For asters, the laboratories contributing the greatest number of reports were those of Kenton Chambers (Oregon State University with Michael Dean and Gerry Allen (now at the University of Victoria, B.C.); reports from the western United States), Almut Jones (University of Illinois; reports from all groups of asters), Ronald Jones (Eastern Kentucky University; reports on virguloid asters), Paul Van Faasen (Hope College; reports from Michigan and the northeastern United States), L. Michael Hill (Bridgewater College; reports from Virginia), and my lab (primarily with Luc Brouillet (now at the Institut de Recherche en Biologie Végétale de l'Université de Montréal) and Jerry Chmielewski (now at Slippery Rock University); all groups of asters, especially Ontario and the adjacent states and provinces, California, Colorado, and Florida). Brouillet and his students (MT) have made many counts for aster taxa, primarily from eastern Canada. For goldenrods, two laboratories have done most of the work: that of the now retired Jean Beaudry (l'Université de Montréal; all groups of goldenrods, especially from Québec) and my laboratory (all groups of goldenrods, especially from Ontario, Québec, Colorado, and California). Low numbers of reports have been published by numerous other laboratories not concentrating their research efforts on asters and goldenrods. Contributions made by D. Ward and D. Spellenberg (New Mexico State University) for some species of *Solidago* from New Mexico and surrounding regions are important. Scott Sundberg (University of Washington) has made valuable cytotaxonomic contributions on *Aster* subg. *Oxytripolium.* Askell and Doris Löve did not publish large numbers of reports for asters and goldenrods, but they did determine chromosome numbers for most taxa in Manitoba; this accounts for the high percentages of taxa counted in that province.

Unpublished data from several active laboratories were not included in the data files and matrices. John Morton (University of Waterloo) has accumulated numerous chromosome number determinations for goldenrods, especially members of the *Solidago canadensis* complex. When these are published, the total number of counts for goldenrods from parts of western North America and eastern Canada will increase significantly. Because most of the taxa involved have been sampled at least once in most provinces and states, the percentages of taxa sampled will not change greatly, with the exception of those from Newfoundland.

Brouillet is also known to have numerous unpublished counts for asters from eastern Canada, especially Québec, where at least 63% of the aster taxa have already been sampled. As noted above, more than 600 unpublished counts for particular species complexes of asters and goldenrods made by my laboratory were included in the data base.

Lastly, it should be noted that my laboratory will gratefully receive viable achenes of any taxon of aster or goldenrod, preferably with a voucher. These will facilitate continuing work on the cytogeography of asters and goldenrods from North America and elsewhere.

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ORGANIC FLUVIAL SEDIMENT: PALYNOMORPHS AND "PALYNODEBRIS" IN THE LOWER TRINITY RIVER, TEXAS[1]

Alfred Traverse[2]

ABSTRACT

In 1961–1962, the author studied the lower Trinity River, Texas, for palynomorph content, as a model of how pollen, spores, and palynodebris reach depositional areas for incorporation in sedimentary rocks. The river was selected partly because it was at that time relatively undisturbed by industry and damming. Three stations were selected for surface and mid-depth water sample collection, 00 in Trinity Bay, 04 on the Trinity River delta, and 09 on the lower Trinity River. Palynomorph loads at 04 and 09 were especially high, often reaching 10^5 or more per 100 liters of water. Water of the bay station usually contained much lower concentrations of palynomorphs. A wide range of pollen and spore types occurred in the water, dominated by major floral elements of the lower Trinity River area, but including forms from farther upstream. Reworked pollen and spores, eroded from rocks hundreds of kilometers north and northwest of the sampling localities, were regularly recovered. *Engelhardia/Momipites*-type pollen of Paleogene age was an especially significant reworked form. There were seasonal changes in the composition of the palynoflora, reflecting flowering peaks such as that of *Taxodium* (swamp cypress) in late winter and Poaceae (grass) in summer. In 1985–1986, the same stations were once again sampled. Since the earlier sampling, damming upstream had created Lake Livingston, which acts as a huge settling basin, resulting in decreased palynomorph load in the water at all stations in the lower river. Fungal spores as well as pollen apparently have been reduced in concentration. A sampling in 1986 of the lake itself and of the river at its inlet tends to confirm that the lake acts as a settling basin for waterborne palynomorphs. Rivers deliver a sampling of the terrestrial flora, via palynomorphs and palynodebris, to the continental shelf. In total, this particulate organic matter is an important part of the earth's budget of buried carbon. Studies of the palynomorph-palynodebris load of streams therefore contribute to understanding the origin and fate of organic matter in sedimentary rocks.

The carbon, or organic, cycle normally returns most organic matter to the hydrosphere and atmosphere as CO_2 and H_2O, with the release of energy. Cellulose and related compounds of the earth's biomass locked up in terrestrial plant tissues, especially wood, provide a relatively brief exception or delay to the cycle, but the interruption in the case of old trees can be much longer than it is for animals. Also, the total bulk of carbon tied up in living land plants is much greater than that stored in animals—most biomass is forest biomass. Furthermore, plant tissues incorporated in peat can remove carbon from the organic cycle for millions of years, in the form of peat, lignite, and higher-rank coal deposits. Coal deposits are a relatively rare geologic phenomenon, requiring an environment of deposition in which water depth remains in the tens-of-centimeters range for long periods, approximately 10^5–10^6 years for thick, commercially exploitable coal beds. Palynologists, as "dissolvers" of rock, have long been aware that sediment delivered by streams to the continental shelf, there producing the ubiquitous sandstones and shales of the geologic record, is almost always rich in

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[1] William A. McHale's help in field and laboratory during 1985–1986 was indispensable to the completion of the project. Elizabeth I. Traverse and Ann Williams also helped with various aspects of the work. Martin B. Farley assisted with concentration calculations. Officials of the Trinity River Authority of Texas were most helpful during sampling at Lake Livingston. Joan W. Nowicke suggested a number of improvements to the manuscript. Lee R. Kump provided information on the relative importance of categories of organic sediments. Shell Development Company, Houston, Texas, generously released for publication the 1961–1962 information, which was the subject of two company reports. Walter H. Lewis, then of Stephen F. Austin State College, Nacogdoches, Texas, and the late Lloyd H. Shinners, then of the Herbarium, Southern Methodist University, Dallas, Texas, were especially helpful during the Shell project in my efforts to understand the flora of the Trinity River basin.

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plant tissues of all sorts. Bits of wood are the most common ingredient, but leaf fragments, especially cutinized epidermal pieces, bark residues, spores and pollen, as well as amorphous, more or less degraded plant material, are also common. It is this organic residue from sedimentary rock, especially of silty shale, that provides the subject matter of paleopalynology. Such plant debris, dispersed in the sedimentary rock, usually comprises a minor constituent by weight of the rock, less than 2% on average (Degens, 1965: 203). The organic matter content of sedimentary rocks varies from 0% for a very clean, nonorganic shale or sandstone, to 50% in a highly carbonaceous shale, to 97% in a few very pure coals. Palynologists usually refer to the pollen and spores either as "palynomorphs," a category that technically includes many other sorts of things representing all of the kingdoms of organisms except Monera, or as "sporomorphs," exclusively embryophyte pollen and spores. The rest of the microscopic plant organic matter, or detritus, dispersed in sedimentary rock is sometimes called "palynodebris."

Sporomorphs and palynodebris clearly have a lot to tell us about various environmental factors that operate during and after deposition of sediment. The spore and pollen floras indicate much about the environments pertaining on the land surfaces from which they were derived. The younger the sediments (and thus the more closely related the vegetation is to modern floras), the more accurately this information can be applied. For Pleistocene sediments it is possible now to reconstruct from the pollen record the source forest composition and dynamics with great precision (Bradshaw, in press; Jackson, in press; Traverse, 1988: 386–389). In older sediments we are not so certain of the autecological implications of each fossil plant taxon. Nevertheless much valuable information can be derived from ancient palynofloras about the environmental conditions on land where the producing plants grew, especially when the palynological information is coupled with data about megafossil plants (Phillips & DiMichele, 1981; Phillips et al., 1974, 1985; Scott, 1978, 1979). This is analogous to the fact that Pleistocene palynology depends on information from modern botanical studies.

Spore/pollen floras also reveal information about the *sedimentary* environment(s) by means of which they found their way to their final resting place. In 375 × 10^6-yr.-old Devonian shale-sandstone deposits of New York State and vicinity, Schuyler & Traverse (1990) have shown that spores are most abundant in river channel sediments, where they were quickly and "efficiently" covered, and least abundant in overbank (flood) deposits, where atmospheric oxygen had too good a chance to destroy the sporopollenin of the spore exines before they could be covered. The concentration of spores in these Devonian sediments was, however, about 10% of comparable Cenozoic sediments. Other studies back to the time of Hoffmeister (1954) and Muller (1959) have demonstrated that palynomorph concentration is related to proximity of ancient shorelines, water turbulence, and current directions (see Traverse, 1988, Chapter 17). Though the subject is in its infancy, investigations of nonspore palynodebris promise to yield even more information about the sedimentary environments responsible for its deposition. It is now reasonably clear that terrestrial plant biomass is a major source, probably *the* most important source of organic matter in sedimentary rocks (Deuser, 1988; Ittekot, 1988; Kump, 1988). At least part of this carbon bankroll may lead to hydrocarbon generation—petroleum and natural gas.

The magnitude of the accumulation of organic debris on the continental shelf is suggested by Chmura & Liu (1990), who report that one large river, the Mississippi, delivers about 1 × 10^{19} palynomorphs annually to the Gulf of Mexico. Assuming this is correct, it is easy to calculate by several techniques that about 4 × 10^4 metric tons of palynomorphs per year are deposited in this way on the Gulf shelf—a sizable annual increment of sporopollenin—but this is only a fraction of all plant debris so sedimented. For comparison it should be noted that all of the major rivers of the world are estimated to carry to the continental shelves about 150 × 10^6 metric tons of chemically resistant particulate organic matter (POC; Deuser, 1988; Ittekot, 1988). Mostly this is what palynologists call palynodebris. It is therefore obviously of interest to trace the movement of plant debris, most of which is microscopic in size, in streams, from the source vegetation to the site of deposition, usually on the continental shelf.

TRINITY RIVER, TEXAS

RATIONALE FOR SELECTION AND DESCRIPTION OF SITES

Trinity River (see Fig. 1) was selected for study in about 1960, because at that time there had been relatively little disturbance of the watercourse by dams, levees, and industry (Traverse, 1990). Originally, multiple stations and multiple depths of sampling for a program of repeated collections were planned. Preliminary studies quickly indicated that

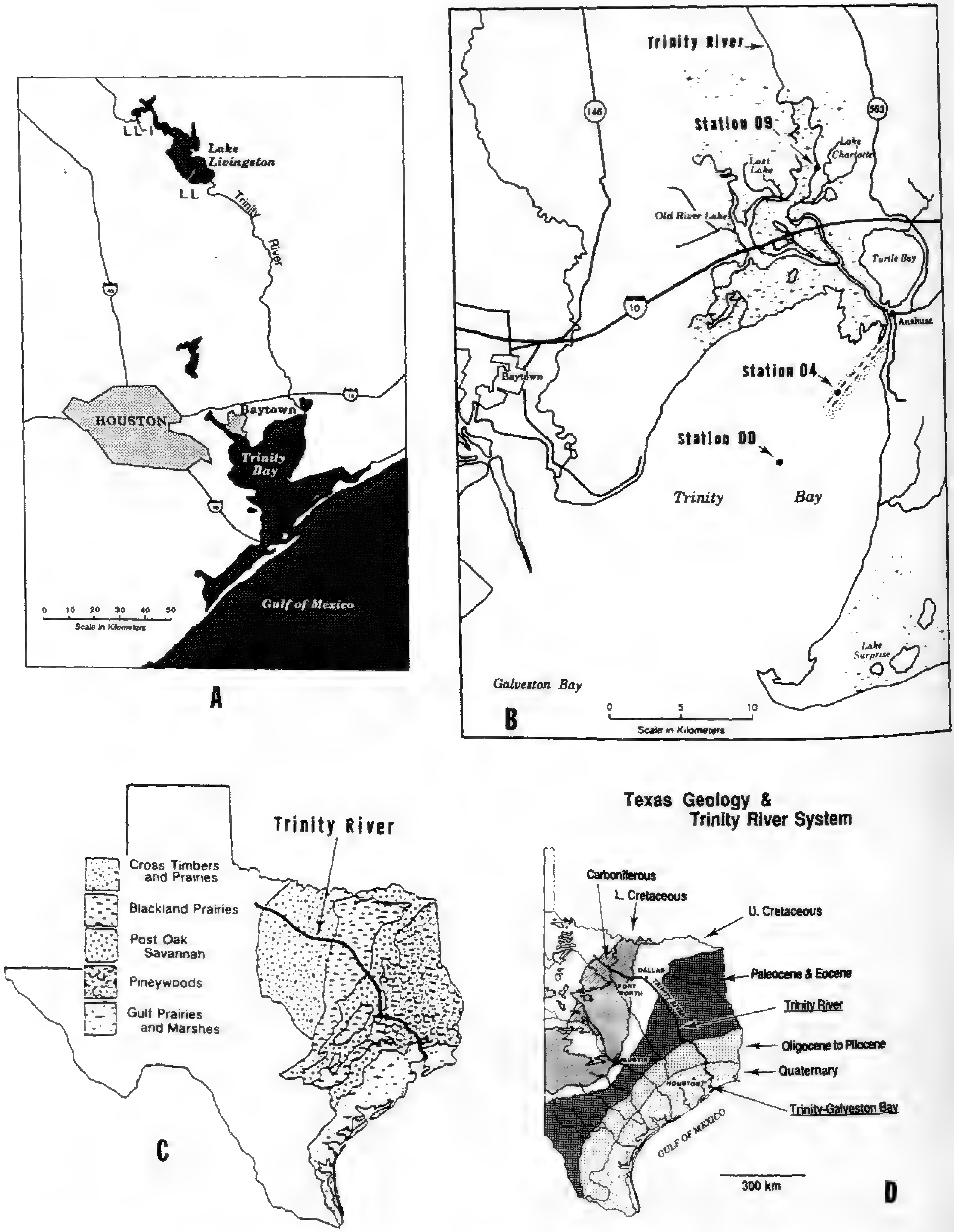


FIGURE 1. Geographic-botanical-geologic-setting for the lower Trinity River.—A. Lower Trinity River with Lake Livingston. Collection sites for Lake Livingston located by arrows. LL-I: inlet in middle of the river, where it discharges into the lake. LL: about 2 km north of the impounding dam. See B for details of collecting sites in the lower river and bay.—B. Lower Trinity River and Trinity Bay, showing sampling stations: 09, near Lake Charlotte, about 5 km north of highway I-10; 04 on the channeled deltaic extension; 00 in the center of Trinity Bay.—C. Vegetation areas through which the Trinity River passes. Station 09 is in piney woods near the Gulf prairies and marshes. Plant geographic information from Nixon & Willett (1974). For distances compare with D.—D. Course of the Trinity River from its source northwest of Ft. Worth to Trinity-Galveston Bay, showing the course of the river from older to younger rocks, Permo-Carboniferous to Pleistocene. (These illustrations first appeared in Traverse, 1990, and are reproduced here by permission of Elsevier Science Publishers.)

this was redundant, and sampling was limited to surface and mid-depth at three stations: 00 in the open bay, 04 on the outer Trinity River delta, and 09 on the lower river near Lake Charlotte. Each of these stations is still identifiable by prominent landmarks: an oil well head near station 00, navigational markers near 04, and an easily measurable distance north of a tributary at 09 (see Fig. 1). Therefore, the 1961–1962 collections could be compared to samples taken from the same stations in 1985–1986.

The area studied is a typical flat portion of the Gulf Coastal Prairie (see Fig. 1C, D). Extensive stands of pine (*Pinus*)–oak (*Quercus*)–sweet gum (*Liquidambar*)–hickory (*Carya*) forest typical for east Texas are present on the higher ground east and north of Turtle Bay and west of Old River Lake. The area immediately west of our station 09 consists of a *Spartina* grass prairie plus patches of standing water, with backswamps in which the dominant trees are *Taxodium distichum* (L.) Richard (cypress), *Salix nigra* Marshall (willow), and *Forestiera acuminata* (Michaux) Poiret (swamp privet). To the east of station 09, backswamps of this composition extend to Lake Charlotte.

Station 04 lies in the dredged Trinity River channel just off the lower part of the delta of the river, the vegetation on exposed parts of which is dominated by the giant grass ("reed"), *Phragmites communis* Trin., and other grasses (Poaceae), as well as sedges (Cyperaceae) and rushes (Juncaceae). The overwhelming bulk of this study area is covered by sedges and grasses. A gallery forest along the river as far south as Anahuac consists of *Salix nigra* Marshall, *Fraxinus pennsylvanica* Marshall (ash), *Taxodium distichum* (L.) Richard, *Carya aquatica* (Michaux f.) Nutt. (hickory), and other trees and shrubs. Backswamps near station 04 have vegetation like that of the galleries described above. Some shell banks support a flora atypical for the area, more reminiscent of limestone areas of central Texas, and characterized by *Diospyros texana* Scheele (Texas persimmon).

Beyond our study area, the Trinity River has its source northwest of Fort Worth and drains part of the Texas portion of the Great Plains, the Cross Timbers region (mostly forested with oaks), blackland prairies southeast of Dallas, extensive blackjack oak and post oak woodlands, and large areas of east Texas timber country, including the famed "Big Thicket." This east Texas forest is dominated by species of oak, pine, hickory, and sweet gum. Vegetation of this aspect extends south into our area, where it occurs as patches on deep sandy soils (Fig. 1C).

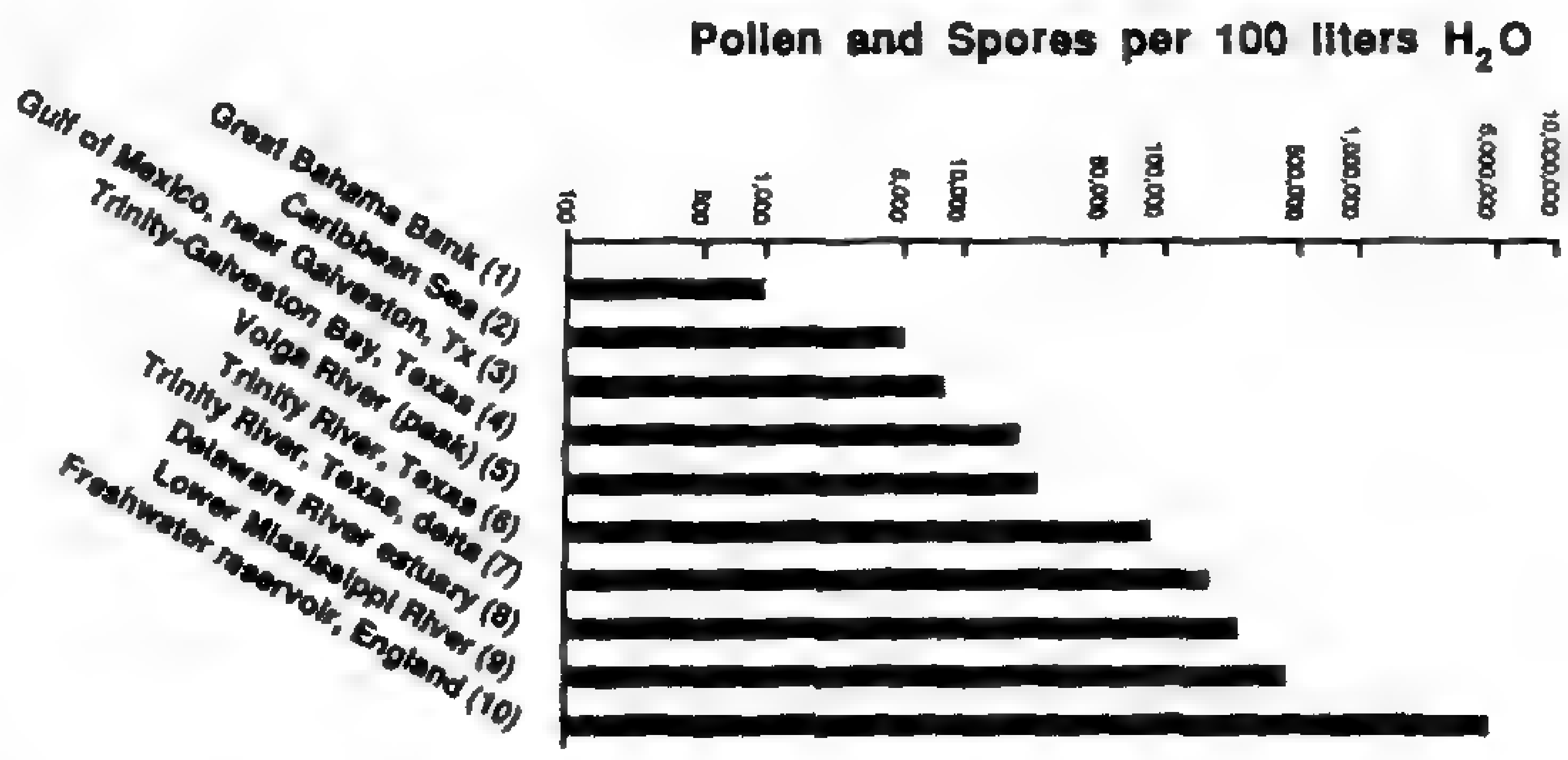


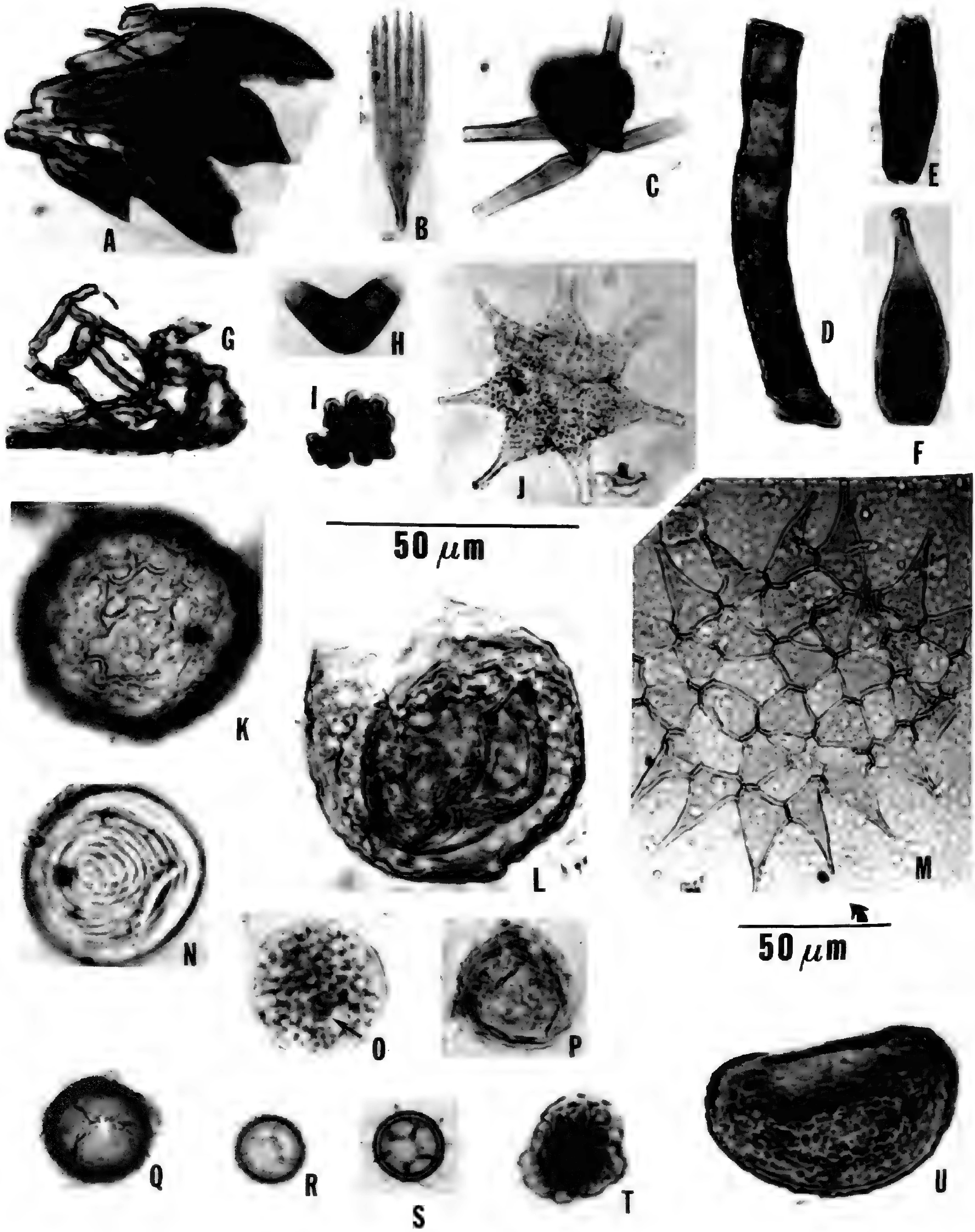
FIGURE 2. Pollen and spores in the water in various *sedimentary* situations. The concentration of palynomorphs per volume of water varies considerably from season to season and in response to storms and other factors. Therefore, all of the data with the exception of (5) are estimated averages for multiple measurements. Pollen and spores are expressed per 100 liters of water, as the numbers so generated are then similar to those for palynomorphs per gram of sediment. The data are plotted logarithmically. Water from mid-ocean localities would presumably contain at least an order of magnitude less per 100 liters than even the water of Great Bahama Bank. The reading of 5×10^6 per 100 liters of water for a small reservoir in England (10) is an indication of the high density that can be obtained in water with limited influx, closely surrounded by pollen-producing vegetation. Sources for data: (1) Traverse & Ginsburg (1966); (2) Farley (1987); (3, 4) Traverse (1990); (5) Fedorova (1952); (6, 7) Traverse (1990); (8) Groot (1966); (9) Chmura & Liu (1990); (10) Peck (1973).

STUDY OF PALYNOMORPHS AND "PALYNODEBRIS" PRESENT IN TRINITY RIVER WATER

MATERIALS AND METHODS

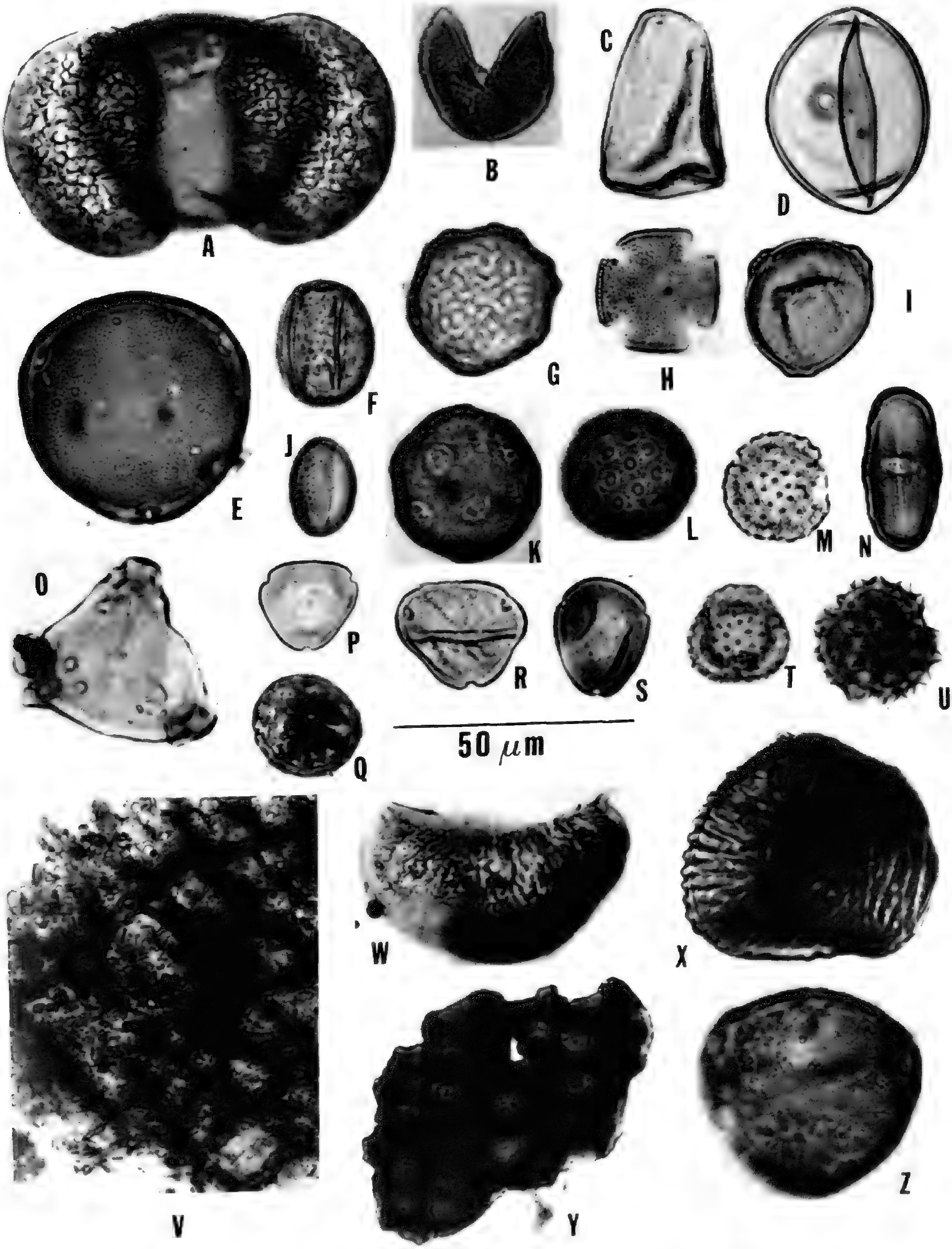
Approximately 20-liter (5-gallon) samples of water were taken. Mid-depth samples were obtained with gasoline-powered pumps. During 1961–1962 a specially designed outfit was used, but by 1985–1986 adequate commercially rentable gasoline pumps were available. In both instances a weighted, calibrated hose was used for collection at mid-depth. Surface samples were obtained by immersing a 20-liter tank directly in the water. The water was processed in 1961–1962 by boiling to a sludge and then processing the sludge by normal HCl-HF palynological procedures (see schedules in Traverse, 1988). In 1985–1986 some samples were boiled to a sludge, but most samples were filtered through silica filters, which were later dissolved in HF. Both techniques work well, but boiling is less trouble if the water contains much debris, because filters then clog quickly. The boiling technique requires careful monitoring, however.

The concentration of palynomorphs is expressed per 100 liters of water, because this yields numbers that are in the same range as palynomorphs per gram of sediment in rock samples. This convention



FIGURES 3 AND 4. Photomicrographs of the most important constituents of the palynoflora of the water of the lower Trinity River. Bars under 3I–J and 4R–S indicate the size of all of the specimens except for 3M, which has a separate bar.

FIGURE 3.—A. Chitinous, animal mouth part, perhaps of a polychaete worm.—B. Probably chitinous, though nearly colorless, lepidopteran wing scale. C–I. Brownish, chitinous fungal remains.—C. Possible germinating spore body.—D–F, H. Spore bodies.—G. Mycelia.—I. Sporeling.—J. Green algal coenobium, presumably *Pediastrum* sp.—K, L. Cyst or cystlike bodies, presumably algal, sometimes very abundant. The inner body seen in L is a frequent feature.—M. *Pediastrum* sp. coenobium.—N. Algal cystlike body. This form is commonly encountered in the Trinity River and in the water of other Texas streams investigated. Practically identical forms have been described as fossils, for example, as *Concentricystes* Rossignol.—O. Probable algal sphere, always with a condensed "eye" (arrow), often



abundant, not resistant-walled.—P. Baglike algal? cell, often abundant.—Q. Algal cystlike body, often having an operculum or pylome (arrow).—R, S. Algal cystlike body, two levels of focus of one specimen.—T. *Botryococcus braunii* Kützing, algal colony, related to green algae.—U. Monolete fern isospore with verrucate sculpture.

FIGURE 4.—A. *Pinus* sp., distal view of this abundant bisaccate form.—B. *Taxodium* sp., usually splits open in this fashion in water.—C. Typical pear-shaped cyperaceous pollen.—D. Poaceae pollen displaying the invariable annulate single pore and thin walls that collapse into folds during sedimentation.—E. Polar view of *Carya*, triporate hickory or pecan pollen (this example probably pecan).—F. *Quercus*, tricolporate pollen, equatorial view.—G. Polar view of *Ulmus*, multipored pollen with characteristic ridged sculpture.—H. Polar view of *Fraxinus* pollen with four

has been followed in previous publications on pollen in the water (Federova, 1952; Traverse & Ginsburg, 1966; Farley, 1987; Traverse, 1988). For pollen a ratio was also calculated to the "pollen sum," the total of wind-pollinated tree pollen. *Taxodium* was excluded from the pollen sum, because Shell Oil Co. palynologists, with whom I was associated at the time of the 1961–1962 research, excluded it for Cenozoic palynofloral studies, having noticed frequent, erratically occurring peaks of abundance of this pollen form in Neogene rock samples, which masked significant trends in other taxa.

MAJOR PALYNOFLORAL "PALYNODEBRIS" CONSTITUENTS

Pollen and spores are abundant in all streams and other bodies of water near-shore. Because sporopollenin is perhaps the most durable organic compound in existence, sporomorphs also are important in organic residues of sedimentary rock, ranging commonly from $1-2 \times 10^3$ per gram of sediment for Devonian shales to as high as 5×10^6 per gram for some Cenozoic coals (Traverse et al., 1961; Traverse, 1988). In water, pollen and spores range from about $1-5 \times 10^3$ per 100 liters in the open ocean (Farley, 1987; Traverse & Ginsburg, 1966) to 5×10^6 per 100 liters for some very small lakes in flood stage, when surrounding vegetation is flowering (see Fig. 2).

Figures 3 and 4 illustrate the major constituents of the waterborne palynoflora/palynodebris of the lower Trinity River. All kingdoms of organisms are represented except Monera: annelid worm mouth parts (3A), lepidopteran insect scales (3B), and abundant fungal spores and hyphae (3C–I), *Botryococcus* colonies (3T), and other algal material such as monads that would be classified by the palynologist as "acritarchs" (= "unknown origin") (3N–S), *Pediastrum* and related coenobia (3J, M) and some algal cystlike forms (3K, L); no certain fresh-water dinoflagellate cysts were encountered, however. Fern spores (3U) and gymnosperm pollen (4A, B) are abundant, and a great variety of monocot and dicot pollen, especially of wind-pollinated forms such as Poaceae, *Quercus, Ulmus, Carya, Ambrosia* and *Iva* (ragweed) (see Fig. 4). Pollen of animal- (mostly insect-)pollinated angiosperm taxa is also represented, but always in comparatively low numbers. The Trinity River flows through a considerable variety of vegetation types from its source in north-central Texas to the Gulf of Mexico (Fig. 1C). However, the dominant pollen and spore forms represent genera of plants that are found in the piney-woods and Gulf-prairie-and-marsh vegetational areas of the lower Trinity course relatively near the collection stations.

Palynodebris is a term not favored by all palynologists, because cellulosic plant tissues of many sorts are included, not just those with sporopollenin walls such as "true" palynomorphs have. Nevertheless, palynodebris is descriptive for pieces of wood and other tissue particles that are sedimented along with silt and sand-sized mineral particles. Such particles are abundant in all organic residues from the Trinity River (see Fig. 4V, Y). It seems obvious that if such matter is incorporated in anoxic sediment, or is covered by sediment quickly enough to prevent oxidation, considerable carbon-sinks on the continental shelves can be derived from palynomorphs and palynodebris.

Also noteworthy is the small but significant occurrence of obviously recycled forms (Fig. 4O—S, X), such as the Pennsylvanian spore *Triquitrites* sp., probably Cretaceous *Cicatricosisporites*, and Paleogene *Engelhardia* (*Momipites*). These are clearly derived from weathering and erosion of

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colpi and reticulate exine pattern. Also occurs commonly as tricolpate.—I. Polar view of 3-pored *Myrica* pollen.—J. *Salix*, equatorial view of tricolporate, reticulate pollen.—K. *Liquidambar*, multipored pollen with reticulate sculpture.—L. Multipored pollen of sort that many genera of Chenopodiaceae/Amaranthaceae produce.—M. Polar view of tricolporate, echinate (spiny) pollen produced by ragweed (*Iva* and *Ambrosia*, family Asteraceae), cf. T.—N. Equatorial view of tricolporate Umbelliferae (carrot) pollen with characteristic shoebox shape.—O. Proximal view of *Triquitrites* sp., a spore reworked from Pennsylvanian rocks.—P. Polar view of 3-pored fossil *Engelhardia/Momipites*-type pollen, reworked from Paleogene rocks.—Q. Chenopodiaceae pollen (cf. L), with many pyritic crystals inside.—R. 3-pored fossil juglandaceous pollen (*Engelhardia/Momipites*-type?) reworked as P.—S. Another example of 3-pored fossil juglandaceous pollen (*Engelhardia/Momipites*-type?); compare P and R.—T. Ragweed pollen as M.—U. Polar view of long-spined, insect-pollinated Asteraceae pollen.—V. "Clumpy" amorphous, partly degraded plant tissue infested with fungal mycelia.—W. Separated *Pinus* saccus (cf. A) containing pyrite crystals.—X. Characteristically ridged *Cicatricosisporites* spore, probably reworked from Cretaceous rock—the darker color of these spores distinguishes them from spores of extant ferns found in my samples; however, the illustrated form is very similar morphologically to spores of *Anemia mexicana* Kl., a fern still found in the Edwards Plateau of Texas, cf. Dettmann & Clifford (1991).—Y. Fragment of wood.—Z. *Carya* (cf. E) pollen showing extensive biological degradation (bacterial and/or fungal).

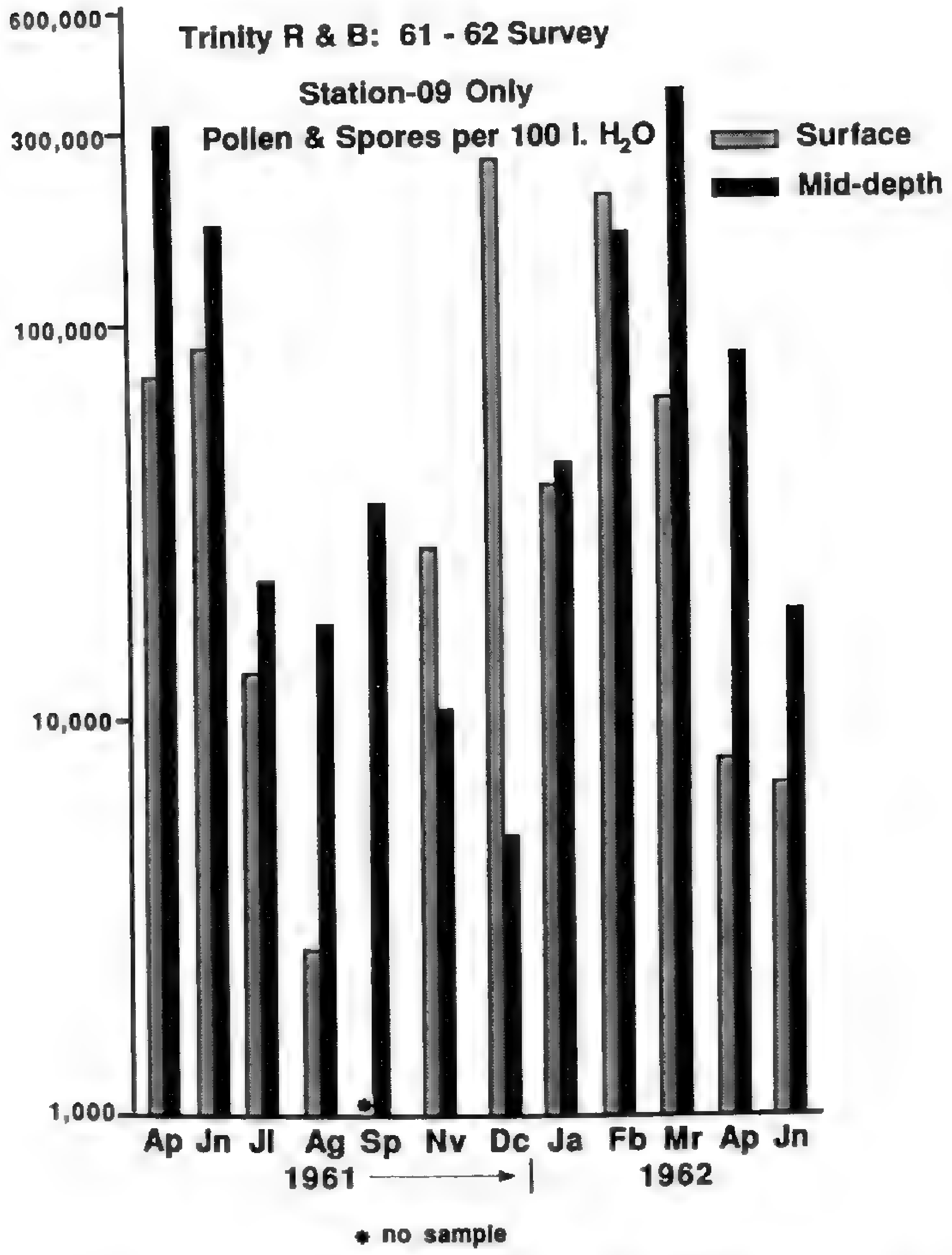

FIGURE 5. Amounts of pollen and spores per 100 liters of water at station 09 (see Fig. 1B for location), 1961–1962. Plotted logarithmically.

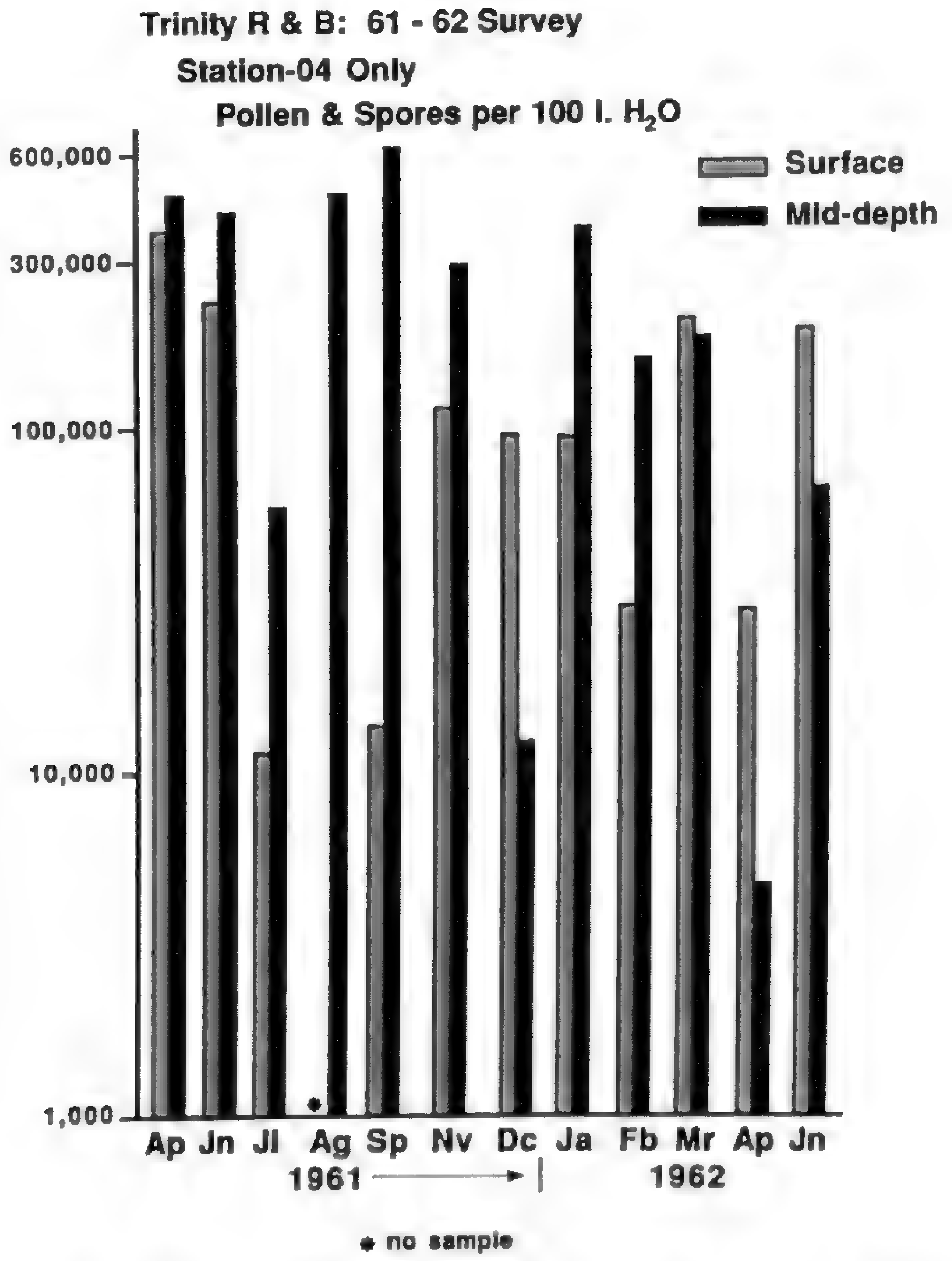

FIGURE 6. Pollen and spores per 100 liters of water at station 04 (see Fig. 1B for location), 1961–1962. Plotted logarithmically.

rocks in the Trinity course, which means that the *Triquitrites* has traveled some 750 km, *Cicatricosisporites* perhaps 500 km, and *Engelhardia* 200–300 km. Burgess (1987) has shown that in the Mississippi River, coal beds are eroded far upstream, probably more than 1,500 km, and particles of the coal-containing Pennsylvanian spores reach the Gulf of Mexico in fair abundance as "coffee grounds." Pyrite-filled grains, or parts of grains (Fig. 4Q), show that bacterial action under reducing conditions has occurred. Partially corroded spores and pollen (Fig. 4Z) demonstrate attack by microorganisms or by oxidation. Such fossils indicate that palynomorphs are affected by a variety of local environmental conditions during their eventful travels down the Trinity.

SEASONAL CHANGES

Station 09 in 1961–1962. Figure 5 illustrates the seasonal changes observed in 1961–1962 at station 09 in the river proper (Fig. 1). Note that pollen load frequently reached over 1 × 10^5 per 100 liters of water and was above 3 × 10^5 per 100 liters in April 1961 and March 1962. With few exceptions (November–December 1961, February 1962) the mid-depth water contained more pollen than surface water, meaning that for most of the year transportation consists predominantly of palynomorphs coming to the stream a day or many days before sampling. Surface samples include pollen newly arrived by air, and by runoff water, from the surrounding vegetation, as well as palynomorphs stirred up from below when flow is turbulent. In the late fall and winter months (January 1962 was only a slight exception), pollen in the superficial runoff water predominated over pollen in the mid-depth load of the river.

Station 04 in 1961–1962. Figure 6 shows the 1962–1962 seasonal changes at station 04, on the delta front (Fig. 1B). Observe first that the numbers are in general the largest for any of the three stations, reflecting continued discharge from the river into the delta channel, as well as pollen rain from abundant neighboring anemophilous vegetation. Mid-depth water contained more pollen than surface water except in December 1961 and March–June 1962. There is considerable tidal influence at station 04, and the relatively low mid-depth water pollen concentrations for some months may be accounted for by incoming, deeper, tidally influenced water, depleted of pollen. Also, because of tidal influence, fresh river water tends to "ride" out over the brackish, deeper water before mixing with it.

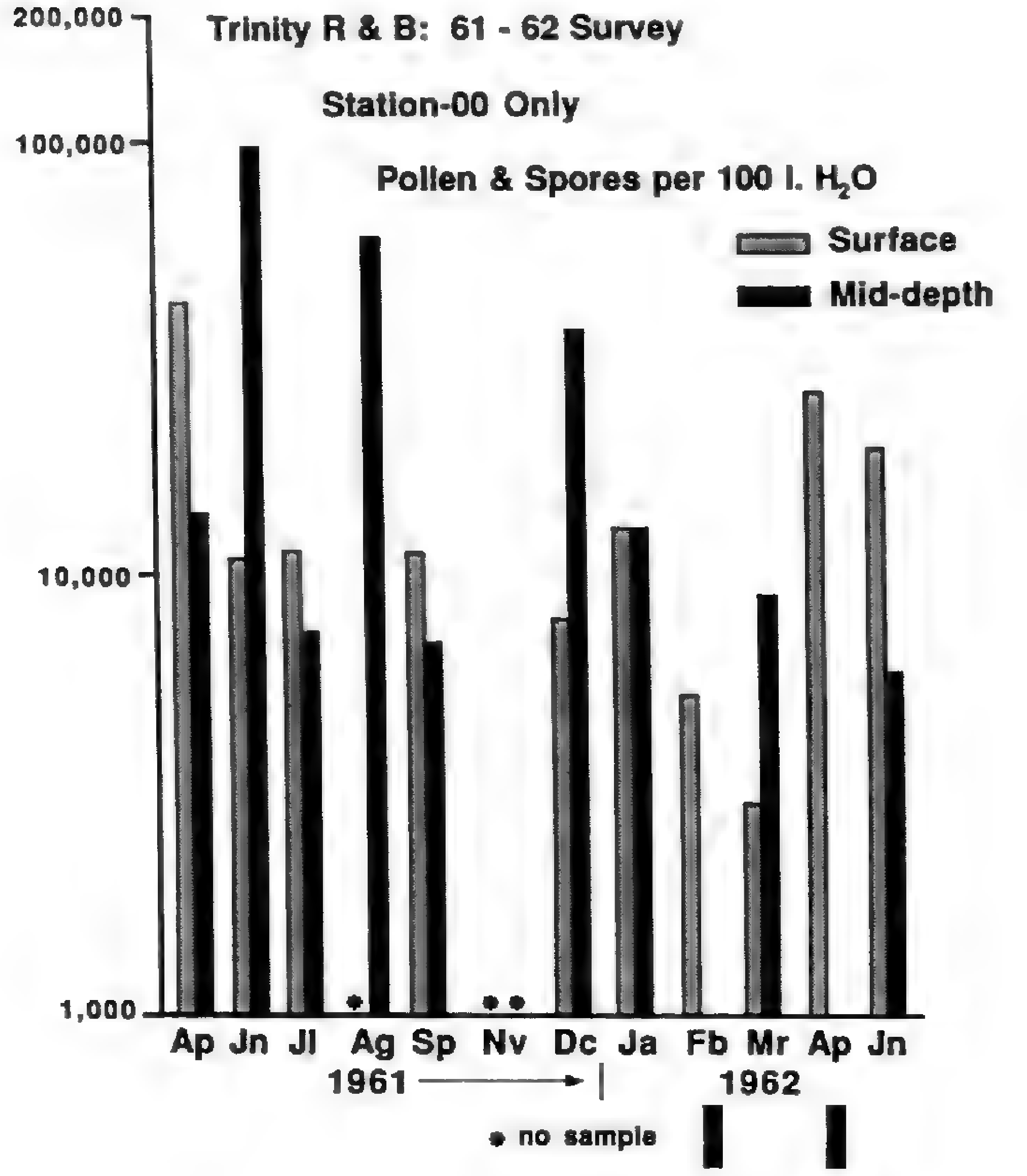

FIGURE 7. Pollen and spores per 100 liters of water at station 00 (see Fig. 1B for location), 1961–1962. Plotted logarithmically. The mid-depth readings for February and April 1962 are extremely low (less than 1,000), and they therefore plot below the 1,000 line.

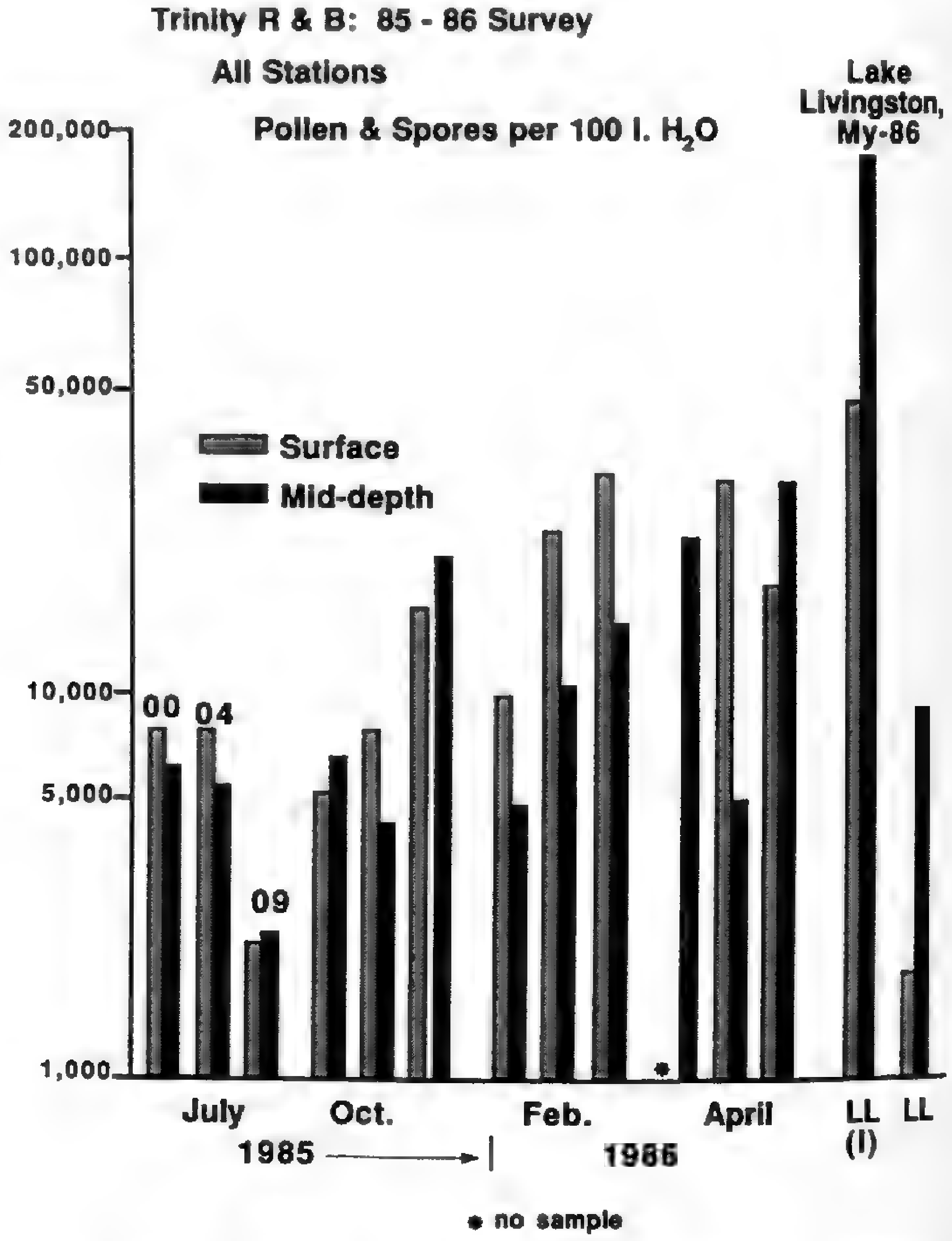

FIGURE 8. Pollen and spores per 100 liters of water, stations 09, 04, 00, and Lake Livingston, 1985–1986. The sequence of stations is the same for October 1985 and February–April 1986, as displayed for July 1985. See Figure 1A for Lake Livingston collecting sites. Plotted logarithmically.

Station 00 in 1961–1962. Figure 7 shows pollen concentration at station 00 in the open Trinity Bay (Fig. 1B). These are the lowest values for any of the stations, no sample exceeding 1 × 10^5 per 100 liters. Most were far less, as the water here is depleted of pollen by settling out (sedimentation). In contrast to other stations, most surface samples exceeded mid-depth samples in concentration. Two of the mid-depth samples (February and April 1962) contained the fewest palynomorphs of any of the 1961–1962 samples. Here, in the open bay, tidal movements probably greatly influence the relative pollen content, especially of mid-depth water.

Observations on pollen load of water at all stations in 1985–1986. In 1968, the U.S. Army Corps of Engineers completed a dam impounding a huge, artificial lake called Lake Livingston (see Fig. 1A). In 1985–1986, I made a few return visits to stations 00, 04, and 09, in order to sample the river under the presumably altered conditions. The results are displayed in Figure 8. Obviously, the pollen load of the lower river, now merely an outlet for Lake Livingston, is significantly depleted, by comparison with the pre-dam river. The conclusion, though based on only one year of measurements, seems obvious. The distributions of surface versus mid-depth concentrations do not seem greatly different from those observed in 1961–1962. However, the total reduction in palynomorph load by interpolation of Lake Livingston as a gigantic settling basin for sediment of all kinds, including pollen and spores, presumably tells the story. Note in Figure 8 that Lake Livingston water at the *inlet* is comparable to 1961–1962 values for the river proper (station 09). Water from well out in Lake Livingston taken the same day displays pollen load comparable to the present-day lower Trinity River, or to water taken from central parts of large lakes generally.

COMMENTS ON SPECIFIC TAXA

In 1961–1962, seasonal variation, and differences depending on position of the stations, were studied for some of the important sorts of pollen. The limited number of samplings in 1985–1986 seem to follow the same pattern, despite the considerable curtailment of total pollen load in 1985–1986, as compared to 1961–1962.

PROMINENT TREE POLLEN

A. *Quercus* (Figs. 9, 4F). Oak pollen is a major component at all stations and in all seasons. Oaks

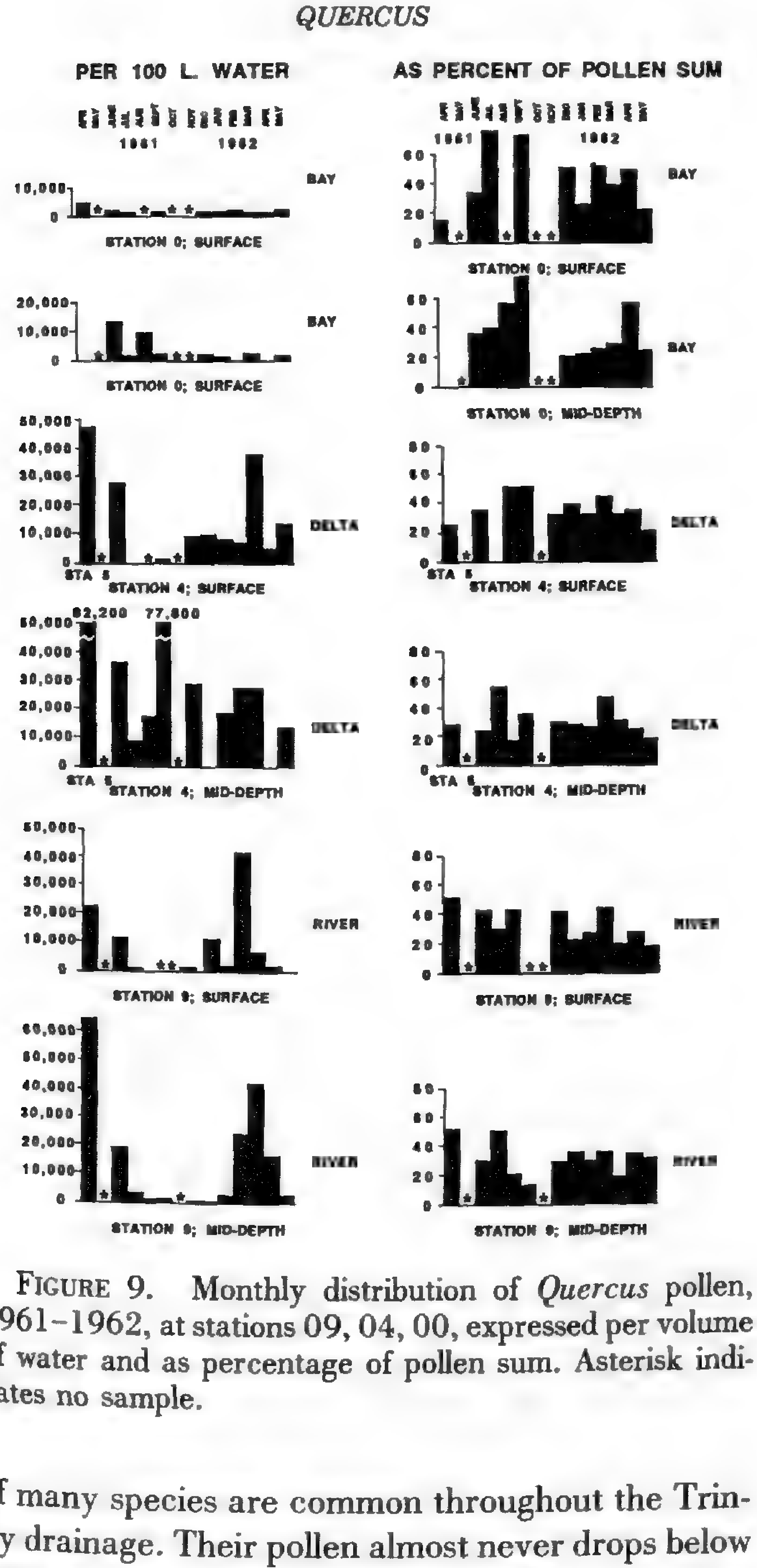

FIGURE 9. Monthly distribution of *Quercus* pollen, 1961–1962, at stations 09, 04, 00, expressed per volume of water and as percentage of pollen sum. Asterisk indicates no sample.

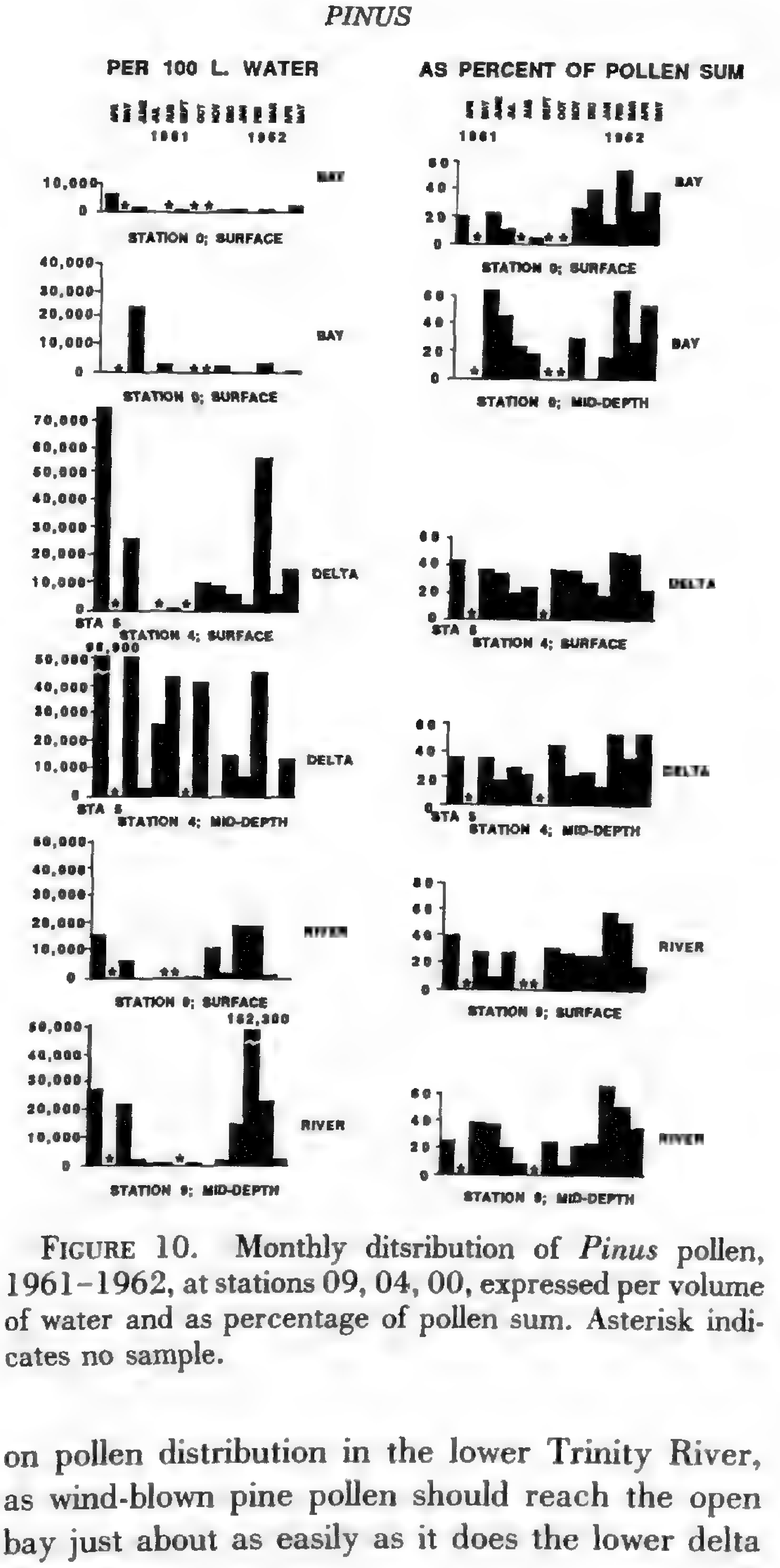

FIGURE 10. Monthly ditsribution of *Pinus* pollen, 1961–1962, at stations 09, 04, 00, expressed per volume of water and as percentage of pollen sum. Asterisk indicates no sample.

of many species are common throughout the Trinity drainage. Their pollen almost never drops below 20% of total palynoflora and is usually higher. On the basis of pollen per 100 liters of water, however, marked differences are observable. Relatively small amounts of *Quercus* pollen remain in the water of the bay. At the river station (09) and at the surface on the delta, the summer and fall concentration of *Quercus* pollen is low, whereas during the spring flowering period, amounts are high. Mid-depth water on the delta has anomalously high values during some summer months, presumably because of pollen being stirred up with other sediment from the bottom.

B. *Pinus* (Figs. 10, 4A). The distribution of pine pollen, both as to percentage, and as an amount of pollen per 100 liters of water, is very similar to that just described for oak pollen. The two are codominants of the pollen flora. *Pinus* species are also abundant in the drainage area. The low values per 100 liters of water in the bay confirm the overwhelming importance of hydrodynamic effects on pollen distribution in the lower Trinity River, as wind-blown pine pollen should reach the open bay just about as easily as it does the lower delta at station 04.

C. Ulmaceae (Figs. 11, 4G). This category includes several species of *Ulmus* and of the closely related *Planera aquatica* (Walt.) J. Gmelin (water elm). (*Celtis* pollen, although ulmaceous, is different morphologically and in distribution of the trees; it was counted separately.) The late fall and winter flowering periods of different species of elm are reflected in percentages and amount per 100 liters of water. Mid-depth values for the delta station (04) show the same stirring-up phenomenon described for *Quercus* and *Pinus* above.

D. *Taxodium* (Figs. 12, 4B). Swamp cypress pollen provides a clear-cut reflection of flowering time of the producing trees. Cypress produces pollen in January and February in the area studied. Significant amounts of *Taxodium* pollen at other times in mid-depth delta water must represent some combination of: (1) pollen stirred up with other

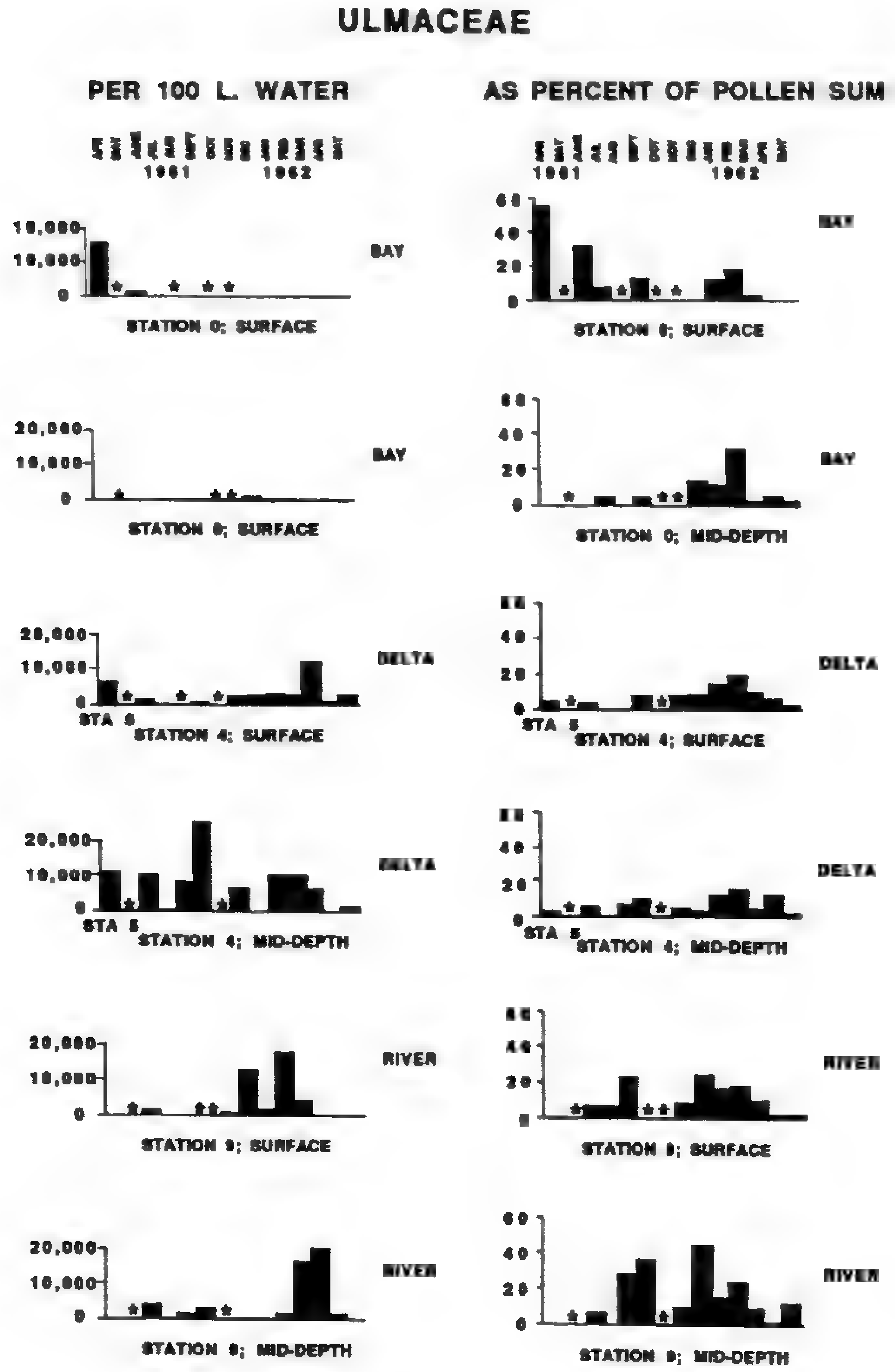

FIGURE 11. Monthly distribution of Ulmaceae pollen, 1961–1962, at stations 09, 04, 00, expressed per volume of water and as percentage of pollen sum. Asterisk indicates no sample.

sediment in the delta by river and tidal action, as in A–C above, or (2) pollen washed off of surfaces upstream.

E. *Carya* (Figs. 13, 4E). This genus includes all the hickory species of the area, as well as pecan. The record bespeaks the April–May flowering of the genus in this area, plus what I interpret as an influx of reworked *Carya* pollen in summer and fall that fits in quite well with records for *Engelhardia/Momipites*-type, a known reworked Paleogene form (see below). *Carya* pollen is known to be robust and frequently reworked.

F. *Engelhardia/Momipites*-type (Figs. 14, 4P, R?, S). This pollen type was produced by trees related to *Juglans* (walnut) and *Carya*. *Engelhardia* itself is, however, now extinct in the United States. (The genus, or closely related juglandaceous trees making pollen of the *Engelhardia/Momipites*-type, still exists in Asia, Mexico, and Central America.) Therefore, this pollen is obviously reworked from older, probably Paleocene–Oligocene deposits. Plotted with the pollen distribution is the approximate monthly total rainfall at Riverside, Texas, on the Trinity River, near the boundary between Oligocene and Eocene rocks. Occurrences of *Engelhardia/Momipites*-type are perhaps related to preceding heavy rains in these areas upstream. It is worth noting that there is no certain way to distinguish reworked pollen of *Quercus*, *Pinus*, and other extant genera from their recently produced counterparts (cf. especially *Carya*, above). The regular occurrence of reworked forms in surface water samples proves that the whole palynomorph load of the river is thoroughly mixed by turbulence when the rate of flow is sufficiently high.

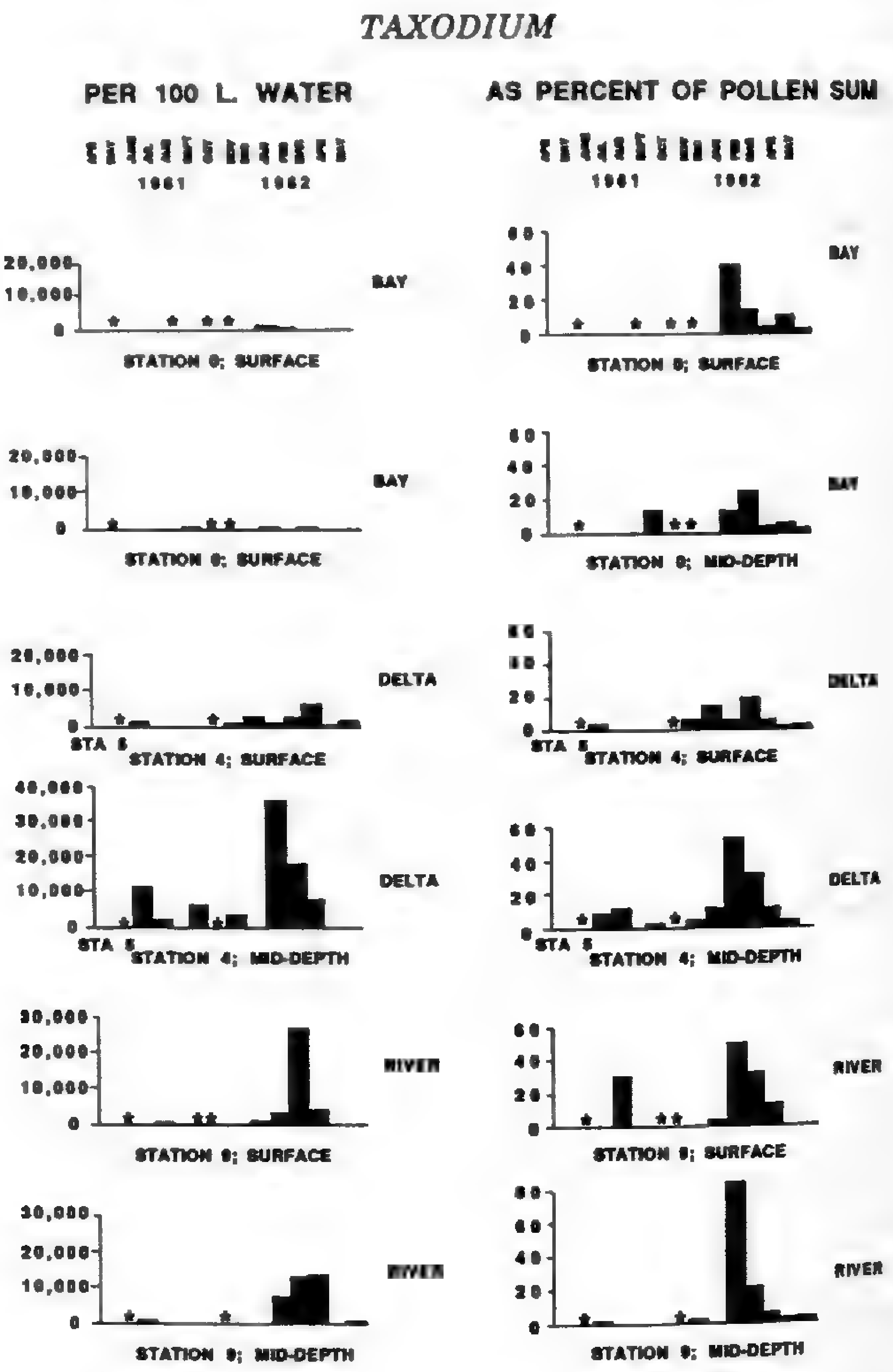

FIGURE 12. Monthly distribution of *Taxodium* pollen, 1961–1962, at stations 09, 04, 00, expressed per volume of water and as percentage of pollen sum. Asterisk indicates no sample.

PROMINENT HERBACEOUS FORMS

A. Poaceae (Figs. 15, 4D). Grass pollen is very difficult to separate as to genus, and this is not ordinarily attempted in palynological analysis. Grass pollen in Trinity River water shows strong seasonality, reflecting its summer–fall flowering. This is especially obvious in percentage-of-pollen sum calculations. The record for Cyperaceae (Fig. 4C) is very similar to that for grass, and both data sets show rather small concentrations of pollen in the water at station 09, presumably a reflection of the prevailingly wooded area in that vicinity and north of it.

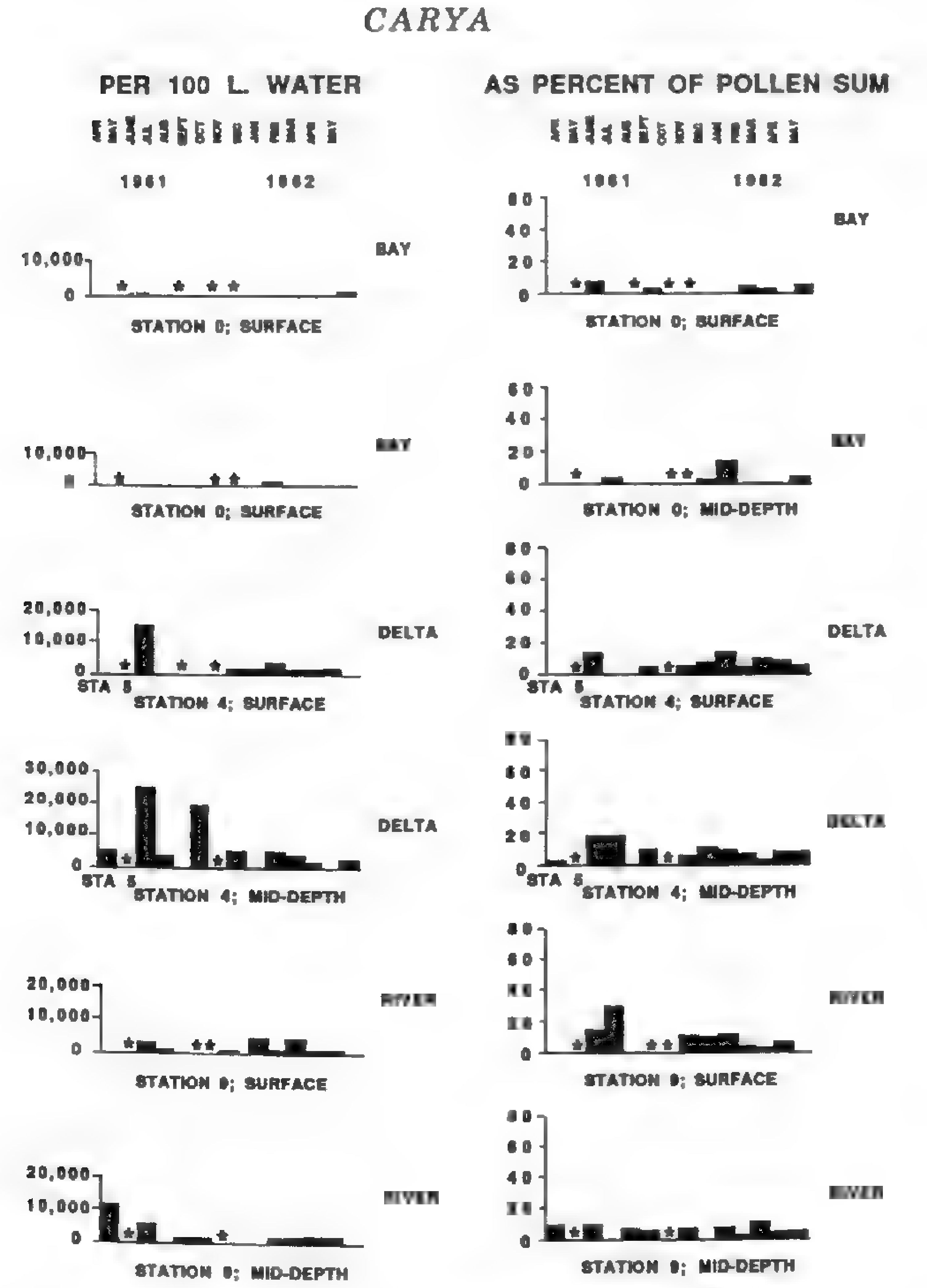

FIGURE 13. Monthly distribution of *Carya* pollen, 1961–1962, at stations 09, 04, 00, expressed per volume of water and as percentage of pollen sum. Asterisk indicates no sample.

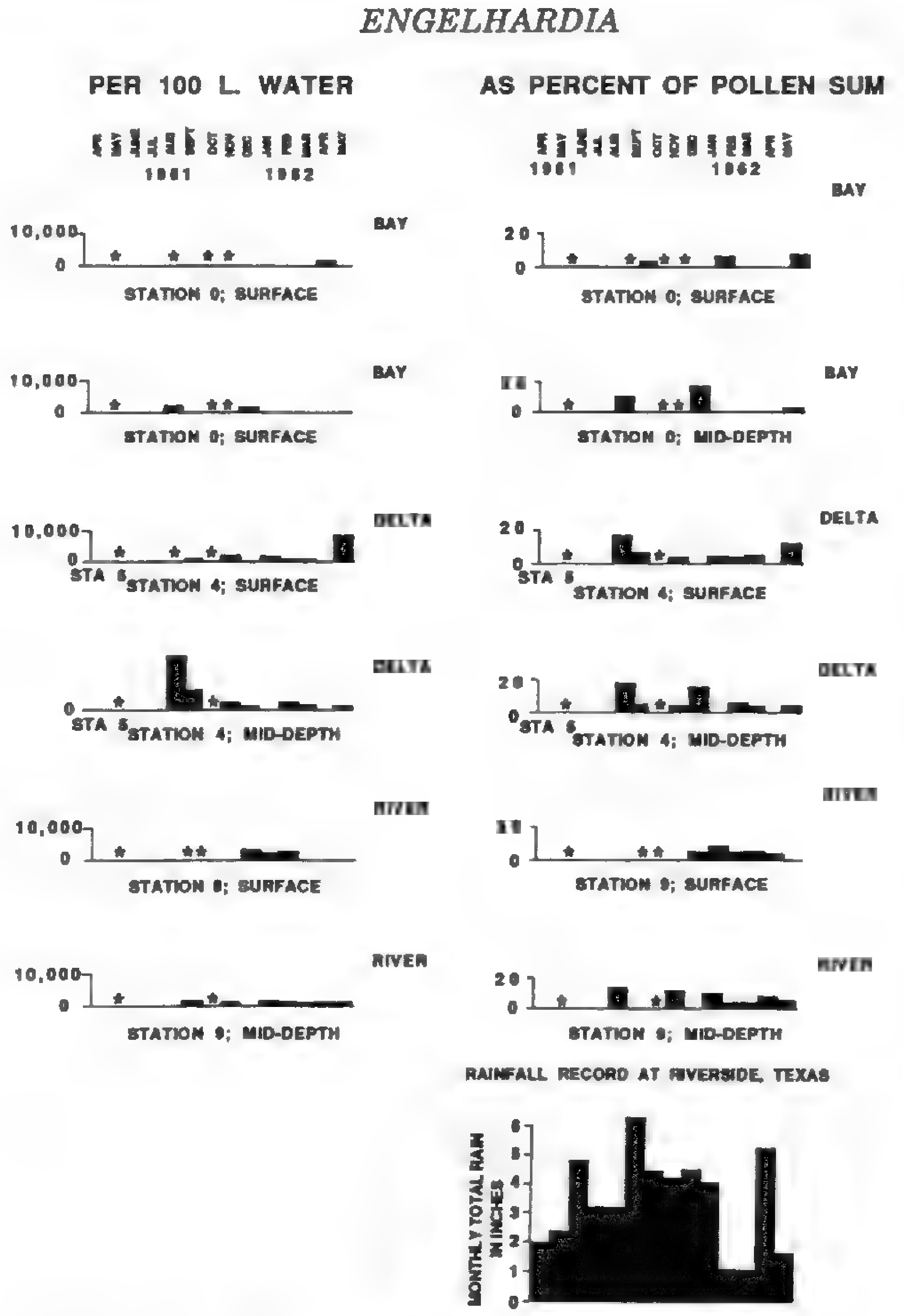

FIGURE 14. Monthly distribution of the reworked pollen of *Engelhardia/Momipites*-type, 1961–1962, at stations 09, 04, 00, expressed per volume of water and as percentage of pollen sum. The monthly rainfall record for Riverside, Walker County, Texas, upstream on the Trinity River, is plotted below. The reworked pollen record probably reflects erosion upstream. Asterisk indicates no sample.

B. Asteraceae (Figs. 16, 4M, T, U). This large family includes thistles (*Cirsium horridulum* Michaux), groundsel bushes (*Baccharis halimifolia* L.) and many others occurring in the subject area, both wind-pollinated forms such as ragweed (*Iva* spp. and *Ambrosia* spp.), which produce huge quantities of pollen, and insect-pollinated forms such as sunflower (*Helianthus* spp.), which produce relatively little. The common wind-pollinated composites flower in the summer and fall. This flowering pattern is reflected better as a percentage of pollen sum than in concentration per volume of water, which is influenced by other factors such as water velocity and turbulence.

C. Chenopodiaceae (Figs. 17, 4L, Q). The chenopod record probably consists partly of freshly produced pollen, a phenomenon of spring and early summer, and partly of reworked pollen, an expression of erosion. The pollen of this family characteristically has thick exine and high sporopollenin percent, making it very "robust" (durable). This durability is reflected in the large number of reworked examples from Recent, Pleistocene, and older salt marsh deposits upstream. *Salicornia* (saltwort), a salt marsh plant, clearly produces much of the chenopodiaceous pollen in these samples. (It should be noted that pollen of the Amaranthaceae is very similar to that of the Chenopodiaceae. Therefore, the two are usually united in pollen analyses as "cheno/ams." I have not done that in this study, because my fieldwork convinced me that most of the periporate pollen of this type was coming from *Salicornia*.)

FUNGAL SPORES (FIGS. 18, 3D–F, H, I)

These chitinous-walled spores are mostly produced by saprophytes, and the walls are comparable in robustness to sporopolleninous exines of pollen. Muller (1959) noted their prevalence on deltas and their scarcity offshore, implying that they do not transport well. Muller postulated that perhaps the chitinous-walled spore coats have a relatively high specific gravity (there are, however, many *non*-chitinous-walled fungal spores that are abundant aerosol particles worldwide). The lower Trinity record for 1961–1962 shows that fungal spores are abundant in the water with no obvious

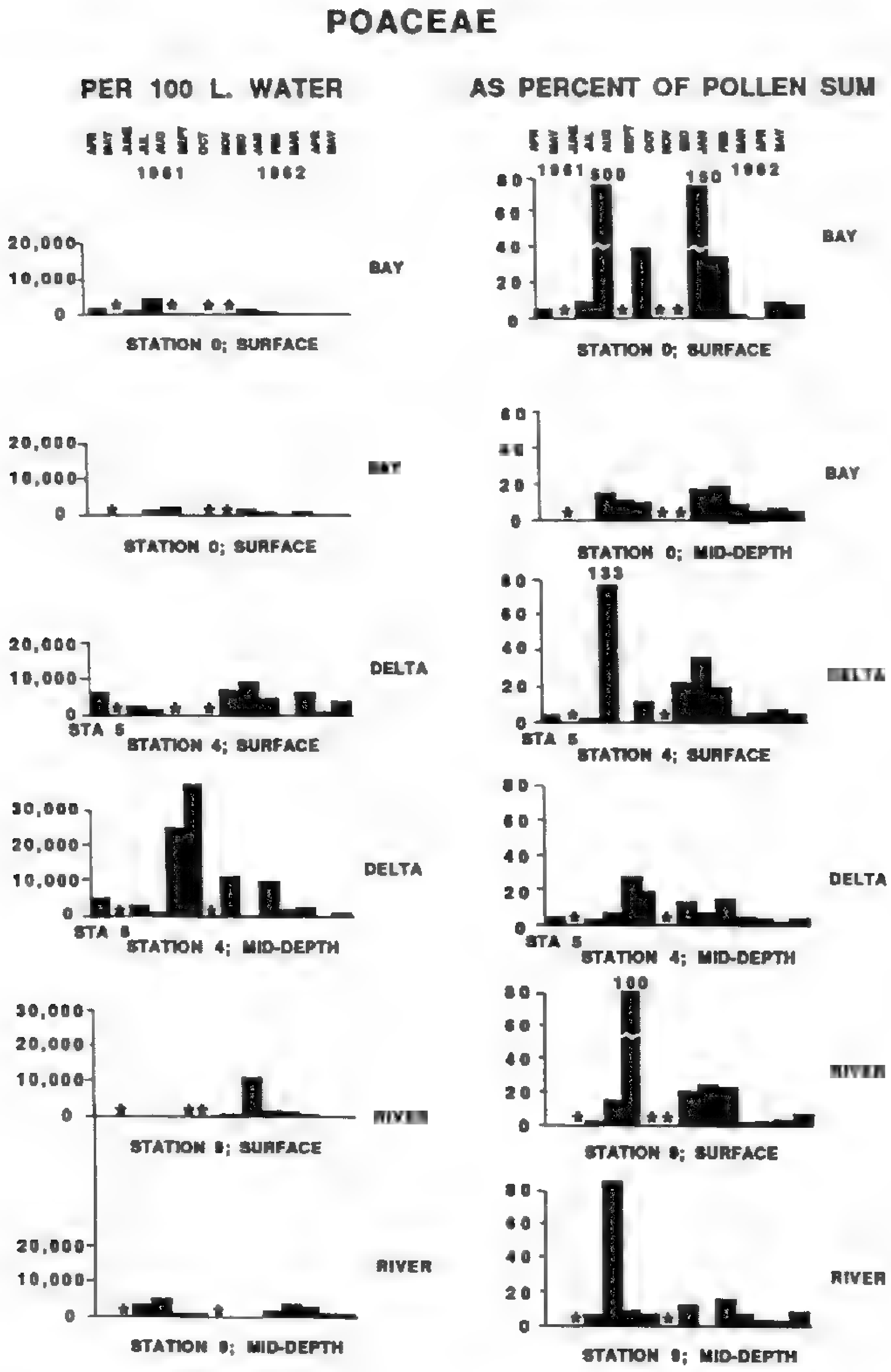

FIGURE 15. Monthly distribution of Poaceae pollen, 1961–1962, at stations 09, 04, 00, expressed per volume of water and as percentage of pollen sum. Asterisk indicates no sample.

seasonal pattern. They are not expressed as a percentage of (tree) pollen sum, as they represent a category of fossils totally unrelated to the plant-pollen of the pollen sum. The 1985–1986 record for fungal spores shows for the most part the same sort of overall reduction in concentration per volume of water as is seen for pollen and spores, when compared to 1961–1962.

SUMMARY AND CONCLUSIONS

The concentration of palynomorphs per volume of water in Trinity River and Bay fluctuates greatly. The total amount per 100 liters of water in the river channel just off the delta (station 04) sometimes was as high as about 5 × 10^5 per 100 liters of water in 1961–1962 and sometimes as low as about 1 × 10^4 per 100 liters of water. This should be compared with the average report for four stations on the Volga River above the delta: 2.4 × 10^4 per 100 liters of water (Fedorova, 1952), and with an average concentration for the lower Mississippi River of about 4.5 × 10^5 per 100 liters of water (Chmura & Liu, 1990). Marine water on the Great Bahama Bank averaged 9.6 × 10^3 per

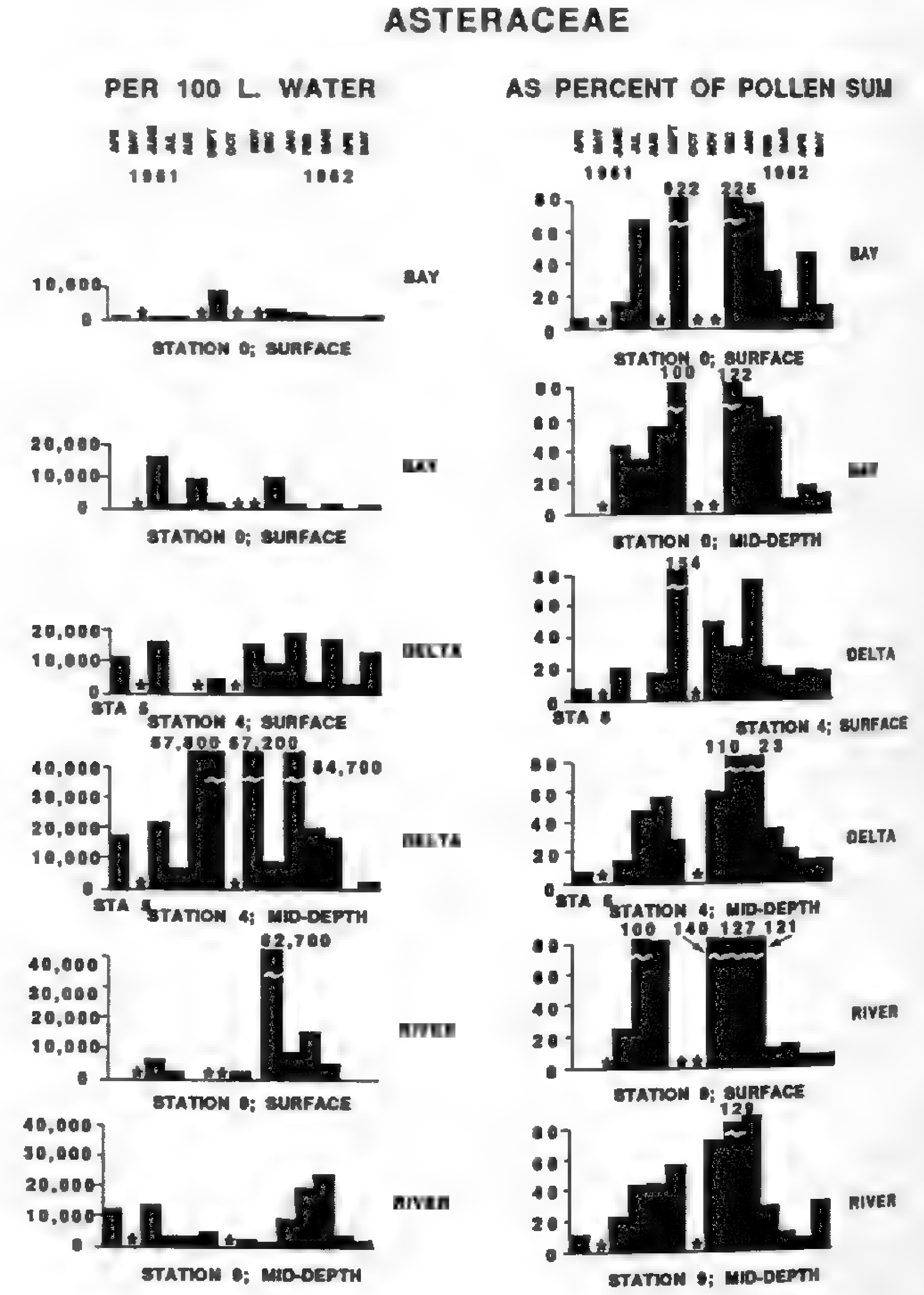

FIGURE 16. Monthly distribution of Asteraceae pollen, 1961–1962, at stations 09, 04, 00, expressed per volume of water and as percentage of pollen sum. Asterisk indicates no sample.

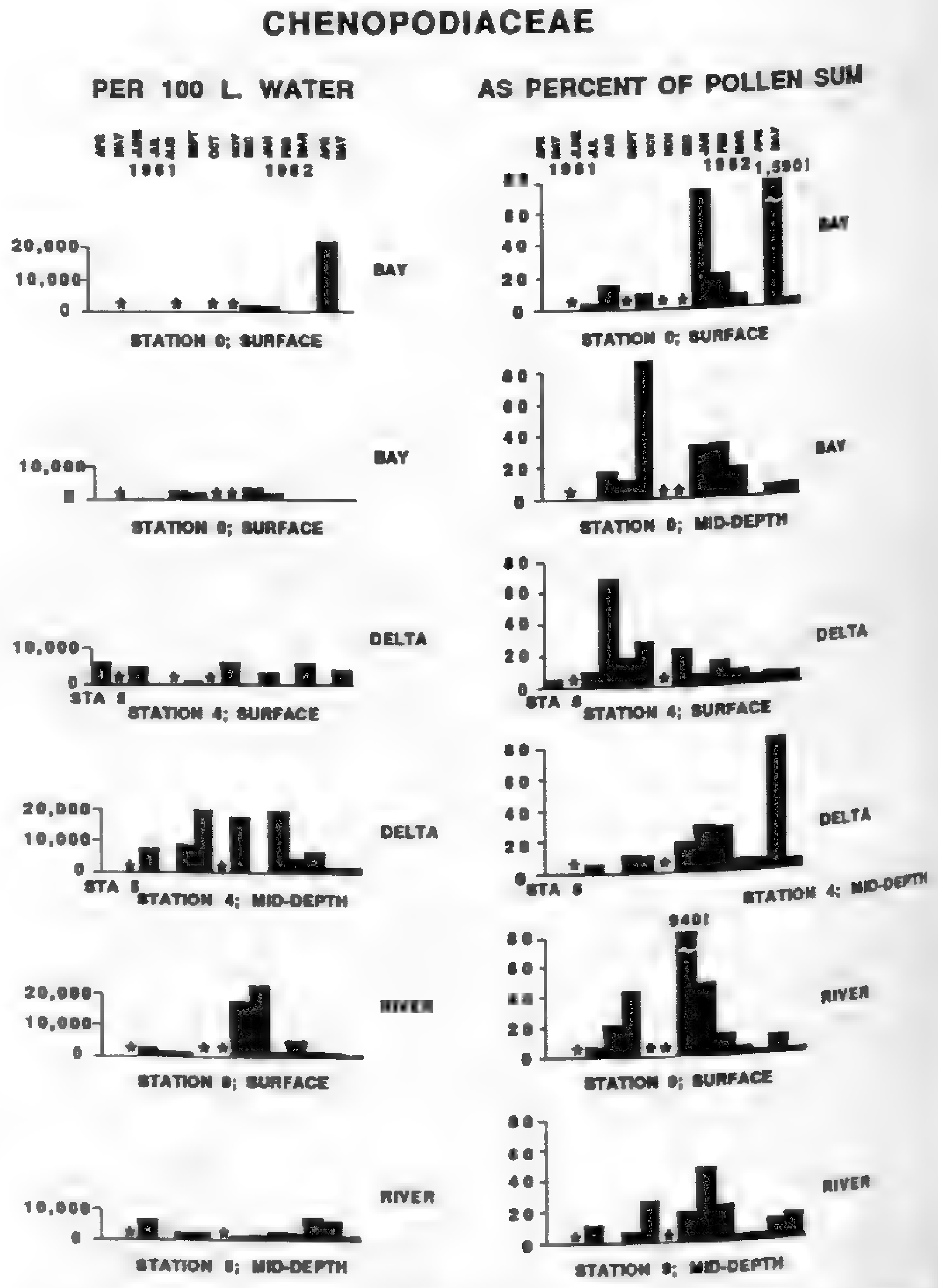

FIGURE 17. Monthly distribution of Chenopodiaceae pollen, 1961–1962, at stations 09, 04, 00, expressed per volume of water and as percentage of pollen sum. Asterisk indicates no sample.

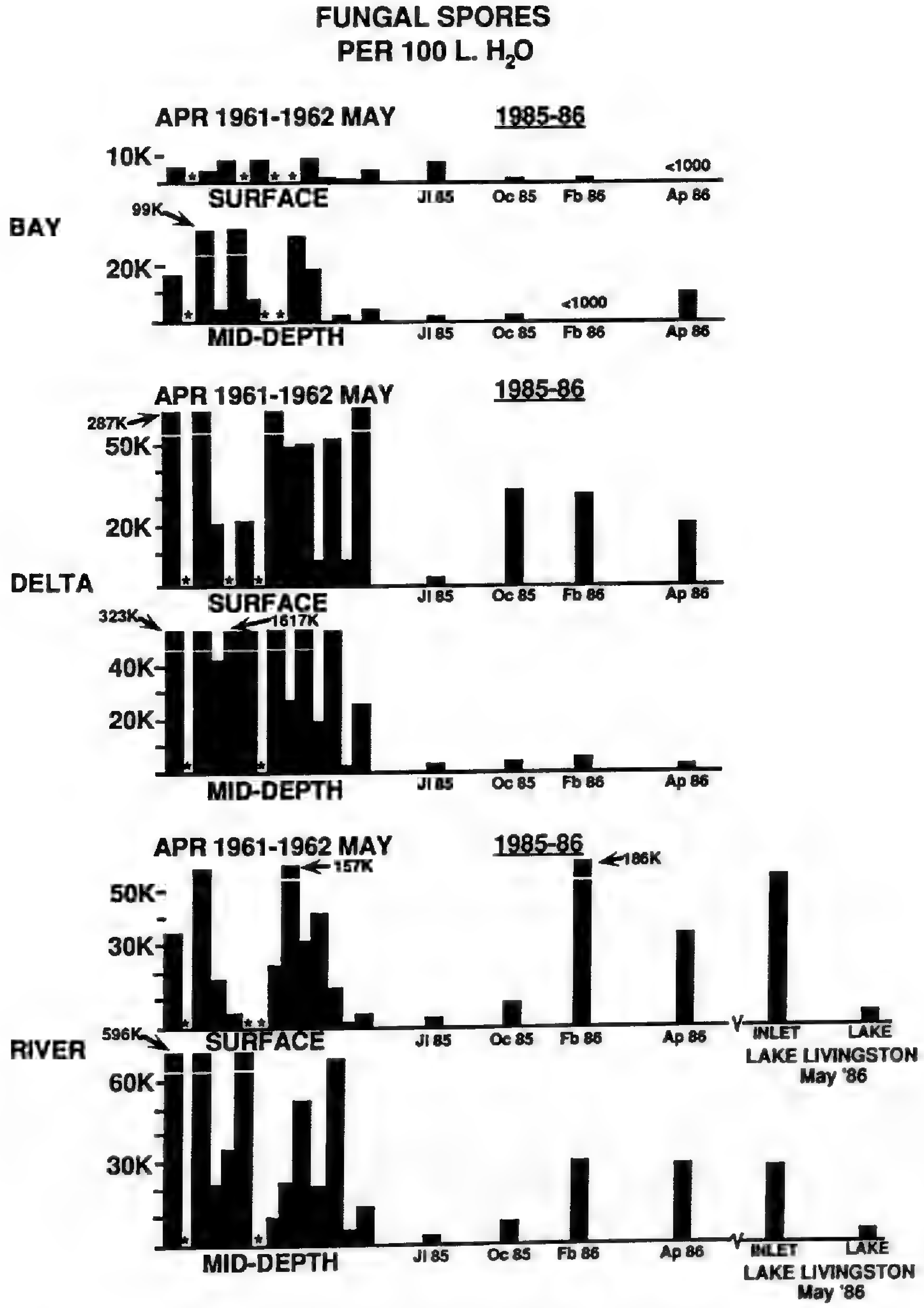

FIGURE 18. Fungal spores per 100 liters of water, 1961–1962 versus 1985–1986, for lower Trinity River and in 1985–1986 for Lake Livingston. Sampling stations as shown in Figure 1A, B.

100 liters of water (Traverse & Ginsburg, 1966). Two samples from the Gulf of Mexico near Galveston averaged 8 × 10^3 per 100 liters of water (Traverse, 1988). Presumably the higher pollen content of Gulf water reflects its high sediment content, compared with the relatively clear water of the Great Bahama Bank. As discussed in Traverse (1990), the impoundment in 1968 of Lake Livingston about 200 km north of the study area seems to have considerably reduced the palynomorph load of the water in the lower Trinity. At the same time, the proliferation of algae such as *Botryococcus* in the water of the lower Trinity since impoundment has been notable.

Water in the river channel (station 04) at the edge of the delta contains more pollen than either water from the bay (station 00) or in the river proper (station 09). As the river water discharges into the bay and loses turbulence, the pollen load settles out very quickly. As a result, the pollen content of water in the bay is usually much less than that of water from the river on the delta: in 1961–1962, station 00 (bay) averaged 1.9 × 10^4 per 100 liters of water; station 04 (delta) averaged 1.8 × 10^5 per 100 liters of water; station 09 (lower river) averaged 9 × 10^4 per 100 liters of water.

The pollen spectra of water in the river (station 09) are sometimes rather different from those of the bay (station 00), for example, in the case of Asteraceae. A complex of influences could be responsible. One possibility suggested here is that the Asteraceae pollen in the bay is mostly wind-borne, whereas that of the river is mostly a product of water action. If this is true, seasonal flowering peaks will be better represented in the bay, which seems to be the case for Asteraceae. On the other hand, for *Pinus* and *Quercus* pollen, seasonality of flowering is much more nearly reflected in the river (station 09) than in the delta (station 04) or bay (station 00). This may represent a reverse trend of that for Asteraceae, in that the tremendous quantities of pine and oak pollen formed in the immediate vicinity of the river have more of an impact on the pollen spectra there than they do in the bay.

Taxodium pollen shows a good correspondence at all locations between abundance in the water and in flowering peaks of the producing trees.

Pinus and *Quercus* pollen grains are relatively abundant in the water at all seasons. Because pine and oak pollen are the major constituents of the pollen sum, expression of these forms as ratios to the pollen sum (percentages) masks their greater absolute abundance in the spring of the year. This is especially evident at station 09. On the other hand, Asteraceae pollen shows seasonality in the percentage plots that it does not show when plotted per volume of water. Both of these examples underline the importance of interpreting pollen percentages with caution. However, it must also be emphasized that plotting pollen per volume of water has the drawback of being governed by the amount of water. For example, low pollen per volume can simply mean more water than normal.

Engelhardia/Momipites-type pollen is a reworked, presumably Paleogene, form, and its distribution is seemingly a record of erosion. Periods of abundance of this fossil in the water in the area studied may reflect previous high rainfall levels in a part of the Trinity River drainage in which Paleocene–Oligocene rocks occur. Considerable evidence of other reworked forms has been found. Foraminiferal inner tests are occasionally found in the water of Trinity River at station 09, where they are almost certainly reworked. The distribution of *Carya* pollen indicates dependence partly on the flowering peaks of the genus and partly on reworking of fossil *Carya* pollen. A similar mixed origin is suggested for Chenopodiaceae pollen, which has an extremely durable exine. Reworked chenopod pollen is probably in large part from Recent, Pleistocene, and older sediments, originally deposited under salt marsh conditions. This category may well also include some amaranthaceous pollen, as the two are virtually indistinguishable in routine analyses.

The complex of palynomorphs and palynodebris in river water near its discharge is an important reflection of: (1) events affecting the vegetation of the land which the river drains; and (2) changes in the assortment of plant biomass types sedimented, an expression of conditions and events in stream regimes.

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BIOLOGY OF *SCOLIOPUS* (LILIACEAE) I. PHYTOGEOGRAPHY AND SYSTEMATICS[1]

Frederick H. Utech[2]

Abstract

Comparisons of a wide variety of vegetative, floral, and reproductive characters of *Scoliopus* reveal consistent differences between the Californian *S. bigelovii* and the Oregonian *S. hallii*, whose distributions are mapped. With leaf numbers greater than two reported, a spiral, rather than opposite, leaf arrangement is demonstrated. The floral morphology and geometry, which involve intricate pollination subunits, are related to an outbreeding pollination system. A pollination subunit is established by the terminally recurved stylar arms, the versatile, extrorse anthers, the unusual triangular gynoecium, and the nectariferous, petaloid outer tepals. The myrmecochorous dispersal patterns in *Scoliopus* based on subterranean stems, elongate twisting pedicels, capsules dehiscing in the upper duff layers, and elaiosomal seeds are discussed. The taxonomic relationship to *Paris*, *Trillium*, and *Medeola* is deemed remote.

Scoliopus Torrey, a genus of two herbaceous perennials, occurs in the coastal montane regions of western North America, with the larger *S. bigelovii* Torrey restricted to California and *S. hallii* S. Watson to Oregon.

Detailed information on the distribution of *S. bigelovii* (Utech, 1979), floral vascular anatomy (Utech, 1979), pollination biology (Berg, 1959; Moldenke, 1976; Mesler et al., 1980), karyology (Johansen, 1932; Cave, 1966, 1970), seedlings (Rimbach, 1902), embryology, and dispersal (Berg, 1959, 1962b) has been published. However, beyond limited floristic accounts (Abrams, 1940; Peck, 1961; Hitchcock et al., 1969; Hitchcock & Cronquist, 1973), comparable data on *S. hallii* are lacking. Since 1979, *S. hallii* has been a watch-listed species among Oregon's rare, threatened, and endangered plants (Siddall et al., 1979; Eastman, 1990). Furthermore, *S. hallii* has been used by the federal Bureau of Land Management as a key indicator species for monitoring riparian plant communities in western Oregon.

Scoliopus is poorly represented in herbaria because it blooms very early in spring. With more populations now located and specimens of *S. hallii* available for study, as well as detailed field observations completed, a critical assessment of this interesting genus is now possible.

Materials and Methods

Populations of *Scoliopus* from south of San Francisco, California, northward to Portland, Oregon, were marked and sampled. This study occurred during the early spring and summer of 1988 and 1990. Mass collections, where appropriate, were made for morphometric analysis throughout the ranges of *S. bigelovii* and *S. hallii*. Life history herbarium specimens of flowering and fruiting individuals from the same site were also made (Utech et al., 1984). Alcoholic collections, using FAA as the fixative, were made for anatomical (Johansen, 1940; Sass, 1958; Utech, 1979) and reproductive studies (Ohara & Kawano, 1986a, b; Kawano et al., 1986; Ohara & Utech, 1986, 1988; Ohara, 1989). Voucher specimens have been deposited at Carnegie Museum of Natural History (CM).

Fifty-six populations of *Scoliopus* were located: 35 for *S. bigelovii* and 21 for *S. hallii*. The *S. bigelovii* sites were in the following counties of California: Humboldt (9), Marin (4), Mendocino (7), San Mateo (4), and Sonoma (11). The *S. hallii* sites were in the following counties of Oregon: Benton (2), Clatsop (1), Douglas (2), Lane (4), Lincoln (1), Linn (5), Polk (3), and Tillamook (4). The exact locations of these study and/or collection sites are cited in the specimens examined section.

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[1] The author thanks the curators of the following herbaria for their hospitality during visits or for loaning specimens: CAS, CM, DS, GH, HSC, JEPS, MO, NY, ORE, OSC, PH, ROPA, UC, US, WILLU, and WTU. I particularly thank W. Brown, K. L. Chambers, J. Erwin, I. Knight, W. Knight, L. Scofield, D. H. Wagner, and P. Zika for field, herbarium, and logistic support and acknowledge the Museum's Botany O'Neil Field and M. Graham Netting Research Funds for essential funding. Portions of the fieldwork were further supported by a cooperative grant from the Japanese Ministry of Education (Japan Overseas Project 01041053) to S. Kawano (KYO).

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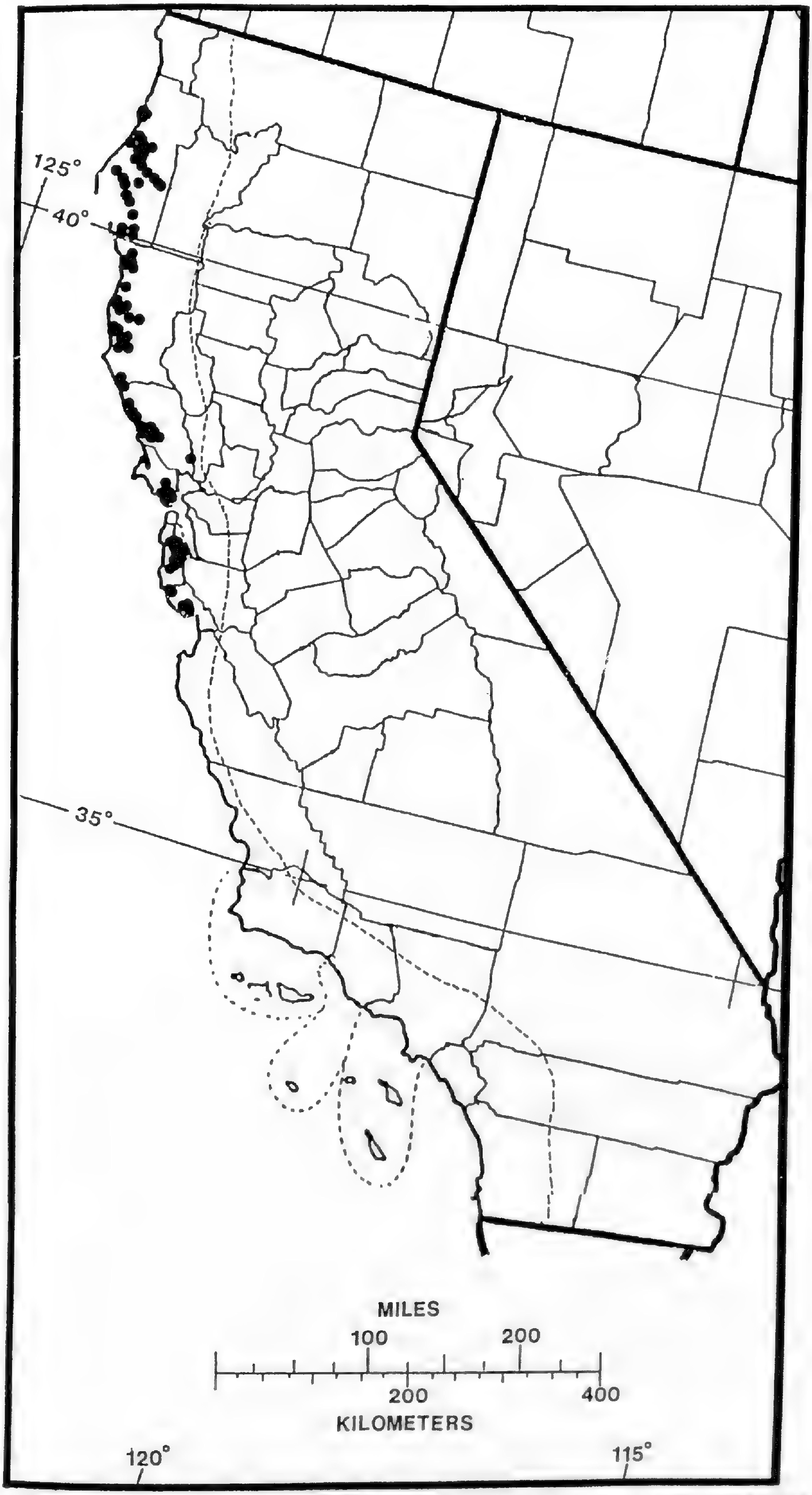

FIGURE 1. Distribution of *Scoliopus bigelovii* along the northwestern California coast. Crest of Coastal Mountain Range indicated by dashed line.

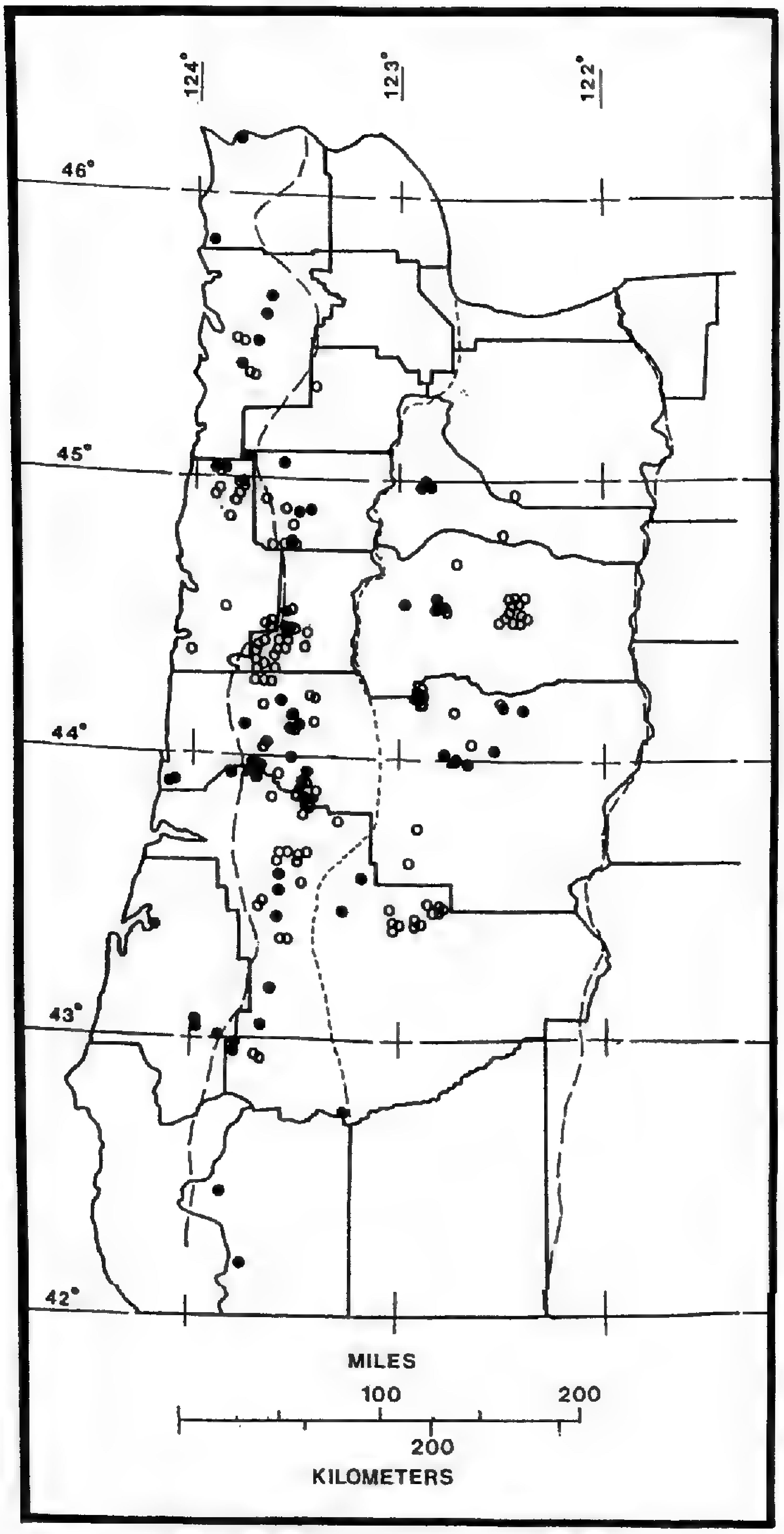

FIGURE 2. Distribution of *Scoliopus hallii* in western Oregon. Solid circles are herbarium-based locations, open circles are site records from the Bureau of Land Management (BLM) data base. Crests of Coastal and Cascade mountain ranges are indicated by long dashed lines, the Willamette River Valley by short dashed lines.

RESULTS

1. HABIT AND HABITAT

This small genus of two distinct species of perennial herbs occurs primarily in the old growth coniferous forests of far western North America. In the shady mesic understory slopes of the coastal Californian redwood forests (Stebbins & Major, 1965; Barbour & Major, 1977; Raven & Axelrod, 1978), from Humboldt County south to the Santa Cruz Mountains, *Scoliopus bigelovii* is relatively common (Fig. 1). According to my field observations and the ecological work of Smith (1957), its more common redwood understory associates include *Polystichum munitum*, *Clintonia andrewsiana*, *Trillium ovatum*, *Dentaria integrifolia*, *Oxalis oregana*, *Viola sempervirens*, and *Trientalis latifolia*.

The Oregonian endemic, *S. hallii*, on the other hand, occurs in mixed coniferous habitats along both sides of the Coastal Mountain Range and on the western slope of the Cascade Mountains (Fig. 2), but is definitely lacking in the intervening Willamette River Valley and only approaches the northernmost limit of *S. bigelovii*. Never far from running water and mossy alluvial slopes, *S. hallii* is typically associated with the following: *Tsuga heterophylla*, *Picea sitchensis*, *Pseudotsuga menziesii*, *Alnus rubra*, *Acer circinatum*, *A. macrophyllum*, *Polystichum munitum*, *Oxalis oregana*, *Oplopanax horridum*, *Rubus spectabilis*, *Osmaronia cerasiformis*, and *Senecio triangularis*.

Both of these *Scoliopus* species are under studied and undercollected because they begin flowering very early within their respective habitats. The earliest flowering records are mid January for *S. bigelovii* and late February for *S. hallii*. Flowering, or more precisely continuous floral presentation, can last for three months in both species. A month after the emergence of the first flowers, it is common to see fruits, flowers, and even buds arising from a given individual.

2. VEGETATIVE AND FLORAL MORPHOLOGY

Classical descriptive morphology of *Scoliopus* has been largely confined to scattered floristic works (Abrams, 1940; Hitchcock et al., 1969; Hitchcock & Cronquist, 1973; Jepson, 1922; Munz, 1959; Peck, 1961) and to the biosystematic work on *S. bigelovii* by Berg (1959) and Utech (1979). Summaries of major vegetative and floral characters are presented here to support the comparative systematic descriptions and to build a base for future sister-group comparisons.

Roots and Rhizomes. Associated with the short, simple rhizomes of both species are extensive networks of long-lived, contractile roots. These roots are relatively long and thick in comparison to the thin, hard rhizome and effectively anchor the plants into the compacted, alluvial soils of their riparian habitats. New roots originate annually near the growing proximal tip and contract within the first year (Rimbach, 1902). Small annual growth increments resulting from cataphyll and leaf scars are identifiable along the rhizome. Because decay occurs distally, precise maximum aging is difficult.

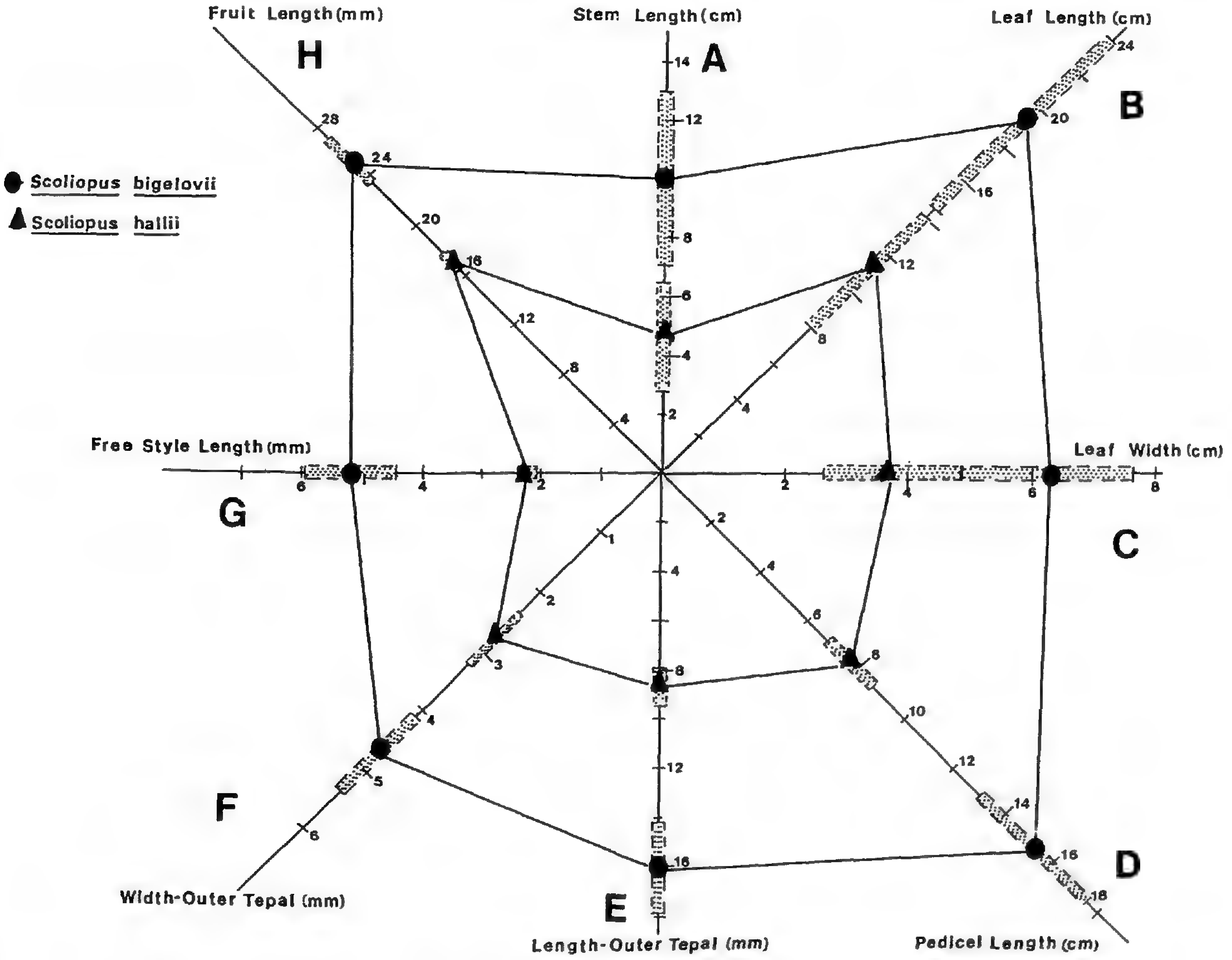

FIGURE 3. Variation polygon comparing morphological characters in *Scoliopus bigelovii* (circles) and *S. hallii* (triangles).—A. Stem length (cm), N = 50.—B. Leaf length (cm), N = 50.—C. Leaf width (cm), N = 50.—D. Fruiting pedicel length (cm), N = 50.—E. Outer tepal length (mm), N = 35.—F. Outer tepal width (mm), N = 35.—G. Free style length (mm), N = 35.—H. Fruit length (mm), N = 35. Shaded bars = standard deviation units.

However, ages of 20 years can be frequently established for mature individuals of both species.

Flowering and/or fruiting individuals of each species often occur so close together they appear to have a common rhizome. When such clumped individuals are dug and their root systems carefully washed, separate rhizomes and associated roots are evident.

Rarely in both species, rhizomes that had accidentally split or forked at the proximal growing tip were discovered. Subsequently, upon progressive decay of the rhizome's distal portion, two separate, vegetatively produced individuals result. These resulting plants have a common, genetic rootstock system, as demonstrated in *Smilacina* and *Polygonatum* (Kawano, 1975, 1985), and shoots that have an identical phenology. Other modes of vegetative reproduction were not observed in either species.

Stems. The unbranched stems in *Scoliopus* are short, vertical and, more importantly, subterranean, a significant adaptation to the high frequency of flooding in their environments. Each monopodial stem extends from its more or less horizontal rhizome to the upper duff layer.

Stem lengths generally coincide with rhizome depths. They vary from 5.5 to 20.5 cm (average 10.0 cm) in *S. bigelovii* and from 2.5 to 10.0 cm (average 4.6 cm) in *S. hallii* (Fig. 3). The average ratio of stem : cataphyll length was 1.76 in *S. bigelovii* (SD = 0.45) and a similar 1.75 in *S. hallii* (SD = 0.43). Slight increases in stem length occur in both species following anthesis.

An elongated, tawny brown stem sheathing cataphyll plus the remaining cataphyll fibers from previous years are found at the stem's base. At maturity, the current year's cataphyll lengths average 5.8 cm (3.5–8.5 cm) in *S. bigelovii* and 2.7 cm (1.5–5.0 cm) in *S. hallii*.

The whitish green, subterranean stems are fragile and not highly differentiated, being composed of large, thin-walled parenchyma cells with large

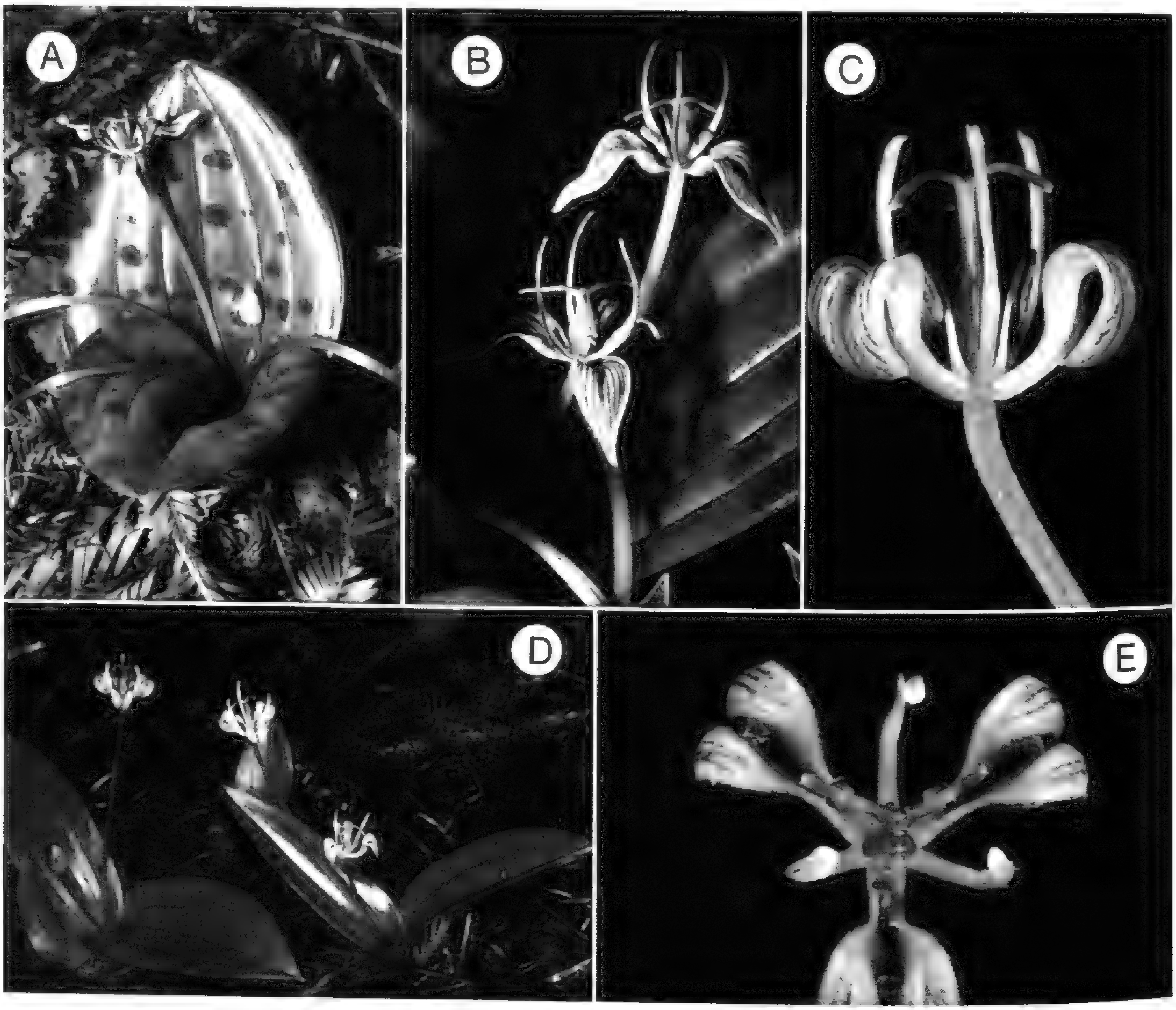

FIGURE 4. Habit and floral geometry in *Scoliopus*.—A. Redwood understory habitat of *S. bigelovii* in flower.—B. Enlarged view of *S. bigelovii* showing the relationship of tepals to stamens.—C. Enlarged side view of *S. hallii* showing the spatial relationship of floral parts.—D. Mossy coniferous understory habitat of *S. hallii*.—E. Axial floral view of *S. hallii* showing the recurved stylar arms and nectariferous glands on the outer tepals. (Photographs A, B courtesy W. Knight; C–E, J. Erwin.)

intercellular spaces which surround the vascular tissue. A subepidermal layer of collenchyma cells that occurs in several longitudinal ridges does provide some mechanical support. With their stems subterranean and totally out of view, both species of *Scoliopus* are thus functionally acaulescent, but not so morphologically.

Leaves. The emerging leaves are very short as the earliest buds reach anthesis. Leaf enlargement, and particularly elongation, occur during, and especially after, the flowering of the last bud. Lengths of 15–24 cm and widths of 5–8 cm are typical in *S. bigelovii* and 11–14 cm by 3–5 cm in *S. hallii* (Figs. 3, 4; Hooker, 1897). Though there is greater leaf variation in *S. bigelovii*, the length : width (L : W) ratios for the two species show nearly identical proportions (Table 1).

The elliptic to oblong leaves have obtuse to apiculate tips and basally sheath and subterranean stem. The dark green upper leaf surfaces of *S. bigelovii*, which are paler below, are mottled with brownish purple spots (Fig. 4A), while those of *S. hallii* are frequently not mottled (Fig. 4D). The mature leaves of *S. hallii* are more petiolate than the elongate, clasping ones in *S. bigelovii*. Stomata occur only on the lower, and paler, leaf surfaces of both species.

Leaf venation in *Scoliopus* is parallel. The major and parallel veins are interconnected with numerous, nearly transverse minor veins. The resulting venation pattern is definitely not reticulate. In *S. bigelovii*, there are seven to nine of these large, longitudinal veins. Of these, five are sunken into the laminal surface. The lower leaf surfaces are thus ribbed or keeled by these veins. Only three such sunken veins occur in *S. hallii*. In both species, these major sunken veins fuse at the leaf apex, while the other parallel veins simply end.

TABLE 1. Comparative *Scoliopus* morphometrics.

Character	Taxa	
	S. bigelovii	*S. hallii*
Leaf		
Length (cm)	19.20 ± 4.67* (14.5–23.9)* N = 50*	11.04 ± 3.04 (8.0–14.1) N = 50
Width (cm)	6.27 ± 1.42 (4.8–7.7) N = 50	3.73 ± 1.11 (2.6–4.8) N = 50
L:W ratio	2.98 ± 0.92 (2.0–7.1) N = 50	3.00 ± 0.47 (2.1–4.0) N = 50
Pedicel length (cm) (flowering)	15.32 ± 2.20 (11.0–22.0) N = 50	7.73 ± 0.95 (6.0–9.8) N = 50
Flower number/ plant (herbarium and field)	4.49 ± 2.32 (1–15) N = 400	2.06 ± 1.04 (1–5) N = 287
Outer tepal		
Length (mm)	16.15 ± 1.94 (12.6–19.3) N = 50	8.69 ± 0.76 (6.8–10.0) N = 50
Width (mm)	4.75 ± 0.65 (3.0–6.0) N = 50	2.79 ± 0.42 (2.0–3.3) N = 50
L:W ratio	3.44 ± 0.52 (2.6–5.1) N = 50	3.19 ± 0.55 (2.1–4.4) N = 50
Inner tepal		
Length (mm)	15.47 ± 1.85 (11.6–19.0) N = 50	7.48 ± 0.71 (6.0–9.0) N = 50
Width (mm)	0.54 ± 0.09 (0.3–0.7) N = 50	0.35 ± 0.10 (0.2–0.8) N = 50
L:W ratio	29.32 ± 6.05 (16.6–46.7) N = 50	22.56 ± 5.02 (10.0–37.5) N = 50
Filament length (mm)	3.76 ± 0.41 (2.3–4.3) N = 50	3.13 ± 0.39 (2.0–3.7) N = 50
Anther length (mm)	2.39 ± 0.22 (2.0–2.8) N = 50	2.17 ± 0.15 (1.9–2.3) N = 50
Free stylar arm length (mm)	5.26 ± 0.81 (4.5–6.1) N = 50	2.26 ± 0.18 (2.1–2.4) N = 50
Fruit		
Length (mm)	25.17 ± 1.93 (22.5–29.5) N = 50	17.21 ± 0.66 (16.0–18.5) N = 25
Width (mm)	7.66 ± 0.58 (6.3–9.0) N = 50	6.63 ± 0.66 (5.5–7.5) N = 25
L:W ratio	3.31 ± 0.36 (2.8–4.0) N = 50	2.62 ± 0.28 (2.1–3.4) N = 25

* Mean ± s.d., range of values, sample size.

Leaf arrangement in *Scoliopus* is spiral and not, as often stated, paired or opposite. Such terminology implies a derived two-leaved whorl or opposite state and thus a relationship to the multi-leaved whorls of other Paridean genera with reticulate venation, e.g., *Paris* or *Trillium*.

Individuals of *S. bigelovii*, with four leaves, and *S. hallii*, with three, have been observed and collected from throughout their respective ranges. Population samples establishing the frequency of leaf numbers for both species are presented in Table 2. The three-leaved condition is relatively common in mature individuals and stable populations of *S. bigelovii*. Though Berg (1959) encountered plants with only two leaves in his study of *S. bigelovii*, historical accounts note three-leaved (Eastwood, 1932) and four-leaved (Brandegee, 1891) plants. In plants of either species with more than two leaves, the sheathing leaves have an observable, spiral arrangement at their insertion on the subterranean stem, though their internodes are greatly reduced.

Inflorescence. Examination of a stem's subterranean crown, from which the numerous pedicels appear to arise, reveals several fascicles of pedicels. Each axillary fascicle, up to three in *S. bigelovii* and two in *S. hallii*, is composed of 2–5 pedicels separated by short internodes. The flowers of the upper fascicles bloom later than those of the lower. A leaf is associated with each fascicle. Bracts are lacking throughout the inflorescence. Plants with more leaves tend to have more flowers. Berg's (1959) morphological analysis of the crown showed that a fascicle might be either a contracted bostryx or a contracted cincinnus. Another possibility, which I envisioned, is a contracted raceme.

The maximum number of flowers per plant is best determined by counting pedicels at the end of flowering, since the order of flowering is irregular and prolonged. A frequency distribution comparing the number of flowers (i.e., pedicels) for both spe-

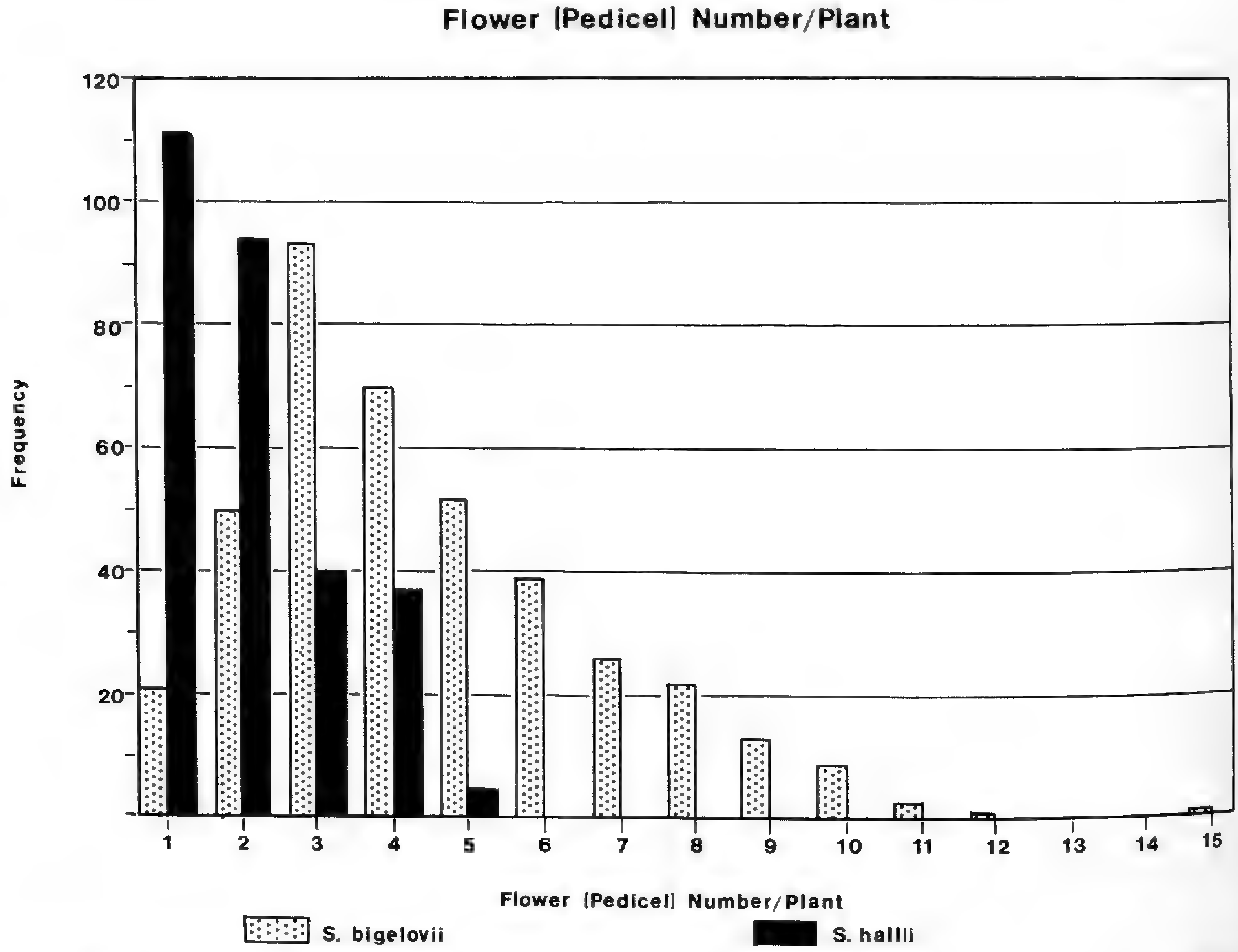

FIGURE 5. Frequency distribution showing the number of flowers (or pedicels) per plant in *S. bigelovii* (shaded bars) and *S. hallii* (solid bars).

cies is presented in Figure 5. A greater range occurs in *S. bigelovii* (1–15) than in *S. hallii* (1–5), though their averages are less dissimilar: *S. bigelovii* (4.5) versus *S. hallii* (2.1) (Table 1).

Floral Morphology and Anatomy. The showy, ill-scented flowers of *Scoliopus* are tetracyclic and thus deviate from the typical liliaceous arrangement in lacking three inner stamens.

The flowers of *S. bigelovii* are significantly larger than those of *S. hallii*, though both exhibit a similar proportion in their floral geometry. While the lengths and widths of the large, petaloid outer tepals of *S. bigelovii* are nearly twice as large as those of *S. hallii* (Figs. 3, 4), their respective length : width ratios are nearly identical. The lengths of the narrowly erect inner tepals of *S. bigelovii* are nearly twice as large as those of *S. hallii*, though their widths differ only slightly (Table 1).

The three outer stamens opposite the outer tepals are basally adnate to these tepals for 0.5 mm in *S. bigelovii* and 0.2 mm in *S. hallii*. The free filaments are short (averaging 3.7 mm in *S. bigelovii* and 3.1 mm in *S. hallii*; Table 1), slightly dilated in transverse section, and curved outwards at the level of anther attachment (Fig. 4B, C, E).

The greenish yellow, oblong anthers are adaxially attached near their mid-lengths. The connective tissues between the anther sacs are flat, though the sacs are free, versatile, and divergent basally. The endothecial cells lining the anther sacs have banded thickenings. Extrorse dehiscence is via two vertical abaxial slits. The tepals and anthers are not persistent.

Unlike most tricarpellate, syncarpous, liliaceous gynoecia in which the dorsal regions correspond to the corners or ribbed portions of the pistil, the dorsal regions in *Scoliopus* are laterally flattened or compressed, and the ventral regions occupy the corners of the triangular pistil. The strongly triangular gynoecium is formed by limited fusion along the ventral/septal margins, which subsequently form the corners (Fig. 6). Raphides were not observed in floral tissue of either species.

Most liliaceous gynoecia with laterally fused septal wings that protrude extensively into the common locular space have some type of axial placentation

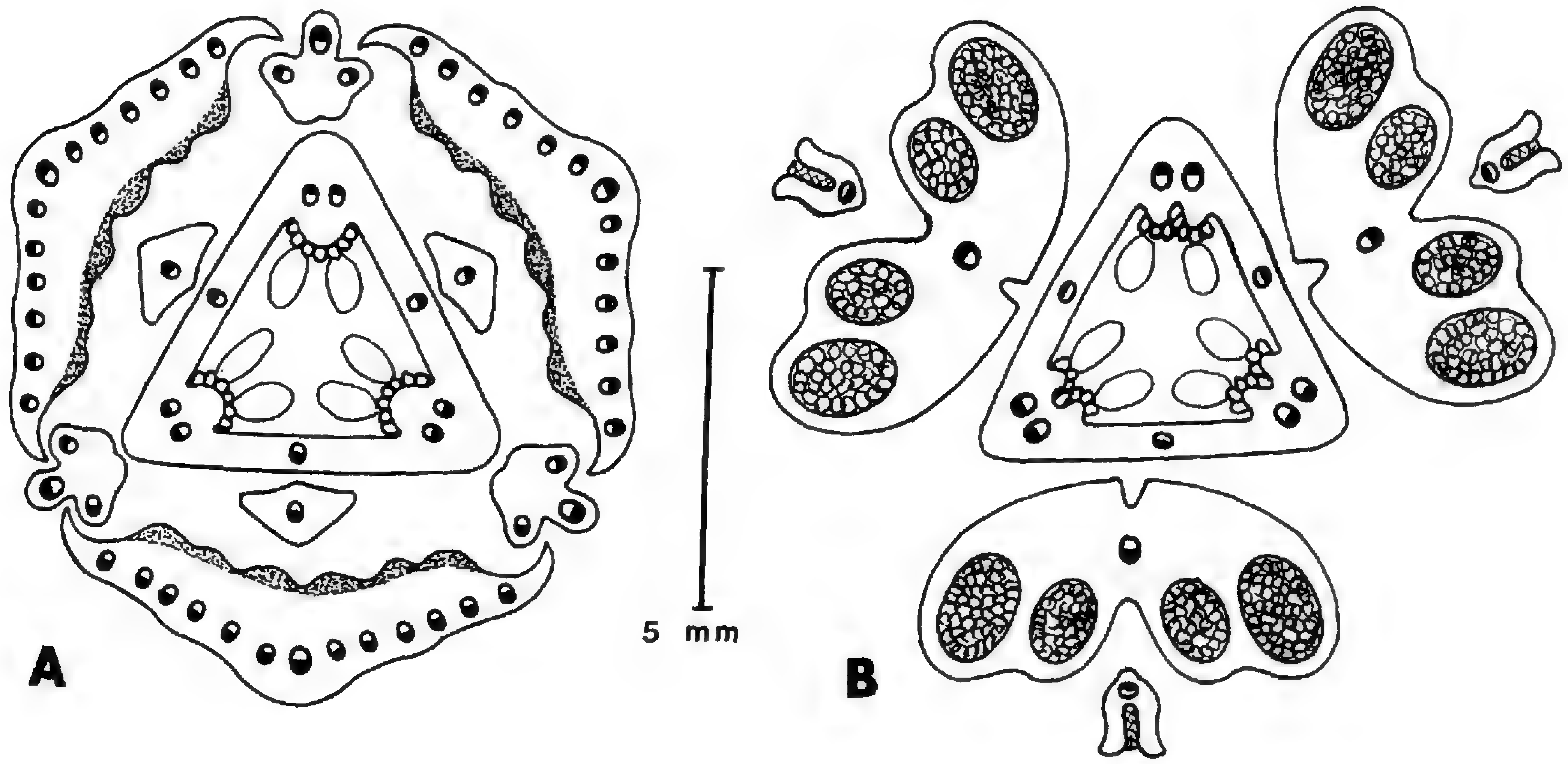

FIGURE 6. Transverse sections showing floral morphology and geometry in *Scoliopus bigelovii.*—A. Section through lower floral envelope and triangular gynoecium showing the large, petaloid outer tepals with numerous veins and nectariferous surfaces (shaded), three outer stamens (inner stamen lacking) opposite the flush dorsal surfaces, and the unilocular gynoecium with three sets of two ranked ovules.—B. Section through middle floral envelope and gynoecium showing the position of the three recurved stylar arms with reversed conducting elements and the extrorse anthers of a pollination subunit. (Adapted from Utech, 1979.)

and three locules. Septal glands often occur between these lateral wings when septal fusion is incomplete.

In *Scoliopus*, the broadly unilocular gynoecium is highly unusual (Berg, 1959; Utech, 1979). Placentation is parietal, since the ventral bundles are in the corners and protruding septal wings are lacking (Fig. 6). Basally, the locules open initially outwards from the center along the dorsal radii, a hint of loculicidal dehiscence.

The shared ascending styles are short and subdivided along the dorsal radii into three, recurved stylar arms or branches. The stylar arms are longer in *S. bigelovii* (5.3 mm) than in *S. hallii* (2.3 mm) (Table 1). Terminally localized on the upper and inner surface of each arm are minute stigmatic zones (Figs. 4B, C, E, 8B), an obvious adaptation for outbreeding. Stigmatoidal tissue is continuous from the three recurved stigma tips down through the shared style and along the inner funicular-ventral margins.

The anatropous, bitegmic ovules are loosely arranged in two ascending rows in each of the three ventral corners (Fig. 6). The number of ovules per

TABLE 2. Leaf number variation in populations of *Scoliopus.*

Species and populations	Number of leaves and percentage of population						Total number of plants
	2	%	3	%	4	%	
S. bigelovii							
Kings Mt.	16	64.0%	8	32.0%	1	4.0%	25
Camp Meeker	20	80.0%	5	20.0%	0	0.0%	25
Kneeland	20	80.0%	5	20.0%	0	0.0%	25
Herbarium	267	82.9%	55	17.1%	0	0.0%	322
Total	323	81.4%	73	18.4%	1	0.3%	397
S. hallii							
Siuslaw Creek	99	99.0%	1	1.0%	0	0.0%	100
McDowell Creek	100	100.0%	0	0.0%	0	0.0%	100
Herbarium	86	98.9%	1	1.1%	0	0.0%	87
Total	285	99.3%	2	0.7%	0	0.0%	287

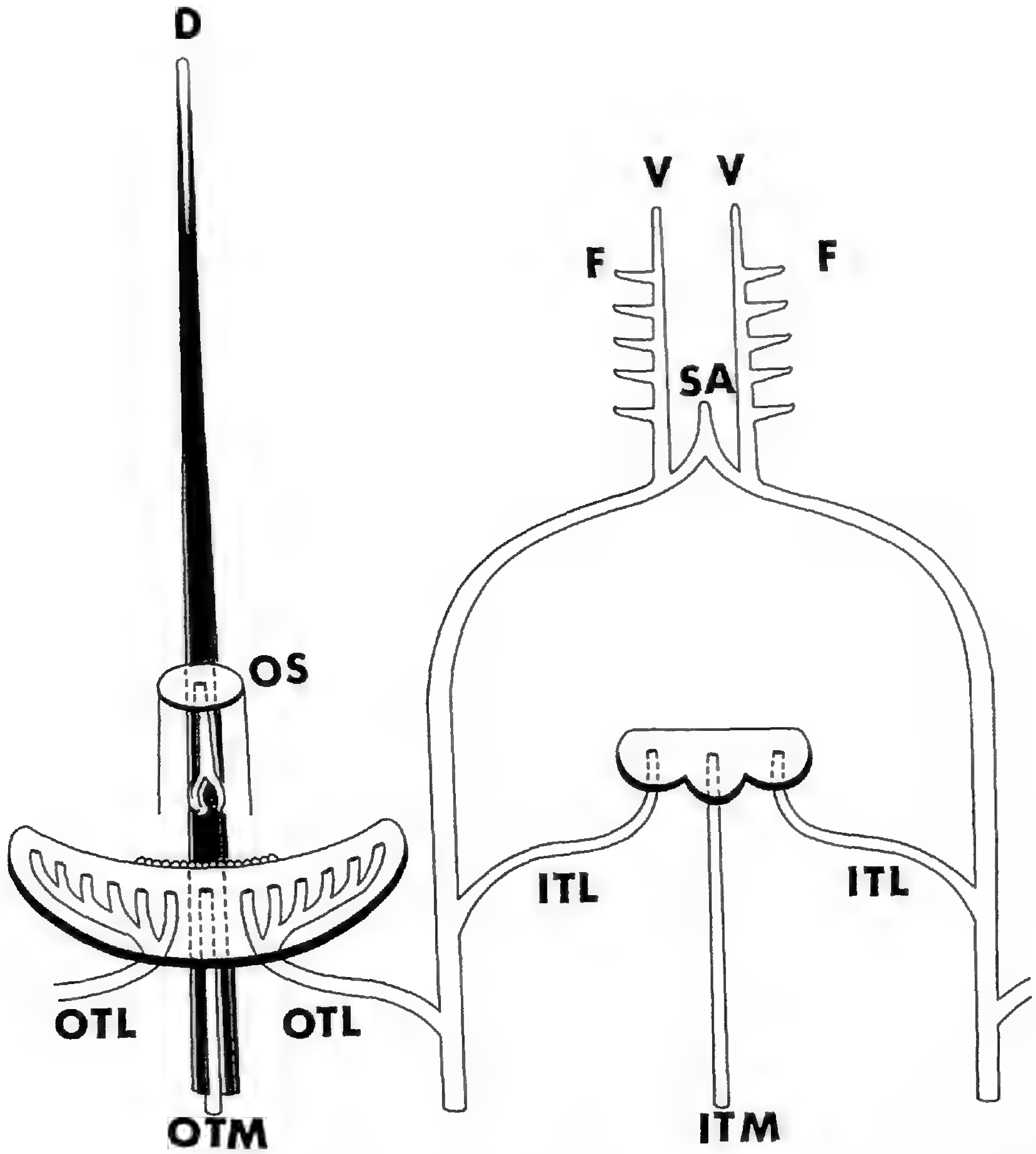

FIGURE 7. Summary longitudinal diagram showing the floral vascularization in *Scoliopus*. One-third of the floral network is presented. The basal portion of the bundle from which a dorsal (D) and an outer stamen (OS) are derived is not connected with an outer tepal medium (OTM) within the flower. There is no interconnection within the gynoecium of the dorsal and ventral supplies. The dorsals (D) are recurved outwardly into the stylar arms. Bundle codes: OTM = outer tepal median, OTL = outer tepal lateral, ITM = inner tepal median, ITL = inner tepal lateral, OS = outer stamen, D = dorsal, V = ventral, SA = septal axial, and F = funicular. (Adapted from Utech, 1979.)

pistil varies between 21 and 38 in *S. bigelovii* and between 20 and 32 in *S. hallii,* though their averages are nearly identical (Table 3). Embryo sac formation is of the *Polygonum* type, and endosperm formation is nuclear and unlike that in *Paris* and *Trillium* (Berg, 1959, 1962b).

The oblong to lanceolate, mature fruits are strongly three-angled and terminated by the persistent style. The mature fruits are generally larger in *S. bigelovii* than *S. hallii* (Table 1). The number of mature seeds per fruit is higher in *S. bigelovii* (Table 3). This is correlated to fruit size, since the seeds of both species are approximately the same size (Table 3).

The thin, membranous pericarp tissue dehisces or decays irregularly between the dorsals and ventrals. A maximum of six such zones occur per fruit (Fig. 6). One or two openings per fruit can expose all the seeds, since the capsules are unilocular. This irregular splitting or degeneration of parenchyma tissue does not follow the normal zones of weakness along the dorsal (loculicidal dehiscence) or the ventral (septicidal dehiscence) lines.

The *Scoliopus* fruit should be considered a capsule for the following reasons: it dehisces; it remains attached to the pedicel; and it possesses no pulpy tissue. Berg (1959) used the term "untypically loculicidal" for this type of capsule dehiscence and added further that "in comparison with other liliaceous capsules, the *Scoliopus* capsule must be considered highly reduced, because of its lack of sclerenchyma and normal dehiscence."

TABLE 3. Reproductive characteristics in *Scoliopus bigelovii* and *S. hallii.*

	Taxa	
Criteria	*S. bigelovii* California. Sonoma Co.: Camp Meeker	*S. hallii* Oregon. Linn Co.: McDowell Creek
Number of ovules/pistil	27.35 ± 3.77* (21.0–38.0)*	27.27 ± 3.07 (20.0–32.0)
Number of pollen grains/flower	2.10×10^4	1.65×10^4
Pollen number : ovule number (P : O) ratio	750 : 1	600 : 1
Number of seeds/fruit	14.28 ± 3.14 (10.0–22.0)	11.40 ± 1.20 (10.0–14.0)
Seed number/ovule number (%)	52.5%	41.8%
Seed weight (mg)	4.47 ± 0.31 (3.86–5.00)	3.15 ± 0.03 (3.10–3.20)
Seed L : W ratio	2.10 ± 0.15 (1.86–2.45)	2.05 ± 0.12 (1.86–2.25)

* Mean ± s.d., range of values.

3. FLORAL VASCULATURE

The floral vascularization of both *Scoliopus* species is similar to that presented in detail for *S. bigelovii* (Utech, 1979; Fig. 7). The floral vasculature is established from a 15-bundled, axial pedicel configuration, which consists of an outer zone of 12 bundles and an inner one of three large bundles. Six of the outer zone bundles depart directly as three outer tepal medians (OTM) and three inner tepal medians (ITM).

Each of the six remaining outer zone bundles undergoes two successive radial divisions whereupon 12 tepal laterals (6 OTL and 6 ITL) and six ventrals (V) are formed. Basally each of the six tepals receives three bundles, i.e., a median and two laterals, though the outer and inner tepals are quite dissimilar morphologically. Several radial divisions occur laminally among the outer tepal laterals (OTL) in *S. bigelovii* to create a maximum of 13 bundles, i.e., 12 laterals (OTL) and a median (OTM). No such subsequent radial divisions occur among the inner tepal laterals (ITL; Fig. 6A). The outer tepals of *S. hallii,* on the other hand, typically have a maximum of nine bundles, i.e., eight laterals (OTL) and a median (OTM).

Between each of the three pairs of ventrals (V) a fusion septal axial (SA) of short vertical duration is formed. Two-ranked, horizontal funicular traces (F) depart directly from each of the paired ventrals (V).

While the ventral vasculature has an outer zone origin, the three dorsal bundles (D) and the three outer stamen bundles (OS) are division products of the three large inner zone bundles. No vestigial traces for inner stamen bundles nor for staminodes were observed in the material examined for this study of either species. The dorsals (D) are unbranched and terminate in the tips of the three recurved stylar arms. The dorsal (D) and ventral (V) supplies are not interconnected within the gynoecium.

4. FLORAL BIOLOGY

Many aspects of *Scoliopus* floral morphology are highly derived, advanced, or reduced and relate to specialized pollination (fungal gnats) and seed dispersal (myrmecochory). The structural geometry and adaptive significance of these showy, ill-scented flowers correlate with their mode of pollination. Berg (1959) correctly demonstrated for *S. bigelovii* (which also applies to *S. hallii*) that a single *Scoliopus* flower functions as three independent flowers, or pollination subunits, a feature usually associated with *Iris* (Figs. 4B, C, E, 7). This unusual partitioning of floral parts into subunits is described below.

Each of the three petaloid outer tepals is lined adaxially with nectariferous tissue. A broad floral cup or shallow tube is formed via the interpenetrating of the lateral edges of the outer tepals into grooves on the narrow, abaxial surface of the inner tepals (Fig. 6A). Because the triangular gynoecium is ridged along three outer ventral surfaces, which are opposite the narrow, appressed inner tepals and flattened along three dorsal surfaces (Fig. 6A), which are opposite the outwardly expanded outer tepals and extrorse anthers (Fig. 6B), a configuration of three independent pollination subunits is established.

The three versatile, extrorse anthers dehisce along two vertical abaxial slits (Fig. 6B). Pollen dispersal zones are therefore defined between the flattened dorsal regions of the gynoecium and the expanded nectariferous grooves on the outer tepals. Each of the three stylar arms recurves over the top of an anther and exhibits a reversal in the xylem to phloem arrangement (Fig. 6B). However, the minute stigmatic surfaces are located terminally and thus are removed from the pollen dispersal zone.

The recurved styles, extrorse anthers, unusual triangular gynoecium, and large, nectariferous outer tepals form a pollination subunit and are all interrelated for outbreeding. The pollen : ovule (P : O) ratios of 750 : 1 for *S. bigelovii* and 600 : 1 for *S. hallii* (Table 3), further assert limited outbreeding.

Scoliopus bigelovii has been shown to be self-incompatible (Berg, 1959; Mesler et al., 1980). Fungal gnats in the closely related families Mycetophilidae (*Mycetophila* sp.) and Sciarideae (*Sciara* sp., *Corynoptera* sp.) were regarded as pollinators, not merely nectar thieves, because of high seed set and because they contacted anthers and stigmas while feeding. Individuals captured on the flowers carried pollen grains (Mesler et al., 1980). The author has also observed fungal gnats working the flowers of *S. hallii.*

Mesler et al. (1980) believed the high fruit and seed set in *S. bigelovii* to be due primarily to the abundance of fungal gnats and the corresponding large number of flower visits. They thought the frequency of pollination per individual gnat was probably very low, but this was compensated for by the large number of swarming gnats.

In the cool, moist redwood forests, where floral resources are widely scattered, large, efficient but energetically expensive pollinators, such as bumble bees, are uncommon (Moldenke, 1976). Under such habitat conditions, many plants could be expected to rely on small, relatively inefficient, but presumably energetically cheaper vectors (Stebbins, 1974). Small dipterans, such as fungal gnats, would be effective pollinators, both in terms of overall fruit set and outcrossing potential, at least when such insects are present in large numbers. Seed setting percentages, based on the number of seeds produced per ovule from the same sampled population, were 52.2% in *S. bigelovii* and 41.8% in *S. hallii* (Table 3).

5. SEEDS AND SEED DISPERSAL

The elongated fruiting pedicels that twist and recurve to the ground have capsules that usually open within the loose, moist coniferous duff. Pedicel twisting is more pronounced in *S. bigelovii.* By default, those seeds twisted en masse to the ground would be group dispersed. Similar results would also occur if ants progressively moved seeds to their duff-hidden, midden heaps. The high density of observed seedlings and adults in both species is no doubt due to this means of dispersal.

Berg (1959) ably demonstrated that the seeds of *S. bigelovii* were ant dispersed (*Formica fusca* L., *F. fusca argentea* Whlr., *F. rufibarbis occidua* Whlr., *Aphaenogaster subterranea occidentalis* Em.) and documented the anatomy of the seeds' oil-containing appendages or elaiosomes. Ant dispersal (*Formica* sp.) and seeds with similar elaiosomes were observed in *S. hallii.*

Most myrmecochorous plants, like both species of *Scoliopus,* begin flowering very early in spring and continue producing seeds for some time (Thompson, 1981). This phenological adaptiveness insures a continuous supply of ripe seeds when the ants are most abundant and active. The subterranean stems, the fruiting pedicels twisting to the ground, the capsules dehiscing in the upper duff layer, and the elaiosome-appendaged seeds are integrated into an advanced dispersal pattern.

6. KARYOLOGY

Chromosome counts for both species of *Scoliopus* have been reported. Cave (1966) noted a count of $2n = 14$ for *S. hallii.* However, Johansen's (1932) report of $2n = 14$ for *S. bigelovii* was not confirmed by Cave (1966, 1970), who observed counts of $2n = 16$ from several different Californian populations. The karyotype consists of three large and five small chromosome pairs. One population from Humboldt County, for example, had a somatic number of $2n = 16$, but also had extra, or small, meiotic chromosomes indicating a certain proportion of structural hybridity within the northern part of the range.

The chromosomes of *Scoliopus* are small in comparison to those of *Trillium* (Cave, 1970), but detailed karyotypes for both *Scoliopus* species need to be established. The chromosomal base number for *Trillium* and *Paris* is a similar $x = 5$ (Fedorov, 1969), while that for *Scoliopus* should be associated with both $x = 7$ and $x = 8$ until more critical karyological research is done.

CONCLUDING REMARKS

Comparison of the ecological, anatomical, and morphological characteristics of the two *Scoliopus* species shows them to be quite distinct and demonstrates that *S. hallii* is more than a geographically isolated, minor-sized variant of *S. bigelovii* (Fig. 3; Table 1). Both have distinctive geographic distributions, ecological associations, and therefore different, past eco-evolutionary histories.

Two character suites epitomize the reduction and specialization within the genus—one for pollination, the other for ant dispersal. The floral morphology, anatomy, geometry, and phenology of both species attest to outbreeding and an unlikely, dipteran group of fungal gnats as present-day pollinators. The subterranean stems, elongate pedicels and duff dehiscing capsules over a prolonged time period support myrmecochory.

The large number of reduced or advanced characters in *Scoliopus* makes classification and analysis of these character assemblages difficult at times. Character clusters that deviate include tetracyclic flowers with nectariferous, petaloid outer tepals and no inner stamens, extrorse outer anthers, and modified unilocular gynoecia with parietal placentation.

Plants with more than two parallel-nerved leaves do occur in both species, and they are spirally arranged. The inflorescence should be viewed as one with axillary fascicles, not as an umbel.

The diagnostic characters that differentiate *Scoliopus* from *Paris* sensu lato, *Trillium,* and *Medeola* (the Englerian Parideae) have been clearly tabulated and documented (Berg, 1959, 1962a, b; Utech, 1978, 1979). *Scoliopus* is so different from these tribal cohorts that a brief historical and taxonomic review is warranted.

The traditional generic placement of *Scoliopus* in the Englerian Parideae with *Paris* (including *Kinugasa* and *Daiswa*), *Trillium,* and *Medeola* (Engler, 1888; Krause, 1930) or in the segregate family Trilliaceae (Hutchinson, 1934, 1959) has in recent years been questioned (Berg, 1959, 1962a, b; Utech, 1978, 1979; Takhtajan, 1983, 1986; Dahlgren et al., 1985).

Torrey (1857) described *Scoliopus* emphasizing the extrorse anthers and the axial placentation of the unilocular gynoecium and placed the genus tentatively at the end of the family Melanthaceae (Gray, 1856). Baker's view of Colchicaceae (1875, 1879) was similar to the above Melanthaceae, but included several "aberrant tribes," which did not fit. One was the monotypic Scoliopeae. In Watson's (1879) treatment of the North American Liliaceae, a linkage among *Trillium, Medeola,* and *Scoliopus* was made. Recognizing the remote relationship between *Scoliopus* and the other two genera, *Scoliopus* was placed in its own subtribe Scoliopeae, apart from *Trillium* and *Medeola* in the tribe Trillieae.

Bentham & Hooker's (1883) acceptance of Watson's (1879) inclusion of *Scoliopus* in the Medeoleae (= Trillieae) was subsequently followed by Engler (1888), Krause (1930), Hutchinson (1934, 1959), and others. Hooker alone (1897) noted that *Scoliopus* was not closely allied to any of the group.

The aberrant and suspect tribal association of *Scoliopus* deserves revision. Few character sets of the tribe Parideae or the family Trilliaceae match those of *Scoliopus* or convey its proper taxonomic position. Following Watson, a tribal status coequal to *Trillium* and *Paris* would be one orthodox solution. Shifting *Scoliopus* as a monotypic tribe to the Uvulariaceae (Dahlgren et al., 1985; Takhtajan, 1986; Cronquist, 1988) would be another.

SYSTEMATIC TREATMENT

Scoliopus Torrey, Pacif. Rail. Rep. 4: 145, pl. 22. 1857. TYPE: *Scoliopus bigelovii* Torrey.

Glabrous, perennial herbs with short slender rhizomes; roots elongate, contractile. Stems short, unbranched, subterranean, not persistent. Leaves 2–3(–4), elliptic to broadly lanceolate, sessile-clasping to subsessile, apically obtuse to apiculate, parallel-veined with numerous transverse veins, dark green above, paler below, ± mottled with purple spots. Inflorescences contracted with several axillary fascicles of elongated, twisting pedicels. Flowers tetracyclic, showy, ill-scented. Perianth segments 6, in 2 series, dissimilar, distinct, deciduous; outer series 3, petaloid, many-nerved, striped, spreading, with basal nectariferous glands; inner series 3, erect, linear, 3-nerved, converging over the pistil. Stamens 3, opposite and adnate basally to outer segments; filaments free, hypogynous, filiform-subulate; anthers oblong, yellowish green, 2-celled, versatile, attached mid-length, extrorse, dehiscing via vertical abaxial slits. Ovary sessile, strongly 3-angled, unilocular, placentae 3-parietal, in locular angles; styles short, connate, erect; stylar arms 3, linear, horizontally spreading to recurved, channeled on the inner stigmatic surface; ovules 20–38, anatropous, bitegmic, in 2 rows on each placenta. Capsules brownish purple, beaked by persistent style and stylar arms, strongly 3-angled, thin-walled, opening irregularly, more by decay than dehiscence. Seeds 10–22, oblong, slightly curved, sulcate-striate longitudinally, eliaosomes present. [Greek *skolios*, crooked, and *pous*, foot, allusion to the recurved, fruiting pedicels.]

KEY TO THE SPECIES OF *SCOLIOPUS*

1a. Leaves 14.0–24.0 cm long; outer petaloid segments 12.5–19.0 mm long; free stylar arms 4.5–6.0 mm long; coastal northwestern California .... 1. *S. bigelovii*
1b. Leaves 8.0–14.0 cm long; outer petaloid segments 6.5–10.0 mm long; free stylar arms 2.0–2.5 mm long; coastal mountains and western Cascade slopes of Oregon .... 2. *S. hallii*

1. **Scoliopus bigelovii** Torrey, Pacif. Rail. Rep. 4: 145, pl. 22. 1857 (fig. 8). SYNTYPES: U.S.A. California: Marin Co., Tamul Pass (Mt. Tamalpais), 1853, *Bigelow s.n.* (lectotype, NY, designated by Utech, 1979: 69; isolectotype, GH; photos CM). California: Sonoma Co., redwoods, Feb. 1856, *Samuels s.n.* (GH, NY, photos CM).

Stems subterranean, 6–20 cm long. Leaves 2(–4), elliptic to oblanceolate, sheathing at base, often mottled with purple, 14–24 cm long, 4.8–7.7 cm wide. Pedicels 3–12(–15), shorter than leaves at anthesis, greatly elongated, becoming strongly recurved to twisted in fruit, 11–22 cm long. Outer perianth segments ovate-lanceolate, mottled with green and lined with purple, up to 13-nerved, 12.5–19.0 mm long, 6.8–10.0 mm wide; inner segments linear-subulate, 11.5–19.0 mm long, 0.5 mm wide. Filaments 2.3–4.3 mm long, anthers 2.0–2.8 mm long. Capsules 22.5–29.5 mm long, 6.3–9.0 mm wide; stylar arms strongly recurved, 4.5–6.0 mm long; seeds 10–22. $2n = 16$.

Illustrations. Torrey (1857), Hooker (1897), Regel (1875), Abrams (1940), Parson (1907), Berg (1959), Utech (1979).

Representative specimens examined. CALIFORNIA: Coast Range, *Bolander s.n.* (MO), *Vasey s.n.* (GH, US). HUMBOLDT CO.: Hubbard's Station, *Davy & Blasdale 5399* (UC); T4N, R2E, S27, *Anderson 1938* (HSC); Bald Mt. Road, T6N, R2E, *Anderson 2397* (HSC); Indian Creek on Kneeland-Bridgeville Road, T2N, R4E, S6, *Anderson 2904* (HSC); Cow Creek fire-trail, headwaters Bear Creek, *Constance 836* (JEPS); Dinsmores, *Eastwood & Howell 4778* (CAS); Carlotta, *Hawver s.n.* (CAS); 200 ft., *Tracy 6144* (UC); 6 mi. S of Pepperwood, T1S, R2E, S14, 500 ft., *Johnson 108* (HSC); S Fork Bear Creek, 2.5 mi. S of Shelter Cove, 1,840 ft., *Kelly 301* (HSC); Kneeland Prairie, 2,000 ft., *Kildale 520* (DS); 2,500 ft., *Tracy 4060, 14808, 16862* (UC); Camp Bauwer Park, 0.25 mi. NE of Korbel, 190 ft., *Miller 1* (HSC); E of US 101 from Seawood Drive, T8N, R1E, S8, *Miller 128* (HSC); Eureka, *Paulson s.n.* (DS); 1.5 mi. N of Trinidad, US 101, T8N, R1W, S14, *Plett 30* (HSC); 3 mi. E of Bridgeville, *Roderick 60-220* (JEPS); S of Kneeland, T3N, R3E, S19, 2,200 ft., *Rogers 29* (HSC); Redwood Creek, Garberville, *Shapovalov & Woodhull s.n.* (DS); 3 mi. E of Redwood Creek on old CA 299, *Spellenberg et al. 1361* (HSC); 1 mi. E of CA 299 on Lindsay Road, T6N, R1E, *Stevens 2* (HSC); 3 mi. SE of Korbel, Snow Camp Road, T6N, R2E, S34, *Styskel 6* (HSC); Van Duzen River, opposite Buck Mt., 1 mi. W of Dinsmores, 2,500 ft., *Tracy 18611* (UC, WTU); Hydesville, 200 ft., *Tracy 4017* (GH, NY, UC, US, WTU); 300 ft., *Tracy 5419* (UC); Glendale, Mad River, 0–500 ft., *Tracy 2156* (UC); Big Lagoon, 300 ft., *Tracy 10941* (UC); Dinsmores Ranch, Van Duzen River, opposite Buck Mt., 2,500 ft., *Tracy 4223* (UC, WTU); Lawrence Creek, Kneeland Prairie, 2,000 ft., *Tracy 6615* (UC); 20 mi. W of Pepperwood, US 101, 65 m, *Utech 88-025* (CM); Durphy Creek junction S Fork Eel River, US 101, 50 m, *Utech 88-019* (CM); Fisher Redwood Grove, 110 m, *Utech 88-027* (CM); 0.1 mi. N of Meyers Flat, S Fork Eel River, 60 m, *Utech 88-023* (CM); Cheatham Redwood Grove, 90 m, *Utech 88-026* (CM); Clark Redwood Grove, 40 m, *Utech 88-024* (CM); 1.5 mi. S of Miranda on US 101, 85 m, *Utech 88-022* (CM); S Fork Bear Creek, 2.5 mi. S of Shelter Cove, 1,840 ft., *White 16* (HSC). MARIN CO.: W end Alpine Lake, *Berg s.n.* (UC); Mill Valley, *Brandegee s.n.* (UC); Cascade Canyon, 0.75 mi. from Mill Valley Station, 350 ft., *Breedlove 2331* (DS); Lagunitas Creek, *Chestnut & Drew s.n.* (UC); Alpine Dam, *Covel s.n.* (CAS), *Doutt 137* (CM); Mt. Tamalpais, *Davy 795* (UC); Mill Valley, *Eastwood 2450* (CAS, GH, NY, UC, US); Sausalito, *Edwards s.n.* (NY); Phoenix Lake Road, 1 mi. below Lake Lagunitas, *Ewan 9424* (WTU); Mill Valley, *Grant s.n.* (GH, US); Mt. Tamalpais, *Greene s.n.* (CM, DS, MO, NY, UC, US, WTU); Sausalito, *James s.n.* (NY, US), *Kellogg s.n.* (JEPS), *Kellogg s.n.* (CAS), *Kellogg & Harford 984* (CAS, GH, NY, US), *LeRoy s.n.* (NY); Mill Valley, *Jepson s.n.* (JEPS, NY, US, WTU), *Jepson s.n.* (JEPS, NY), 100 ft., *Rose 34020* (WTU), *39008* (UC), *Zeile s.n.* (CAS); Mt. Tamalpais, Lagunitas Road, *Mason 1231* (GH, UC); Sequoia Canyon, *Michener & Bioletti 203* (GH, NY, UC); Kentfield, *Nelson s.n.* (ROPA), *Parsons s.n.* (CAS); Mt. Tamalpais, *Parks s.n.* (UC); 2 mi. SE of Nicasio on Lucas Valley Road, *Rentz 4* (CAS); Mt. Tamalpais, Pipeline trail, *Schreiber 112* (UC); Mt. Tamalpais, N end of Catarack trail, *Serpa 9* (ROPA); W side of Bolinas Ridge, E of Bolinas Lagoon, 750 ft., *Sharsmith 5174* (UC); W slope of Mt. Tamalpais, 1 mi. past Alpine Dam, 200 m, *Utech 88-016* (CM); W slope of Mt. Tamalpais, between Rock Springs and Alpine Dam, 430 m, *Utech 88-014* (CM); Nicasio Valley Road, San Geronimo to Nicasio, 90 m, *Utech 88-017* (CM); SW end of Alpine Lake, 320 m, *Utech 88-015* (CM); Tamalpais, T1N, R6W, 300 ft., *Yates 5039* (UC). MENDOCINO CO.: Ft. Bragg, *Arnold s.n.* (ROPA); Kaisen District, *McMurphy 182* (DS, NY); S Fork Big River, T17N, R17W, S29, 5 ft., *Seacat & Seymour 195* (HSC); Masonite Demonstration Forest off CA 128, 50 ft., *Smith & Wheeler 5143* (CAS); Hendy Woods State Park, *Smith & Wheeler 5136* (CAS); Faulkner County Park, 2.3 mi. W of Booneville, 290 m, *Utech 88-038* (CM); 2.7 mi. W of Comptche, 10 m, *Utech 88-036* (CM); 1.0 mi. W of Hollow Tree on CA 1, 350 m, *Utech 88-028* (CM); 1.7 mi. E of Flynn Creek Road on CA 128, 25 m, *Utech 88-037* (CM); 5.0 mi. past Rockport on CA 1 to Leggett, 5 m, *Utech 88-030* (CM); near Usal on CA 1, 80 m, *Utech 88-029* (CM); Dora Creek, Smith Redwood Grove, 140 m, *Utech 88-018* (CM); SSE of Albion, 4.7 mi. E on Navarro Ridge Road, 175 ft., *Utech et al. 84-069*

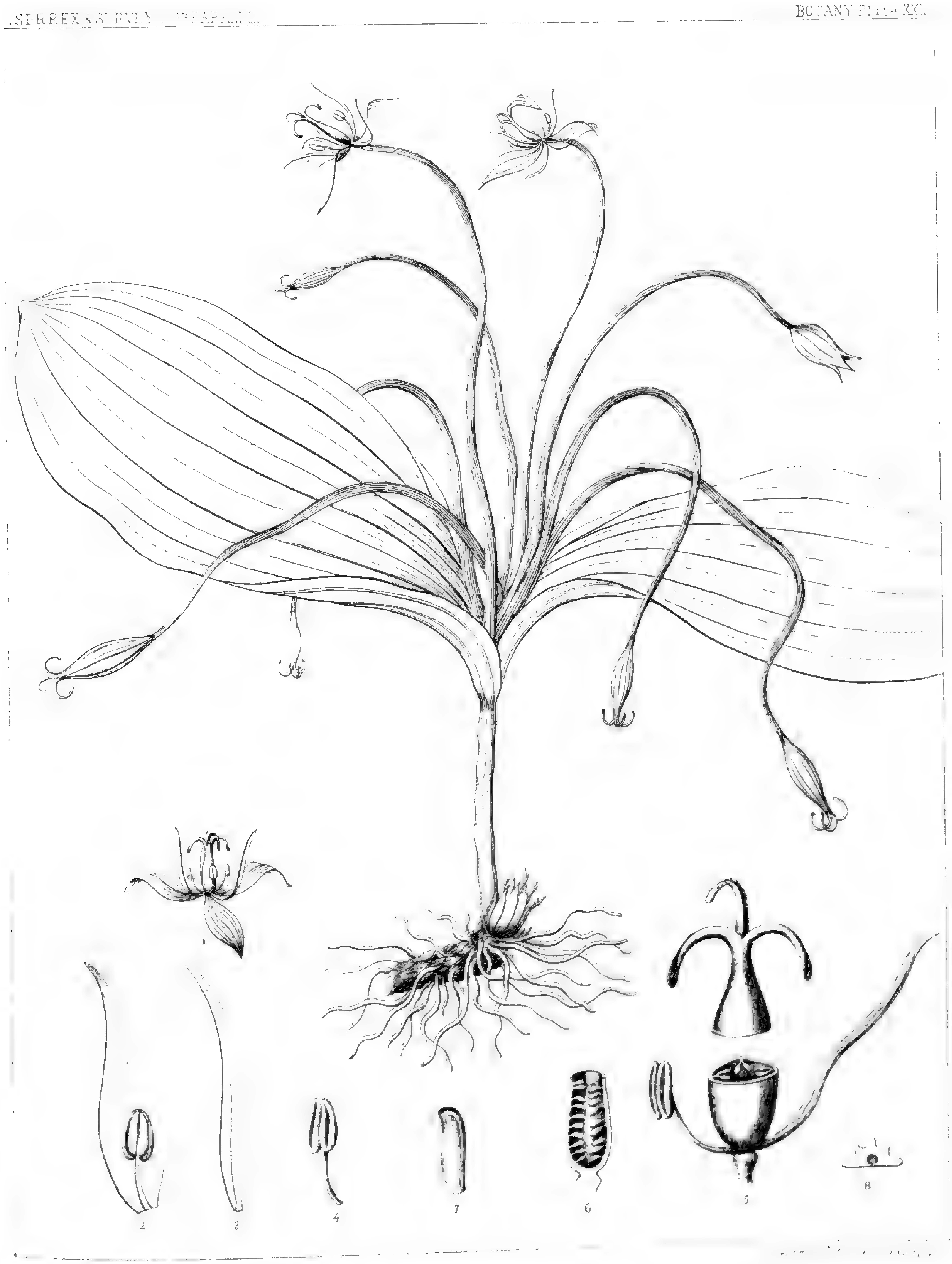

FIGURE 8. Type illustration of *Scoliopus bigelovii* from Torrey (1857).

(CM); SSE of Albion, 4.3 mi. E on Navarro Ridge Road, 220 m, *Utech et al. 84-056A* (CM); Jackson State Forest, N Fork of S Fork of Noyo River, 200 ft., *Wheeler 972* (CAS); Reeves Canyon Road, 3 mi. W of US 101, 1,100 ft., *Wheeler & Smith 2051* (CAS); Hendy Woods State Park, 150 ft., *Wheeler & Smith 780* (CAS); Haven's Neck, 4 mi. N of Gualala, 75 ft., *Wheeler & Smith 1187* (CAS); Hales Grove, NW of CA 208, 1,150 ft., *Wheeler*

& Smith 1142 (CAS); 10 mi. W of Laytonville to Branscom, *Wiggins 11592* (DS, WTU); Albion, 3 ft., *Wyrick 95* (HSC). SAN MATEO CO.: Kings Mt., *Abrams 2283* (DS, GH, MO, NY, US), *Atkinson s.n.* (US), *Baker 322* (CAS, DS, GH, MO, NY, UC, US), *Block s.n.* (CAS), *Dudley s.n.* (DS), *Elmer 4113* (MO, NY, US), *Elmer 4559* (CAS, DS, MO, NY, UC, US), *Howell 265* (CAS); 2,000 ft., *Rose 64000* (CAS, NY), *Thomas 194* (DS), *Wright 53* (US); Bear Gulch, *Abrams s.n.* (CM, DS, MO, WTU); Woodside, *Applegate 737* (DS); Redwood City, *Bolander s.n.* (NY); McGarvey Gulch, Kings Mt., *Browne s.n.* (WTU); Summit Springs, *Burnham s.n.* (GH); La Honda Road to Skyline Drive, *Demaree 8918* (CM, MO); La Honda Creek, *Dudley s.n.* (DS); Lake Pilarcitos, *Eastwood s.n.* (CAS, DS, GH, NY, UC), *Ebright s.n.* (UC), *Pitelka s.n.* (UC); Butomo Canyon, *Eastwood s.n.* (CAS); Woodside, *Edwards s.n.* (WTU), *Leithold s.n.* (DS); Portola, La Honda Road, *Hoover 3897* (NY, UC, US); Searsville Lake, La Honda Road, 1,000 ft., *Keck 1359* (DS, MO, OSC, WTU); N of La Honda, *Kraeger s.n.* (JEPS); below Kings Mt., *McMurphy s.n.* (DS); Pilarcitos Canyon, *Oberlander 87* (DS); NW of Woodside, SE of Half Moon Bay, 0.2 mi. N of King Mt., *Roderick 61-015* (JEPS); Fire Trail Road, 2.1 mi. W from Skyline Blvd., SE of Half Moon Bay, *Roderick 61-019* (JEPS); San Mateo Creek, SE end Buriburi bridge, *Rossbach 214* (UC); Hillsboro, *Smith s.n.* (GH, US), *Smith s.n.* (JEPS); Kings Mt., 0.5 mi. below Skyline Drive, 2,000 ft., *Thomas 8539* (DS); 0.5–3.3 mi. on Kings Mt. Road from Skyline Drive to Woodside, 250–580 m, *Utech 88-039, 88-040, 88-041* (CM). SANTA CRUZ CO.: Glenwod, *Davis s.n.* (CAS); Glenwood, *Demaree 7356* (CM); Camon Camp, Waddell Creek, *Dudley s.n.* (DS); Aptos Creek, 2.5 mi. N of Capitola, 120 ft., *Penalosa 1480A* (CAS); Big Tree Grove, *Sonne s.n.* (UC); Bean Creek, 1 mi. SW of Glenwood, 900 ft., *Thomas 3842* (DS); 3.5 mi. from mouth of San Lorenzo River, 300 ft., *Thomas 2897* (UC); San Lorenzo River valley, 3.5 mi. N of Santa Cruz on CA 9, *Thomas 1896A* (DS). SONOMA CO.: Pocket Canyon, *Baker s.n.* (ROPA); Guerneville, *Baker s.n.* (UC); Redwood Canyon, 2.5 mi. S of Ft. Ross, 100 ft., *Gould 562* (UC); Sturgeon's Mills, 3 mi. NW of Sebastopol, *Hagg 3* (ROPA); W of Sebastopol, *Heller & Brown 5128* (DS, MO, NY, US); 0.5 mi. N of Occidental on road to Camp Meeker, 150 ft., *Lloyd 2044* (JEPS); Occidental, *Lobenstein s.n.* (UC); Duncan's Mill, *Rattan s.n.* (CAS); 6 mi. NW of Occidental along Willow Creek Road, *Roderick 63-1020* (JEPS); E of Plantation, Gualala River, *Roderick 60-135* (JEPS); Duncan's Mill, *Rubtzoff 3297* (CAS); S of Guernevillle, *Rubtzoff 1407* (CAS); 0.5–3.0 mi. S of Ft. Ross on CA 1, 50–100 m, *Utech 88-011, 88-012* (CM); Stillwater Cove Park, 10 m, *Utech 88-013* (CM); 2.75–6.0 mi. W on Willow Creek Road, Occidental to Bridgehaven, 60–130 m, *Utech et al. 88-005, 88-006, 88-007* (CM); 0.3 mi. WNW of Camp Meeker on Bohemian Road, Dutch Bill Creek, 50 m, *Utech et al. 88-004* (CM); WNW of Sebastapol, 0.2 mi. S of Occidental, Sturgeon's Mill, 80 m, *Utech et al. 88-002* (CM); 0.1 mi. SE of East Avenue, Occidental to Camp Meeker, 140 m, *Utech et al. 88-003, 88-182, 90-224* (CM).

2. **Scoliopus hallii** S. Watson, Proc. Amer. Acad. 14: 272. 1879. TYPE: U.S.A. Oregon: Cascade Mountains, 1871, *Hall 518* (holotype, GH; isotypes, MO, NY, photos CM).

S. bigelovii Torrey forma *minor* Baker, J. Linn. Soc. Bot. 17: 492–493. 1879. TYPE: U.S.A. Oregon: Cascade Mountains, 1871, *Hall 518* (GH, MO, NY).

Stems subterranean, 2.5–10.0 cm long. Leaves 2(–3), elliptic to oblong, basally sheathing to subsessile, rarely mottled with purple, 8–14 cm long, 2.5–4.8 cm wide. Pedicels 1–5, elongating to 6.0–10 cm long in fruit. Outer perianth segments lanceolate to oblanceolate, mottled with yellowish green and lined with purple, up to 9-nerved, 6.5–10 mm long, 2.0–3.3 mm wide; inner segments linear-spatulate, 6–9 mm long, 0.3 mm wide. Filaments 2.0–3.7 mm long, anthers 1.9–2.3 mm long. Capsules 16.0–18.5 mm long, 5.5–7.5 mm wide; stylar arms recurved, 2.1–2.4 mm long; seeds 10–14.

Illustrations. Abrams (1940), Hitchcock et al. (1969), Eastman (1990).

Representative specimens examined. OREGON: BENTON CO.: foot of Mt. Alsea, *Barss s.n.* (OSC), *Cook 10554* (OSC), *Fleischman s.n.* (WTU), *Stutz s.n.* (OSC); 6 mi. W of Philomath, *Steward 6031* (OSC); NE slope Mt. Alsea, 6.5 mi. SW of Philomath, T13S, R7W, 200 m, *Utech 88-042* (CM); NE slope Mt. Alsea, T13S, R7W, S2, 240 m, *Utech 88-043* (CM); N slope of Mary's Peak, *Peck 10703* (WILLU). CLATSOP CO.: Astoria, *Bowen s.n.* (ORE); Onion Peak, T10W, R4N, S22, 3,064 ft., *Chambers 3218* (OSC). COOS CO.: Coos River, above Fish Hatchery, *Sheldon 11760* (ORE); Coquille River, Myrtle Point, *Sweetsen & Henderson s.n.* (ORE); 14 km E of Myrtle Point, T28S, R9W, S13 SWSE, 700 m, *Sundberg & Christensen 430* (ORE); 1.0 mi. E of Remote and 1.0 mi. NE on Rock Creek Road, T29S, R10N, S36 SENW, 125 m, *Utech 88-406* (CM). DOUGLAS CO.: *Howell s.n.* (CAS, DS, ORE); Oakland, *Howell 3887* (NY, ORE, US, WTU); Elk Head, *Woodson s.n.* GH; Glendale, *Henderson 12217* (ORE); Umpqua River, T25S, R7W, 500 ft., *Detling 3935* (ORE, OSC); Sugarpine Mt., Lookinglass to Reston, *Williams s.n.* (ORE); 14 km E of Florence, Kentucky Creek, T19S, R9W, S15 NWSE, 550 m, *Sundberg & Christensen 375* (ORE); Wagoner Creek, 13 km S of Elkton, T23S, R8W, S35 SWNW, 135 m, *Sundberg & Christensen 387* (ORE); 8 km E of Remote, W of Kenyon Mt., T30S, R9W, S6, 660 m, *Sundberg 915* (OSC); 8 km S of Elkton, T23S, R7W, S19 NE, 320 ft., *Sundberg 769* (OSC); Bear Creek Recreation Area, 31 mi. W of Roseburg on OR 42, 200 m, *Utech 88-407* (CM); summit of Camas Mt., 2 mi. E of Camas Valley, T29S, R8W, S3 NESW, 440 m, *Utech 88-408* (CM). JOSEPHINE CO.: 3 mi. up New Fiddler Mt. Road from Josephine Creek Road, T38S, R9W, S23 SESE, 910 m, *White 587A* (ORE); Mud Springs, S Fork Silver Creek, Flat Top, T36S, R9W, S19, *Stansell & Planets s.n.* (OSC). LANE CO.: Cougar Bend, Coast Fork of Willamette River, *Taylor 625* (WILLU); Indian Creek, Swisshome, *Henderson 16873* (ORE); Big Fall Creek, *Henderson 18460* (ORE); Big Fall Creek, gravel pit, *Henderson 18504* (ORE); Elk Creek, 1.7 mi. W of Noti, T17S, R6W, S30, 450 ft., *Ireland 1796* (ORE); Elk Creek, Noti, T17S, R6W, 450 ft., *Detling 5092* (ORE); Wendling, Georgia Pacific tree farm, *Mason 10446* (ORE); Alderwood State Park, 15 mi. SW of Junction City, *Mason*

10412 (ORE); Gunshot Creek, Mabel, *Mason 10414* (ORE); Mt. Popocatepetl, T19S, R10W, S17 SESE, *Auler s.n.* (OSC); 13.7 km NE of Lowell, N Fork Fall Creek, T18S, R1E, S25 NENE, 317 m, *Christy 2404* (ORE); 11.7 mi. W of Lorane on Siuslaw River Road, T20S, R6W, S3 NESW, 200 m, *Utech 88-045* (CM); Whittaker Creek, 0.5 mi. SW of OR 62/US 126, T18S, R8W, S16 SWSE, 130 m, *Utech 88-046, Utech 88-450* (CM); Doris wayside, McKenzie River and OR 15/US 126, T16S, R3E, S31 NESW, 250 m, *Utech 88-047* (CM); Shotgun Creek, 0.6 mi. SW of Marcola Road, T15S, R1W, S32 NWSW, 260 m, *Utech 88-048, Utech 88-463* (CM); Fall Creek, *Wynd 45* (UC). LINCOLN CO.: Van Duzen Forest along OR 18 and Salmon River, T6S, R9W, S20, 100 m, *Utech 88-051, Utech 88-527* (CM). LINN CO.: Lebanon, *Haskin 110* (ORE); Lacomb, 1.5 mi. E of Hammond Camp, T12S, R1E, S22 SESE, *Willis s.n.* (OSC); McDowell Creek Falls Park, 8.6 mi. E of US 20, T12S, R1E, S36, 270 m, *Utech 88-044, Utech 88-497* (CM). MARION CO.: Silverton, *Howell 577* (CM); Silverton, *Howell s.n.* (CAS, ORE, OSC); along stream, 1 mi. E of Silverton, *Nelson 2124* (GH). POLK CO.: along Luckiamute River, 1 mi. above Fisherman's Camp, T9S, R7W, S34, *Steward 6695* (OSC); Dutch Creek, ca. 2.5 mi. NNW of Falls City, T8S, R6W, S17 NESW, 220 m, *Utech 88-049* (CM); Little Luckiamute River, 2.0 mi. NW of Falls City, T8S, R7W, S23 SENE, 320 m, *Utech 88-050* (CM); Van Duzen Forest along OR 18 and Salmon River, T6S, R8W, S10, 100 m, *Utech 88-053* (CM). TILLAMOOK CO.: bank of Wilson River, 15 mi. from Tillamook, *Thompson 4117* (CAS, CM, MO, NY, ORE, US, WTU); Van Duzen Forest along OR 18 and Salmon River, T6S, R9W, S17, 110 m, *Utech 88-052* (CM); Trask River, 10 mi. E of Tillamook, 120 m, *Utech 88-054* (CM); Wilson River at Keenig Creek, 18 mi. NE of Tillamook, T1N, R8W, S25, 120 m, *Utech 88-055* (CM); Munson Creek Falls County Park, 100 m, *Utech 88-540* (CM).

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PHYLOGENETIC ANALYSIS OF THE SOUTH AFRICAN GENUS *SPARAXIS* (INCLUDING *SYNNOTIA*) (IRIDACEAE–IXIOIDEAE), WITH TWO NEW SPECIES AND A REVIEW OF THE GENUS[1]

Peter Goldblatt[2]

ABSTRACT

Restricted to the western Cape Province of South Africa, *Sparaxis* comprises 13 species of small seasonal geophytes, seven belonging to section *Sparaxis* and six to section *Synnotia.* Until now treated as a separate genus, *Synnotia* is separable from *Sparaxis* section *Sparaxis* (i.e., *Sparaxis* sensu stricto) only by the degree of zygomorphy of their flowers. Species of the two sections have similar karyotypes with $x = 10$; specialized scarious, brown-streaked bracts; an unusual leaf anatomy in which the leaves lack marginal sclerenchyma but have a specialized, heavily thickened marginal epidermis; and similar fruit and seed characteristics. Vegetatively, they have a common gestalt and cannot be distinguished. In section *Sparaxis* the perianth is always actinomorphic, but in two species the stamens are asymmetrically arranged with the anterior stamen opposed to the posterior tepal and the style curved behind it. In section *Synnotia* the stamens are unilateral and arcuate with parallel, contiguous anthers, and the perianth is zygomorphic. Maintenance of *Synnotia,* based solely on this minor distinction, is unacceptable and is inconsistent with the variation in several other genera of Iridaceae–Ixioideae, for example, *Babiana, Gladiolus, Lapeirousia, Watsonia, Geissorhiza,* and *Tritoniopsis,* all of which include species with either actinomorphic or medianly zygomorphic flowers. Cladistic analysis of *Sparaxis* using either *Tritonia* or *Ixia* as outgroups for character polarization produces the same internal configuration, but it is more parsimonious to regard *Tritonia* as the immediate outgroup, unless characters such as karyotype are weighted. Cladistic analysis shows that the species clusters recognized as section *Synnotia* and section *Sparaxis* are not phylogenetically equivalent; the two sections are thus recognized for their taxonomic utility.

Restricted to the winter-rainfall region of southern Africa, *Sparaxis* is a genus of small geophytic perennials with cormous rootstocks, a fan of fairly succulent leaves, few-flowered spikes of large, usually brightly colored flowers, and scarious, brown-streaked, long-cuspidate bracts. Until now regarded as comprising just six species with completely regular perianths (Baker, 1896; Goldblatt, 1969), *Sparaxis* is here expanded to include *Synnotia* as section *Synnotia.* As a genus, *Synnotia* is distinguished from *Sparaxis* only by having flowers with a zygomorphic perianth with an enlarged upper tepal. Including *Synnotia,* in which Lewis (1956) recognized five species, and adding two new species, *Sparaxis maculosa* (sect. *Sparaxis*) and *S. caryophyllacea* (sect. *Synnotia*), there are now 13 species of *Sparaxis* and four subspecies.

HISTORY AND RELATIONSHIPS

The close relationship between *Synnotia* Sweet and *Sparaxis* Ker has been generally acknowledged (Baker, 1896: 134; Lewis, 1956) and, when first described in 1804 by John Bellenden Ker (Ker-Gawler), *Sparaxis* included two of the species later to be assigned to *Synnotia* by Robert Sweet (1826). In Lewis's (1956: 138) revision of *Synnotia,* she echoed Baker's comment in *Flora Capensis* that *Synnotia* differed from *Sparaxis* [only] in its irregular perianth. Although all the species

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of *Sparaxis* sensu Goldblatt (1969) have an actinomorphic perianth, the filaments of *S. grandiflora* and *S. bulbifera* are unilateral, the abaxial stamen is curved to lie opposite the adaxial tepal, and the style is displaced to lie between this stamen and the adaxial tepal. In *Synnotia,* the perianth is zygomorphic with at least the upper tepal enlarged and differentiated from the other five, and the stamens are unilateral with the lateral filaments lying close to the displaced abaxial stamen so that the anthers are parallel and more or less contiguous. The difference in zygomorphy between *Synnotia* and the above two *Sparaxis* species is one of degree and is not a valid criterion for generic separation. In other genera of Iridaceae, for example, in *Babiana* and *Gladiolus,* both indisputedly monophyletic genera, there are several species with completely actinomorphic flowers and a greater number with zygomorphic flowers (Lewis, 1959; Lewis et al., 1972). *Watsonia* and *Tritoniopsis* each have a single actinomorphic species that is often segregated subgenerically (Lewis, 1958; Goldblatt, 1989) or sectionally from its zygomorphic congeners. There are similar examples in *Lapeirousia, Geissorhiza,* and *Tritonia.* It is clear that zygomorphy has evolved repeatedly in several monophyletic lines in Iridaceae-Ixioideae and may even have been lost in some cases (Hilliard & Burtt, 1991: 36): it is therefore an unsound criterion for the recognition of a genus. This is particularly so in the case of *Sparaxis* and *Synnotia,* where there is a clear progression from actinomorphy to complete floral zygomorphy.

Sparaxis and *Synnotia* are so similar vegetatively that they cannot be distinguished except in flower. The floral bracts, often good indicators of relationship in Ixioideae, are similarly specialized in both. They are scarious and more or less pale-membranous but are irregularly streaked with brown, and are often lacerate and long-cusped. Similar bracts occur in the tropical and southeastern African *Dierama,* for which reason it has been considered related to *Sparaxis.* In *Ixia,* thought to be closely related to *Dierama* (Lewis, 1962), the bracts are usually pale-membranous and short-cusped. These four genera have angular to globose seeds with a surface in which the outline of the epidermal cells is nearly to completely obliterated, a fairly typical seed type in Ixioideae. In *Sparaxis* and *Synnotia* the seeds are completely spherical and perfectly smooth.

Lewis assigned *Synnotia* together with *Sparaxis, Streptanthera, Ixia,* and *Dierama* to subtribe Ixiinae of the Ixieae. Since then composition of Ixiinae has not changed except that *Streptanthera* and *Sparaxis* are considered congeneric (Goldblatt, 1969). Lewis's treatment was supported by karyology (Goldblatt, 1971: 412), all genera having $x = 10$ and a similar karyotype of small chromosomes.

Studies of leaf anatomy (Rudall & Goldblatt, 1991) have now cast doubt on the validity of Ixiinae. Several genera of Ixioideae have a derived leaf margin structure with columnar epidermal cells with very thick anticlinal walls and without subepidermal sclerenchyma. These include *Sparaxis* (and *Synnotia*), *Crocosmia, Chasmanthe,* most species of *Tritonia* (a few have marginal epidermal cells matching those of the laminar epidermis), *Freesia,* and *Anapalina. Tritoniopsis* (Goldblatt, 1990; Rudall & Goldblatt, 1991) has columnar and thickened marginal epidermis, but some species also have subepidermal marginal sclerenchyma. *Ixia* and *Dierama* have unmodified marginal epidermal cells and subepidermal sclerenchyma, both considered basal features for Iridaceae. In addition, *Dierama* has an unspecialized leaf anatomy, and its leaves usually lack midribs. In this paper I develop a phylogeny of *Sparaxis* using both *Ixia–Dierama* and *Tritonia* as possible outgroups for polarizing characters. The choice of outgroup makes no difference to the structure of the tree (although the evolution of some characters differs), and the immediate generic relationships of *Sparaxis* remain uncertain.

REVIEW OF TAXONOMIC CHARACTERS AND CHARACTER POLARIZATION

CORM TUNICS

In most species the relatively small corms are enclosed in fine, pale, netted fibers, which outgroup comparison with either *Tritonia* or *Ixia* suggests is the basal condition. In section *Synnotia, S. roxburghii* and *S. galeata* have the tunic extending upward in a neck around the base of the plants and the tunics accumulate in an unusually dense mass, particularly in the latter. In *S. villosa, S. caryophyllacea,* and *S. variegata* the corm tunics are composed of thicker and harder fibers, especially thickened below, thus resembling claws. This tunic structure is probably an important specialization and is evidence for uniting these three species in a single clade.

LEAVES

Difficult to describe objectively, the leaves of *Sparaxis* can usually be distinguished from other Iridaceae in their somewhat succulent (soft but firm) nonfibrotic texture. They are always a rather pale green, and the fine, pale lateral veins are perhaps part of the reason for their being easily recognized. In sunlight the leaves seem sprinkled with gold, probably a reflection of the light from the epidermal papillae. Most species of the genus also have obtuse leaves generally obliquely apiculate, unlike both possible outgroups in which the leaves are acute. These leaf characters probably have a basis in internal anatomy, but in any event should be regarded as derived. The leaf margin epidermis of the several species examined anatomically is unusual. As in the case of *Tritonia* and its close allies *Crocosmia* and *Chasmanthe* (de Vos, 1982, 1984) and *Tritoniopsis* (Goldblatt, 1990), the marginal epidermal cells differ from the laminar epidermal cells, being columnar and heavily thickened on the anticlinal walls. The margins lack subepidermal sclerenchyma, as do the margins in the *Tritonia* group but not *Tritoniopsis* (Goldblatt & Manning, 1990; Rudall & Goldblatt, 1991). Both leaf margin features are regarded as apomorphic and strongly link *Sparaxis* to the *Tritonia* group, especially because morphology is equivocal concerning relationships in most Ixioideae. *Ixia*, thought to be allied to *Sparaxis* (Lewis, 1962; Goldblatt, 1969), has the plesiomorphic leaf margin anatomy, with the epidermis no different on margin and lamina, and well-developed subepidermal sclerenchyma associated with a marginal vein.

INFLORESCENCE AND BRACTS

There is nothing remarkable about the inflorescence of *Sparaxis*, a spike, but the patterns of branching are variable. In most members of section *Sparaxis* branching is restricted to the base, although plants may produce up to five axes per corm and this seems to be the basic condition in the genus. In *S. bulbifera* and section *Synnotia*, branching, when it occurs, is cauline, presumably a reversal to the basic kind of branching in Iridaceae including the possible outgroups of the genus. Flowers are more or less spirally arranged on a flexuose axis in section *Sparaxis*, but the spike is secund in those species with a zygomorphic perianth (sect. *Synnotia*). The two characters may be correlated, but are here regarded as separate synapomorphies.

The bracts of *Sparaxis* are perhaps the most striking feature of the genus. They are dry and firm in texture, somewhat creased, and usually long-cusped (Fig. 1). In addition, they are irregularly streaked with medium to dark brown on the pale translucent background. The bracts are remarkably similar to those of *Dierama*, which is presumed to be convergent. Bracts of *Ixia* and *Tritonia* are typically membranous and uniformly pale or with the veins a darker color, and in both genera the bracts are most often short-cusped. Three species of section *Sparaxis* stand out in having especially large but non-cusped bracts. Instead, the margins are rather irregularly lobed. This condition is assumed here to be the plesiomorphic state. In *S. fragrans* and *S. maculosa* the margins of the bracts including the cusps are irregularly fringed (Fig. 1A). The condition is distinctive enough to make it possible to identify the species from the bracts alone and must be regarded as apomorphic.

PERIANTH

The somewhat fleshy perianth is actinomorphic in section *Sparaxis*, but is medianly zygomorphic (Figs. 2, 3), a derived condition, in section *Synnotia*, in which the flowers face to the side, the upper tepal is always largest, and the lower three tepals are typically smaller, united to one another for a short distance, and grooved proximally. All members of section *Sparaxis* have a fairly short perianth tube, as do several of section *Synnotia*. An elongate tube characterizes *S. roxburghii* and the two subspecies of *S. variegata*, and in the latter the tube is bent sharply (geniculate) at the top of the lower cylindric part of the tube (Fig. 3B).

Floral variation in section *Sparaxis* is limited. All seven species have a regular perianth, and five have actinomorphic flowers with erect stamens symmetrically oriented around the central style. Two species have asymmetrically arranged stamens, described below.

In the flowers of section *Synnotia* the tepals are unequal, the adaxial tepal being largest and the lower three small, united for a short distance, and grooved. The stamens are unilateral and more or less contiguous, lying close to the posterior tepal.

Perianth colors of red to orange or pink, found in *Sparaxis tricolor*, *S. elegans*, and *S. pillansii*, are probably plesiomorphic, corresponding as they do to the predominant perianth colors in *Tritonia* and *Ixia*. The remaining species of *Sparaxis* have yellow to white or purple perianths.

I have not included floral odor in this analysis because the scents in the three fragrant species, *S. fragrans*, *S. caryophyllacea*, and *S. galeata*, seem different, and thus poor evidence for relationship. Moreover, based on all other criteria, the three scented species do not seem to be immediately related.

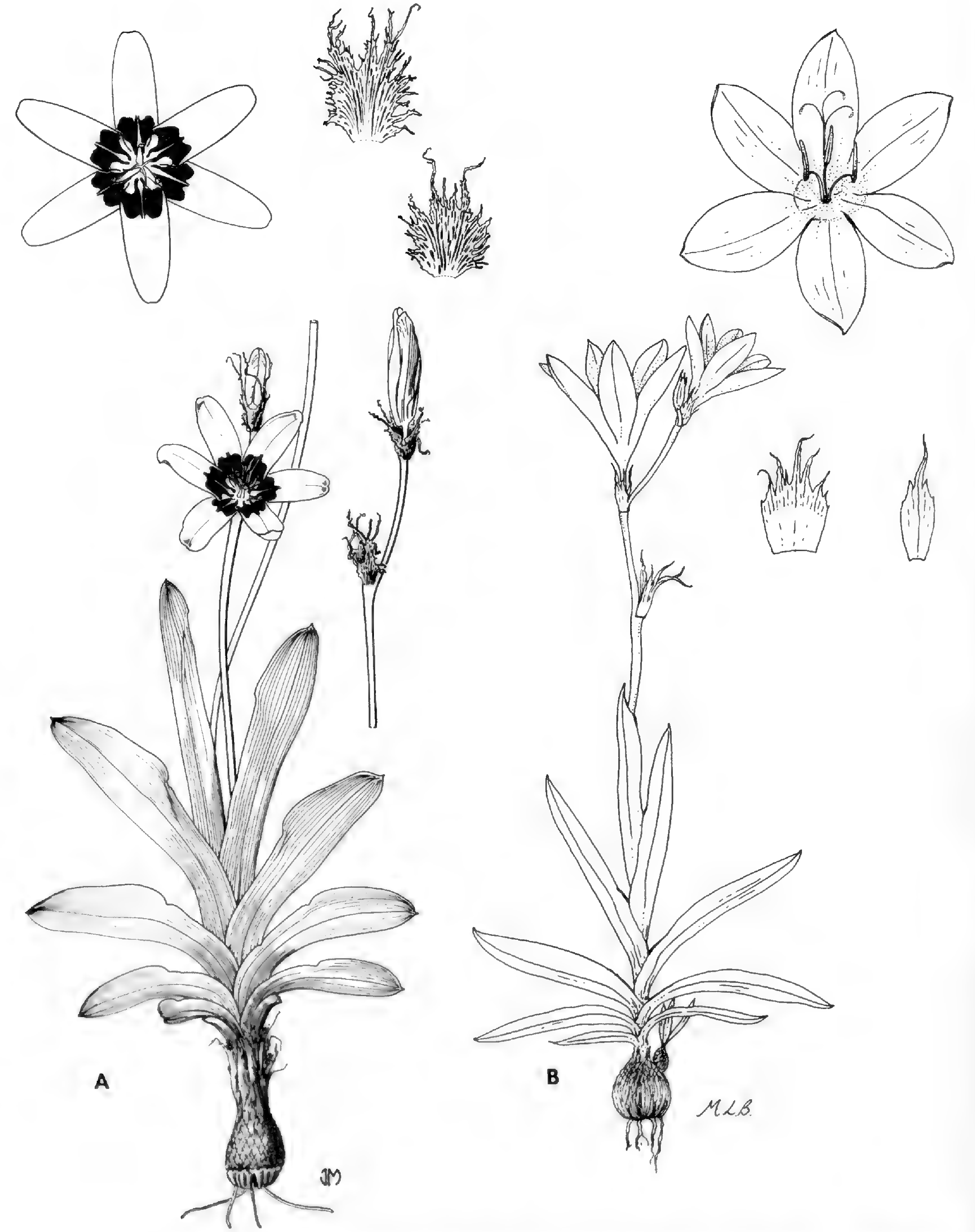

FIGURE 1. Habit and floral details of *Sparaxis maculosa* (A) and *S. bulbifera* (B). Habits ×0.5; single flowers and separated inner and outer bracts full size. (Drawn by J. C. Manning and M. L. Branch.)

STAMENS AND STYLE

Whereas in most species of section *Sparaxis* the stamens are arranged symmetrically around the central style, in *S. grandiflora* and *S. bulbifera* the stamens and style are asymmetrically arranged. The lower (abaxial) stamen is curved across the flower to lie opposite the upper (adaxial) tepal, and the style lies between this stamen and the posterior tepal (Fig. 1B). This condition is probably a step

FIGURE 2. Habit and floral details of *Sparaxis villosa* (A) and *S. caryophyllacea* (B). Habits ×0.5; single flowers and separated inner and outer bracts full size. (Drawn by M. L. Branch.)

toward the arched unilateral and more or less contiguous stamens of section *Synnotia* (Figs. 2, 3). In *S. grandiflora* and *S. bulbifera* and section *Synnotia* the anthers face inward and are introrse at anthesis, unlike the other species of section *Sparaxis*, which have extrorse anthers, the basal condition for Iridaceae. In *S. pillansii* the anthers are slightly coiled (S-shaped), and in *S. elegans* they are strongly twisted around the style (Goldblatt, 1969).

Three species of section *Sparaxis*, *S. tricolor*, *S. elegans*, and *S. pillansii*, have short, terminally expanded style branches, different from the filiform, relatively long style branches that characterize the rest of the genus (Goldblatt, 1969). Comparison with *Tritonia* suggests that the long filiform style branches are the basal condition and that the short branches are derived. A similar interpretation seems reasonable with *Ixia* as outgroup.

POLLEN

The pollen grains of several species examined are sulcate with a 2-banded operculum, and the exine has a perforate and minutely verrucate tectum (Goldblatt et al., 1991). In all these features the grains correspond fairly closely to the presumed basal condition in Ixioideae, although contrasting with *Ixia*, which has unusually small grains with a single banded operculum.

FRUIT AND SEEDS

The thin-walled capsules are unremarkable in Ixioideae and are more or less barrel-shaped to

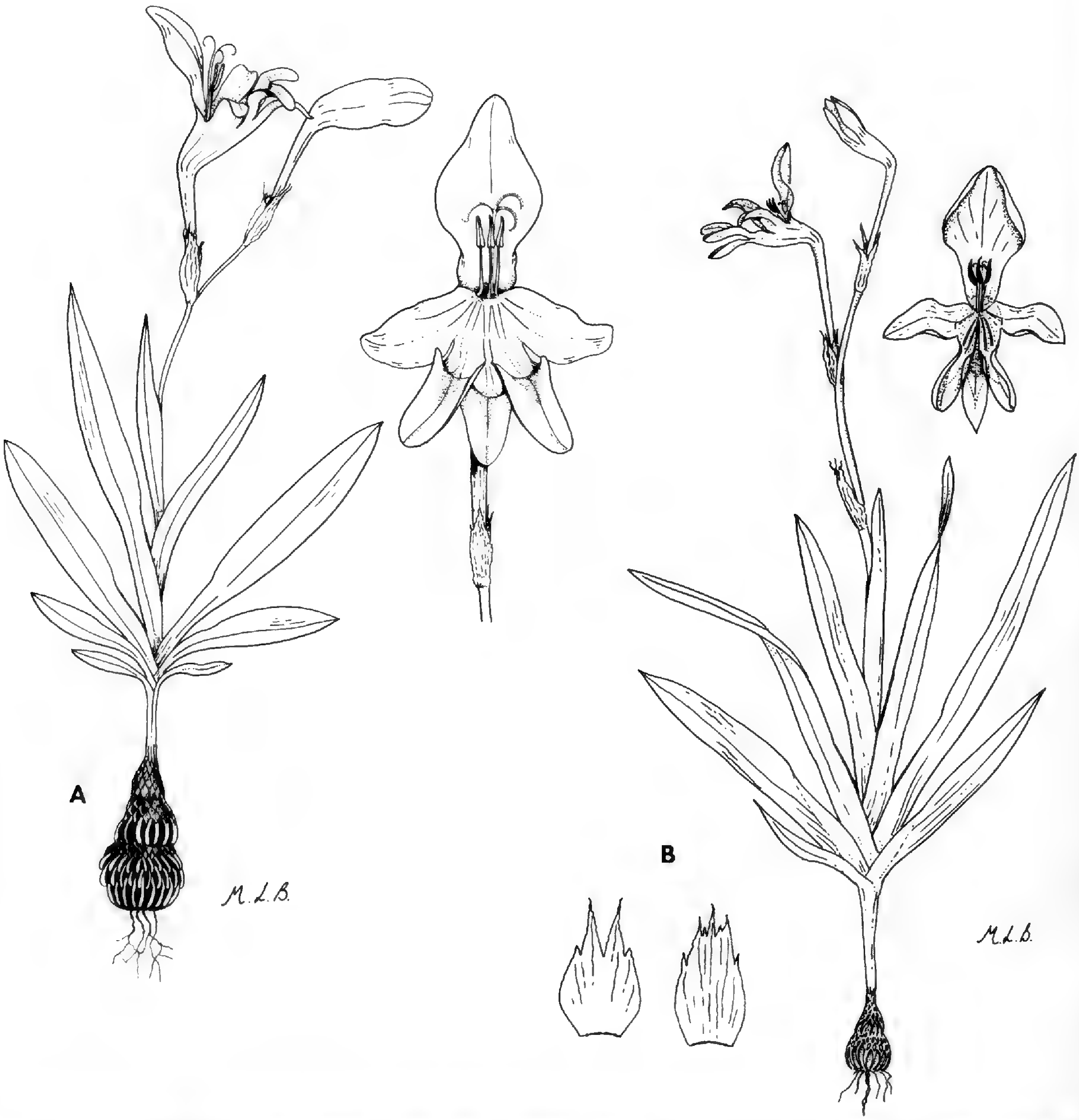

FIGURE 3. Habit and floral details of *Sparaxis variegata* subsp. *variegata* (A) and subsp. *metelerkampiae* (B). Habits ×0.5; single flowers and separated inner and outer bracts full size. (Drawn by M. L. Branch.)

subglobose, but 3-lobed when seen from above. The translucent membranous walls of the ripe capsules show clearly the rounded impression of the seeds, a consequence of seed shape and texture rather than of any intrinsic feature of the capsule itself. The seeds of both sections *Sparaxis* and *Synnotia* are spherical, hard, and shiny. The raphe remains conspicuous, and there is a slight swelling around the micropyle. Color is medium brown to deep red-brown. Seed number is remarkably constant in a species, with an average of 8–10 seeds per locule (24–30 per capsule). Fewer seeds are found in *S. parviflora* (4–6 per locule) and *S. galeata* (2–4 per locule) and *S. variegata* subsp. *variegata* (5–6 per locule), while subspecies *metelerkampiae* has capsules with a greater number of seeds than the average (10–12 per locule). Size varies a little between the species, but the large seeds of *S. parviflora*, up to 2.5 mm diam., are clearly apomorphic. The small seeds of *S. variegata* subsp. *metelerkampiae*, 1.6–1.8 mm diam., are probably also apomorphic. Curiously, the above two taxa, one with many small seeds and the other with few large seeds are also the most strongly self-compatible and autogamous species in the genus.

KARYOLOGY

Basic chromosome number in *Sparaxis* is $x = 10$ (Goldblatt, 1969, 1971). The chromosomes are small and exhibit a small range in size. Original counts here for two species of section *Synnotia*, *S. caryphyllacea* and *S. variegata* subsp. *metelerkampiae*, both $2n = 20$, conform to the pattern already described for the genus. This karyotype accords closely with that of *Ixia* and *Dierama*. *Tritonia* and *Crocosmia* have $x = 11$, but otherwise have a similar chromosome morphology. It is only a small change from $x = 11$ to $x = 10$, and there is ample precedent for single-step decreasing dysploid events in flowering plants, including several within Iridaceae.

PHYLOGENY OF *SPARAXIS*

The characteristics outlined above and summarized in Table 1 form the basis for the cladistic analysis. Characters were initially polarized using both *Ixia* and *Tritonia* as the outgroup. A more parsimonious resolution was obtained with *Tritonia*. The use of *Ixia* as outgroup is founded largely on karyotypic similarity, and the resulting cladogram thus assumes the convergent development of the two evidently unlinked and striking leaf anatomical characters, columnar marginal epidermal cells, and lack of subepidermal epidermis at the margins in *Sparaxis* and in the *Tritonia* lineage. I prefer to assume that a single decreasing dysploid event occurred in the *Sparaxis* line, resulting in the apparently identical karyotypes of *Ixia* and *Sparaxis*. The cladogram (Fig. 4) was produced by hand and verified using Hennig86. The computer analysis produced three trees of equal length, the one figured, a second that is not supported by the data, and a third that is discussed below, that have a tree length of 31 and a consistency index (CI) of 0.77, ignoring non-informative characters for the ingroup. Ignorance of seed type (character 25) in *S. roxburghii* and *S. variegata* makes it impossible to resolve completely the *Synnotia* clade. Depending on the character state for these two species a shorter tree length of 30 and CI of 0.8 can be obtained (as is figured), assuming many small seeds for *S. variegata* and few large seeds for *S. roxburghii*.

The most significant point of difference between the three computer-generated trees is the position of *Sparaxis parviflora*. Its position as sister clade to the remaining species of section *Synnotia* (Fig. 4) where it is defined by two parallelisms is the one I prefer. But in one tree *S. parviflora* is the sister clade to *S. galeata–S. roxburghii*, and the cluster is supported by the presumed presence of few large seeds (character 25). Ignorance of the seeds of *S. roxburghii* renders informed comment on the tree impossible.

A notable parallelism in the tree is the elongate perianth tube in *S. roxburghii* and *S. variegata*, species which have different types of corms. A longer tree results when these two species are treated as related by their long tubes, for there is then a reversal in corm tunic texture and two parallelisms, one for an erect upper tepal and another for tunics thick and forming a neck. Other parallelisms in the tree, including a small flower in *S. parviflora* and *S. villosa*, spotted leaf bases in *S. galeata* and *S. caryophyllacea*, and few and large seeds in *S. parviflora* and *S. galeata*, are not unusual for plants in general. The presence of cauline branching for the clade including the *Synnotia* group and *S. bulbifera* is treated as a reversal, basal branching being regarded here as apomorphic for *Sparaxis*. The reversal of one of the basal characters for *Sparaxis*, oblique apiculate leaf apices, in *S. fragrans* is not surprising in view of its narrow leaves, which leave little opportunity for the expression of the character.

The analysis confirms the integrity of *Synnotia* as a monophyletic assemblage. The *Synnotia* clade is supported by three synapomorphies, all related to floral zygomorphy and thus perhaps intimately linked. The analysis also indicates that while the genus *Sparaxis* is monophyletic and is supported by five synapomorphies, none evidently linked, the seven species of *Sparaxis* sensu Goldblatt (1969), i.e., excluding *Synnotia*, do not themselves constitute a single lineage, but rather consist of four clades, more or less equivalent to the *Synnotia* clade.

Treatment of these seven species as a section *Sparaxis* is taxonomically convenient, although phylogenetically unacceptable because section *Sparaxis* as so constituted is paraphyletic. The recommended phylogenetic solution, to recognize these seven species as four sections equivalent to section *Synnotia* (or no sections at all) has little practical merit. Excepting the basal clade that includes *S. tricolor* and its two relatives, the lineages are supported by only one synapomorphy each. On grounds of taxonomic utility, I suggest treating *Sparaxis* as two sections, section *Synnotia* and a residual and paraphyletic section *Sparaxis*. It must be noted that within the latter, the *S. tricolor* line stands out from the remaining four species, which though constituting three primary clades, are in fact so closely related that they are in practice often difficult to distinguish, and their validity as separate species has not always been accepted (e.g., Lewis, 1950). Recognition of a third section *Tri-*

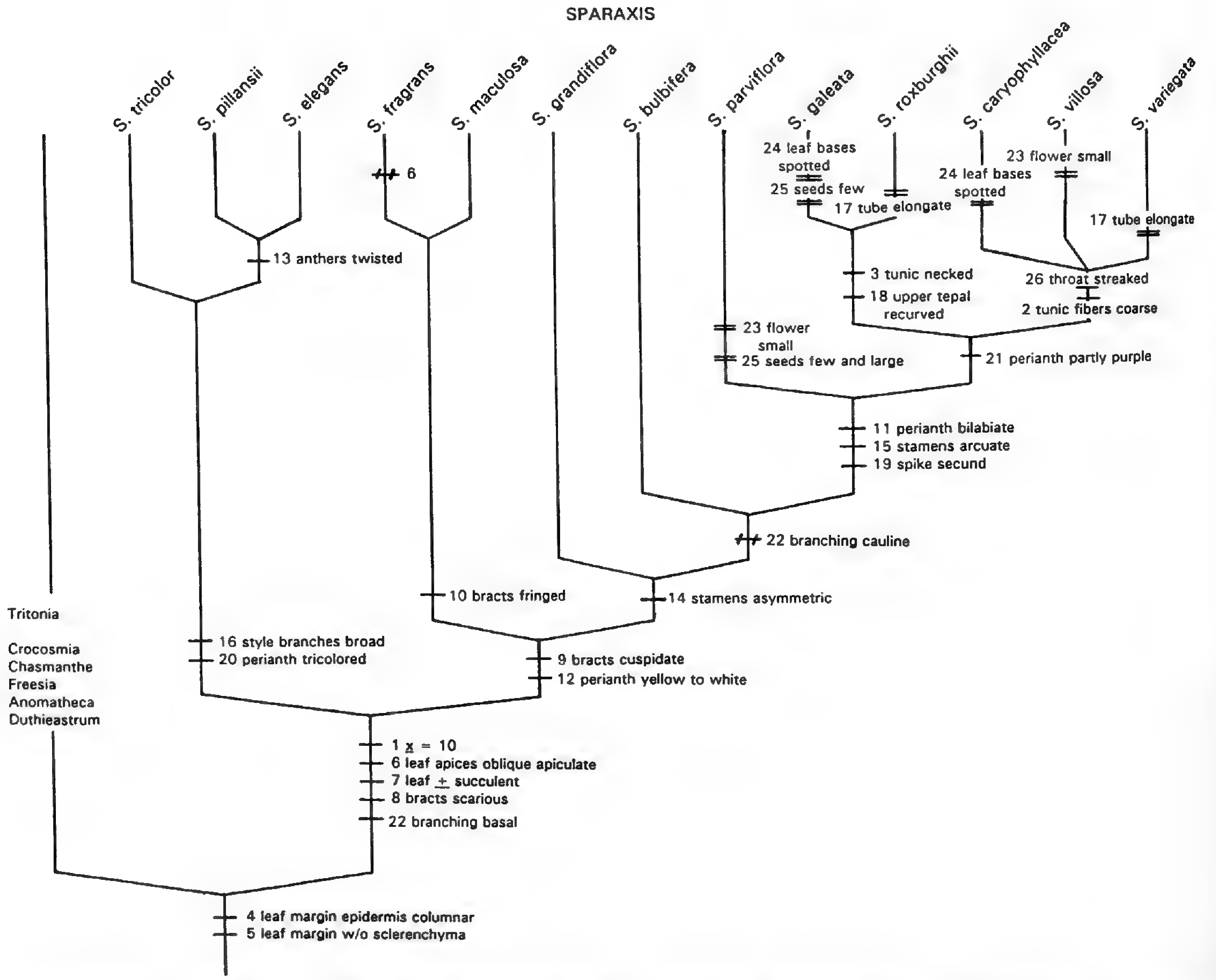

FIGURE 4. Phylogeny of *Sparaxis*, with *Tritonia* and its close allies (*Crocosmia, Chasmanthe, Freesia,* and *Anomatheca*) as outgroup. The cladogram is based on the character list and data matrix presented in Table 1. Tree length is 30 and the consistency index (CI) is 0.8, with autapomorphies excluded for the manually constructed cladogram. Parallelisms are indicated by double lines and reversals by barred lines.

color has merit, but because of its small size formal treatment seems unnecessary at present.

SYSTEMATIC REVIEW

The species of *Sparaxis* are dealt with briefly below in taxonomic sequence. Because full descriptions are provided in a treatment of the genus for *Flora of Southern Africa* (Goldblatt, in press) they are not repeated here. Only brief synonymy is given except where new combinations are presented. Extended descriptions are provided for two new species, *S. maculosa* and *S. caryophyllacea* and for *S. variegata*, which has a complex pattern of variation. Complete species descriptions and ample citation of specimens are included in revisions of *Synnotia* (Lewis, 1956) and *Sparaxis* in part (Goldblatt, 1969). I have not included sectional descriptions here because they have little utility in a small genus like *Sparaxis* and would call for near repetition of the generic description except for the fact that the section *Sparaxis* has an actinomorphic perianth and section *Synnotia* has a zygomorphic one.

Sparaxis Ker, Curtis's Bot. Mag. 15: t. 548. 1802, & Konig & Sims, Ann. Bot. 1: 225. 1804 as 1805. Klatt, Linnaea 32: 747. 1863, & Abh. Naturf. Ges. Halle 15: 389 (Erganz. 56). 1882, not including *Synnotia* or *Streptanthera*. Baker, Handb. Irid. 196. 1892, & in Flora Cap. 6: 115. 1896, not including *Synnotia* or *Streptanthera*. Goldblatt in J. S. African Bot. 35: 219–252. 1969, not including *Synnotia*; Contr. Bolus Herb 13: 57. 1991. TYPE SPECIES: *S. bulbifera* (L.) Ker (lectotype, here designated).

Streptanthera Sweet, Brit. Fl. Gard. ser. 1, 3: t. 209. 1827, Klatt, Abh. Naturf. Ges. Halle 15: 390 (Erganz. 56). 1882. Baker, Handbk. Irid. 160 (1892) & in Flora Cap. 6: 86. 1896. E. Phillips, Gen. S.

TABLE 1. Data matrix and character list for the cladogram (Fig. 4). The derived condition is denoted by 1; ancestral by 0; state unknown by ?. Polarity of characters is discussed in the text. Autapomorphies are not included. Abbreviations for species will be evident from the text and Figure 4.

Taxon	Character number																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Tritonia	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sparaxis																										
tric.	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0
eleg.	1	0	0	1	1	1	1	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0
pill.	1	0	0	1	1	1	1	1	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0
frag.	1	0	0	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
macu.	?	0	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	?	0
grand.	1	0	0	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0
bulb.	1	0	0	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
parvi.	?	0	0	1	1	1	1	1	1	0	1	1	0	1	1	0	0	0	1	0	0	0	1	0	1	0
gale.	1	0	1	1	1	1	1	1	1	0	1	1	0	1	1	0	0	1	1	0	1	0	0	1	1	0
roxb.	?	0	1	1	1	1	1	1	1	0	1	1	0	1	1	0	1	1	1	0	1	0	0	0	?	0
vill.	1	1	0	1	1	1	1	1	1	0	1	1	0	1	1	0	0	0	1	0	1	0	1	0	0	1
caryo.	1	1	0	1	1	1	1	1	0	0	1	1	0	1	1	0	0	0	1	0	1	0	0	1	0	1
varie.	1	1	0	1	1	1	1	1	1	0	1	1	0	1	1	0	1	0	1	0	1	0	0	0	?	1

Characters: the derived (apomorphic) states listed first followed by the presumed ancestral (plesiomorphic) condition.

1. basic chromosome number $x = 10$—$x = 11$
2. corm tunics of coarse fibers thickened below—tunics fibers fine
3. corm tunics forming a neck and accumulating in a dense mass—tunics not forming a neck nor a dense mass
4. leaf margin epidermis columnar—epidermis normal
5. margins without subepidermal sclerenchyma—subepidermal sclerenchyma present
6. leaf apices obtuse and oblique apiculate—apices acute
7. leaves ± succulent and gold-reflecting—leaves firm, not gold-reflecting
8. bracts scarious, creased and brown streaked—bracts membranous and self-colored
9. bracts long-cuspidate and lacerate—bracts not cuspidate or hardly scarious
10. bract edges irregularly serrate-fringed—bract edges smooth
11. perianth zygomorphic and bilabiate—perianth actinomorphic
12. perianth shades of yellow to white or purple—perianth with red, orange or pink
13. anthers weakly twisted—anthers straight
14. abaxial stamen opposed to adaxial tepal and style arcuate—stamens and style symmetrically arranged
15. stamens unilateral and arcuate—stamens not unilateral
16. style branches short and broad above—style branches filiform
17. perianth tube elongate—perianth tube short
18. upper tepal erect-recurved—upper tepal hooded
19. spike secund—spike spiral
20. perianth vividly marked (tricolored)—perianth usually drably marked (uni- or bicolored)
21. perianth with at least upper tepal partly purple—perianth without purple marks
22. branching basal only—branching cauline
23. flowers especially small—flowers fairly large
24. leaf bases spotted—leaf bases self-colored
25. seeds few and large—seeds many and moderate-sized
26. perianth throat streaked—throat not streaked

Afr. Fl. Pl. ed. 2: 218. 1951. TYPE SPECIES: *S. elegans* Sweet (= *Sparaxis elegans* (Sweet) Goldblatt).

Synnotia Sweet, Brit. Fl. Gard. 2: t. 150. 1826 (as *Synnetia*), corr. *Synnotia* by Sweet in Hort. Brit. ed. 2: 501. 1827. Klatt, Linnaea 32: 750. 1863. Baker, Flora Cap. 6: 134–135. 1896. Lewis, Ann. S. African Mus. 40: 137–151. 1956. TYPE SPECIES: *S. variegata* Sweet (= *Sparaxis variegata* (Sweet) Goldblatt).

Anactorion Raf., Fl. Telluriana 34. 1838 (as 1836). TYPE: *A. bicolor* (Thunb.) Raf. (= *Sparaxis villosa* (Burm. f.) N. E. Br.).

Geophytic perennials with small globose corms rooting from the base; *corm tunics* of fine to moderately fine netted fibers or of coarse hard fibers, thickened and clawlike below. *Leaves* several, mostly basal, but sometimes also cauline, the lowermost 2–3 membranous and sheathing (thus cataphylls), the remaining laminate and green, lanceolate to linear or falcate, obtuse to acute, acuminate, often obliquely so, glabrous, with many closely set fine secondary veins, the midrib prominent. *Stem* firm and relatively thick, ± erect, glabrous, simple or branched, then either from near the base or above the ground, sometimes with a few large axillary cormlets below, or many small cormlets in all axils. *Spike* (1–)few- to several-flowered, lax, distichous in bud, loosely spiral or nearly secund in bloom; *bracts* scarious and creased, pale with brown streaks, ± entire to lightly lacerate, or deeply lacerate with long tapering cusps, the outer (abaxial) larger than the inner (adaxial). *Flowers* actinomorphic or zygomorphic, then with either the stamens alone asymmetrically arranged or the perianth also asymmetric, then the upper (adaxial) tepal larger and often hooded and the lower three tepals smallest, with contrasting marking and extended forward ± horizontally; *perianth tube* short to long, funnel-shaped (cylindric below and expanded above), sometimes obliquely so, or elongate, much exceeding the bracts and dimorphic, the lower part cylindric and abruptly bent and widened above; *tepals* with the whorls ± equal or the upper largest and the lower three smallest, lanceolate to obovate or spathulate, acute to obtuse. *Stamens* inserted at the base of the expanded part (throat) of the tube, symmetrically or asymmetrically disposed; *filaments* filiform, straight and surrounding the style, or curved outwards and the abaxial twisted to lie opposite the adaxial tepal, or all three filaments ± parallel and opposite the adaxial tepal; *anthers* straight, curved or spirally coiled, subbasifixed, extrorse or introrse. *Ovary* ovoid; *style* filiform, straight and erect or unilateral, the branches either short, often with expanded apices, or long and filiform. *Capsules* barrel-shaped to oblong, firm-membranous, showing the outline of the seeds; *seeds* (2–)4–15 per locule, globose, relatively large, smooth, usually shiny. *Chromosome number* $x = 10$.

A genus of 13 species, all in South Africa and restricted to the southwestern Cape, southern Namaqualand, and the western Karoo.

KEY TO THE SPECIES

- 1a. Perianth actinomorphic; stamens either symmetrically disposed around a central style or the abaxial stamen lying opposite the adaxial tepal, and style opposite the adaxial tepal (section *Sparaxis*).
  - 2a. Bracts entire to slightly lacerate; stamens symmetrically disposed around erect style (this includes when anthers are coiled).
    - 3a. Anthers spirally coiled and reaching only to apex of the style .... 3. *S. elegans*
    - 3b. Anthers straight or slightly twisted and curved, extending well past style branches.
      - 4a. Anthers straight, yellow to ochre; spikes 2–5-flowered; tepals orange, marked with yellow and black .... 1. *S. tricolor*
      - 4b. Anthers incurved and slightly twisted, red to brown; spikes (2–)5–10-flowered; tepals rose pink, marked with yellow and red to purple .... 2. *S. pillansii*
  - 2b. Bracts deeply lacerate with cusps at least as long as the rest of the bract; stamens symmetrical or asymmetrical but not coiled.
    - 5a. Bract edges irregularly serrate (fringed); stamens symmetrically arranged around style.
      - 6a. Tepals 27–35 × 8–10 mm; leaves oblong to lanceolate, 9–12 mm wide and obliquely apiculate .... 5. *S. maculosa*
      - 6b. Tepals 18–25 × 5–8 mm; leaves linear to narrowly lanceolate, 2–5(–9) mm wide and acute .... 4. *S. fragrans*
    - 5b. Bract edges ± entire, not serrate or fringed; stamens asymmetrically disposed.
      - 7a. Stem usually branched in mid-axis and bearing a cauline leaf; many small cormlets produced after flowering at all nodes .... 7. *S. bulbifera*
      - 7b. Branches if present produced from base, and axes lacking a cauline leaf; cormlets not produced in numbers and never above ground .... 6. *S. grandiflora*
- 1b. Perianth zygomorphic, with the adaxial (upper) tepal largest, erect, and often hooded, and lower three tepals smallest and ± horizontal; stamens unilateral and arcuate, with the anthers parallel and ± contiguous (section *Synnotia*).
  - 8a. Narrow part of perianth tube more than 25 mm long, well exserted from the bracts; tube bent abruptly (geniculate) at apex of the slender part .... 13. *S. variegata*
  - 8b. Narrow part of perianth tube less than 25 mm long, exserted or included in the bracts; tube gently to sharply curved at the apex of the narrow part.
    - 9a. Corm tunics of fine fibers; flowers small, the tepals less than 10 mm long .... 8. *S. parviflora*
    - 9b. Corm tunics either of fine or coarse fibers thickened into claws below; flowers usually larger, the upper tepals at least 15 mm long, but if shorter the corm tunics of coarse fibers.
      - 10a. Corm tunics of hard reticulate fibers not extending upwards in a neck; upper tepal directed forward and somewhat hooded over the stamens.
        - 11a. Upper tepal ca. 16 mm long, bases of the leaves uniformly colored; style dividing opposite the lower half of the anthers, the style branches ca. 2 mm long .... 11. *S. villosa*
        - 11b. Upper tepal 22–24 mm long; bases of the leaves lightly speckled with purple (not

visible in dry material); style dividing near anther apices, the style branches ca. 5 mm long .... 12. *S. caryophyllacea*

10b. Corm tunics of fine fibers, usually extending upwards in a neck; upper tepal erect or directed backwards.

  12a. Cylindrical part of perianth tube less than 8 mm long; leaf bases spotted red to purple (sometimes fading on dry specimens) .... 9. *S. galeata*

  12b. Cylindrical part of perianth tube 15–25 mm long; leaf bases uniformly colored .... 10. *S. roxburghii*

SECTION 1. *SPARAXIS*

1. **Sparaxis tricolor** (Schneev.) Ker, König & Sims, Ann. Bot. 1: 225. 1804. Baker, Flora Cap. 6: 117. 1896. Goldblatt, J. S. African Bot. 35: 230. 1969. *Ixia tricolor* Schneev., Icon. Pl. Rar. t. 39. 1795. Ker, Curtis's Bot. Mag. 11: t. 381. 1797. *Streptanthera tricolor* (Schneev.) Klatt, Abh. Naturf. Ges. Halle 15: 390 (Erganz. 56). 1882. TYPE: illustration in Schneevogt, Icon. Pl. Rar. t. 39.

Restricted to the northern end of the Bokkeveld Escarpment, northwest of Nieuwoudtville in the northwestern Cape, occurring on clay soils in renosterveld. Readily identified by the characteristic orange-red flowers with yellow and blackish tepal markings. Widely cultivated in southern Africa and elsewhere; most *Sparaxis* hybrids were derived from crosses that included *S. tricolor.*

2. **Sparaxis pillansii** L. Bolus, S. African Gard. 22: 57. 1932. Goldblatt, J. S. African Bot. 35: 232. 1969 & Ann. Missouri Bot. Gard. 68: 563. 1981. TYPE: South Africa. Cape: near Nieuwoudtville, *L. Bolus s.n.* (holotype, BOL-19182).

Endemic to the Calvinia District in the northwestern Cape, it is most common in the rocky hills east of Nieuwoudtville but is also found near Calvinia. Occurring in heavy red clay waterlogged for most of the growing season, often in standing pools. Closely related to *S. tricolor,* and with flowers having similar, though smaller markings, *S. pillansii* is easily distinguished by differences in tepal coloring (orange and blackish in *S. tricolor,* rose and reddish in *S. pillansii*), and by its weakly twisted anthers.

3. **Sparaxis elegans** (Sweet) Goldblatt, J. S. African Bot. 35: 233. 1969. *Streptanthera elegans* Sweet, Brit. Fl. Gard. ser. 1, 3: t. 209. 1827. Baker, Flora Cap. 6: 86. 1896. TYPE: figure in Brit. Fl. Gard. ser. 1, 3: t. 209.

Streptanthera cuprea Sweet, Brit. Fl. Gard. ser. 2, 2: t. 122. 1831 (Sweet, Hort. Brit. ed. 2: 501. 1830, nom. nud.). Baker, Flora Cap. 6: 86. 1896. Pole-Evans in Fl. Pl. South Africa 8: pl. 320. 1928. *Sparaxis cuprea* (Sweet) Klatt, Linnaea 35: 378. 1868. TYPE: figure in Brit. Fl. Gard. ser. 2, 2: t. 122.

Streptanthera cuprea var. *non-picta* L. Bolus, S. African Gard. 22: 276. 1932. Marais, Curtis's Bot. Mag. 177: t. 557. 1969. TYPE: South Africa. Cape: Nieuwoudtville, *Buhr s.n.* (holotype, BOL 19443).

Endemic to the Bokkeveld Plateau in the northwest Cape, extending from about Nieuwoudtville southward some 25 km; occurring in light to heavy clay soils. Easily recognized by the distinctively marked flowers, the coiled anthers twisted around the style and the unusually broad style branches. The more common form with salmon-pink flowers occurs in the Nieuwoudtville area, and the white-flowered form occurs in the south of its range, sometimes in pure stands, or mixed with the pink.

4. **Sparaxis fragrans** (Jacq.) Ker, König & Sims, Ann. Bot. 1: 225. 1804. Baker, Flora Cap. 6: 117. 1896. Goldblatt, J. S. African Bot. 35: 235. 1969. *Ixia fragrans* Jacq., Icon. Pl. Rar. 2: t. 274. 1793. TYPE: figure in Jacquin, Icon. Pl. Rar. 2: t. 274.

Ixia sordida Hornem., Hort. Hafn. Suppl. 6. 1819. TYPE: South Africa, without precise locality, *Hornemann s.n.* (holotype, C).

Gladiolus odorus Schrank, Denkschr. Königl.-Baier Bot. Ges. Regensburg 2: 206. 1822, nom. illeg. non Salisb. (1796) nec *Gladiolus fragrans* Jacq. (1797). Type as for *Ixia fragrans* Jacq.

Endemic to the Caledon District in the southwestern Cape, extending from Botrivier and Villiersdorp in the west to the east end of the Caledon Swartberg in the east; occurring on clay flats and slopes, usually waterlogged in the winter months. Distinguished by the small yellow to buff, unpleasantly scented flowers with symmetrically disposed stamens and narrowly acute leaves. Closely related to *S. maculosa* (below) which has similar fringed to serrate bract margins.

5. **Sparaxis maculosa** Goldblatt, sp. nov. TYPE: South Africa. Cape: farm Stettyn, between Worcester and Villiersdorp, *Perry & Manning 3603* (holotype, NBC; isotypes, K, MO, PRE). Figure 1A.

Plantae 10–20(–30) mm altae, cormo globoso ca. 15. cm diam., foliis 7–9, lanceolatis, 9–12 mm latis, spica 1–2(–3)-flora, bracteis scariosis laceratis cuspidatis, floribus actinomorphis stellatis, flavis in medio atromarroninis, filamentis erectis, antheris ascendentibus 9.5–11 mm longis, ramis stylorum inter antheris recurventibus.

Plants 10–20(–30) cm high. *Corm* globose, ca. 1.5 cm diam., tunics of fine, pale, closely matted fibers. *Foliage leaves* 7–9, all ± basal, about 2/3 as long as the spikes, the upper longest, lanceolate(–oblong), 9–12 mm wide, abruptly expanded adaxially above the sheath, obtuse, obliquely apiculate. *Stem* nearly erect, flexed above the first flower, leafless above the ground, simple or with 1–2 branches produced from below ground level. *Spike* 1–2(–3)-flowered, weakly flexuose; *bracts* scarious, translucent with light brown streaks toward the margins, the outer 3-cuspidate, the inner 2-cuspidate, both lacerate, and the edges lightly and irregularly serrate, 2–2.5 mm long, the cusps slightly exceeding the rest of the bract. *Flowers* actinomorphic, stellate, bright yellow, the tepals each with a dark maroon heart-shaped mark with a central yellow streak in the lower third; *perianth tube* funnel-shaped, 6–7 mm long, the lower part ca. 2.5 mm long; *tepals* ± oblong, 27–35 mm long, 8–10 mm wide. *Filaments* 6–7 mm long, erect, contiguous around the style; *anthers* linear, 9.5–11 mm long, pale yellow. *Ovary* globose, ca. 2.5 mm long, *style* filiform, dividing opposite the lower third of the anthers, branches 4.5–5 mm long, arching between the upper anthers. *Capsules* and *seeds* unknown. *Chromosome number* unknown.

Discovered in 1988, *Sparaxis maculosa* is known only from the farm Stettyn, north of Villiersdorp, in the Worcester valley. It grows on clay soils in seasonally waterlogged conditions and blooms in September. It is closely related to *S. fragrans*, and the basic form of their actinomorphic flowers is identical. Their bracts are also similar, being long-cuspidate and irregularly lacerate with the edges lightly and irregularly serrate (or somewhat fringed), a feature that alone makes it possible to identify the two species.

As circumscribed by Goldblatt (1969), *Sparaxis fragrans* includes slender plants with linear to narrowly lanceolate (or falcate), acute leaves 2–8 mm wide and a spike of 1–3(–5) scented, pale yellow to buff flowers. The tepals are uniformly narrow, the stamens symmetrically disposed with the filaments contiguous and surrounding the lower part of the style, and the anthers divergent. The style branches are relatively long and curve outwards over and between the anthers. Occasionally the flowers have a small single or paired dark mark at the base of each tepal, while the outer or both whorls of tepals may be flushed with purple on the reverse. Unlike *S. fragrans*, the leaves of *S. maculosa* are short, oblong to lanceolate, and obtuse and obliquely apiculate, and the stems have one or rarely two flowers, which are larger than any known in *S. fragrans*, although the perianth tube is about the same length in both. In *S. maculosa* the clear, bright yellow tepals each have a large heart-shaped, dark maroon mark in the lower third.

The single known population is relatively small but quite uniform for these characters. The question arises whether it is simply a divergent population of *S. fragrans*, or whether it is sufficiently distinct to merit taxonomic recognition. Comparison with variation patterns among taxa within *Sparaxis* suggests that the differences in the leaves alone would merit taxonomic separation at subspecific rank. Less pronounced leaf differences exist in *S. grandiflora* between subspecies *grandiflora* and subspecies *violacea*, which are also separated by small differences in tepal shape (Goldblatt, 1969, in press). The substantial leaf and floral differences including tepal width, length, and patterning, style arm length, and level of division relative to the anthers make it seem preferable to accord the Stettyn population recognition at the species rank. The distinction in leaf shape, tepal size, and relative proportion of other floral characters are absolute. There is no overlap in any floral or leaf characters. Additional exploration in suitable sites in the southern Worcester valley may yield further populations that render this decision liable to revision, but until then specific rank for the population seems preferable.

6. **Sparaxis grandiflora** (Delaroche) Ker, König & Sims Ann. Bot. 1: 225. 1804 (Sept.–Nov.) & Curtis's Bot. Mag. 20: t. 779. 1804 (Oct.). Baker, Flora Cap. 6: 116. 1896. G. Lewis, Fl. Cape Penins. 245. 1950, in part including *S. bulbifera*. Goldblatt, J. S. African Bot. 35: 239. 1969. *Ixia grandiflora* Delaroche, Descr. Pl. Nov. 23. 1766. Ker, Curtis's Bot. Mag. 15: t. 541. 1801. TYPE: South Africa. Cape: near Tulbagh Road Station, *Goldblatt 303* (neotype, designated by Goldblatt (1969), BOL; isoneotype, MO).

Ixia uniflora L., Mant. 27. 1770. TYPE: without precise locality, Herb. Linnaeus 58/19 (holotype, LINN).

Widespread in the southwestern Cape from Clanwilliam in the northwest to Breadasdorp in the southeast, occurring on heavy clay soils, often waterlogged in the winter; flowering August to September. The species is variable, and four allopatric subspecies were recognized by Goldblatt (1969). Although finely drawn, each seems to represent a separate race of the species, geographically isolated from the others by mountain and soil barriers. The subspecies will be fully treated in the *Flora of Southern Africa* treatment (Goldblatt, in press), which will include the extensive and complex synonymy, key, and descriptions.

Subspecies *grandiflora*, with plum-colored flowers, is restricted to the Tulbagh valley; subspecies *fimbriata*, with cream flowers, occurs along the western Cape coastal plain; subspecies *violacea*, which has either purple or white flowers, in the Caledon district, east of the Houw Hoek Mountains; and subspecies *acutiloba*, with yellow (rarely violet) flowers, occurs to the north, in the Olifants River valley.

7. **Sparaxis bulbifera** (L.) Ker, König & Sims, Ann. Bot. 1: 225. 1804. Baker, Flora Cap. 6: 116. 1896, in part excl. *S. grandiflora* subsp. *violacea* as variety B, *violacea*. Goldblatt, J. S. African Bot. 35: 236. 1969. *Ixia bulbiflera* L., Amoen. Acad. 300. 1756. *Belamcanda bulbifera* (L.) Moench (as *Belemcanda*), Suppl. Meth. 214. 1802. TYPE: without precise locality, Herb. Linnaeus 58/16 (neotype, designated by Goldblatt (1969), LINN). Figure 1B.

Ixia anemonaeflora sensu DC. in Redouté, Liliac. 2: t. 85. ca. 1804, non Jacq. (1793) (= *Ixia campanulata* Houtt.).

Sparaxis albiflora Ecklon, Topogr. Verz. 28. 1827. TYPE: cited as *Zeyher s.n.* (isotype, SAM) by Goldblatt (1969), but uncertain.

Widespread in the southwestern Cape, extending from Darling in the west to Bredasdorp in the east, occurring on flats and lower slopes of hills and mountains, and mostly in sandy ground, waterlogged in winter, occasionally on wet clay soils. Often confused with white-flowered forms of *Sparaxis grandiflora* and sometimes distinguished only with difficulty in early flower by its taller stature and preference for wet, sandy habitats; identification is easier after the aerial branch and small axillary cormlets develop.

SECTION 2. *SYNNOTIA*

Sparaxis sect. **Synnotia** (Sweet) Goldblatt, Contr. Bolus Herb. 14: 57 (1991). *Synnotia* Sweet, Brit. Fl. Gard. 2: t. 150. 1826 (as *Synnetia*), corr. *Synnotia* by Sweet in Hort. Brit. ed. 2: 501. 1827. TYPE SPECIES: *S. variegata* Sweet (= *Sparaxis variegata* (Sweet) Goldblatt subsp. *variegata*).

8. **Sparaxis parviflora** (G. Lewis) Goldblatt, comb. nov. Basionym: *Synnotia parviflora* G. Lewis, Ann. S. African Mus. 40: 140–142. 1956. TYPE: South Africa. Cape: between Darling and Mamre, *Lewis 3556* (holotype, SAM 65637; isotype, K).

Restricted to the coastal plain between Cape Town and Saldanha Bay and occurring in sandy, granite-derived soils, often in rock outcrops, where it flowers fairly early in the season, beginning in mid-August. Easily recognized by its tiny cream and pale yellow flowers, the smallest in the genus, and the finely fibrous corm tunics, *Sparaxis parviflora* is a strongly autogamous species. The seeds are the largest in the genus.

A form of *S. villosa* with unusually small flowers can be distinguished from *S. parviflora* by its thickened and clawed corm tunics and flowers with the upper tepals flushed with purple.

9. **Sparaxis galeata** Ker, König & Sims, Ann. Bot. 1: 225–226. 1804, as nom. nov. pro *Gladiolus galeatus* Jacq., Icones Pl. Rar. 2: t. 258. 1794 et Coll. Bot. 4: 167. 1792 (as 1790), nom. illeg. non *G. galeatus* Burman f. 1768 (= *Gladiolus alatus* L.). *Synnotia galeata* (Ker) Sweet, Hort. Brit. ed. 1, 398. 1827. Pole Evans, Fl. Pl. Africa 5: pl. 162. 1925 (as *Synnotia villosa*). Lewis, Ann. S. African Mus. 40: 143–146. 1956. *Anactorion galeatum* Raf., Fl. Telluriana 4: 34. 1838 (as 1836). TYPE: illustration in Jacq., Icones Pl. Rar. 2: t. 258.

Restricted to the lower Olifants River valley more or less between Clanwilliam and the foot of the Bokkeveld (Nieuwoudtville) Escarpment, *Sparaxis galeata* occurs on dry, arid, stony clay flats and gentle slopes. Unlike most species of *Sparaxis*, *S. galeata* is self-incompatible and it sets few, if any, seeds unless cross-pollinated. Seed set via deliberate or accidental selfing is infrequent. The unusually small capsules, 5–7 mm long, contain only 2–3(–4) seeds per locule. In addition to the capsules, it is easily distinguished by the corm tunics that accumulate in a dense mass and extend upwards to ground level in a neck, a character shared in *Sparaxis* only with *S. roxburghii*. The large, brightly colored and intensely fragrant, short-tubed flowers bloom from early August to mid-September.

10. Sparaxis roxburghii (Baker) Goldblatt, comb. nov. Basionym: *Synnotia bicolor* var. *roxburghii* Baker, Handbk. Irid. 198. 1892; Flora Cap. 6: 135. 1896. *Synnotia roxburghii* (Baker) G. Lewis, Ann. S. African Mus. 40: 146–147. 1956. TYPE: South Africa. Cape: 15 mi. N of Citrusdal, *Lewis 5207* (neotype, here designated, NBG; isoneotype, MO) (*Roxburgh s.n.*; the original type, without precise locality, has not been located).

Except for the type, from an unknown source, *Sparaxis roxburghii* has apparently been recorded from a single locality, a shale ridge near Alpha in the Olifants River valley between Citrusdal and Clanwilliam, flowering from late August to mid-September. It is rare and has not been collected for over 30 years. The species must be regarded as seriously endangered until its status can be assessed by on-site investigation. Its fine corm tunics that form a neck around the base and erect to reflexed, rather than hooded, upper tepal suggest that *S. roxburghii* is most closely related to *S. galeata*, but it can be distinguished immediately by its long perianth tube and differently colored and proportioned flower. Capsules and seeds of *S. roxburghii* are unknown.

11. Sparaxis villosa (Burman f.) Goldblatt, comb. nov. Basionym: *Gladiolus villosus* Burman f., Flora Cap. Prod. 2. 1768. *Synnotia villosa* (Burman f.) N. E. Br. Kew Bull. 133. 1929. Lewis, Ann. S. African Mus. 40: 142–143. 1956. TYPE: South Africa. Cape: without precise locality, illustration in Breyne, Prodr. Fasc. Rar. Pl., Icones 22: t. 8 f. 2. 1739 (lectotype effectively designated by Brown, 1929). Figure 2A.

Gladiolus bicolor Thunb., Diss. de Gladiolo no. 16, t. 2, f. 1. 1784. Jacquin, Ic. Pl. Rar. 2: t. 240. 1794. *Ixia bicolor* (Thunb.) Ker, Bot. Mag. 15: t. 548. 1802, nom. illeg. superfl. pro *Gladiolus villosus* Burman f. *Sparaxis bicolor* (Thunb.) Ker, König & Sims, Ann. Bot. 1: 225. 1805. *Synnotia bicolor* (Thunb.) Sweet, Hort. Brit. ed. 1: 398. 1827. Baker, Flora Cap. 6: 134–135. 1896, excl. syn. *Gladiolus galeatus* & var. *roxburghii*. *Anactorion bicolor* (Thunb.) Raf., Fl. Telluriana 4: 34. 1838 (as 1836). TYPE: South Africa. Cape: Groene Kloof, *Thunberg s.n.* (holotype, UPS).

(Figure 162 in Fl. Pl. Africa 5. 1925, identified as *Synnotia bicolor*, is *Sparaxis galeata*.)

The most widespread member of section *Synnotia*, *S. villosa* extends from the Cape Peninsula northward along the west coast and through the Tulbagh and Olifants River valleys as far north as Citrusdal. It occurs in renosterveld on heavy clay and granite-derived soils, often in rocky sites but also under low shrubs where it blooms more erratically than plants in open habitats. It flowers from late August to the end of September.

A small-flowered form in the Saldanha district can be confused with *S. parviflora*, but that species has corm tunics of fine-netted fibers unlike the coarse fibers with their clawlike thickenings characteristic of *S. villosa*.

12. Sparaxis caryophyllacea Goldblatt, sp. nov. TYPE: South Africa. Cape: middle slopes of the Nardouw Mountains, north of Clanwilliam, *Goldblatt 3851* (holotype, NBG; isotypes, K, MO, PRE). Figure 2B.

Plantae 12–30 cm altae, cormo 13–18 cm diam, spica 2–4-flora, floribus luteis, tepalo superiore violascente, faucibus atromaculatis, tubo perianthii ca. 20 mm longo, tepalo superiore ca. 20 mm longo erecto-arcuato, antheris ca. 4.5 mm longis.

Plants 12–30 cm high. *Corm* 13–18 cm diam., tunics of hard, coarse fibers oriented vertically, usually thickened below into clawlike ribs. *Foliage leaves* 5–7, basal except the upper 1–2, these inserted in the mid part of the stem, broadly lanceolate, 10–15 mm wide, usually obtuse, apiculate, sometimes obliquely so. *Stem* simple or with 1–2 branches produced in the axils of cauline leaves, usually inclined and slightly flexed above the leaves. *Spike* 2–4-flowered, straight or barely flexuose, ± secund; *outer bracts* pale below with whitish veins, becoming feathered light brown above, 12–14 mm long, lacerate, usually with a prominent central cusp, inner bracts similar, usually 2-cusped. *Flower* pale yellow with the upper tepal shading to violet in the upper half, the upper lateral tepals cream above the base, and the lower tepals deep yellow, fading to cream at the apices, the throat yellow with dark streaks, sweetly carnation-scented; *perianth tube* funnel-shaped, the upper part curving outward, ca. 20 mm long; *tepals* unequal, the upper largest and erect to slightly hooded, ca. 20 mm long, the upper laterals 16 mm long, directed forward, the lower tepals united for 3 mm, ± horizontal proximally, ca. 12 mm long, distally flexed downward and channeled. *Filaments* unilateral and arcuate, whitish, ca. 12 mm long; *anthers* white, ca. 4.5 mm long, only the upper parts exserted from the mouth of the tube; pollen cream. *Ovary* ca. 3.5 mm long, ovoid-trigonous; *style* arched behind the filaments, white, dividing just below the apices of the anthers, branches diverging and recurved in the upper half, spread above the anthers, conduplicate below, becoming narrowly channeled toward the upper third and the margins sparsely ciliate in the wider upper half. *Capsule* rotund, 10–11 mm long, 6–7 mm at the widest; *seeds* 1.8–2.2 mm diam., middle brown, usually 10 per locule. *Chromosome number* $2n = 20$.

Apparently very localized, *Sparaxis caryophyllacea* is known only from the western slopes of the Nardouw Mountains in the Olifants River valley between Bulshoek and the confluence of the Doorn River near Trawal where it was first collected in 1976. It grows in stony clay, below the contact line with the lowermost band of Table Mountain Sandstone that caps the range. The large flowers are produced from early August to mid-September and are sweetly scented. *Sparaxis caryophyllacea* is self-compatible and sets full capsules, containing ca. 30 seeds, when hand-pollinated with its own pollen, and is sometimes autogamous in the greenhouse, presumably when the stigmatic surfaces of styles of wilting flowers come into contact with pollen. In nature the species is probably outcrossing and pollinated by bees.

The flowers most closely resemble those of *Sparaxis villosa* (Fig. 2A), and it is to this species that *S. caryophyllacea* is probably most closely related. It can be readily distinguished by size, the upper tepals ca. 20 mm long compared with 12–16 mm in *S. villosa*. In addition the perianth is conspicuously striped with black in the throat and is strongly carnation-scented. Another diagnostic feature is the red speckling on the sheaths of the lower leaves. This character is also present in *S. galeata*, presumably due to convergence, for the two do not seem immediately related. *Sparaxis caryophyllacea* would make a fine container or rock garden subject. It is as easy to grow as the *Sparaxis* hybrids available in the horticultural trade.

13. **Sparaxis variegata** (Sweet) Goldblatt, comb. nov. Basionym: *Synnotia variegata* Sweet, Brit. Fl. Gard. 2: t. 150. 1826. Baker, Flora Cap. 6: 135. 1896. Lewis, Ann. S. African Mus. 40: 147–149. 1956. TYPE: illustration in Brit. Fl. Gard. 2: t. 150. Figure 3.

A relatively common species of the western Cape interior, *S. variegata* extends from the upper Olifants River valley through the Cedarberg to the Nieuwoudtville escarpment, occurring on sandstone-derived soils or in sandstone outcrops; flowering mid-August through September. It stands out because of its corms with coarsely fibrous tunics and flowers with a long perianth tube with a strong geniculate bend at the apex of the slender, cylindric part of the tube (Fig. 3).

Lewis's (1956) treatment of this species as comprising two infraspecific taxa is followed here. She treated *Synnotia metelerkampiae* as a variety of *S. variegata*, but I prefer subspecies rank because the two taxa are for the most part easily separated, and they appear biologically as well as morphologically distinct. Subspecies *variegata* has larger, more brightly colored flowers and smaller capsules with fewer, large seeds and is self-incompatible, whereas subspecies *metelerkampiae* has smaller, less brightly colored flowers and larger capsules with numerous fairly small seeds and is autogamous. In this latter taxon, the style divides opposite the anthers, and the stigmatic surfaces of the rather short style branches are in contact with the pollen throughout anthesis. In subspecies *variegata* the style branches are generally longer and held above the anthers.

1a. Flowers with upper tepal 25–30 mm long; anthers 5–7 mm long; style at least as long as or exceeding the anthers, and style branches 4–7 mm long spreading above the anthers 13a. subsp. *variegata*
1b. Flowers with upper tepal 14–17 mm long; anthers 3–4 mm long; style not exceeding the anthers, and style branches 2–3 mm long and tangled in the anthers 13b. subsp. *metelerkampiae*

13a. Subspecies variegata

Sparaxis wattii Harvey, Gen. S. African Pl. ed. 1: 33. 1838. TYPE: South Africa. Cape: without precise locality, *Watt s.n.* (holotype, TCD; isotypes, GH, K). Figure 3A.

Plants 10–18(–30) cm high. *Spike* 3–8-flowered, the branches always with fewer flowers; *bracts* 20–25 mm long. *Flowers* either predominantly purple with the throat and bases of the lower tepals yellow or predominantly yellow with the upper tepals and the tips of the lower tepals becoming purple; *perianth tube* with the cylindric part 30–32 mm long, the upper part ca. 12 mm long, slightly inflated, ca. 12 mm wide at the mouth; *tepals* with the upper 25–30 mm long, 16–18 mm at the widest, upper laterals ca. 20 mm long, ca. 10 mm wide, the lower tepals united for 5–7 mm more than the upper, ca. 12 mm long. *Filaments* ca. 20 mm long; *anthers* 6–7 long, whitish with purple on the angles. Style dividing near the apex of the anthers, the branches 4–5 mm long, usually arching above the anthers. *Capsules* 9–10 mm long, 5–6 mm diam.; *seeds* ca. 2 mm diam., brown, 5–6 per locule.

The large flowers have partly to predominantly yellow flowers. The tepals are at least tipped with violet and sometimes are predominantly violet with relatively little yellow coloration (the types of both *S. variegata* and the synonym *S. wattii* correspond to the latter). Perianth color, the larger size of the tepals and anthers, and a style that divides near the anther apices distinguish subspecies *variegata* from subspecies *metelerkampiae*. The longer style with the branches arched above the anthers makes self-pollination unlikely, but the subspecies is genetically self-incompatible. The relatively small capsules contain 5–6 large seeds per locule. Subspecies *variegata* is centered in the lower Olifants River valley between Clanwilliam and Bulshoek, and occurs in sandstone rocks, sometimes in the courses of temporary streams.

13b. Subspecies metelerkampiae (L. Bolus) Goldblatt, comb. et stat nov. Basionym: *Synnotia metelerkampiae* L. Bolus, Ann. Bolus Herb. 3: 77. 1923. Pole Evans, Fl. Pl. S. Africa 3: t. 98. 1923. *Synnotia variegata* var. *metelerkampiae* (L. Bolus) G. Lewis, Ann. S. African Mus. 40: 148. 1956. TYPE: South Africa. Cape: Eendekuil, *Metelerkamp s.n.* (holotype, BOL 16039; isotypes, K, PRE). Figure 3B.

Sparaxis orchidiflora Lodd., Bot. Cab. 11: t. 1099. 1825, nom. nud.
Sparaxis luteoviolacea Ecklon, Topogr. Verz. 27. 1827. nom. nud. (*Ecklon & Zeyher 76.8*, C, E, G, GH, P).

Plants 15–30 cm high. *Spike* 2–5-flowered; *bracts* 15–18 mm long. *Flower* violet-purple with cream to yellow (rarely reddish) markings on the lower tepals; *perianth tube* with the cylindric lower part 35–40 mm long, the upper part ca. 10 mm long, 6–7 mm wide at the mouth; *tepals* unequal, the upper largest and erect with the margins incurved, 14–17 mm long, 8–10 mm wide, the upper laterals 12 mm long, ca. 5 mm wide, directed forward in the upper half, the lower tepals united for 3 mm more than the upper, ± horizontal, ca. 12 mm long, 4–5 wide, flexed downward distally. *Filaments* 10–12 mm long, purple, reaching to the top of the tube or slightly exserted; *anthers* 3–4 mm long, purple. *Style* dividing opposite the lower part of the anthers, purple, branches diverging, 2–3 mm long, extending between the anthers. *Capsule* cylindric-trilobed, 12–15 mm long, 5 mm wide; *seeds* 1.3–1.6 mm diam., 10–12 per locule, brown.

Subspecies *metelerkampiae* has largely purple flowers with the lower tepals each with a white longitudinal streak, at the center of which is a pale yellow mark (reddish in the type figure). The tepals are smaller than those of typical subspecies *variegata*, and the style branches are short and in contact with the anthers. Greenhouse studies have shown that this form is fully self-compatible and sets full capsules with 10–12 seeds per locule without deliberate self-pollination.

There is some variation in flower size and coloration in *Sparaxis variegata* and it is not always clear to which subspecies populations are best referred. Lewis (1956) assigned large-flowered plants, irrespective of perianth color, to subspecies *variegata* and smaller-flowered plants to subspecies *metelerkampiae*. Some of the variation in perianth size may be due to growing conditions, but as Lewis pointed out, the existence of these variants makes it impossible to maintain *S. metelerkampiae* as a separate species, despite the striking differences, both in morphology and reproductive biology, in the extremes. *Sparaxis variegata* needs more study in the field and laboratory.

Subspecies *metelerkampiae* is relatively widely distributed in the western Cape, extending from Eendekuil and Piekeniers Kloof north through the Olifants River valley and the adjacent valleys of the Cedarberg north to the Gifberg, and the Nieuwoudtville Escarpment. It grows in sandy and stony ground in well-drained situations.

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A REVISION OF *ATRACTANTHA* (POACEAE: BAMBUSOIDEAE: BAMBUSEAE)[1]

Emmet J. Judziewicz[2]

ABSTRACT

A revision of the South American woody bamboo genus *Atractantha* is presented, including a key to the species, and descriptions, illustrations, and distribution maps for all five recognized taxa. The Bahia (Brazil) species *A. aureolanata* and *A. cardinalis*, both with large, attenuate florets but differing in culm leaf morphology, foliage leaf blade width, and lemma indument, are newly described. Possible affinities of *Atractantha* with *Alvimia*, *Arthrostylidium*, and *Elytrostachys* are discussed.

Its pungent, needlelike florets, often arrayed in elegant, fan-shaped clusters or capitate heads, make *Atractantha* McClure (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae) one of the most easily recognizable genera of American bamboos. It is a characteristic element of the rich Bahian (Brazil) bamboo flora (Soderstrom et al., 1988). First collected in 1943 by Ricardo de Lemos Fróes (Soderstrom & Londoño, 1987), the genus was described by McClure (1973) on the basis of *A. radiata* McClure (the type species) and *A. falcata* McClure. Explorations in Bahia by C. E. Calderón and T. R. Soderstrom in the 1970s made it evident that several more taxa of this genus awaited description. Thus, Calderón & Soderstrom (1980) estimated 9–10 species for the genus; Clayton & Renvoize (1986), about 10 species; while Soderstrom & Londoño (1988) noted that there were 5–6 "additional" species. Except for the newly described, Amazonian *A. amazonica* Judziewicz & L. G. Clark (Judziewicz et al., 1991), the *Atractantha* folders in the U.S. National Herbarium, Smithsonian Institution (US) have for many years borne Soderstrom's unpublished names for six new Bahian species of *Atractantha*. An opportunity to evaluate this abundant material resulted in the decision to validate only two of these names as new species and enabled the completion of this first formal revision of the genus.

Most collections of *Atractantha* were made during the years 1972–1983 by Soderstrom, Calderón, and the Brazilian botanists acknowledged above. The first set of specimens is in the herbarium of the Centro de Pesquisas do Cacau (CEPEC), Itabuna, Brazil, where they were examined during a February 1986 visit. The ample duplicates were studied at US using classical alpha taxonomic methods before being distributed to numerous herbaria. Unless noted, all collections cited are sterile.

MORPHOLOGY AND ANATOMY

HABIT AND BRANCHING

Species of *Atractantha* are caespitose woody bamboos from sympodial rhizomes. The slender, flexible culms are scandent, vining, and are ultimately pendent from or curtaining upon trees (Figs. 6, 12). Branching and rebranching is profuse from the middle and upper nodes. Soderstrom & Londoño (1988) discussed in some detail the functional adaptations of the culm leaf sheath girdle (Figs. 2C, D, 4C, 5), promontory (Fig. 2B), and branching patterns found in climbing bamboos in general and *Alvimia* Soderstrom & Londoño in particular, and

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many of their generalizations apply to the closely related *Atractantha* as well.

CULMS

Although most are typically solid (Fig. 4B), an unusual feature in the culms of several species of *Atractantha* is the presence of small but well-developed peripheral air canals (Fig. 2A). The canals are most frequently seen in *A. aureolanata* Judziewicz but occasionally develop in *A. cardinalis* Judziewicz and *A. radiata* (*Calderón et al. 2452*) as well. Air canals are not common in New World bamboos but are known from the rhizomes and culm bases of *Arundinaria gigantea* (Walter) Muhl. (North America), as well as from throughout the culms of an undescribed species of *Rhipidocladum* McClure (Amazonian Peru; *Dillon et al. s.n.*, US). In both of these species there is a central canal in addition to the peripheral canals, and all are much larger than those found in *Atractantha*. Air canals are well developed in the roots of Old World bamboos such as *Arundinaria densifolia* Munro (Sri Lanka) and *Thamnocalamus tesselatus* (Nees) Soderstrom & R. P. Ellis (South Africa). These species, as well as *Arundinaria gigantea*, grow in wet swamps and bogs quite unlike the dry, terrestrial habitat of the Bahian species of *Atractantha*.

CULM LEAVES

The culm leaves are caducous to tardily deciduous. In several of the Bahian species (e.g., *A. aureolanata, A. cardinalis*) a prominent, dark, corky, swollen sub-basal callus is located on the abaxial surface of the sheath (Fig. 4E, F), while in *A. cardinalis* one basal margin of the sheath is auricled (Figs. 4E, 7). The blades are variable. In *A. amazonica* they are erect, triangular, persistent, and not subtended by sheath summit oral setae (Fig. 1F); in *A. radiata*, they are absent or represented by a tiny mucro (Fig. 2G); and in *A. aureolanata, A. cardinalis*, and *A. falcata* the blades are horizontal becoming reflexed, linear to narrowly lanceolate, readily deciduous, and often subtended by prominent oral setae (Figs. 2C–G, 4D). *Atractantha aureolanata* is noteworthy for its prominently flattened, basally confluent culm leaf sheath oral setae.

FOLIAGE LEAVES

The foliage leaves consist of a sheath, a small, indurate outer ligule, a membranous inner ligule, rather delicate, curling oral setae (Figs. 11C, 14B), and a linear-lanceolate to lanceolate-ovate blade. The blades are similar to those of other arthrostylidioid genera, which can often be easily recognized by the absence of a prominent midvein, and the frequent presence of a narrow, lighter or darker zone of tissue along one margin.

INFLORESCENCES

The inflorescences of the Bahian species of *Atractantha* are compound and consist of a few to numerous partial inflorescences produced from all leafy axes and sometimes at branch and culm nodes as well. Individual partial inflorescences are either loosely to densely fascicled (*A. aureolanata, A. cardinalis*, and *A. falcata*) or densely capitate (*A. radiata*). McClure (1973) interpreted the inflorescences of *A. falcata* and *A. radiata* (Figs. 11D, 15D) to be composed of iterauctant pseudospikelets that rebranch in either distichous or sympodial fashion. *Atractantha amazonica* has semelauctant inflorescences with true spikelets produced in spicate racemes.

FLORETS

Atractantha has particularly distinctive florets. Each pseudospikelet or spikelet is 1- or occasionally 2-flowered, with a large, slender, spindlelike, falcate, indurate, obscurely nerved, pungent, functional lower floret, and, if present, a tiny, rudimentary upper floret borne on an elongate, bristlelike prolongation of the rachilla. The lemma is typically rounded on the back and externally nerveless, but *A. radiata* (Fig. 15B, C, E, F) is exceptional in its raised midnerve and occasionally raised lateral nerves. Although the florets of all species normally disarticulate intact from the summit of the rachilla, in *A. aureolanata* (Fig. 3D), *A. cardinalis*, and *A. falcata* there is a small area of tissue on the back of the lemma near its base where the nerves are prominent for a short distance and separated by depressed, fragile areas of thin tissue. The floret sometimes pulls apart in this zone of weaker tissue before it disarticulates from the rachilla.

FLOWERS

The flowers of *Atractantha* consist of three relatively large, lanceolate lodicules (*A. amazonica* may lack lodicules), three stamens, and a gynoecium with one style and two hispidulous stigmas.

FRUITS

The fruit of *Atractantha* has not been described until now. Based on *Calderón et al. 2402* (*A.

TABLE 1. Comparison of *Atractantha* with putatively related genera.

Character	*Alvimia*	*Arthrostylidium*	*Atractantha*	*Elytrostachys*
Habit	Delicate, vining	Delicate, scandent or uncommonly erect, arching	Delicate, scandent	Robust, erect and arching (but not self-supporting)
Culms	Nearly solid with a small lumen	Hollow with a small lumen, uncommonly solid	Solid, or with a ring of peripheral air canals, or rarely with a small lumen	Hollow with a large lumen
Culm node promontory	Present	Present	Present	Absent
Oral setae, culm and foliage leaves	Curling, not prominent	Curling, not prominent	Curling, not prominent except on culm leaves of some species	Straight, prominent
Inflorescence	Diffuse	Spicate raceme	Diffuse, capitate, or rarely a spicate raceme	Diffuse
Pseudospikelets	Present	Absent	Present (rarely absent)	Present
Florets/spikelet	10–30	3–10	1(–2)	1(–2)
Floret texture	Membranous	Membranous	Indurate	Firmly membranous, slightly inflated
Floret shape	Elliptical, acute	Lanceolate to elliptical, acute to acuminate	Lanceolate, pungent	Elliptical, acute
Rachilla internode prolonged past last floret bearing rudimentary spikelet?	No	Yes, moderately large	No or yes, very small	No or yes, very small
Stamen number	2	3	3	6
Fruit type	Fleshy	Dry	Dry	Dry
Distribution	Brazil (Bahia)	Mexico and West Indies to Bolivia and central Brazil	Brazil (Amazonas, Bahia) and Venezuela (Amazonas)	Central America, Colombia, Venezuela, Peru, and Bolivia

cardinalis), it is a dry, narrowly fusoid, slightly dorsally compressed caryopsis with a small, basal embryo and an elongate linear hilum extending the full length of the fruit (Fig. 3K–M). The slender beak appears to represent the remnants of the summit of the ovary.

LEAF ANATOMY

The foliage leaf blade cross-sectional anatomy of *Atractantha* clearly places it within the Arthrostylidiinae (Soderstrom & Ellis, 1987). In addition to typically bambusoid features such as fusoid cells and arm cells, an anatomical slide of *A. aureolanata* (*Calderón & Pinheiro 2256*, US slide collection) exhibits arthrostylidioid characters such as the presence of intercostal sclerenchyma subjacent to both epidermises and an inconspicuous midvein with simple vasculature.

RELATIONSHIPS

Of the 11 genera of arthrostylidioid bamboos, only *Atractantha*, *Alvimia* Soderstrom & Londoño (Soderstrom & Londoño, 1988), and *Elytrostachys* McClure (McClure, 1942, 1973) have some or all species with pseudospikelets instead of true spikelets. Table 1 compares these three taxa with *Arthrostylidium* Rupr., an unspecialized and heterogeneous genus that may be the paraphyletic core group of the subtribe (Judziewicz & Clark, in press).

Arthrostylidium and *Atractantha* have similar vegetative branching patterns in which a promontory produces one to several main branches that quickly rebranch to produce numerous smaller secondary and tertiary branchlets. *Arthrostylidium* differs in producing semelauctant, spicate racemes of true spikelets, each with three to many membranous florets lacking the specialized morphology of those of *Atractantha*. *Atractantha amazonica*, with true semelauctant spikelets borne in spicate racemes, is a possible intermediate between the two genera. In their decision to describe this species in *Atractantha* rather than in *Arthrostylidium*, Judziewicz et al. (1991) chose to emphasize the distinctive and presumably uniquely derived floret morphology shared by *A. amazonica* and all Bahian species, and stressed the possibility that, by reduction, true spikelets may have evolved from pseudospikelets several times in the bamboos. Aside from its determinate inflorescences, *A. amazonica* differs from its Bahian congeners in its culms with a small, central lumen and culm leaves with triangular, erect, persistent blades. Further study could indicate that this anomalous species requires recognition as a separate genus.

Another possible relative of *Atractantha* is *Elytrostachys*. This genus is occasionally encountered in wet forests at elevations from 0 to 900 m in Central America, but is quite rare at elevations from 100 to 1,700 m in Andean South America (Fig. 9); examination of US material suggests that the two described species are not distinct and that *E. clavigera* McClure should be united with the type species *E. typica* McClure. Similarities between *Atractantha* and *Elytrostachys* include narrow, reflexed culm leaf blades, often subtended by prominent oral setae; setose, laminiferous pseudospikelet bracts; and the single "pedicellate," readily disarticulating floret, often with a setose prolongation of the rachilla internode bearing a rudimentary spikelet. *Elytrostachys* differs from *Atractantha* in its erect, arching, only semiscandent habit; more robust culms with a large central lumen; apsidate branch complements with many equal-sized branches not situated on a promontory; and the rigid and straight rather than flexible and curling oral setae.

Alvimia is clearly related to *Atractantha* (Soderstrom & Londoño, 1988). Both genera share a vining habit, similar branching morphologies, pseudospikelets, and sympatric distributions. In fact, the range of *Alvimia* lies wholly within that of *Atractantha* (Fig. 9). *Alvimia* differs from *Atractantha* most strikingly in its olive-sized, fleshy fruits, but other differences include the presence of two rather than three stamens and very elongate pseudospikelets with numerous, small, membranous florets. Each of these observed differences can be interpreted as representing derived character states in *Alvimia*, when compared with those found in *Atractantha*. As discussed under that species, *Atractantha radiata* frequently exhibits a diverse array of intriguing flowering teratologies, and in some of these the proliferated partial inflorescences produce elongate, apparently several-flowered pseudospikelets with firmly membranous (rather than indurate), distant florets slightly reminiscent of those of *Alvimia*. The available evidence does not exclude the possibility that *Alvimia* evolved from a species of *Atractantha*, perhaps even directly from *A. radiata* or a related species.

TAXONOMIC TREATMENT

Atractantha McClure, Smithsonian Contr. Bot. 9: 42. 1973. TYPE SPECIES: *A. radiata* McClure.

Small- to medium-sized, caespitose woody bamboos. Rhizomes short-necked, sympodial, pachymorph. Culms scandent to vining and pendent, slender, either solid, or with a ring of small air canals near the epidermis, or uncommonly with a small, central lumen. Midculm nodes solitary with a horizontal nodal line, initially bearing a single branch bud at the summit of a promontory, this rebranching to form secondary and tertiary branchlets. Culm leaves deciduous or persistent; sheaths clasping culm, the base attached to the culm by a dark, thickened girdle; oral setae absent to abundant; blades either absent or present; if present, then small, narrow, reflexed, and caducous to less commonly triangular, erect, and persistent. Branching intravaginal. Foliage leaves with both inner and outer ligules present, membranous; oral setae usually short, numerous, and curling; blades linear to lanceolate-ovate. Inflorescence a group of 1–several partial inflorescences, each consisting of a capitate head, a fascicled or scorpioidal cluster, or a spicate raceme, iterauctant (producing pseudospikelets) or less commonly semelauctant (producing true spikelets); if iterauctant, pseudospikelets with branching axes subtended by a glumelike bract, each bearing a prophyllate bract as the first lateral appendage, and 1–several gemmiparous bract(s) above this. Spikelets or pseudospikelets with one functional floret and occasionally a second, tiny, sterile rudiment on a filiform prolongation of the rachilla; floret with lemma narrowly lanceolate, falcate, attenuate, indurate, smooth, glabrous to pubescent, abaxially obscurely 7–15-nerved, mucronate to short-awned, basally clasping and nearly concealing the palea. Palea about as long as lemma, narrowly lanceolate, the apex acute to bifurcate, bicarinate, the margins strongly inrolled and overlapping, the keels set close together and usually concealing the prolongation of the rachilla (if present) in the dorsal sulcus. Lodicules (0–)3,

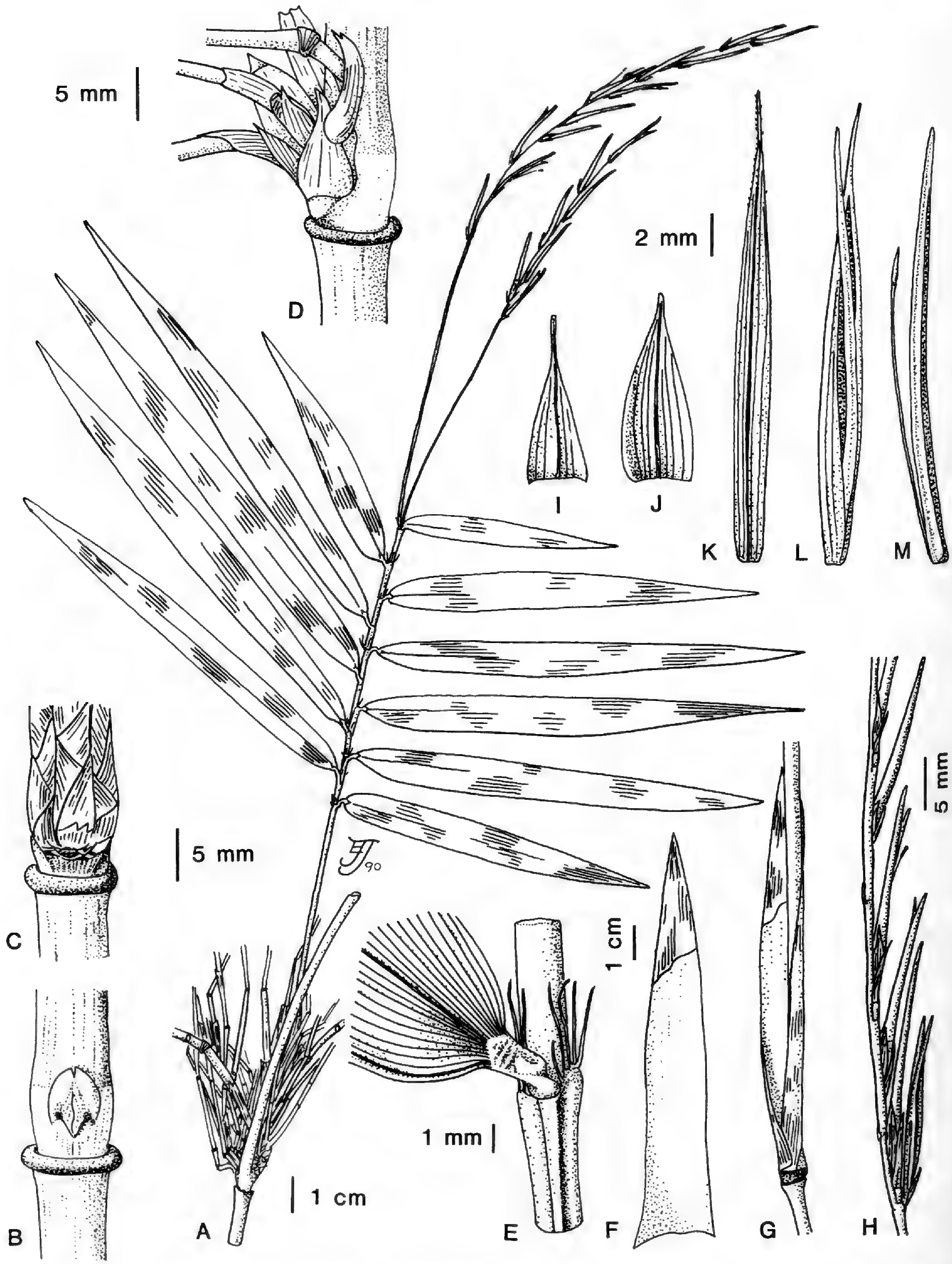

FIGURE 1. *Atractantha amazonica.*—A. Habit of fertile foliage leaf complement.—B. Culm node with bud.—C. Culm node with three main branches.—D. Branch complement, lateral view.—E. Foliage leaf, ligular area.—F. Culm leaf, spread.—G. Culm leaf, in situ.—H. Portion of raceme.—I. Lower glume.—J. Upper glume.—K. Lemma, dorsal view.—L. Floret, showing palea protruding from lemma.—M. Palea (right) and rachilla internode with rudimentary spikelet (left), lateral view. (A, E, H–M based on *Kubitzki et al. 79-222*; B–D, F, G based on *Kubitzki et al. 79-209.*)

rather large, lanceolate, acuminate, membranous to diaphanous, sometimes ciliate on the apical margins, otherwise glabrous. Androecium with stamens 3, the filaments free, the anthers linear, basifixed. Gynoecium with ovary glabrous below, glabrous to puberulent above; style 1; stigmas 2(–3), hispidulous. Fruit a fusiform caryopsis; embryo small, basal; hilum linear, extending the full length of the fruit; endosperm solid. Chromosome number unknown.

Distribution. *Atractantha* is a genus of five species known from Venezuela (Amazonas) and Brazil (Amazonas and Bahia) (Fig. 9). Calderón & Soderstrom (1980) also give northern Espírito Santo (Brazil) as part of the range but no collections have been examined from that state.

Habitat. The Bahian species of *Atractantha* grow at elevations from 0 to 650 m in several forest types but are most characteristic of the sandy "restinga" and "mata littorânea" vegetation types. Some species are locally dominant and cover the tree canopy, hanging down in festoons and curtains (Figs. 6, 12). The Amazonian *A. amazonica* is a scandent plant found along riverbanks in "igapó" forest. All Bahian species are doubtlessly threatened by forest destruction (Mori et al., 1983).

KEY TO THE SPECIES OF *ATRACTANTHA*

1a. Inflorescence a simple spicate raceme of true spikelets; culms with a small, central lumen; Amazonian Brazil and Venezuela .... 1. *Atractantha amazonica*
1b. Inflorescence a complexly branched, fascicled or capitate group of pseudospikelets; culms solid or with a ring of tiny peripheral air canals; Atlantic coastal Brazil (Bahia).
  2a. Florets 27–36 mm long, the apex of the lemma and keels of the palea 2–5 mm long, curving, attenuate, and awnlike.
    3a. Foliage leaf blades 1–2(–2.8) cm wide; florets glabrous to sparsely and minutely hispidulous; culms smooth or siliceous below the nodes; bracts subtending secondary and tertiary branchlets greenish or stramineous, rarely slightly reddish; culm leaf sheaths with finely ciliate lower margins, bases lacking auricles, and leaf-base girdles usually with prominent skirts of retrorse, golden cilia that remain attached to the culm after the leaf has fallen .... 2. *Atractantha aureolanata*
    3b. Foliage leaf blades 0.4–0.8 cm wide; florets densely pubescent; culms ± harshly asperous throughout; bracts subtending secondary and tertiary branchlets bright reddish; culm leaf sheaths with glabrous lower margins, bases with one side auricled, and glabrous leaf-base girdles .... 3. *Atractantha cardinalis*
  2b. Florets 11–17(–19) mm long, the apex of the lemma and keels of the palea acuminate-attenuate to pungent or acute, not awnlike and straight.
    4a. Inflorescences loosely to densely fascicled, the rachises sympodially inserted, with 5–25(–40) pseudospikelets; foliage leaves with sheaths pubescent and not maculate, the blades (0.4–)0.7–1.1 cm wide, linear-lanceolate, symmetrical at the base; lemmas with midnerve not raised and evident abaxially .... 4. *Atractantha falcata*
    4b. Inflorescences densely capitate, the rachises distichously inserted, with 50–250 pseudospikelets; foliage leaves with sheaths glabrous and maculate, the blades (2–)3–5 cm wide, lanceolate, asymmetrical at the base; lemmas with midnerve raised and evident abaxially .... 5. *Atractantha radiata*

1. **Atractantha amazonica** Judziewicz & L. G. Clark, Novon 1: 76–87. 1991. TYPE: Brazil. Amazonas: Rio Marié ca. 40 km above confluence with Rio Negro, right bank beyond rapids and cachoeira, clumps at edge of river in igapó forest [ca. 0°35′S, 66°40′W], ca. 100 m, 10 Sep. 1979 (fl), *K. Kubitzki, C. E. Calderón & H.-H. Poppendieck 79-222* (holotype, INPA; isotypes, B, CANB, COL, CTES, F, G, INPA, ISC, K, LE, MO, NY, P, PE, PRE, SI, SP, TULV, US—2 sheets, USCH, W, WIS). Figure 1.

Densely caespitose woody bamboo, the clumps up to 1 m diam., with up to 20 culms per clump; rhizomes not seen, presumably sympodial. Culms erect at first, later scandent and pendent, climbing in vegetation to at least 6 m; internodes hollow with a small lumen, cylindrical, glabrous, smooth to siliceous, 4–8 mm diam., straight and rather rigid; nodal line slightly annular, corky, dark; bud positioned about 2–4 mm above the nodal line. Bud at midculm node initially producing 3 subequal, widely spreading branches, these soon rebranching so that the upper portions of the culm appear to have 20–40 branches at each node. Culm leaves papery, stramineous, glabrous, deciduous, appressed to the culm; sheaths 7–9 cm long, 2 cm wide (spread width), rounded on the back, confluent with the base of the much smaller blade; inner ligule 0.2–0.3 mm long, very oblique, rimlike, glabrous; oral setae and outer ligule absent; blades 3–5 cm long, 1.4–1.6 cm wide, triangular, acute, erect, persistent. Foliage leaves in complements of

5–9; sheaths glabrous and rounded on the back below, prominently keeled at the summit, ciliolate on the margins; inner ligule ca. 0.5 mm long, membranous, brown; outer ligule rimlike, inconspicuous; oral setae 3–6 mm long, numerous, delicate, golden-brown; pseudopetioles 1.5–3 mm long, glabrous, brownish, slightly winged, sometimes deflexed; blades 10–17 cm long, 1–1.4 cm wide, linear-lanceolate, acute to obtuse above the pseudopetiole, acuminate at the apex, glabrous, the upper surface slightly scaberulous near the base, the lower surface slightly whitened, the midnerve evident only in the lower ⅓ of the blade, the margins scabrous. Inflorescences abundantly produced on peduncles 5–13 cm long, each consisting of 1(–2) spicate racemes terminal to leafy branches; individual racemes 7–15 cm long, alternately bearing 8–13 loosely overlapping, short-pedicelled spikelets, often twisted so that the spikelets appear to be secund; rachis glabrous, shiny; pedicels 0.5–1 mm long, indurate, stout, shiny. Spikelets 20–28 mm long, linear-lanceolate, coriaceous, nearly glabrous, loosely appressed to or slightly divergent from the rachis, 1- or rarely 2-flowered, the lower floret functional, if present the upper floret a tiny, long-pedicelled rudiment; glumes subequal, persistent, membranous, keeled above the middle, one or both short-awned, separated by a distinct internode ca. 1 mm long; lower glume 6–9 mm long (including awn), triangular-elliptical, rounded on the back, 5-nerved, the prominent, raised midnerve prolonged into an awn 1.5–3.5 mm long; upper glume 8–10 mm long, lanceolate-ovate, 7-nerved, the apex mucronate or prolonged into an awn up to 3 mm long; rachilla internodes separating the upper glume from the lower floret 2–3.5 mm long, persistent, slightly obcuneate at the apex. Functional floret bisexual, 18–23 mm long, 1.2–2 mm wide, slenderly lanceolate, slightly falcate, indurate, brownish, deciduous; lemma smooth, shiny, and obscurely nerved below, 7–11-nerved above with minutely ciliolate margins, the base with a squat, peglike callus ca. 0.3 mm long, the apex pungent or the midnerve abruptly prolonged into an awn up to 3 mm long; palea slightly shorter to as long as the lemma, enclosed within it or prominently protruding, linear, 4-nerved, 2-keeled, the keels ciliolate; rachilla internode (if present) slender, filiform, prolonged beyond the lower floret by 10–20 mm, tipped by a rudimentary spikelet up to 1.5 mm long. Lodicules not apparent. Androecium with stamens 3; anthers 4–10 mm long. Gynoecium with ovary 1.5–2 mm long, stipitate, glabrous; style 1; stigmas 2. Fruit not seen.

Distribution. Endemic to affluents of the Río Negro in southwestern Amazonas, Venezuela, and northwestern Amazonas, Brazil (Fig. 9).

Habitat. Occurring at elevations from 80 to 100 m in wet, lowland, seasonally flooded forests (vegetation type known as "igapó" in Brazil).

Additional specimens examined. VENEZUELA. AMAZONAS: Dept. Río Negro, middle part of Río Baria, margin of flooded forest around small laja, ca. 1°05'N, 66°25'W, 80 m, 29 June 1984 (fl), *Davidse & Miller 26846* (MO, US, VEN). BRAZIL. AMAZONAS: Rio Marié, 30–40 km above confluence with Rio Negro, near Macobeta village, climbing bamboo in forest on high river banks, in sandy soil [ca. 0°35'S, 66°40'W], ca. 100 m, 9 Sep. 1979, *Kubitzki et al. 79-209* (B, INPA, ISC, K, LE, MO, NY, P, SI, SP, TULV, US, USCH).

The generic placement of this species is only tentative; see comments in the introduction.

2. **Atractantha aureolanata** Judziewicz, sp. nov. TYPE. Brazil. Bahia: Munic. Belmonte, 31 km SW of Belmonte, 84 km E of Itapebí, low forest on white sand above creek, 30 m, 11 Apr. 1976 (fl), *T. R. Soderstrom, G. F. Russell & J. Hage 2148* (holotype, CEPEC; isotypes, B, C, CANB, COL, F, G, ISC, K, LE, MO, NY, P, PE, PRE, SGO, SI, SP, US—4 sheets, W, WIS). Figures 2A–E, 3A–G, 5, 12.

Bambusa lignosa. Culmi graciles, scandentes, viminei, usque ad 20 m longi, 5–20 mm diametro. Vaginae culmorum 6–25 × 1.5–4.5 cm, a cingulo incrassato aureofimbriato affixa; setis oralibus prominentis; laminae culmorum 3–12 × 0.4–1.2 cm, attenuatae. Ramificatio intravaginalis. Laminae foliorum (6–)9–17(–23) × 1–2(–2.8) cm. Inflorescentiae ad apices ramulorum foliosurum vel aphyllorum omnium ordinum iterauctantes, diffusae, ex pluribus pseudospiculis constantes; rachidibus omnium ramificationium et bracteatis et prophyllatis, omnis rachidis segmento terminali pro pedicello flosculi consistenti. Flosculi 27–36 × 1.7–2.3 mm, decidui, indurati, lanceolati, attenuati, glabri. Paleae apice bifurcatae, dorso sulco angustissimo instructae. Lodiculae 3, 3.5–5 mm longae, lanceolatae, acuminatae. Stamina 3, antherae 10–13 mm longae, lineares. Stylus 1, stigmata 2. Caryopsim non vidi.

Delicate, vining woody bamboo forming loose to dense clumps, erect at the base, then scandent, turning upwards and climbing into trees up to 20 m, abundantly rebranching, finally pendent in curtains. Culms 5–20 mm diam., slender, flexible, solid or often with a ring of 7–20 tiny air canals subjacent to the epidermis, circular to slightly elliptical in cross section; internodes dark green to blackish or occasionally violet, either glabrous, puberulent, or uncommonly densely pubescent, smooth to si-

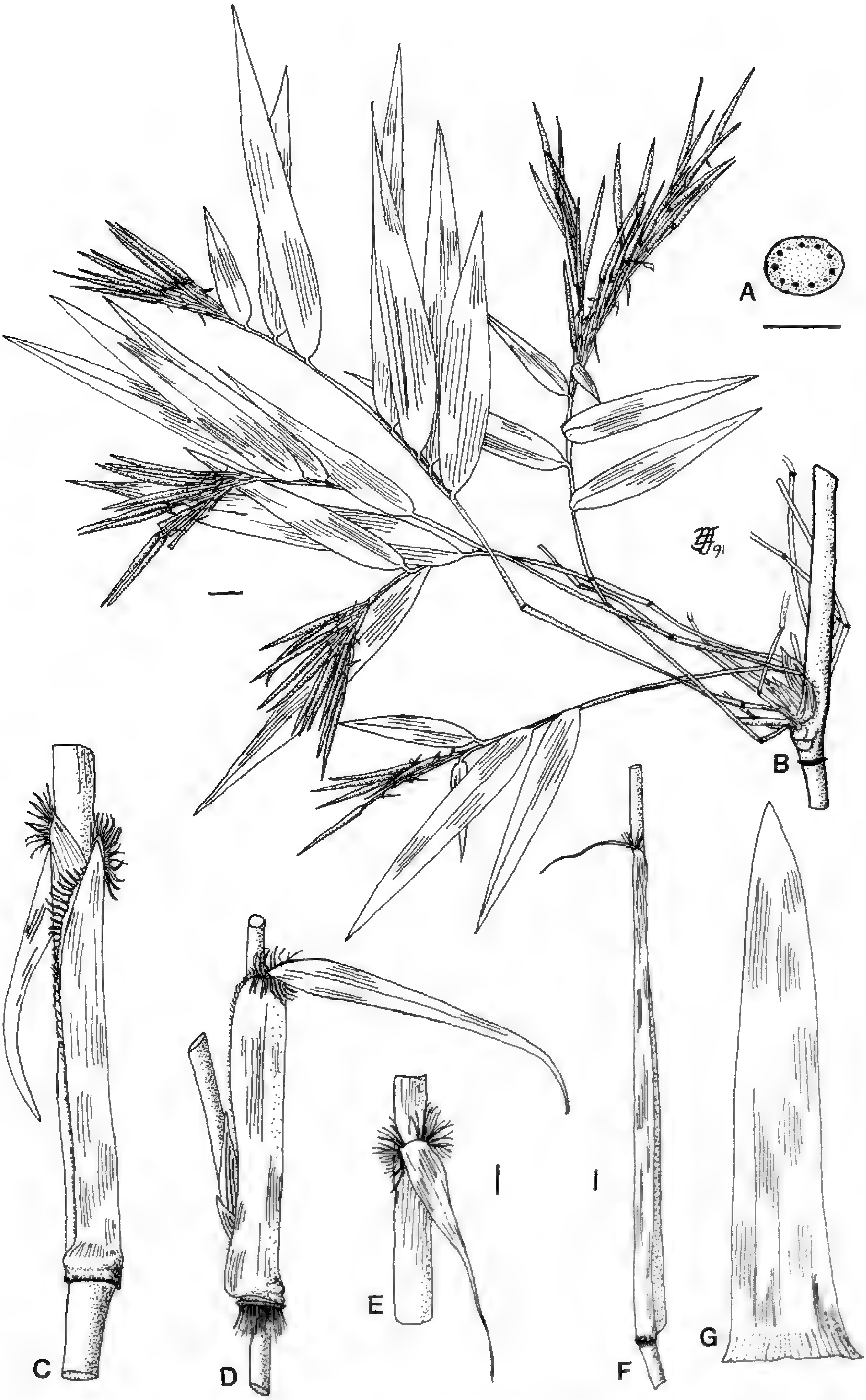

FIGURE 2. A–E. *Atractantha aureolanata.*—A. Cross section of culm showing peripheral air canals.—B. Fertile foliage leaf complement.—C–E. Culm leaves. F. *Atractantha falcata.*—F. Culm leaf in situ. G. *Atractantha radiata.*—G. Culm leaf, spread. (All scale bars = 1 cm; A, B based on *Calderón & Pinheiro 2233*; C, E based on *Calderón et al. 2377*; D based on *Calderón & Pinheiro 2256*; F based on *Calderón et al. 2408*; G based on *Calderón et al. 2442*.)

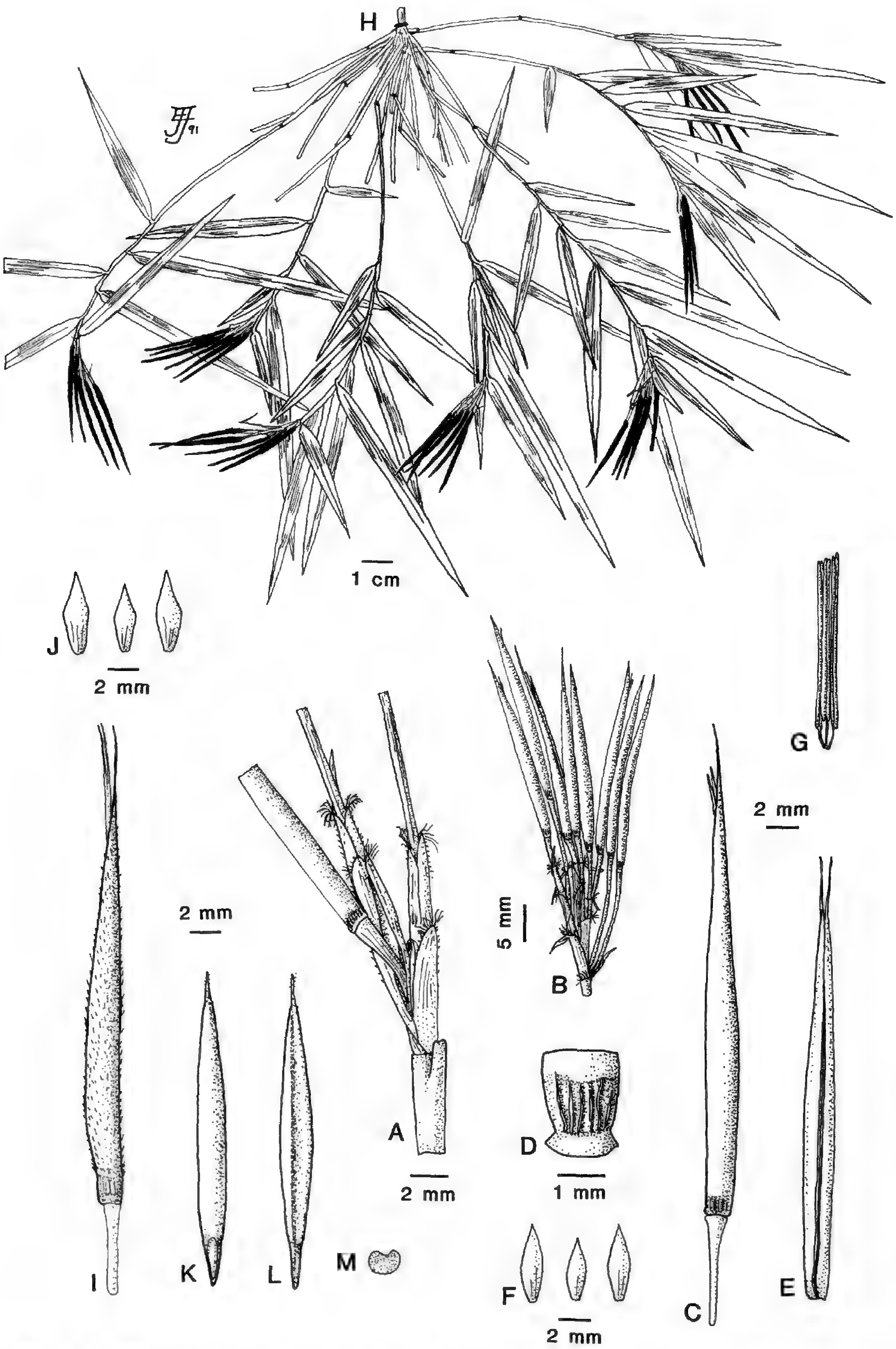

FIGURE 3. A–G. *Atractantha aureolanata.*—A. Bases of three pseudospikelets.—B. Cluster of pseudospikelets.—C. Floret.—D. Base of lemma, dorsal view.—E. Palea, dorsal view.—F. Lodicule complement.—G. Androecium. H–M. *Atractantha cardinalis.*—H. Fertile foliage leaf complement.—I. Floret.—J. Lodicule complement.—K–M. Caryopsis, dorsal, ventral, and cross-sectional views. (A–G based on *Calderón & Pinheiro 2233*; H–M based on *Calderón et al. 2402.*)

liceous (especially just below the nodes); lowest internodes 0.4–0.7 m long; nodes glabrous; bud positioned 4–10 mm above the nodal line. Culm leaves papery; sheaths 6–25 cm long, 1.5–4.5 cm wide (spread width), persistent or very tardily deciduous, clasping the culm, strongly attached by a flangelike girdle 1–2.5 mm long below the promontory, pushed away by the developing branches above, the base rarely glabrous but much more commonly with a dense band of stiff, silky, retrorse, golden, fimbriate hairs 2–7 mm long remaining on the culm after the leaf has fallen, a thickened calluslike scar also present 2–4 mm above the sheath base, the sheath margins finely ciliate, the back glabrous, adaxially shiny and stramineous, abaxially dull, stramineous to less commonly reddish and occasionally pruinose, widest about ⅔ of the way from the base, tapering to a truncate apex ca. 1 cm wide; outer ligules 0.1–0.2 mm long; auricles present, elliptical, up to 3 mm long, bearing oral setae, developed on one side of the sheath summit only; oral setae abundant, 5–15 mm long, yellowish, flattened, confluent below, present at the sheath summit and along the uppermost 1–2 cm of the sheath margins, antrorsely pubescent, curling; inner ligules 0.5–1 mm long, ciliolate; blades 3–12 cm long, 0.4–1.2 cm wide, much narrower than the sheath summit, narrowly lanceolate, obtuse at the base, attenuate at the apex, horizontal and concave becoming reflexed, caducous. Branching intravaginal, with a central dominant branch many meters long reaching into trees for support, with a cluster of 1–6 smaller secondary or tertiary branchlets at its base, these also rebranching; bracts subtending branchlets often well developed, 1–3 cm long, greenish or stramineous to less commonly reddish. Foliage leaves in complements of 5–13, not wilting quickly when cut; sheaths sparsely to densely pubescent throughout, stramineous or sometimes minutely green spotted, slightly auriculate or not at the truncate summit, auricles if present up to 2 mm long, found on only one side; outer ligules 0.2–0.4 mm long, glabrous; oral setae 2–12 mm long, delicate, whitish to yellowish, crisped apically; inner ligules 0.2–0.5 mm long, membranous; pseudopetioles 1.5–3.5 mm long, adaxially stramineous, glabrous to hispidulous, abaxially glabrous or with one margin hirsute with golden hairs; blades (6–)9–17(–23) cm long, 1–2(–2.8) cm wide, linear-lanceolate to lanceolate, obtuse to less commonly asymmetrically cuneate at the base, acute at the apex, sparingly pubescent on both surfaces near base, elsewhere hispidulous becoming glabrous, adaxially bright green and rarely with scattered pilose hairs 1–1.5 mm long, abaxially bluish green. Inflorescences terminating leafy and nearly leafless branches of all orders, iterauctant, diffuse, congested and often falcate and pendent, the branches sympodially or distichously inserted, consisting of 1–3 partial inflorescences each 3–5 cm long, each partial inflorescence consisting of 7–20 pseudospikelets. Pseudospikelets comprising one subtending bract, a tiny prophyll if present, 1–3 gemmiparous bracts (which may or may not develop into additional pseudospikelets), one functional floret, and (rarely) a setose prolongation of the rachilla internode bearing a tiny rudimentary sterile spikelet at its apex; subtending bract and gemmiparous bracts similar in morphology, 8–17 mm long, lanceolate-elliptical, clasping the rachilla, strongly 7–13-nerved, somewhat inflated, membranous, pubescent, laminiferous, at the summit bearing oral setae 1–4 mm long and a reflexed linear blade 4–8 mm long; rachilla segment between uppermost gemmiparous bract and functional floret 4–12 mm long, 0.5–1.2 mm diam., smooth, glabrous, clavate and cupulate at the apex. Functional floret 27–36 mm long, 1.7–2.3 mm wide, disarticulating from the summit of the rachilla or fragmenting near the base and leaving behind ca. 0.5 mm of the base of the floret on the rachilla; lemma narrowly lanceolate, slightly falcate, near the base on the dorsal side with a squarish patch 0.7–1 mm long with 5–9 strong nerves evidently separated by depressed areas, curving attenuate-aristate at the apex, indurate, shiny, glabrous or sparsely and minutely scabrous-hispidulous, green when young becoming olivaceous or nearly black at maturity, the nerves not evident abaxially (except in the aforementioned basal patch), adaxially finely 11–15-nerved; palea as long as or slightly longer than the lemma, the dorsal sulcus very narrow, glabrous or the keels antrorsely ciliolate, the keels bifurcate at the apex and prolonged 2–4 mm past the sinus. Rachilla internode rarely prolonged ca. 30 mm past the functional floret as a setose bristle. Lodicules lanceolate, acuminate, membranous, finely 2–4-nerved, the apical margins glabrous; anterior pair 4–5 mm long, the posterior one 3.5–4.5 mm long. Androecium with stamens pendent; anthers 10–13 mm long, linear, purplish. Gynoecium with ovary glabrous below, pubescent toward the apex; stigmas hispidulous. Fruit not seen.

Distribution. Endemic to coastal Bahia, Brazil (Fig. 10); the most widespread Bahian species of *Atractantha*, in terms of both geography and ecological amplitude.

Habitat. Occurring at elevations from 30 to

650 m, in low to tall forests or forest edges on loam or white sand ("mata littorânea"), on flat to steep slopes. The plants are sometimes dominant, forming thick masses as they climb over trees (Fig. 12).

Phenology. Apparently, entire populations flower and then die.

Additional specimens examined. BRAZIL. BAHIA: Munic. Itacaré, 10 km SW of Itacaré City, ca. 14°18′S, 39°05′W, 100 m, 19 Mar. 1972, *Calderón & Pinheiro 2180* (CEPEC, US); Munic. Wenceslau Guimarães ex Nilo Peçanha, km 104, rodovía BA-2, 14 km N of Gandú, ca. 13°40′S, 39°27′W, 200 m, 21 Apr. 1972 (fl), *Calderón & Pinheiro 2233* (CEPEC, US); Munic. Jaguaquara, Riacho de Ouro, 22 km SE of Jaguaquara city, ca. 13°38′S, 39°52′W, 625–650 m, 8 May 1972, *Calderón & Pinheiro 2256* (US); 12 Apr. 1976, *Calderón et al. 2377* (CEPEC, US); Munic. Ibirataia, 12 km NW of Ibirataia on connecting road with BR-101, 350–400 m, 3 Apr. 1976, *Calderón et al. 2357* (B, CEPEC, F, G, K, LE, MO, NY, P, SI, SP, TULV, US, USCH); Munic. Jequié, 25 km N of road Ipiaú–Jequié, on road to Apuarema–Jaguaquara, 600–650 m, 8 Apr. 1976, *Calderón et al. 2370* (CEPEC, ISC, SI, SP, TULV, US); Munic. Una, road Una–Olivença, 19 km N of Una, 50 m, 27 Apr. 1976, *Calderón et al. 2399* (B, CEPEC, ISC, K, LE, MO, NY, P, SI, SP, TULV, US, USCH); Munic. Ilhéus, road Olivença–Vila Brasil, 17.3 km SW of Olivença, then 31.2 km to right on side road Sapucaeira–Cururupe, 24 Feb. 1979, *Calderón & dos Santos 2484* (B, CEPEC, F, G, ISC, K, LE, MO, NY, P, PRE, SI, SP, TULV, US, USCH, W, WIS); Munic. Itacaré, rodovía BA-654, 6 km W of Itacaré, ca. 14°18′S, 39°02′W, ca. 60 m, 12 Apr. 1980 (fl), *Plowman et al. 10088* (CEPEC, F, US), *dos Santos et al. 3559* (CEPEC, US); Munic. Pôrto Seguro, Fazenda Carvalho, ca. 26 km W of town of Monte Pascoal, 380–460 m, 15 May 1976 (fl), *Soderstrom et al. 2211* (B, CEPEC, F, G, ISC, K, LE, MO, NY, P, SI, SP, US); Munic. Itacaré, 5 km SW of Itacaré and 25 km E of Taboquinhas, 100 m, 20 May 1976, *Soderstrom et al. 2214* (B, C, CANB, CEPEC, CHR, COL, CTES, DD, F, G, ISC, K, LE, MO, NY, P, PE, PRE, SGO, SI, SP, TULV, US, USCH, W, WIS); Munic. Una, 7 km E of São José do Macuco on road to Una, 140 m, 24 May 1976 (fl), *Soderstrom et al. 2221* (CEPEC, ISC, SI, SP, TULV, US, USCH); Munic. Ilhéus, camino de Olivença a Una, ramal para Vila Brasil, 60 m, 19 May 1985, *Zuloaga et al. 2481* (SI, US); Munic. Una, camino de Olivença a Una, km 35, 50 m, 19 May 1985, *Zuloaga et al. 2484* (SI, US).

The specific epithet, suggested by Soderstrom, refers to the golden, woolly-appearing "skirt" of retrorse cilia that develops on the culm leaf sheath base girdle and remains attached to the culm after the leaf has fallen (Figs. 2D, 5). The skirt is best developed in young shoots, and poorly developed or absent on smaller branches. A similar-appearing feature is the ring of cilia present on the culm nodes of *Arthrostylidium fimbrinodum* Judziewicz & L. G. Clark (Judziewicz & Clark, in press).

Atractantha aureolanata is most closely related to *A. cardinalis.* Besides having the largest florets of any species in the genus, both taxa also have in common culms with tiny, peripheral air canals (Fig. 2A; common in *A. aureolanata,* uncommon in *A. cardinalis*), scorpioid inflorescences, and florets with attenuate lemma apices and attenuate, bifurcate palea keels (Fig. 3C, E, I).

Included in *A. aureolanata* are three unpublished herbarium names used by Soderstrom for US material. "Longispiculata" (*Calderón & Pinheiro 2256*) differs in no discernable way from typical *A. aureolanata,* while "unaensis" (*Calderón et al. 2399*) is a sterile collection with atypically large foliage leaf blades up to 23 cm long and 2.8 cm wide and asperous culms. More problematical is "robusta," collected four times along the Itacaré to Ubaitaba road about 5–10 km SW of Itacaré: these collections are atypical in the usual absence of leaf sheath base skirts (in *Calderón & Pinheiro 2180, Plowman et al. 10088,* and *dos Santos et al. 3559*; but skirts present in *Soderstrom et al. 2148,* an ample collection), pubescent branchlet bracts, large florets 32–36 mm long, and smaller foliage leaf blades only 8–14 cm long and 1–1.6 cm wide. This series of populations tends toward *A. cardinalis* but, based on their glabrous florets, merely siliceous culm internodes, and greenish to stramineous branchlet bracts and culm leaves (reddish in *Soderstrom et al. 2148,* which does have skirts), they appear to be closer to and not well segregated from *A. aureolanata.*

3. **Atractantha cardinalis** Judziewicz, sp. nov.

TYPE: Brazil. Bahia: Munic. Una, road Una–São José, 34 km NW of Una, remains of humid forest partially cut down, with mixed, rich soil, 175 m, 22 Apr. 1976 (fl), *C. E. Calderón, T. S. dos Santos & L. B. de Oliveira 2385* (holotype, CEPEC; isotypes, ISC, K, MO, NY, P, SI, SP, TULV, US—8 sheets, USCH). Figures 3H–M, 4, 6, 7.

Bambusa lignosa. Culmi graciles, scandentes, usque ad 15 m longi, 5–13 mm diametro. Vaginae culmi 13–25 × 1.5–3.5(–4.5) cm, a cingulo incrassato glabro affixa; setis oralibus prominentis; laminae culmi 3–13 × 0.1–0.3 cm, lineares. Ramificatio intravaginalis. Laminae foliorum 6–11 × 0.4–0.8 cm. Inflorescentiae ad apices ramulorum foliosurum vel aphyllorum omnium ordinum iterauctantes, diffusae, ex pluribus pseudospiculis constantes; rachidibus omnium ramificationium et bracteatis et prophyllatis, omnis rachidis segmento terminali pro pedicello flosculi consistenti. Flosculi 29–35 × 1.8–2.3 mm, decidui, indurati, lanceolati, attenuati, pubescentes. Paleae apice bifurcatae, dorso sulco angustissimo instructae. Lodiculae 3, 4.5–5 mm longae, lanceolatae, acuminatae. Stamina non vidi. Stylus 1, stigmata 2. Caryopsis 20 × 1.8 mm, fusiforma sulcataque.

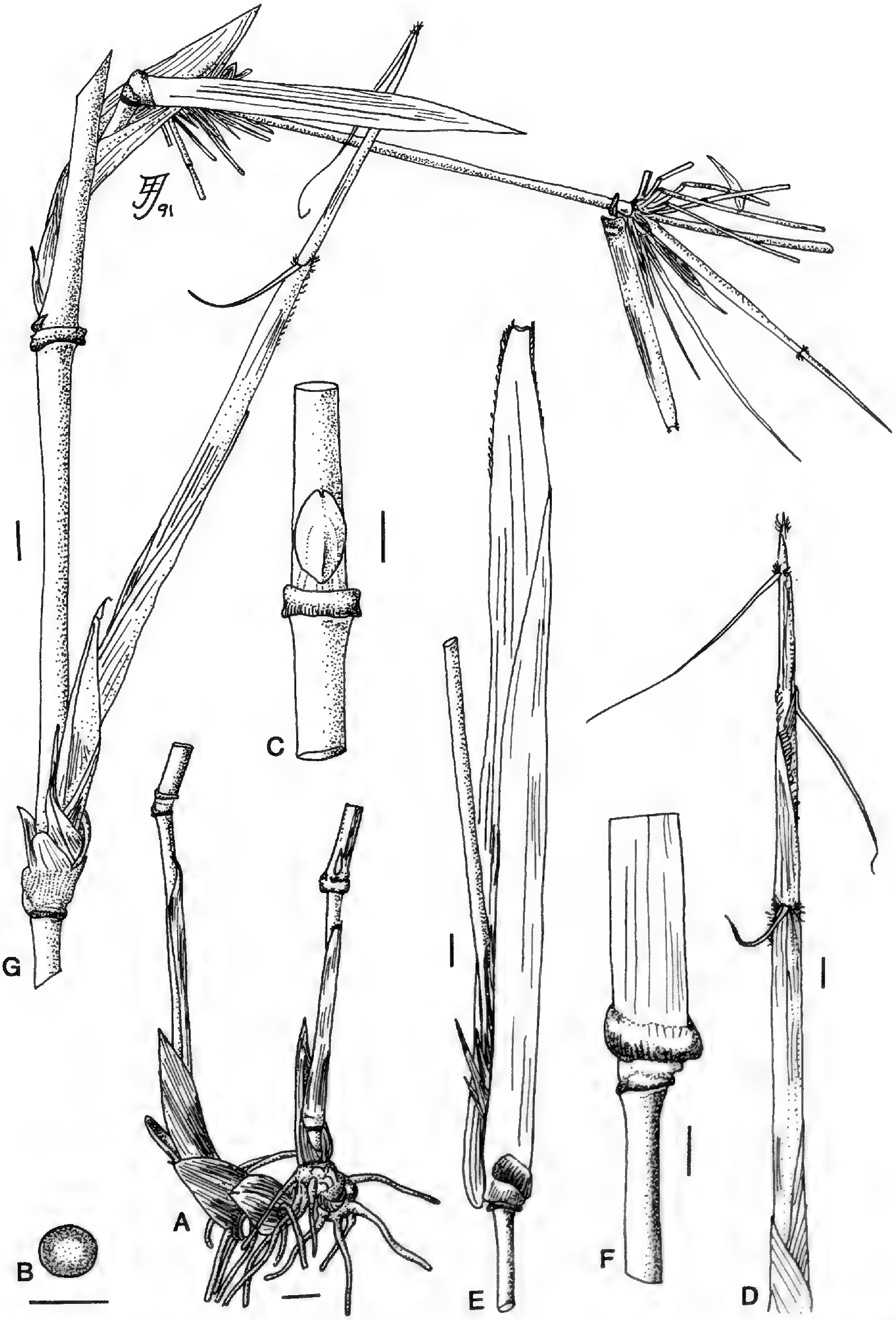

FIGURE 4. *Atractantha cardinalis.*—A. Base of plant.—B. Cross section of culm.—C. Culm node with bud.—D. Shoot with culm leaves.—E. Culm leaf in situ, the blade having fallen; note the auricled sheath base (left).—F. Base of culm leaf sheath.—G. Branching at midculm nodes. (All scale bars = 1 cm; A, B based on *Soderstrom et al. 2159*; C based on *Zuloaga et al. 2486*; D based on *Calderón et al. 2372*; E, F based on *Calderón et al. 2402*; G based on *Calderón et al. 2385*.)

Delicate, scandent woody bamboo forming loose clumps, climbing into trees up to 15 m, profusely rebranching, finally pendent. Culms 5–13 mm diam., slender, solid or occasionally with up to 10 tiny peripheral air canals, terete; internodes dark green to blackish, glabrous to puberulent (especially in upper branches), harshly retrorsely asperous or less commonly siliceous; lowest internodes 0.2–


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FIGURES 5–8. Bahian species of *Atractantha*, photographed and collected by C. E. Calderón.—5. *A. aureolanata*, culm leaf in situ. (Based on *2256*.) 6. *A. cardinalis*, habit. (Based on *2401*.) 7. *A. cardinalis*, culm leaf in situ. (Based on *2372*.) 8. *A. radiata*, plant in full flower. (Based on *2397*.)

0.5 m long, clothed in bright reddish, bladeless sheaths; nodes glabrous; bud positioned 5–10 mm above the nodal line. Culm leaves papery; sheaths 13–33 cm long, 1.5–3.5(–4.5) cm wide (spread width), persistent or very tardily deciduous, clasping the culm, strongly attached by a prominent, glabrous, flangelike girdle 1–2 mm long below the promontory, pushed away by the developing branches above, the base glabrous, one margin projecting slightly downwards by up to 1 cm as an auriculate extension, a prominent, knobby, thickened, calluslike scar present 3–8 mm above the sheath base, the sheath margins glabrous, adaxially smooth, shiny, stramineous, and glabrous, abaxially asperous, dull, reddish, and glabrous or sparsely pubescent near the margins, tapering evenly to the minutely truncate apex ca. 0.5 cm wide; outer ligules 0.1–0.2 mm long; auricles not noted; oral setae 5–10 mm long, those at the sheath summit orangish yellowish, terete, separate, those along the uppermost 3–10 cm of the sheath margins confluent basally, flattened, yellowish, curling; inner ligules ca. 1 mm long, ciliolate; blades 3–13 cm long, 0.1–1.3 cm wide, linear, attenuate, erect or horizontal and concave becoming reflexed, deciduous. Branching intravaginal, with a central dominant primary branch and a cluster of 1–5 smaller secondary or tertiary branchlets at its base, these also rebranching; bracts subtending branchlets often well developed, 1–4 cm long, strongly tinged with red or orange-yellow. Foliage leaves in complements of 5–15, wilting quickly when cut; sheaths sparsely to densely pubescent throughout or only on margins, sometimes stramineous or minutely green spotted, not auriculate at the truncate summit; outer ligules 0.2–0.3 mm long, glabrous; oral setae 3–8 mm long, delicate, yellowish, crisped apically; inner ligules 0.2–0.4 mm long, membranous; pseudopetioles 1–2 mm long, glabrous to hispidulous on both surfaces, adaxially purplish; blades 6–11 cm long, 0.4–0.8 cm wide, linear to linear-lanceolate, obtuse to cuneate at the base, acute at the apex, glabrous, adaxially dark green, abaxially light bluish green. Inflorescences terminating leafy and nearly leafless branches of all orders, iterauctant, congested and often fascicled, often pendent, the branches sympodially or distichously inserted, consisting of 1–5 partial inflorescences each 3–6 cm long, each partial inflorescence consisting of 5–13 pseudospikelets. Pseudospikelets comprising one subtending bract, an inconspicuous prophyll, 1–3 gemmiparous bracts (which may develop into additional pseudospikelets), one functional floret, and (rarely) a setose prolongation of the rachilla internode bearing a tiny rudimentary sterile spikelet at its apex; subtending bract and gemmiparous bracts similar in morphology, 7–20 mm long, lanceolate-elliptical, clasping the rachilla, strongly 7–11-nerved, somewhat inflated, membranous, pubescent, often laminiferous, bearing at the summit oral setae 1–3 mm long and a reflexed linear blade 3–6 mm long; rachilla segment between uppermost gemmiparous bract and functional floret 5–13 mm long, 0.6–1 mm diam., smooth, pubescent, slightly clavate and cupulate at the apex. Functional floret 29–35 mm long, 1.8–2.3 mm wide, densely pubescent, disarticulating from the summit of the rachilla or fragmenting near the base and leaving behind ca. 0.5 mm of the base of the floret on the rachilla; lemma narrowly lanceolate, slightly falcate, near the base on the dorsal side with a squarish patch 0.4–0.8 mm long (Fig. 10).

Habitat. Occurring at elevations from 0 to 320 m in tall forest on rich soil at inland sites, or in low coastal forests in mixed, sandy soil ("mata littorânea").

Phenology. Colonies apparently die after massive flowering.

Additional specimens examined. BRAZIL. BAHIA: Munic. Una, road Una–Olivença 7 km N of Una, ca. 15°15′S, 39°06′W, 50 m, 12 May 1972, *Calderón & Pinheiro 2264* (CEPEC, US); Munic. Jaguaquara, 16 km N of Apuarema on road Apuarema–Jaguaquara, 275 m, 10 Apr. 1976, *Calderón et al. 2372* (CEPEC, ISC, MO, SI, SP, TULV, US, USCH); Munic. Una, road Una–Olivença, 3 km N of Una, 55 m, 28 Apr. 1976, *Calderón et al. 2401* (CEPEC, ISC, MO, SI, SP, TULV, US, USCH); Munic. Una, road Una–Olivença, 5 km N of Una, 55 m, 28 Apr. 1976 (fl), *Calderón et al. 2402* (CEPEC, US); without locality, 15 Mar. 1943, *Fróes 20060* (US) [mixed with *Merostachys* sp.]; estrada de Itabuna a Una, 24 Jan. 1980, *Heringer et al. 3264* (IBGE, US); Munic. Ituberá, ca. 2 km from Ituberá on road to Gandú, Fazenda Inferno Verde, 320 m, 23 Apr. 1976, *Soderstrom et al. 2159* (B, CEPEC, F, G, ISC, K, LE, MO, NY, P, SI, SP, US); Munic. Una, 7 km E of São José do Macuco on road to Una, 140 m, 24 May 1976, *Soderstrom et al. 2222* (CEPEC, ISC, K, MO, NY, P, SI, SP, TULV, US, USCH); Munic. Canavieiras, camino de Canavieiras a Camacã, km 15, 20 m, 20 May 1985, *Zuloaga et al. 2486* (SI, US); Munic. Maraú, camino de Maraú a Ubaitaba, 15 km de Maraú, near sea level, 18 May 1985, *Zuloaga et al. 2470* (SI, US).

The bright reddish bladeless bracts that subtend the secondary branchlets and the often reddish culm leaf sheaths prompted Soderstrom to suggest the specific epithet. In contrast to its close relative *A. aureolanata*, the blades of *A. cardinalis* reportedly curl up quickly upon being cut; see further comments under the former species.

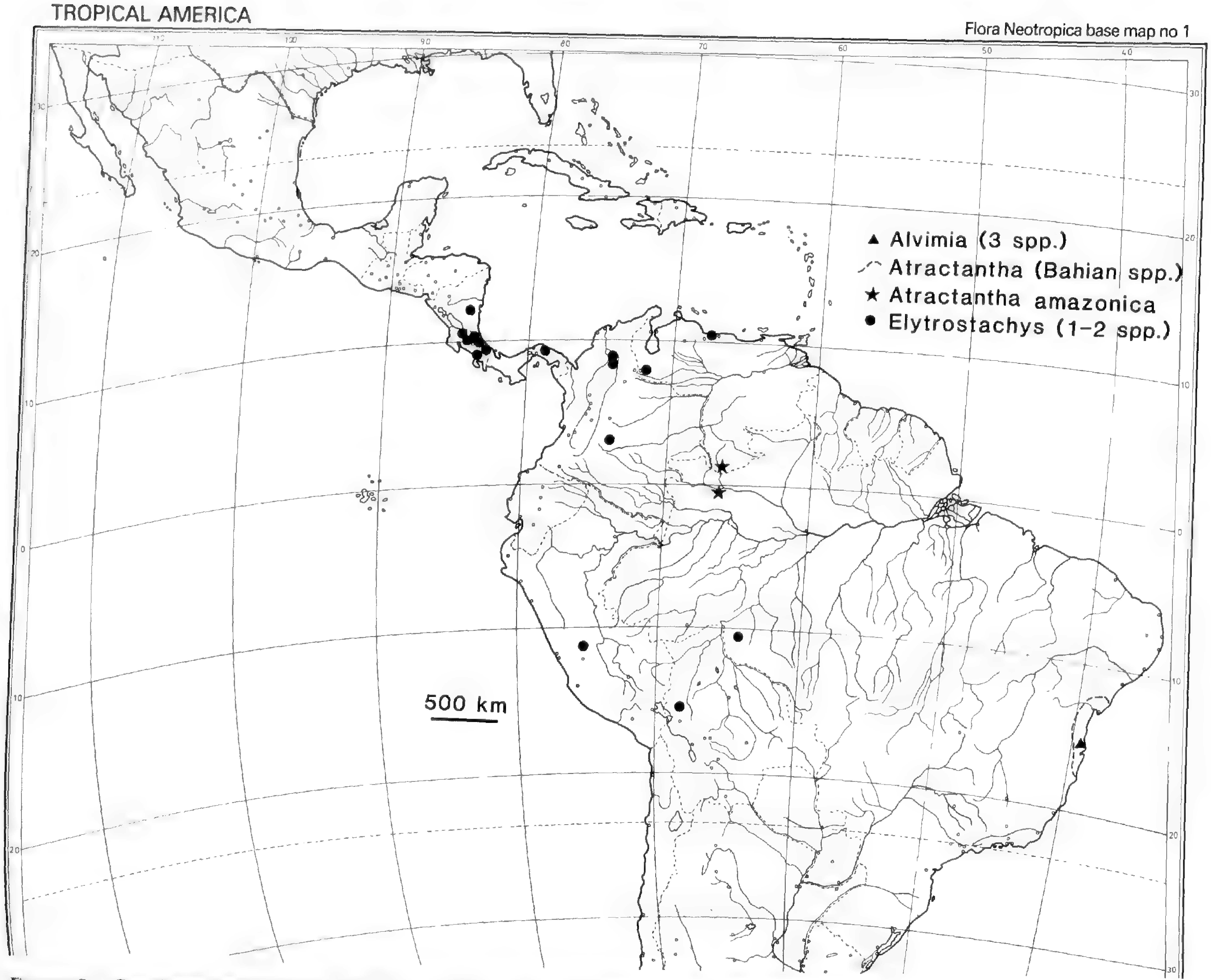


FIGURE 9. Distribution of the genera of Arthrostylidiinae that have members with pseudospikelets.

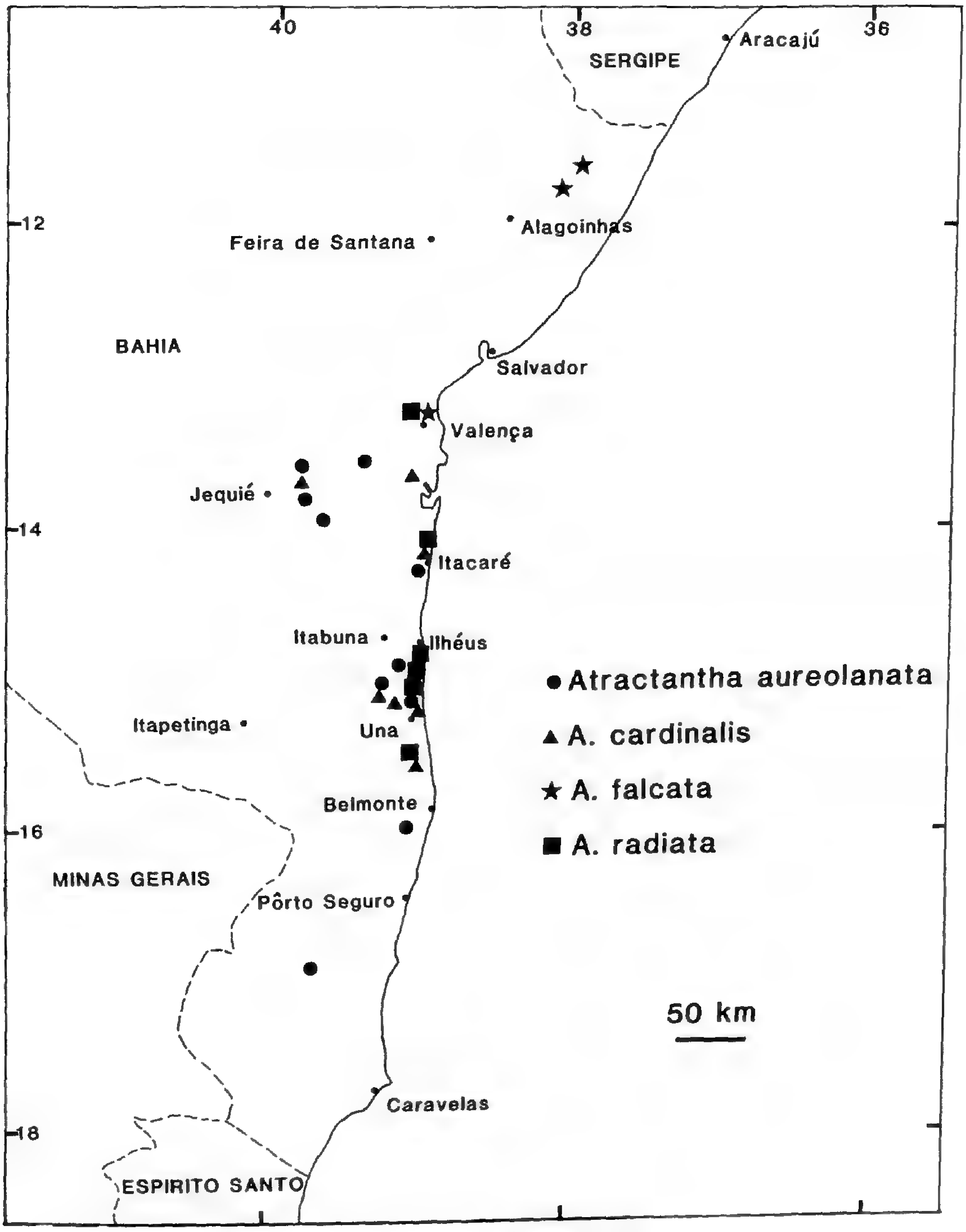
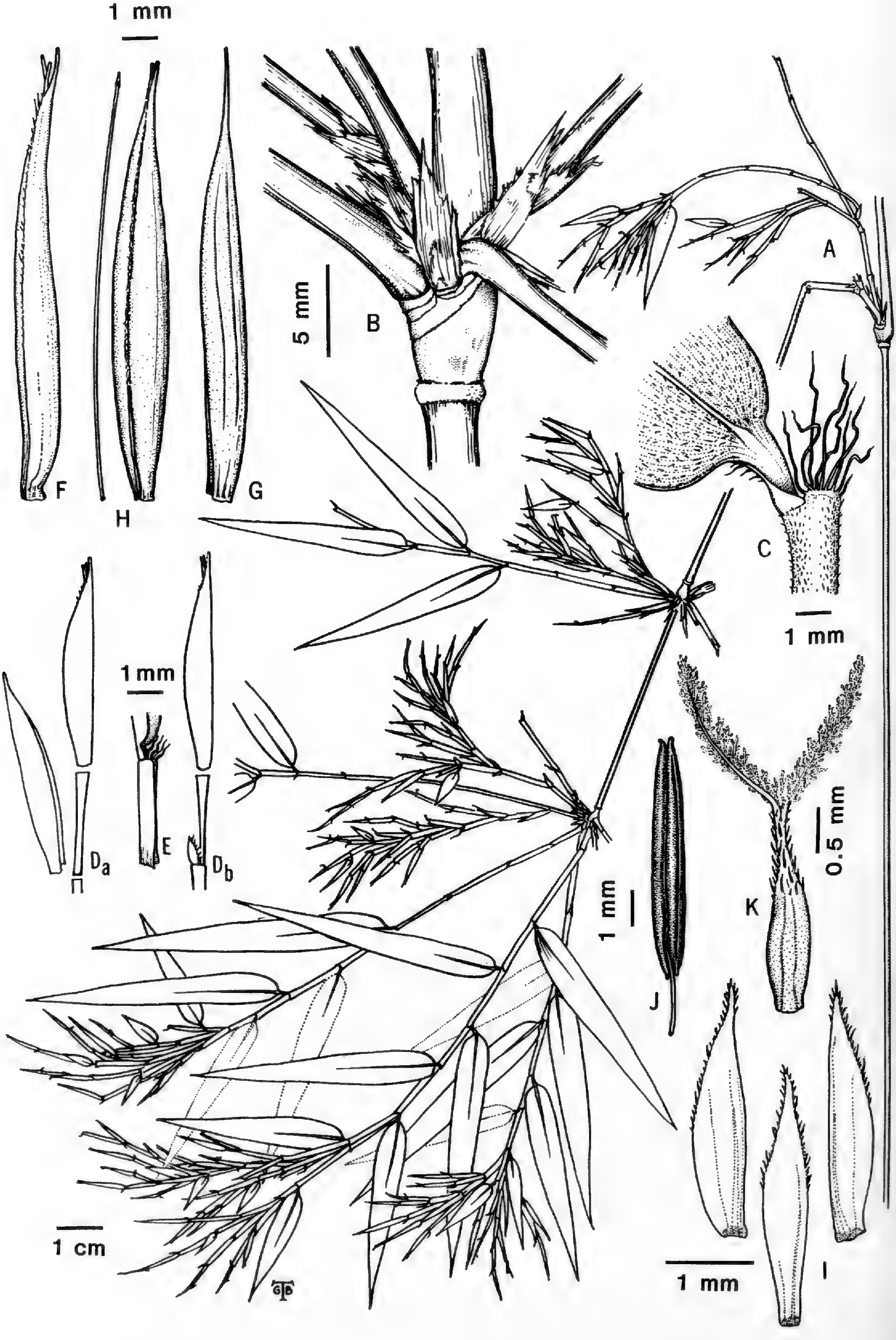


FIGURE 10. Distribution of the Bahian (Brazil) species of *Atractantha*.

4. **Atractantha falcata** McClure, Smithsonian Contr. Bot. 9: 48. 1973. TYPE. Brazil. Bahia: Esplanada, carrascal, anno 1950–1951, *G. Pinto 681* (holotype, US; isotype, CEPEC). Figures 2F, 11, 13.

Climbing woody bamboo forming loose clumps of 3–10 culms, decumbent at the base, arching, scandent, abundantly rebranching, climbing into trees up to 12 m, then pendent in festoons. Culms 5–8 mm diam., slender, solid, terete; internodes asperous and glabrous in the lower parts, smooth and glabrous to pubescent in the upper branches, yellowish; nodes glabrous; bud positioned 5–8 mm above the nodal line. Culm leaves papery; sheaths 20–35 cm long, 2–3 cm wide (spread width), clasping the culm, tapering to a truncate apex, persistent, rotting in place, strongly attached by a flange-like girdle 1.5 mm long below the promontory, pushed away by the developing branches above; outer ligules 0.1 mm long; auricles absent or weakly developed on one side of the sheath summit; oral setae 5–10(–15) mm long, straight, golden-orange, lustrous, antrorsely pubescent below, crisped apically; inner ligules not noted; blades 7–15 cm long, 2–3 mm wide, much narrower than the sheath summit, linear, reflexed, soon deciduous. Branching intravaginal, with a central dominant primary branch and 1–4 smaller secondary or tertiary branchlets at its base, these also rebranching; bracts subtending branchlets often well developed, 1–3 cm long, stramineous to reddish. Foliage leaves in


1 mm
F
H
G
5 mm
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C
1 mm
1 mm
Da
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K
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J
1 cm
I
1 mm
GD

complements of 5–15; sheaths pubescent throughout, sometimes becoming glabrous at maturity, slightly auriculate or not at the summit; outer ligules 0.1–0.3 mm long, minutely ciliolate; oral setae 1–3 mm long, delicate, white to yellow, crisped apically, fragile, easily deciduous; inner ligules 0.2–0.4 mm long, membranous, truncate; pseudopetioles 1.7–3 mm long, adaxially golden, glabrous to hispidulous, abaxially hirsute; blades (4–)6–16 cm long, (0.4–)0.7–1.1 cm wide, linear-lanceolate, obtuse and symmetrical at the base, acute at the apex, sparsely hirsute on both surfaces near base, elsewhere hispidulous becoming glabrous. Inflorescences terminating leafy and nearly leafless branches of all orders, iterauctant, congested and often falcate, sometimes appearing loosely scorpioid, the branches sympodially inserted, consisting of 1–6 partial inflorescences with each 5–25(–40) pseudospikelets. Pseudospikelets comprising one subtending bract, the rachis, one prophyll, one basal gemmiparous bract (which may or may not develop into another pseudospikelet), one functional floret, and (rarely) a setose prolongation of the rachilla internode bearing a tiny rudimentary sterile spikelet at its apex; subtending bract 5–13 mm long, lanceolate, 7–13-nerved, membranous, pubescent, often laminiferous, bearing 1–3 mm long oral setae at its summit, bearing an awn up to 3 mm long or a reflexed linear blade 3–6 mm long; prophyll 3–5 mm long, elliptical, bicarinate, pubescent; basal gemmiparous bract 4–8 mm long, lanceolate, acute, 5–7-nerved, pubescent; rachilla segment between basal gemmiparous bract and functional floret 5–15 mm long, 0.3–0.8 mm diam., smooth, glabrous, shiny, clavate and cupulate at the apex. Functional floret 12–16 mm long, 1.5–2 mm wide, disarticulating from the summit of the rachilla or fragmenting near the base and leaving behind ca. 0.5 mm of the base of the floret on the rachilla; lemma narrowly lanceolate, slightly falcate, near the base on the dorsal side with a patch 0.5–0.9 mm long with 5–9 strong nerves evidently separated by depressed areas, at the apex acuminate-attenuate to pungent, indurate, shiny, glabrous or sparsely and minutely scabrous-hispidulous, green when young becoming olivaceous or nearly black at maturity, the nerves not evident abaxially (except in the aforementioned basal patch), adaxially finely 9–13-nerved; palea as long as or slightly longer than the lemma, the sulcus very narrow, glabrous or the keels antrorsely ciliolate. Rachilla internode often prolonged 10–14 mm past the functional floret as a setose bristle. Lodicules lanceolate-elliptical, acuminate, membranous, diaphanous, weakly 1–2-nerved, the apical margins glabrous to ciliolate; anterior pair 2.7–3.5 mm long, the posterior one 2.5–3 mm long. Androecium with stamens pendent; anthers 5–6 mm long, linear, purple drying to dark brown. Gynoecium with ovary glabrous below, pubescent toward the apex; style exserted from below the stamens, the stigmas hispidulous. Fruit not seen.

Distribution. Endemic to coastal Bahia, Brazil (Fig. 10); this is the most northerly Bahian species of *Atractantha.*

Habitat. Occurring at elevations from 0 to 120 m in white sand "restinga," a vegetation type with small trees and shrubs, an abundance of epiphytes, and a groundlayer dominated by terrestrial Bromeliaceae and Orchidaceae; also found in "carrascal," a dense, relatively dry, low forest on sandy soil.

Phenology. Populations flower massively, then die, with even the smallest shoots bearing inflorescences. The stamens and stigmas are produced simultaneously.

Additional specimens examined. BRAZIL. BAHIA: Munic. Esplanada, N of Esplanada, near BR-101, 120 m, 6 May 1976 (fl), *Calderón et al. 2408* (CEPEC, US); Munic. Entre Rios, 14 km N of Entre Rios, on road intersecting BR-101 across from Fazenda Lagoa Preta, 7 May 1976 (fl), *Calderón et al. 2413* (CEPEC, US); Munic. Valença, 8 km from Valença on road to Guaibim, 24 Apr. 1976 (fl), *Soderstrom et al. 2161* (B, CANB, CEPEC, COL, F, G, K, LE, MO, NY, P, PRE, SI, SP, US, W, WIS).

5. **Atractantha radiata** McClure, Smithsonian Contr. Bot. 9: 50. 1973. TYPE. Brazil. Bahia: Estrada de Bom Gosto a Olivença, 15 Mar. 1943 (fl), *R. de L. Frões 19947* (holotype, US; isotypes, CEPEC, IAN, US). Figures 2G, 8, 14, 15.

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FIGURE 11. *Atractantha falcata.*—A. Culm internode with fertile foliage leaf complement.—B. Branch complement.—C. Apex of foliage leaf sheath and base of blade.—Da, b. Variations in structures forming terminal portion of a twig, diagrammatic.—E. Laminiferous bract from base of branch of inflorescence.—F. Floret, lateral view.—G. Lemma, lateral view.—H. Rachilla internode (left) and palea (right).—I. Lodicule complement.—J. Stamen.—K. Gynoecium. (Illustration by Gesina B. Threlkeld, first published in McClure, Smithsonian Contr. Bot. 9: 51. 1973; all based on *Pinto 681.*)

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FIGURES 12, 13. Bahian species of *Atractantha*, photographed and collected by C. E. Calderón. 12. *A. aureolanata*, habit. (Based on *2256*.) 13. *A. falcata*, inflorescence. (Based on *2413*.)

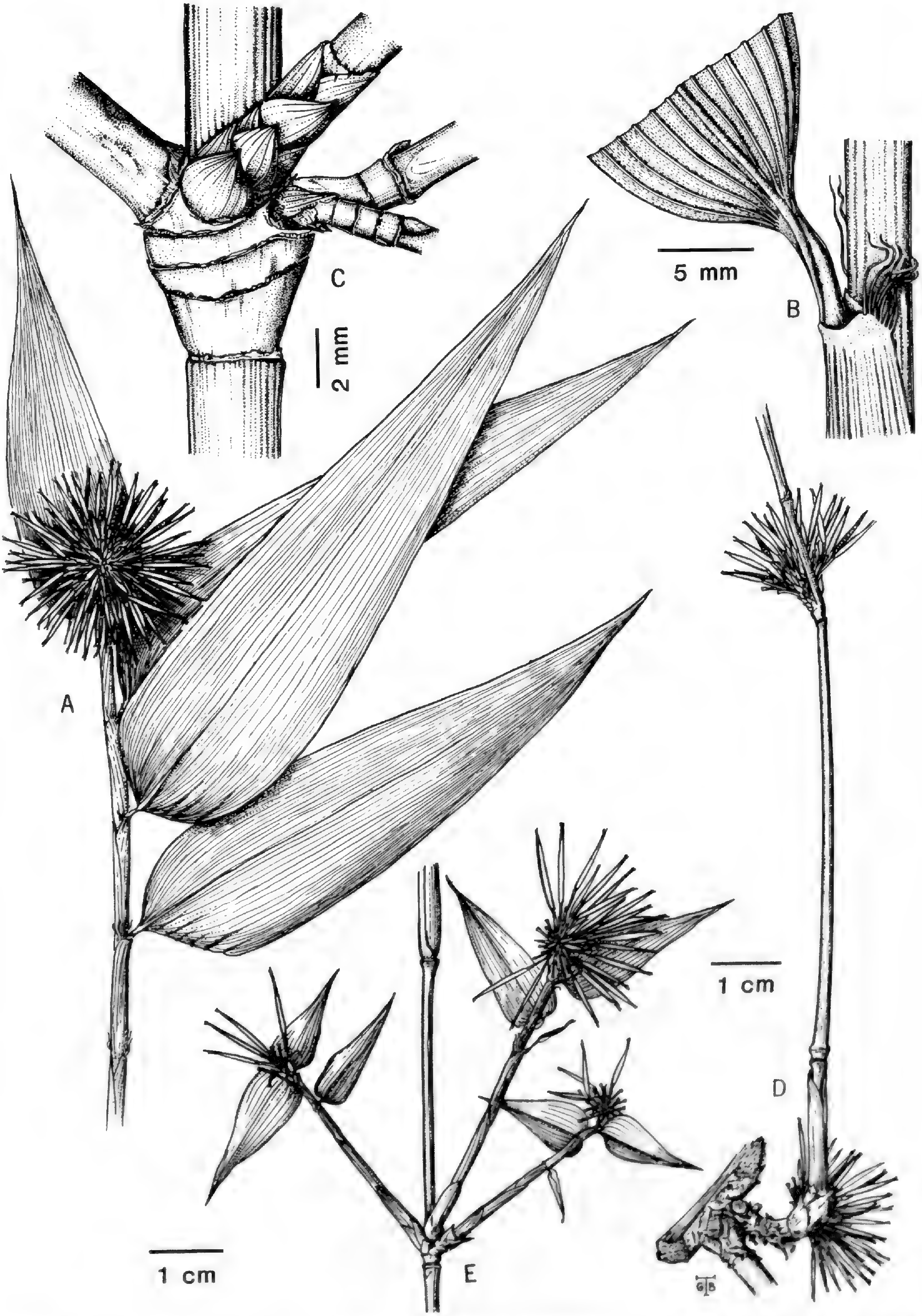

FIGURE 14. *Atractantha radiata.*—A. Fertile foliage leaf complement.—B. Foliage leaf, apex of sheath and base of blade.—C. Base of branch complement.—D, E. Variants of flowering axes. (Illustration by Gesina B. Threlkeld, first published in McClure, Smithsonian Contr. Bot. 9: 52. 1973; all based on *Fróes 19947.*)

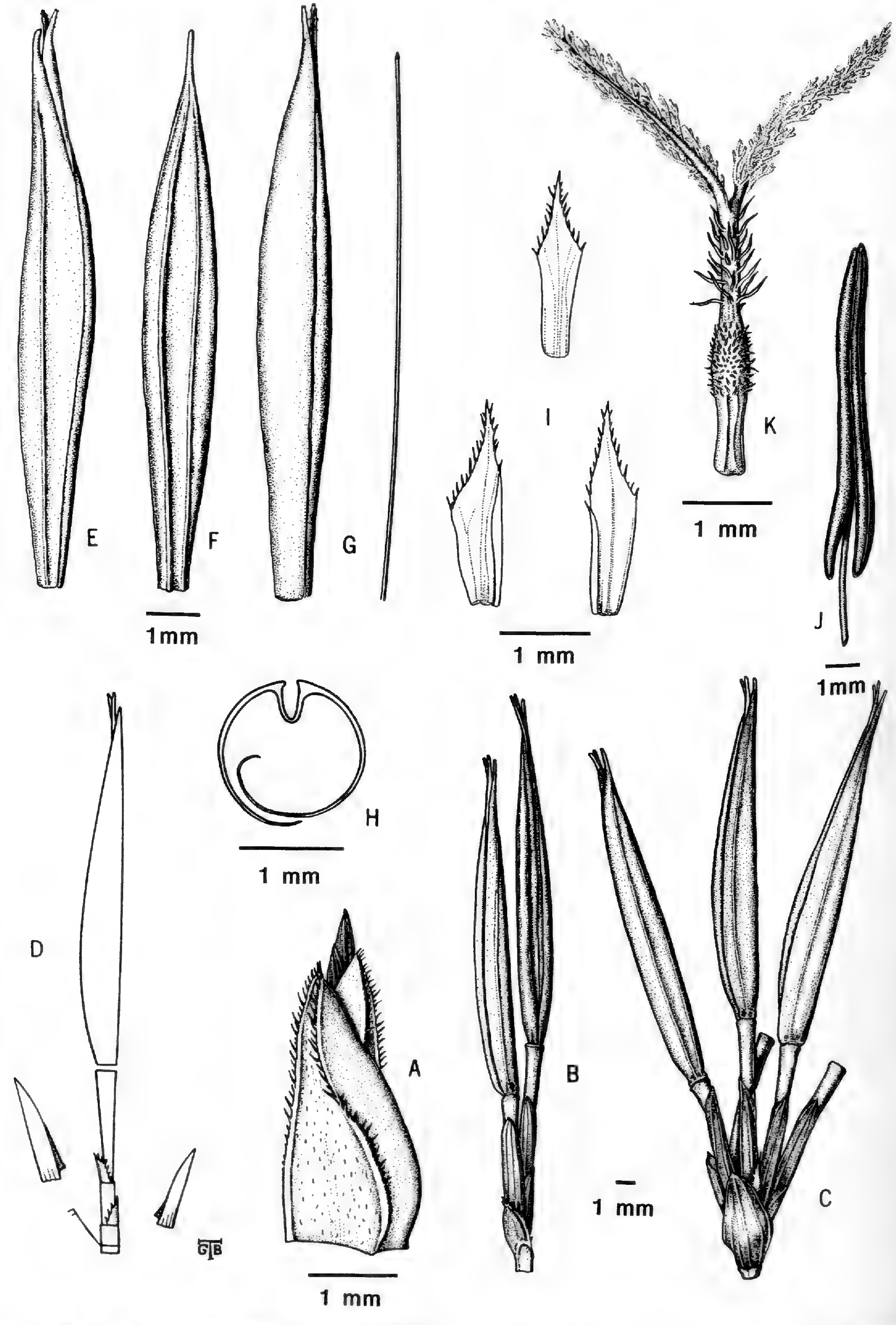

FIGURE 15. *Atractantha radiata.*—A. Pseudospikelet in early stage of development.—B. Two pseudospikelets, showing the prophyll at the base of the one on the left.—C. Cluster of pseudospikelets.—D. Pseudospikelet, dia-

Climbing woody bamboo forming large but rather loose clumps, decumbent at the base, arching, scandent, rebranching, climbing into trees up to 12 m, then pendent. Culms 6–13 mm diam., slender, flexible, solid or rarely with a ring of tiny, peripheral air canals in cross section, terete; internodes stramineous but minutely striate-maculate with green, slightly depressed spots, glabrous, smooth or uncommonly asperous in the upper branches, occasionally glaucous; lowest internodes 0.6–1 m long, the first branches appearing 4–5 m above the base; nodes glabrous; bud positioned 5–12 mm above the nodal line. Culm leaves papery, stramineous, glabrous; sheaths 20–30 cm long, 3–6 cm wide (spread width), loosely clasping the culm, slightly auricled on one side near the base, tapering to a rounded to acute apex, persistent, rather readily deciduous, attached by a flange-like girdle 1 mm long below the promontory, pushed away by the developing branches above; outer ligules, auricles, oral setae, and inner ligules all absent; blades absent, represented by a mucro 1–2 mm long. Branching intravaginal, with a central dominant primary branch and 2–6 smaller secondary or tertiary branchlets at its base, these also rebranching; bracts subtending branchlets 0.5–2 cm long, stramineous to reddish. Foliage leaves in complements of 7–13; sheaths glabrous, stramineous but minutely maculate with green spots, weakly if at all auricled at the summit; outer ligules 0.2–0.3 mm long, glabrous; oral setae 5–10 mm long, fine, delicate, white to orangish, crisped apically; inner ligules 0.3–0.5 mm long, membranous, truncate; pseudopetioles 3–7 mm long, adaxially golden or dark purple, glabrous to puberulent, abaxially glabrous; well-developed blades (10–)15–26 cm long, (2–)3–5 cm wide, lanceolate, asymmetrically obtuse to cuneate at the base, acute at the apex, glabrous. Inflorescences terminating leafy and nearly leafless branches of all orders, iterauctant, congested and capitate, the branches distichously inserted, consisting of 1–7 hemispherical to spherical, often pendent partial inflorescences 4–8 cm diam., each with 50–250 pseudospikelets with ± equal rachises. Pseudospikelets comprising one subtending bract, the rachis, one prophyll, 1–2 basal gemmiparous bracts (which may develop into more pseudospikelets), one functional floret, and (rarely) a setose prolongation of the rachilla internode bearing a tiny rudimentary sterile spikelet at its apex; subtending bract 5–10 mm long, lanceolate, acute, 7–11-nerved, membranous, glabrous, never laminiferous; prophyll 3–4.5 mm long, elliptical, bicarinate, pubescent on keels only; basal gemmiparous bracts 4–6 mm long, elliptical-lanceolate, acute, 3–7-nerved, glabrous; rachilla segment between uppermost gemmiparous bract and functional floret (4–)7–12 mm long, 0.3–0.5 mm diam., smooth, glabrous, stramineous, shiny, clavate and cupulate at the apex. Functional floret (11–)14–17(–19) mm long, 1.5–2(–2.5) mm wide, disarticulating from the summit of the rachilla; lemma narrowly lanceolate to uncommonly ovate-lanceolate, slightly falcate, acuminate-attenuate to pungent at the apex, indurate to less commonly papery, shiny, glabrous, green when young becoming olivaceous, reddish, or nearly black at maturity, the nerves not evident abaxially except for the raised midnerve and occasionally 1–2 pairs of lateral nerves, adaxially finely 5–11-nerved; palea slightly longer than the lemma, glabrous, the sulcus very narrow or less commonly wider, the apex acute. Rachilla internode often prolonged 12–17 mm past the functional floret as a setose bristle, filiform to flattened, rarely bearing a rudimentary sterile spikelet up to 5 mm long. Lodicules lanceolate-elliptical, acuminate, membranous, diaphanous, finely 3–5-nerved, the apical margins ciliolate; anterior pair 2.5–2.7 mm long, the posterior one 2.2–2.4 mm long. Androecium with stamens pendent; anthers 6–9 mm long, linear, yellow drying to orangish or purplish. Gynoecium with ovary glabrous below, pubescent toward the apex; style exserted from below the stamens, the stigmas hispidulous. Fruit not seen.

Distribution. Endemic to coastal Bahia, Brazil (Fig. 10).

Habitat. Occurring at elevations from 10 to 75 m in hilly "mata littorânea" on white sand, often with the bamboo *Alvimia*; in "campos" and "restinga" vegetation, rich in piaçaba palms (*Attalea funifera* C. Martius); in "mata atlântica arrestingada" (secondary forest after restinga is cut), on nearly pure white sand; and in "mata baixa," a low forest type found on sandy soil.

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grammatic.—E. Floret, lateral view.—F. Lemma, dorsal view.—G. Palea (left) and prolongation of rachilla (right), lateral view.—H. Palea, diagrammatic cross section.—I. Lodicule complement.—J. Stamen.—K. Gynoecium. (Illustration by Gesina B. Threlkeld, first published in McClure, Smithsonian Contr. Bot. 9: 54. 1973; all based on *Fróes 19947*.)

Phenology. At the presumed type locality between Una and Olivença, flowering episodes are recorded from 1943 and from 1976 through 1978; a nearby (ca. 200 m away) population at this locality began flowering in 1979, after the death of the 1976–1978 flowering population.

Additional specimens examined. BRAZIL. BAHIA: Munic. Maraú, 5.5 km S of Maraú, ca. 15 km from ocean, 20 May 1976 (fl), *Calderón et al. 2442* (CEPEC, ISC, SI, SP, US), 27 Feb. 1975 (fl), *dos Santos 2928* (CEPEC, US); Munic. Una, road Una–Olivença, 28 km N of Una, passing Rio Maroim, 55 m, 26 Apr. 1976 (fl), *Calderón et al. 2397* (CEPEC, US), 7 Apr. 1977 (fl), *Calderón 2454* (US), 2 Feb. 1978 (fl), *Calderón 2474* (US), 25 Feb. 1979 (fl), *Calderón & dos Santos 2485* (B, C, CANB, CEPEC, COL, CTES, DD, F, G, INPA, ISC, K, LE, MO, NY, P, PE, PRE, SGO, SI, SP, TNS, TULV, U, US, USCH, W, WIS); Munic. Canavieiras, 5 km W from intersection of fazenda side road with main road (40 km S of Una), 75 m, 26 May 1976 (fl), *Calderón et al. 2452* (CEPEC, US); Munic. Ilhéus, road Olivença–Vila Brasil (road to Fazenda Ipiranga), 6 km SW of Olivença, 2 Feb. 1978 (fl), *Calderón 2473* (US); Munic. Ilhéus, road Olivença–Vila Brasil, ca. 18.5 km SW of Olivença, 23 Feb. 1979 (fl), *Calderón & dos Santos 2479* (B, CEPEC, F, G, ISC, K, LE, MO, NY, P, SI, SP, TULV, US, USCH, W); Munic. Maraú, camino de Maraú a Ubaitaba, km 5, 10 m, 18 May 1985, *Zuloaga et al. 2465* (SI, US); Munic. Ilhéus, estrada Olivença–Maruim, km 7–10, 50 m, 19 May 1985, *Zuloaga et al. 2476* (SI, US); without locality or date, *Pirajá da Silva s.n.* ("*Hoehne 28692*") (US).

Flowering teratologies are common in *A. radiata* (e.g., *Calderón et al. 2397, 2442, 2454, 2474, 2479,* and *2485*). In these individuals some to most of the pseudospikelets of a capitate partial inflorescence proliferate into equal-sized branchlets bearing complements of small blades ca. 3 cm long and 0.5 cm wide, and, near the apex, a few loosely spicate pseudospikelets, a few of these strongly resembling a single large pseudospikelet with several, distant florets. There appears to be a complete gradation between this extreme type and shoots with normal inflorescences. *Calderón et al. 2397* has proliferated capitate inflorescences bearing branches with larger foliage leaf blades ca. 6 cm long and 1.3 cm wide, and small, loosely fascicled to capitate inflorescences, while *Calderón et al. 2485* exhibits a full spectrum of inflorescence structure, with different shoots from the same plant bearing spherical, hemispherical, loosely fascicled (reminiscent of *A. falcata*), or spicate racemose partial inflorescences.

Calderón et al. 2452, given the herbarium name "cristata" by Soderstrom, has foliage leaf blades only 2–2.3 cm wide; partial inflorescences with pseudospikelets arrayed in dense, fan-shaped fascicles (cristate) rather than hemispherical or spherical heads; the rachilla internode between the uppermost gemmiparous bract and the floret relatively short (ca. 4 mm long); small (11–13 mm long), papery, gaping, slightly inflated, ovate-lanceolate florets; and paleas with a broad dorsal sulcus embracing a prominent, flattened (up to 0.4 mm wide), sterile prolongation of the internode that often noticeably exceeds the floret. The inflorescence of this collection bears some superficial resemblance to the monotypic arthrostylidioid genus *Athroostachys* Benth. (*A. capitata* (Hook.) Benth., Bahia to Paraná, Brazil), but the latter has true, semelauctant spikelets and lacks a prolongation of the rachilla internode past the functional floret. It is possible that *Calderón et al. 2452* represents a new species distinct from *A. radiata,* but the population from which it was collected was reportedly one from near the end of its flowering period, and perhaps the peculiarities of the inflorescence and floret structure can be accounted for by its senescence. It seems best to await further collections before describing it as new, especially in view of the abundance and diversity of teratological inflorescences exhibited by this species. Several other collections of *A. radiata* with otherwise normal inflorescences and spikelets exhibit tendencies toward cristate partial inflorescences (e.g., *Calderón et al. 2397,* US sheet no. 9) and occasionally have gaping, papery, inflated florets.

A common name is *taboca* (*dos Santos 2928*).

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TRIBAL AND SUBTRIBAL DELIMITATION AND CIRCUMSCRIPTION OF THE GENERA OF ARACEAE TRIBE LASIEAE[1]

A. Hay[2]

Abstract

The Lasieae, comprising a relictual pantropical tribe of aroids, are defined and described. Four subtribes are recognized: neotropical Dracontiinae (*Dracontioides* Engl., *Dracontium* L., and *Anaphyllopsis* A. Hay), Indochinese Pycnospathinae (*Pycnospatha* Thorel ex Gagnepain), Indian Anaphyllinae A. Hay described herein (*Anaphyllum* Schott), and pantropical Lasiinae (*Cyrtosperma* Griff., *Lasia* Lour., *Lasiomorpha* Schott, *Podolasia* N. E. Br., and *Urospatha* Schott). Keys and diagnoses are given for the subtribes and genera, and the latter are described. Seeds are illustrated. Geography of the tribe is discussed; it is suggested that the group is Gondwanan in origin and that, in the Orient, it has arrived in Malesia from both the East and the West. *Dracontium polyphyllum* L. is lectotypified. The combination *Dracontium schomburgkii* (Schott.) A. Hay is made following the reduction of *Echidnium* Schott.

The Lasieae are of critical interest in the Araceae as a relictual pantropical group that shows great range of leaf form, from highly compound to lanceolate, and spathe form from campanulate to hood-forming to bractlike. The flowers show the greatest range in numbers of parts in any hermaphrodite-flowered aroid group. The leaves are frequently armed, a condition to which Corner (1949 et seq.) has drawn attention as a putatively primitive one, and they show an acropetal method of leaf expansion of restricted systematic distribution in Araceae, and of very rare occurrence in the monocotyledons as a whole (Hay, 1986). Two of the four subtribes have extremely restricted distributions, as have nearly half the genera and many of the species—factors that may indicate an ancient group in decline (Scott & Day, 1983).

The group appears to represent a primitive clade of Araceae. While the hermaphrodite tepalate flowers suggest also a primitive grade (in this respect), the Lasieae are nevertheless highly heterobathmic and are thus a vitally important source of information contributing to the development of hypotheses of evolutionary trends in the family as a whole. Indeed, study of this group, particularly in the Old World, has led Hay (1986) and Hay & Mabberley (in press) to propose a radically new hypothesis for the origin of the Araceae.

A cladistic treatment has not been attempted, both for philosophical reasons and for the pragmatic one that one of the larger neotropical genera (*Urospatha*) requires a monograph before its characterization can be established. This work resolves a number of problems in the generic delimitation of the Lasieae and serves to highlight others.

Historical Background

THE GENERA

Of the five species of *Dracontium* in Linnaeus's *Species Plantarum* (1753), two are recognized today as belonging in the tribe Lasieae—*D. poly-*

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phyllum and *D. spinosum*. The remaining three are *Monstera pertusa* (L.) de Vries, *Symplocarpus foetidus* (L.) Nuttall, and *Lysichiton camtschatcensis* (L.) Schott, the first in subfamily Monsteroideae, the latter two considered by Krause (1908) to belong in subfamily Calloideae. Rafinesque (1838) said of Linnaeus's *Dracontium* species that "the scandent species appear the type of *Dracontium* which Adanson changed to *Monstera* perhaps a better name," and so he superfluously renamed *D. polyphyllum* as *Eutereia nigricans* Raf.

In 1790 Loureiro based the genus *Lasia* on a plant collected from near Hanoi, Vietnam. The type species, *L. aculeata*, was recognized by Thwaites in 1863 to be conspecific with Linnaeus's *D. spinosum*, and the new combination *L. spinosa* (L.) Thwaites was made.

In 1851 Griffith described *Cyrtosperma* for a plant from the Malay Peninsula. Then came Schott, who erected *Urospatha* in 1853 for seven neotropical species (including a *Sagittaria*—"*U. friedrichsthalii*"). These (except *U. friedrichsthalii*) are now included in *U. sagittifolia* (Rudge) Schott, which Rudge had described as a species of *Pothos* in 1805 based on a plant collected in Guyana by Martin. In 1857 Schott based *Lasiomorpha* on an African plant and *Arisacontis* on a Pacific one collected by Chamisso (which had already appeared in 1837 without a diagnosis as *Apereoa* Moerenhout). Engler later combined both of these genera with *Cyrtosperma*. *Lasiomorpha* is resurrected here. Also in 1857, Schott based *Ophione* and *Echidnium* on neotropical plants subsequently included in *Dracontium* by Engler (1911) and Bogner (1985) respectively. In 1858 he described *Anaphyllum* based on an Indian plant. Later, in 1865, he extracted his rival K. Koch's *D. asperum*, described the genus *Chersydrium*, and applied the superfluous epithet "*jararaca*," a local name noted also by Spruce (1908) and referring to the snakelike petioles characteristic of the genus. In 1869, Seemann named the gigantic Nicaraguan and Costa Rican geophyte *Godwinia gigas*, which ten years later Engler reduced to sectional status in *Dracontium*. In 1882 N. E. Brown described *Podolasia* from material obtained from Borneo and cultivated in England by Veitch.

Engler (1911) extracted Schott's *Urospatha desciscens* in describing the monotypic east Brazilian genus *Dracontioides*. In 1941, Gagnepain published the genus *Pycnospatha*, described in manuscript by Thorel for two species of atepalate geophytes from Laos and Thailand. Hay (1988a) has erected the neotropical genus *Anaphyllopsis* based on a species of Engler's heterogeneous pantropical *Cyrtosperma* and two new species. Bunting (1988) has created *Urospathella* for a diminutive Venezuelan savanna herb, which is reduced here to synonymy with *Urospatha*.

SUPRAGENERIC GROUPINGS

Schott (1832, 1858, 1860) was the first specialist to arrange the genera of Araceae, putting in a widely expanded tribe "Orontieae" the genera *Chersydrium, Dracontium, Echidnium, Ophione, and Urospatha* (together with *Symplocarpus*) in his subtribe Dracontiinae next to his subtribe Lasiinae, which included *Anaphyllum, Arisacontis, Lasia*, and *Lasiomorpha*.

Engler's reappraisals (1877, 1879, 1911) were based on considerably more material and phylogenetic concepts. He perceived that neither *Orontium* nor *Symplocarpus* had close relationship with the remaining genera, and he combined Schott's subtribes into his (Engler's) Lasieae, at the same time (1877) erecting the subfamily Lasioideae. Ultimately he abandoned subtribal classification. Hutchinson (1934) elevated Schott's subtribes Lasiinae and Dracontiinae to tribal rank, for some unspecified reason including the monsteroid genus *Holochlamys* in his concept of Dracontieae. Subsequently Nakai (1943) recognized Lasieae (ovary unilocular) as including *Anaphyllum, Lasia*, and *Podolasia*; erected "Urospatheae" (ovary 2–6-locular; the name Dracontieae was already available) to include *Dracontioides, Dracontium*, and *Urospatha*; and erected Cyrtospermateae for *Cyrtosperma*, the latter based solely on the character of dehiscent fruit, which he presumably obtained from Engler's inaccurate illustration (1911, fig. 7f) of dehiscent fruits in *C. lasioides* Griff. Neither Hutchinson's nor Nakai's classification of Araceae has had much following by specialists.

When he published *Pycnospatha*, Gagnepain, on the basis of its atepalate flowers, allied it with the north temperate bog-dwelling *Calla*, an affinity which Bogner (1973) denied, noting the greater resemblance to *Dracontium*. Bogner included *Pycnospatha* in Lasieae (sensu Engler), regarding the atepalous condition as sufficient to warrant erecting the monogeneric subtribe Pycnospathinae, and in so doing re-created Lasiinae for the remaining genera. However, it is proposed here that the genera of Lasiinae (sensu Bogner) are sufficiently diverse to warrant either rejecting Bogner's recognition of subtribal status for *Pycnospatha* or subdividing Lasiinae (sensu Bogner) further to reflect the variation. The latter course is adopted here since this best portrays a close-knit and relictual tribe. The subtribes proposed are based on vegetative architecture, leaf, seed, and flower morphology, and distribution.

Within his classification of the family, Engler (1877 et seq.) regarded the Pothoideae and Lasioideae as occupying central positions, separating them on anatomical grounds (laticifers present and absent respectively). He regarded *Pothos* as the most primitive genus in the family. The Lasioideae he regarded as more specialized, being generally more elaborate and sometimes with more specialized floral construction. He recognized hermaphrodite-flowered and monoecious groups in the subfamily, the former represented by the Lasieae, the latter by the Thomsonieae (*Amorphophallus, Anchomanes, Plesmonium, Pseudodracontium, Pseudohydrosme*, and *Thomsonia*), Nephthytideae (*Cercestis, Nephthytis*, and *Rhektophyllum*), and Montrichardieae (*Montrichardia*).

Grayum (1984, 1990), on palynological and other grounds, has suggested that *Amorphophallus, Pseudodracontium, Plesmonium*, and *Thomsonia* be moved from Lasioideae to Aroideae. He further suggested that *Anchomanes* and *Pseudohydrosme* are more closely allied with Nephthytideae, and that Montrichardieae and Nephthytideae may belong nearer Philodendroideae. He tentatively allied Lasieae with Stylochaetoneae (extracted from Engler's Aroideae) and *Symplocarpus* (thitherto considered a member of the enigmatic Calloideae). He concluded that subfamily Lasioideae may be recognized to include three tribes: boreal Orontieae (*Symplocarpus, Lysichiton, Orontium*), Lasieae (as here), and African Stylochaetoneae (*Stylochaeton*). Of these, further evidence is necessary to verify that Orontieae are natural, and there can be little doubt that if these groups form a monophyletic unit it is a profoundly fragmented one.

The great strength of Engler's system is its classification at tribal level, which largely stands today. Arguably it is better to begin formal division of the Araceae at the level of tribe rather than subfamily, and to talk of informal tribal alliances.

LASIEAE

Lasieae Engler, Nova Acta Acad. Leopold.-Carol. 39:144. 1877.

Massive to slender cormous, rhizomatous, or suffruticose terrestrial or semiaquatic plants; stems erect to creeping, sympodial, the modules bearing a prophyll, one to several euphylls and sometimes one or more cataphylls[3]; internodes distinct and then sometimes armed, or very condensed. Leaves small (measured in centimeters) to enormous (a few meters in length), solitary or spirally clustered, with the petioles and blades often armed with scattered or flanged spines or variously spinescent warts, often conspicuously mottled and streaked; blades highly compound to pinnate, hastate, or lanceolate, frequently fenestrate, or with the lobes developed marginally, or both; maturation of the whole leaf markedly acropetal, the blade exposed from the bud at an early stage in its expansion (Fig. 1); venation reticulate; rachis and/or petiole sometimes geniculate; sheath short, infrequently up to ca. 20% of the length of the petiole. Inflorescence solitary, very rarely (and then irregularly) in a cymose pair; peduncles mostly similar in length and texture to the petioles, occasionally much abbreviated; spathe campanulate to hood-forming to spirally twisted to ± bractlike, occasionally armed outside or papillate within, mostly purple-brown, often streaked yellowish, rarely pink or white, persistent, marcescent or caducous; spadix usually shorter than the spathe, stipitate or sessile, mostly a direct continuation of the peduncle, sometimes with the stipe adnate to the adaxial side of the spathe; maturation of flowers and fruits in a basipetal sequence (Fig. 2). Flowers hermaphrodite throughout the spadix, rarely the apical ones sterile (*Dracontium*), (9–)6–4-tepalate (0 in *Pycnospatha*); tepals free, imbricate; stamens 4–12 with distinct anthers and free filaments (except *Lasiomorpha*); anthers extrorse, dehiscent by longitudinal slits to ± apical pores; pollen extruded in ropelike masses, ellipsoid, monosulcate with usually reticulate exine, binucleate and starch-free; ovary 1–6-locular, superior to slightly inferior (*Lasiomorpha*), the locules uni- to multiovulate; placentation axile, basal, parietal or apical; ovules bitegmic, anatropous; stigma buttonlike, unlobed, microscopically papillate or verruculate, wet with or without a pollination droplet, style distinct or none. Fruit with rudimentary spines (*Lasia, Pycnospatha*) or smooth, indehiscent, usually a red berry, 1–several-seeded, ovoid to obpyramidal, sessile on the spadix, rarely expelled (as in *Anthurium*). Seed pachychalazal (sensu Corner, 1976), often with "tegmic" and "testal" layers differentiated within the pachychalaza, hard, ± campylotropous, reni-

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[3] A prophyll is distinguished from a cataphyll by its position at the beginning of an axis and by its bicarinate structure.

FIGURE 1. a. An emerging leaf in *Dracontium polyphyllum.*—b. The blade undergoes some tenfold increase in length during expansion after it has emerged from the cataphylls. Cultivated at the Bogor Botanic Gardens.

form to helical, with an oily strophiole or rudimentary aril at the chalazal end; ovular integuments with the true micropyle forming an operculum over the pachychalazal micropyle; seed coat variously spiny, crested, warty, or smooth; (in *Anaphyllum,* seed ovoid, seed coat membranous); endosperm present or absent; n = 13, or 26 (*Urospatha*).

Differential characters. Terrestrial or semiaquatic habit, early leaf exposure, reticulate venation, basipetal flower and fruit maturation, hermaphrodite flowers, campylotropous pachychalazal seeds, monosulcate heteropolar binucleate, starch-free pollen monads (Grayum 1984: 275–280), x = 13 (Marchant, 1973; Petersen, 1989).

Distribution. Pantropical with subtropical extensions into the Himalayan foothills (*Lasia*); absent from Australia. Distribution is discussed below.

Ecology. Lowland, rarely montane; on floor and edge of and gaps in rainforest, monsoon forest, and semideciduous forest, to open, mostly swampy, sites. Cormous species are sometimes tolerant of seasonal drought. Inflorescences generally present a saproentomophilous pollination syndrome of dark coloration and the smell of decaying organic matter.

Ray (1987) has published a classification of aroid shoot diversity. In his terminology, the axes in Lasieae are anisophyllous sympodial. Growth of the renewal axis after flowering is sylleptic in the subtribe Lasiinae, and hence each module bears first a prophyll, and the subsequent leaf (the mesophyll) and all other leaves are foliage leaves. In the genera of the remaining subtribes, growth of the renewal axis after flowering is proleptic (with the possible exception of *Dracontioides*), and hence at least the mesophyll has the form of a cataphyll. Where flowering occurs after a period of dormancy, the inflorescence is subtended by a number of bracteoles (*Dracontium, Pycnospatha*). Inflorescences are generally solitary throughout the tribe. Where they are paired (in vigorous individuals of certain species, e.g., *Anaphyllopsis americana* (Engler) A. Hay, *Cyrtosperma macrotum* Becc. ex Engler) they are multiplied according to an axillary mo-

FIGURE 2. Basipetal fruit maturation in the spadix of *Anaphyllum wightii* (*Hay s.n.*, FHO). Anthesis also takes place in a basipetal sequence in Lasieae.

nophyllous sympodial plan in *Cyrtosperma*, and have an interposed mesobracteole and bracteole in *Anaphyllopsis* between the subtending prophyll of the second inflorescence and the base of its peduncle. In Ray's system an essentialist's stance is adopted, and the term "leaf" is used for several functionally quite different organs. In the present work, "leaf" means foliage leaf.

KEY TO THE SUBTRIBES

1a. Flowers atepalate, plant cormous, leaf solitary, spathe hood-forming, fruit spinous, seed coat with raphides and druses .... Pycnospathinae
1b. Flowers tepalate, other characters not in the above combination.
  2a. Stems bearing prophylls and euphylls only .... Lasiinae
  2b. Stems bearing cataphylls and prophylls.
    3a. Seed ovoid, smooth, coat membranous; stems clump-forming to rather weakly stoloniferous, leaves never fenestrate .... Anaphyllinae
    3b. Seed ± campylotropous; coat hard, ornate; leaves often fenestrate .... Dracontiinae

SUBTRIBE 1. DRACONTIINAE SCHOTT

Dracontiinae Schott in Schott & Endl., Melet. Bot. 22. 1832. "Dracontiae."

Cormous or rhizomatous, usually solitary herbs. Stems cataphylliferous (?except *Dracontioides*). Leaves usually solitary or paired (except *Dracontioides*), with usually warty, or rarely spiny petioles; blades often highly compound and/or fenestrate, rarely simple and entire. Spathe erect, hood-forming or spirally twisted. Flowers tepalate. Seed campylotropous, albuminous; seed coat thick, usually ornate.

Distribution. Three genera ranging from southern Mexico, through Central America to Brazil, southeast to near Rio de Janeiro.

KEY TO GENERA

1a. Leaves clustered, sagittate, fenestrate with the holes not reaching the margin; spathe hood-forming, ovary bilocular .... *Dracontioides*
1b. Leaves solitary or two together, ternately divided to highly compound.
  2a. Plants cormous; leaves highly compound or if not, then with the posterior lobes each equally bifid; spathe usually erect to hood-forming, sometimes campanulate .... *Dracontium*
  2b. Plants rhizomatous; leaves sagittate and divided by fenestration to pinnate by marginal dissection; spathe spirally twisted .... *Anaphyllopsis*

Dracontium L., Sp. Pl. 967. 1753. TYPE: *D. polyphyllum* L. [Type: Hermann, Paradisus Batavus, fig. 93. 1698 (lectotype, selected here).]

Eutereia Raf., Fl. Tellur. 4: 12. 1838, nom. superf. pro *Dracontium*. TYPE: *E. nigricans* Raf., nom. superf. pro *D. polyphyllum*.

Echidnium Schott, Oesterr. Bot. Wochenbl. 7: 62. 1857. TYPE: *E. schomburgkii* Schott = *Dracontium schomburgkii* (Schott) A. Hay, comb. nov.

Ophione Schott, Oesterr. Bot. Wochenbl. 7: 101. 1857. TYPE: *O. purdieana* Schott = *D. purdieanum* (Schott) Engl.

Chersydrium Schott, Oesterr. Bot. Zeitschr. 15: 72. 1865. TYPE: *C. jararaca* Schott, nom. superf. pro *D. asperum* K. Koch.

Godwinia Seemann, J. Bot. 7: 313, t. 87, 96. 1869. TYPE: *G. gigas* Seemann = *D. gigas* (Seemann) Engl.

Gigantic to slender cormous herbs, with solitary, rarely paired, compound to highly compound leaves; corm hemispherical or ± irregular, concave around the bud, roots arising mostly from the top, commonly bearing scattered to very numerous small bulbils. Leaf to 5 m tall, subtended by several evanescent cataphylls, emerging from these in a very unexpanded state and thereafter undergoing a long exposed period of great expansion; petioles mottled, usually warty, the warts rounded, ± pointed to spinous; blade tripartite, to 4 m across, the petiole divided into three subequal rachises; of these, the anterior undergoing at least one more 3-parted division and forming a pair of opposite lateral secondary rachises, and a continuation of the anterior rachis; posterior rachises forked, rarely not further divided; ultimate branches of the rachises bearing ± pinnately arranged sessile, ovate to rhomboid, or rarely linear leaflets; in addition the rachises bearing scattered leaflets throughout; leaflets with pinnate, brochidodromous venation, often fenestrate, rarely the whole blade entire in bud, the parts separating on expansion, and then the leaflets truncate. Inflorescence solitary, accompanying or alternating with the leaf; peduncle exceeding, equaling or shorter than the petiole, sometimes not extending above ground level, when long similar to the petiole; spathe mostly purple-brown, campanulate to hood-forming to erect, occasionally somewhat twisted in uppermost part, smooth or papillate within; spadix sessile to stipitate, usually disproportionately small, sometimes with the uppermost flowers with enlarged tepals, forming a short appendix bearing ascidiform structures (Fig. 4), putrid-smelling over a lengthy period. Flowers 9–6-tepalate, 12–6-staminate; ovary 6–1-locular, often bearing a long style (to ca. 6 mm); locules 1–few-ovulate; stigmas papillate or not, wet. Fruit mostly obpyramidal, red, smooth, usually accompanied by the ± marcescent spathe, often beaked with the persistent style. Seed campylotropous, crested and/or warty, inner layers of pachychalaza with cell walls thicker than those of the outer ones; endosperm present (Figs. 5a, 6a).

FIGURE 3. Lectotype of *Dracontium polyphyllum* L., from P. Hermann, *Paradisus Batavus* (1698) figure 93.

Typification of Dracontium polyphyllum. Of the elements cited in Linnaeus's *Species Plantarum*, material of this plant in the Clifford Herbarium is sterile and fragmentary. The figure in Plukenet's *Almagestum* (1696, t. 149, fig. 1) is highly stylized, while that in Hermann's *Paradisus Batavus* (1698, fig. 93), reproduced here (Fig. 3), is clearly *D. polyphyllum* in the current sense—with a short peduncle, hood-forming spathe, prominent styles, and no (or few) fenestrations in the leaflets. This illustration is therefore here selected as lectotype.

Distribution. About 15 species from Chiapas, Mexico, through Central America and tropical South America, predominantly in open sites, also in rainforest, tolerant of seasonal drought; mostly at low altitude.

This genus is in need of revision. It shares with Old World *Amorphophallus* the problem of matching fertile and sterile material in those species in which flowering and leafing alternate. This will entail extensive fieldwork and use of living collections. Several species are in cultivation at St. Louis, Kew, and Munich. Most species appear to have very restricted distributions, although this may in part be due to insufficient collecting. Madison (1978) noted that *Dracontium* species tend to occur as rare, easily overlooked single individuals, although the bulbiliferous species form substantial clumps.

There is no available information on the pollination biology. Inflorescence color, smell, and morphology suggest saprocantharophily and sapromyophily. The Panamanian *Dracontium dressleri* Croat, in cultivation at Kew emits an odor of stale meat and dirty socks over a period of about three weeks, in marked contrast to the brief exhalations of the quickly acting monoecious groups (e.g., Meeuse, 1978) and recalling the behavior of *Symplocarpus* (Knutson, 1974). Peduncle lengths ranging from none in *D. dressleri*, for example, to ca. 1.5 m in the Colombian *D. carderi* Hook. f. suggest selection for different pollinators. So do the markedly differing style lengths, where stigmas may be more or less sessile, for example in the recently described Venezuelan *D. changuango* Bunting (Fig. 1), or borne on long styles as in *D. polyphyllum* and *D. gigas* (Engler, 1911). (Long styles are unusual in the Araceae.)

The morphology of the spadix apices in some species in curious. The Mexican *D. soconuscum* Matuda and *D. changuango* have one to several (or sometimes no) stalked asciform structures in place of the upper flowers (Fig. 4), whereas in *D. dressleri* tepals of the upper flowers are much longer than those of the rest, as is sometimes the case in *Cyrtosperma cuspidispathum* Alderw.

Dracontium fruits are characteristically obpyramidal, the upper part of the fruit showing upward and outward expansion above the locules. Similar fruits occur in *Anaphyllopsis americana* (Engler) A. Hay and, less expanded, in *Dracontioides* and *Lasia*. In other Lasieae and in most aroids the pericarp is more even in thickness throughout.

The leaves defy succinct description. Those of the Nicaraguan and Costa Rican *D. gigas* rank with the largest of all, outside the palms, reaching some five meters in height and four meters in blade diameter. In contrast, *D. margaretae* Bogner from Brazil, Venezuela, Bolivia, and Paraguay is a comparatively dwarf species in which the posterior and anterior lobes are only once divided into linear leaflets (Bogner, 1981). Engler (1911) noted that the leaves of *D. gigas* and *D. costaricense* Engl. are entire in bud, and the whole is segmented from within the lamina, as in the similarly elaborate leaves of *Anchomanes* and *Pseudohydrosme*. In *D. polyphyllum*, the main lobing of the leaf appears marginal, and the ultimate divisions are intramarginal, occasionally failing and leaving fenestrate leaflets. These observations are based on unfolding and mature blades, and further evidence of early developmental stages is required.

A striking feature of *Dracontium* leaves is their early emergence from the cataphylls. The branches and segments of the anterior lobe are bunched and point upward in bud, together with the inner/upper product of the first division of each posterior lobe; the outer/lower half is similarly bunched, but points down the petiole. Expansion proceeds over a period of weeks in an acropetal wave up the petiole to the blade; this is in marked contrast to the otherwise rather similar leaves of *Amorphophallus*, which emerge in a late stage of apparently diffuse rather than polar expansion. Mottling is streaked in *Dracontium* versus usually maculate in *Amorphophallus*, perhaps reflecting their differing methods of expansion.

Dracontioides Engl., Pflanzenr. IV. 23C: 36. (Heft 48). 1911. TYPE: *D. desciscens* (Schott) Engl. [Basionym: *Urospatha desciscens* Schott, Oesterr. Bot. Zeitschr. 9: 99. 1859. Type: Brazil. Bahia: Salvador, Itaparica, *Riedl 714* (holotype, LE not seen; isotype, K).]

Robust to rather slender swamp herbs to ca. 2 m high; rhizome erect, sparsely branching, to 40 cm long and ca. 6 cm diam., bearing a crown of several sagittate rarely ± ovate and then auriculate leaves. Leaf blades glossy, in larger leaves fenestrate; fenestrations more numerous in anterior than in posterior lobes; petioles smooth to rough, mottled brownish and green, unarmed, watery, drying thin, with large numbers of easily detached bulbils in their axils; cataphylls present, but very short (shorter than sheath of petiole); sheath membranous. Inflorescence solitary on a peduncle similar to but usually shorter than the petioles; spathe forming a deep hood, brownish green without, deep purple and longitudinally streaked yellowish, becoming pink toward the base, within to 15 cm long; spadix much shorter than the spathe, sessile to shortly stipitate, purple. Flowers 4-tepalate; stamens 4, exserted from the tepals at male anthesis; ovary bilocular with a purple conical style; locules uniovulate with axile placentation; stigma buttonlike, whitish, wet. Fruit reddish, furrowed, usually 2-seeded. Seeds campylotropous, asymmetrical with the micropylar end longer and narrower than the chalazal end, albuminous; seed coat thick, hard, brown with up to 8 sharp longitudinal warty crests (Figs. 5b, 6b).

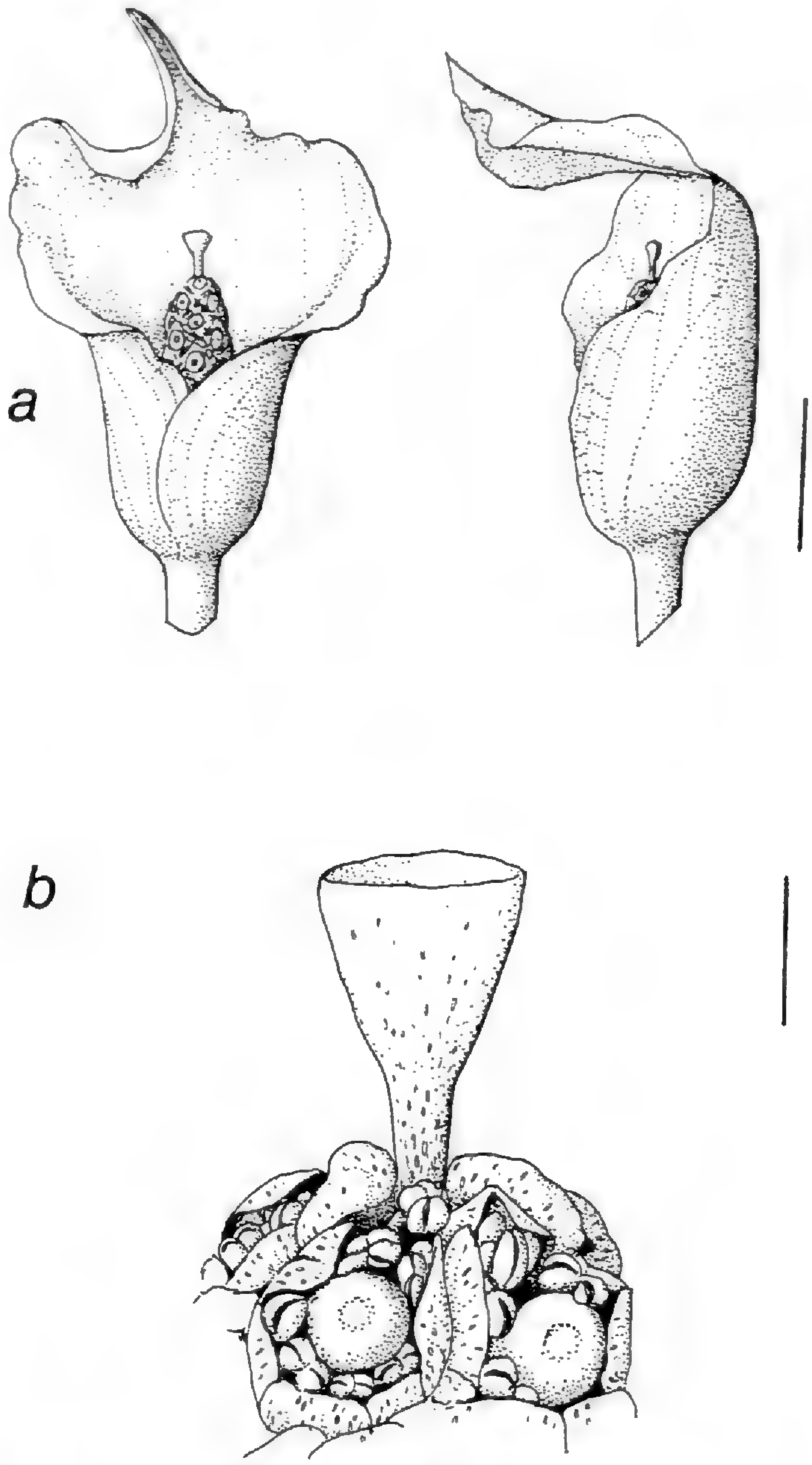

FIGURE 4. The spadix apex of *Dracontium changuango* (*Aristeguieta 12734*, K).—a. The whole inflorescence; scale bar = 2 cm.—b. Apical flowers; scale bar = 3 mm.

Distribution. Riverbanks, swamps, and swamp forest undergrowth in rainforests of eastern Brazil, in Bahia, and near Rio de Janeiro at Tijuca (Mayo, 1978).

Schott (1859) ascribed this species to *Urospatha* because of the bilocular ovary that characterized all species of *Urospatha* then known in the fertile state. Engler, however, noted the albuminous seed (*Urospatha* species were exalbuminous), and that the hood-forming spathe more closely resembled that in *Dracontium*, hence the name *Dracontioides*. The spathe, the fenestrate leaves, and the presence of bulbils indicate closer affinity with *Dracontium* than with any member of the Lasiinae, and the seed and vegetative architecture warrant

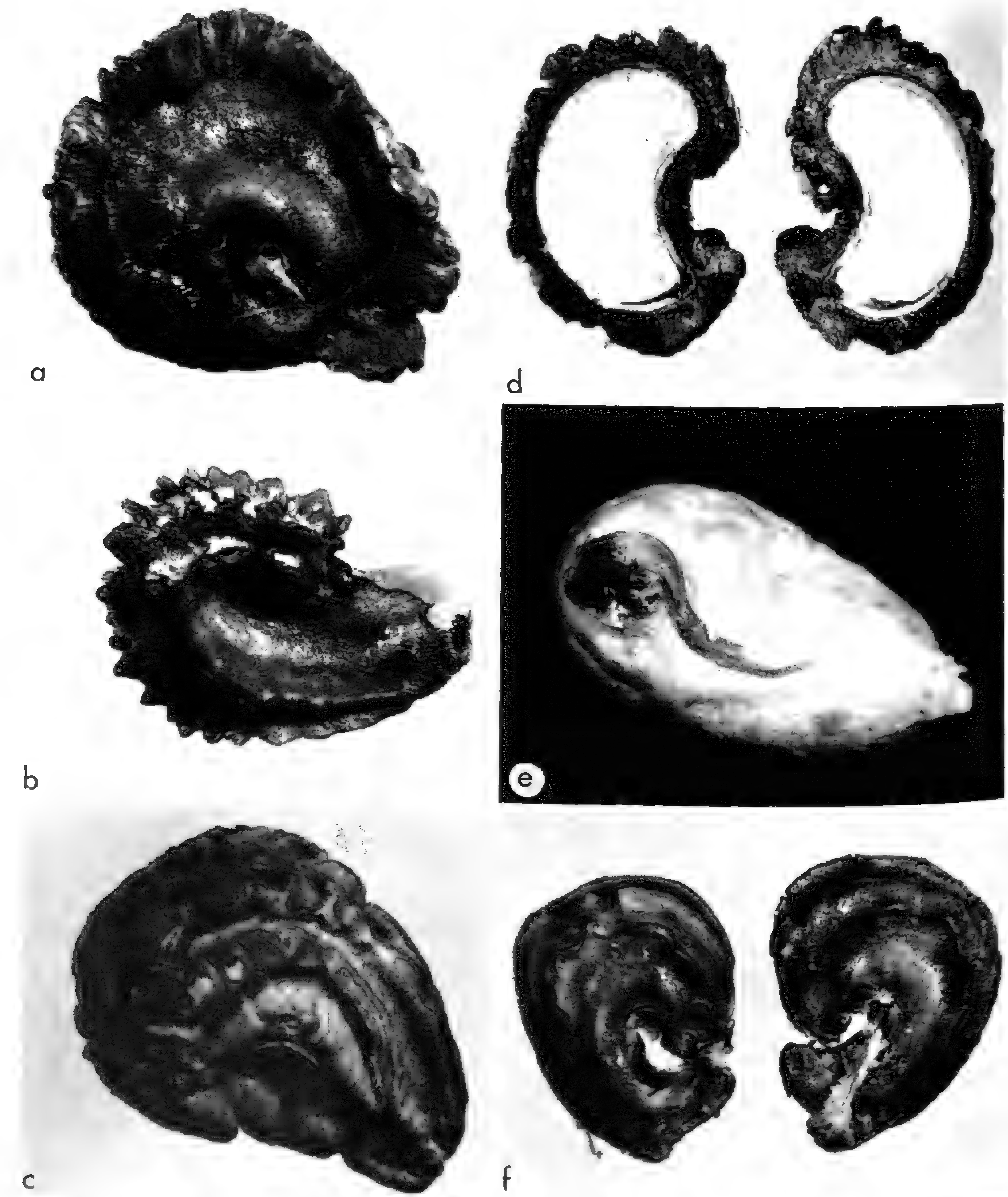

FIGURE 5. Seeds of Lasieae.—a. *Dracontium soconuscum* (*Matuda 17783*, UC).—b. *Dracontioides desciscens* (*Harley et al. 2824*, K).—c. *Anaphyllopsis cururuana* A. Hay (*Anderson 10627*, NY).—d. *Pycnospatha arietina* (*Bogner 395*, K).—e. *Anaphyllum wightii* (*Hay s.n.*, FHO).—f. *Cyrtosperma merkusii* (*Bogner 1363*, K). See Figure 6 for scale.

recognition of *Dracontioides* as a relict descended from a caulescent "pre-Dracontium."

Anaphyllopsis A. Hay, Aroideana 11(1): 25. 1988 and 11(2): 8. 1988. TYPE: *Anaphyllopsis americana* (Engl.) A. Hay [Basionym: *Cyrtosperma americanum* Engl. in Martius, Fl. Bras. 3(2): 117, t. 22. 1878. Type: French Guiana: *Leprieur 152* (lectotype, P, selected by Hay, loc. cit., isolectotype, US).]

Terrestrial or semiaquatic solitary herbs; rhizome erect, subterranean, bearing prophylls, cataphylls, and euphylls. Leaves solitary, rarely paired, with unarmed, usually warty petioles; lamina hastate to pinnate, dissected by fenestration and/or marginal outgrowth. Inflorescences solitary, rarely paired, on long peduncles similar to the petioles; spathe membranous, papery when dry, convolute in the lower part, otherwise spirally twisted; spadix with a stipe adnate for most of its length to the spathe. Flowers hermaphrodite throughout the spadix, with four tepals and four stamens; ovary unilocular, uni- to bi-ovulate with basal placentation; stigma wet. Fruit obpyramidal to ovoid, ripening reddish, with marcescent spathe. Seed campylotropous, pachychalazal, albuminous; coat thick, verruculose to deeply channeled; aril rudimentary, chalazal (Figs. 5c, 6c).

Distribution. Three species from tropical South America: *A. americana* from the Guianas, and two Amazonian species. Apparently all are rare, growing in swamp forest undergrowth, open swamps, riversides, and rainforest floor, at low altitude.

The genus is distinguished from *Dracontioides* by the spirally twisted as opposed to hood-forming spathe, solitary leaf, and unilocular ovary with basal placentation. It is distinguished from *Dracontium* by the rhizome, spathe, and posterior lobes of the leaf, which are never bifid or dichotomous. It is allied with these genera because of fenestration, cataphylls, tepals, and the ornate campylotropous seed.

The presence of both fenestrate and marginal leaf dissection within a single genus is matched by *Dracontium*.

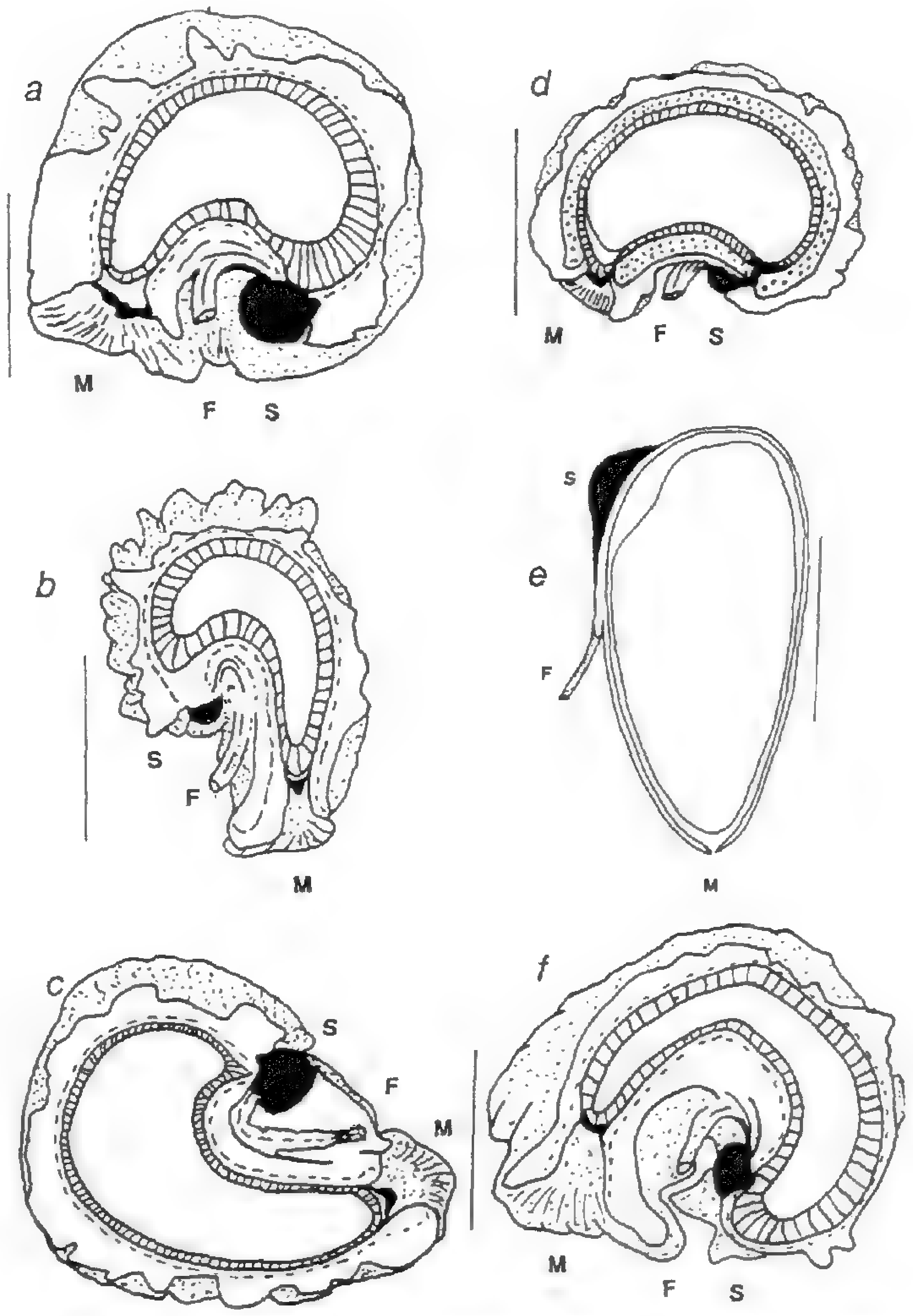

FIGURE 6. Seeds of Lasieae drawn from specimens in Figure 5.—a. *Dracontium soconuscum.*—b. *Dracontioides desciscens.*—c. *Anaphyllopsis cururuana.*—d. *Pycnospatha arietina.*—e. *Anaphyllum wightii.*—f. *Cyrtosperma merkusii.* F = funicle, M = micropyle, S = strophiole. Scale bar = 2 mm.

SUBTRIBE 2. PYCNOSPATHINAE BOGNER

Pycnospathinae Bogner, Oesterr. Bot. Zeitschr. 122:202. 1973.

Cormous plants with solitary, usually highly dissected leaves. Spathe hood-forming. Flowers atepalate. Fruit spiny. Seed campylotropous, albuminous; seed coat hard, warty, containing druses.

Distribution. A single Indochinese genus.

Pycnospatha Thorel ex Gagnepain, Bull. Soc. Bot. France 88: 512. 1941. TYPE: *P. palmata* Thorel ex Gagnepain [Type: Laos: Ben-chom, Sedom, *Thorel* 2404 (holotype, P).]

Cormous herbs with solitary highly dissected leaves on spiny spongy petioles, emerging from the cataphylls early as in *Dracontium* species; posterior lobes forked 3 times, anterior lobe trifid, the central member trifid again, the laterals unequally forked; leaflets sessile, ± confluent, with brochidodromous pinnate venation, or the leaf entire with the anterior lobe trisect with a pair of opposite lateral lobes, and the posterior lobes 1 × pedatifid; rachides with scattered leaflets throughout. Inflorescence solitary, accompanying the leaf, peduncle much shorter than the petiole; spathe sharply hood-forming, purple with pale longitudinal streaks; spadix sessile or shortly stipitate. Flowers hermaphrodite throughout, atepalate; stamens 6+; ovary unilocular, uniovulate with basal to subbasal placentation, style elongated, stigma punctiform. Fruit a reddish spiny berry ca. 1 cm diam. (Fig. 7), pericarp (in spirit material) hard, rather corky,

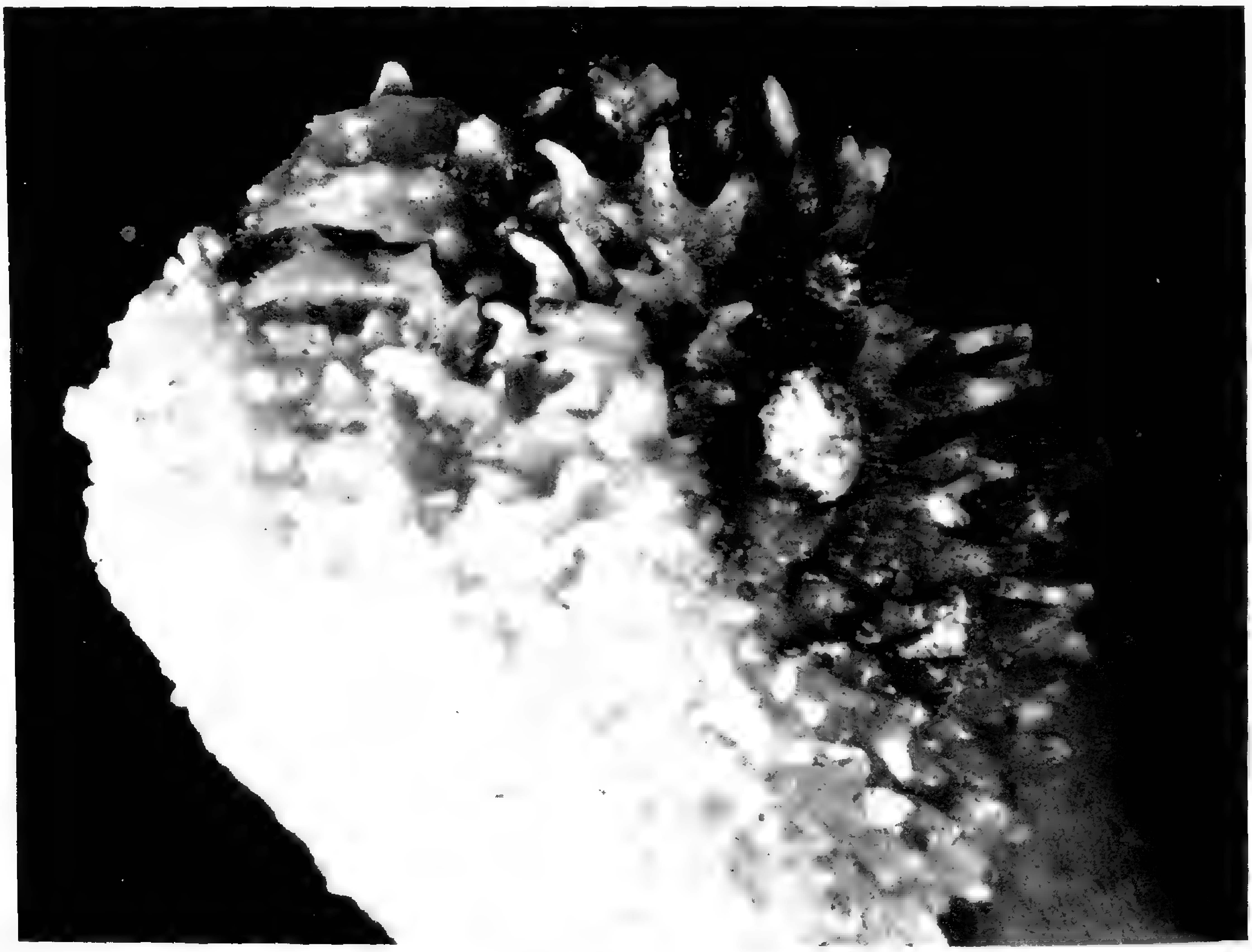

FIGURE 7. Pericarp of *Pycnospatha arietina* (*Bogner 395*, K). The fruit is ca. 1 cm in diameter.

firmly appressed around the seed. Seed black or very dark brown, seed coat hard, thick, warty, containing white druses in "tegmic" layer of pachychalaza (Figs. 5d, 6d).

Distribution. Two species from rather open sites in areas of evergreen forest in Thailand and Laos. Rare. Bogner (pers. comm.) noted that *P. arietina* Thorel ex Gagnepain is locally common in Thailand.

The genus has recently been revised and the species described in detail by Bogner (1973). He recognized two species, reducing *P. soerensenii* S. Y. Hu to synonymy with *P. arietina*. Bogner noted that the genus is close to *Dracontium* on the basis of the corm, highly compound ± solitary leaves, spiny petioles, hooded spathe, and warty seed coat, a conclusion with which I concur. However, the presence of druses in the seed coat, which are unknown in other members of the Lasieae, and the atepalate flowers set the genus apart.

The leaf blade of *P. arietina* is similar to that of some species of *Dracontium*, but at no stage in the juvenile to adult sequence is there any evidence of fenestrate development, hence the segments may be regarded as outgrowths rather than as "cutouts." The posterior rachides are more or less equally divided three times, with the outermost (i.e., those farthest from the anterior lobe) products of each fork somewhat more elaborate than the inner, creating a "tri-pedate" effect. The anterior rachis undergoes a major division into three about a third of the way along its length, and the central member repeats this near the tip. The lateral members of these divisions undergo somewhat irregular forking with some overtopping. Throughout, the rachides are bounded by an irregular narrow wing arising on the adaxial surface on either side of the lamina. Here and there, this wing is thrown into a "leaflet," the costa(e) of which emerge(s) from the adaxial part of the rachis. By contrast, the major divisions of the rachides are complete and more or less equal, including those that produce the ultimate rachillae. Those leaflets that are scattered along the main rachides may be regarded as supernumerary, and their origin is tentatively ascribed to a process of space filling in the tightly folded developing leaf. They also occur in species of *Amorphophallus*, *Dracontium*, and *Taccarum*, and in *Tacca leontopetaloides* (L.) Kuntze (Taccaceae). The leaf construction of the last-mentioned is very similar to that of *Pycnospatha arietina*.

In subadult leaves of *P. arietina*, the anterior lobe is trilobed with two pairs of opposite costae corresponding to the divisions of the mature anterior rachis described above. The posterior lobes are bilobed, with their midribs forked. Adult leaves of *P. palmata* are almost identical with subadult leaves of *P. arietina,* and the species seem otherwise to differ only in the style, which is straight in *P. arietina* and curved in *P. palmata.*

The Monstereae have a preponderance of members with naked hermaphrodite flowers; otherwise, only *Calla* of the enigmatic Calloideae shares this characteristic with *Pycnospatha.* Indeed, Gagnepain (1941) stated that *Pycnospatha* clearly belongs in the Calloideae, although he indicated that the spadix contains a mix of male and female flowers. This was not Krause's view of *Calla,* for which he noted "flores hermaphroditi vel superiores abortu masculi, nudi" (Krause, 1908). Bogner (1973) took the view, followed here, that the flowers of *Pycnospatha* are hermaphrodite.

Spiny fruits are extremely rare in the Araceae, occurring only in this genus and in *Lasia.* In both genera the spines are rudimentary and scarcely seem to have ecological significance. The phylogenetic significance of spiny fruits has been discussed by Corner (1949, 1952–1954, 1964, 1966) in relation to the Durian Theory. The allegedly primitive armed loculicidal capsule of arillate seeds is not known to occur in Araceae, although arillate seeds are known and sarcotestas are common. In the Lasieae the seed has an oily strophiole and the fruits are indeshiscent. That spines appear in a more or less rudimentary state in this relictual group suggests that they may be interpreted as vestigial.

The seed is less strongly curved in *Pycnospatha* than in other members of the tribe (other than *Anaphyllum*), has a slightly enlarged hilum, and its coat is dark brown throughout, whereas in other genera the pigmentation is concentrated in the surface layers of cells. The inclusion of white crystalline druses is unique.

SUBTRIBE 3. ANAPHYLLINAE

Subtribe **Anaphyllinae** A. Hay, subtribe nov.
TYPE: *Anaphyllum* Schott.

Caudex hypogaeus, rhizomatosus, sobolifer vel stolonifer, cataphyllis, prophyllis euphyllisque praeditus; foliorum lamina pinnata vel pinnatipartita, haud fenestrata; spatha spiraliter torta vel plusminusve plana; flores tetrameri; semen anatropum, ovoideum, laeve; integumentum tenue, membranaceum; embryo crassus, rectus; albumen nullum.

Distribution. A single genus, *Anaphyllum,* restricted to southern India.

Anaphyllum Schott, Gen. Aroid. t. 83. 1858.
TYPE: *Anaphyllum wightii* Schott [Type: India. Karnataka: Courtallum, *Wight 2776* (holotype, K).]

Clump- or colony-forming herbs; stem a sympodial series of rhizomes bearing prophylls, cataphylls, and a few foliage leaves. Petioles to ca. 1.5 m tall, smooth to tubercular and then sometimes with warts on distinctly raised flanges, rarely (?)armed; blade pinnate with opposite leaflets, the terminal segment trifid and the posterior lobes sometimes bifid, or the leaf pinnatisect; rachis with a geniculum at the junction with the first and second leaflet pairs, or only at the apex of the petiole. Inflorescence solitary, on a peduncle similar to and about equaling the petiole in length; spathe membranous to coriaceous, marcescent, basally convolute and spirally twisted in the remainder, or the whole ovate and ± flat; spadix much shorter than the spathe, free-stipitate. Flowers tetramerous; receptive stigmas with pollination droplets; ovary unilocular and uniovulate, with parietal placentation. Fruit ovoid, smooth, ripening red. Seed ovoid, filling the locule, anatropous, on a slender funicle thickening toward attachment to seed; seed coat unlignified, membranous, smooth; endosperm absent; embryo stout, straight (Figs. 5e, 6e).

Distribution. Two species from southern India, in evergreen forest and swamp forest undergrowth.

Sivadasan (ined.) recognized three infraspecific taxa in *A. wightii.* The second species, *A. beddomei* Engl., is distinguished by its ovate, open spathe and pinnatifid leaves in contrast to the twisted convolute spathe and usually pinnate leaves of *A. wightii.*

The genus is remarkable for its soft and membranous seed coats, in contrast to the hard ornate campylotropous seeds of other members of the tribe. Monosulcate pollen, early emergence of the leaves, and basipetal maturation of the spadix, however, mark the genus as belonging in the Lasieae.

SUBTRIBE 4. LASIINAE SCHOTT

Lasiinae Schott, Prodr. Aroid. 399. 1860. "Lasinae."

Rhizomatous or suffruticose, solitary, clump-forming, or colonial herbs; leaves and more rarely stems usually armed, sometimes heavily; modules of sympodia multifoliar, with prophylls and euphylls only; leaf blades simple, dissected to hastate;

inflorescence solitary, rarely cymose-paired, on peduncles similar to the petioles; spathes erect to deflected, very rarely hood-forming, sometimes acuminate-twisted, persistent, marcescent, or caducous. Flowers 6–(5–)4-tepalate and -staminate; filaments free, rarely united; ovary bi- or unilocular, multi- to uniovulate; placentation axile, basal, parietal or apical. Fruit a green to red, spiny to smooth, 1-several-seeded berry. Seed campylotropous, reniform, rarely helical, albuminous or not; seed coat hard, pachychalazal, often warty or crested, sometimes smooth.

Distribution. Pantropical excluding Australia. Five genera.

KEY TO GENERA

1a. Stems suffruticose, erect to decumbent, usually with spiny internodes, rarely a condensed rhizome; leaves usually dissected, or hastate; spathe caducous or rarely marcescent; placentation apical; fruit usually spiny. Indomalesia .... *Lasia*
1b. Stem usually a condensed rhizome, rarely with distinct internodes and then unarmed; leaves entire, sagittate to hastate or lanceolate; spathe persistent to marcescent; placentation otherwise; fruit smooth.
  2a. Plants always unarmed; ovary bilocular or rarely unilocular; seed mostly exalbuminous; petioles soft and spongy in the dry state. Neotropics .... *Urospatha*
  2b. Plants nearly always armed (some individuals unarmed); ovary unilocular; seed albuminous or exalbuminous; petioles usually drying rigid. Paleotropics.
    3a. Petioles angular in cross section, armed in rows along the edges; plants stoloniferous, forming large colonies; spathe persistent; filaments of stamens united. Africa .... *Lasiomorpha*
    3b. Petioles ± terete in cross section; armature scattered or in oblique combs; plants solitary or forming small clumps; spathe marcescent or persistent; filaments of stamens free.
      4a. Spines straight and turned downward; rhizome with distinct internodes and roots emerging from between the persistent leaf bases; seed smooth, ± orbicular, to 7 mm diam. West Malesia .. *Podolasia*
      4b. Spines straight and upturned; rhizome condensed; seed crested and/or warty, if smooth then less than 5 mm diam. Malesia to Oceania .... *Cyrtosperma*

An argument could be made for reducing all the genera of the Lasiinae to *Lasia*. The generic limits are narrow. However, the groups here circumscribed appear natural on morphological, geographical, and ecological grounds, and rather than making a large number of new combinations, I have resurrected *Lasiomorpha* to maintain the status quo. The Old World genera have recently been revised by Hay (1988a).

Cyrtosperma Griff., Notul. 3: 149. 1851 & Icon. Pl. Asiat. t. 169. 1851. TYPE: *C. lasioides* Griff. [Type: Malaysia: Malacca, *Griffith 5059* (holotype, K).] = *C. merkusii* (Hassk.) Schott.

Arisacontis Schott, Bonplandia 5: 129. 1857. TYPE: *A. chamissonis* Schott (= *C. merkusii*).

[*Apereoa* Moerenhout, Voyages aux Îles du Grand Ocean 2: 16. 1837, nom. nud.]

Massive to slender rhizomatous herbs, usually solitary, occasionally clump-forming; rhizome thick, condensed, creeping, the older parts long-persistent or quickly rotting. Leaves several, on spiny petioles to ca. 3 m long; blades hastate to sagittate, with a prominent geniculum at apex of petiole. Inflorescence solitary, rarely paired, on peduncles similar to the petioles; spathe erect, rarely somewhat hood-forming, occasionally with the upper part long-acuminate and twisted, convolute or not in the lower part, blackish purple to white; spadix sessile to stipitate. Flowers 6–(5–)4-tepalate and -staminate; filaments free; receptive stigmas wet; ovary unilocular, multi- or uniovulate; placentation basal or parietal. Seed strongly campylotropous, reniform to orbicular to helically twisted, pachychalazal, crested, warty or smooth, albuminous (Figs. 5f, 6f).

Distribution. Eleven species: *C. merkusii* from the Malay Peninsula, Borneo, Sumatra, Java, the Philippines, and Oceania, the rest Papuasian. None is recorded from Sulawesi, Halmahera, or Australia.

Cyrtosperma giganteum Engl. has multiovulate locules. The remaining species are bi- or uniovulate. In part of its range, which has apparently been greatly extended by humans, *C. merkusii* (syn. *C. chamissonis* (Schott) Merr., *C. edule* Schott) is cultivated for the edible and sometimes huge (to ca. 60 kg) rhizome. *Cyrtosperma johnstonii* (Bull) N. E. Br. is cultivated as an ornamental, and there are no wild collections of it, apart perhaps from a seedling from Buka Island in the Papua New Guinea Solomon Islands. *Cyrtosperma cuspidispathum* Alderw. is remarkable for its huge size (the leaves may reach 4 m in length) and for its fruits, which are expelled from the spadix at maturity and remain attached to it by the inner

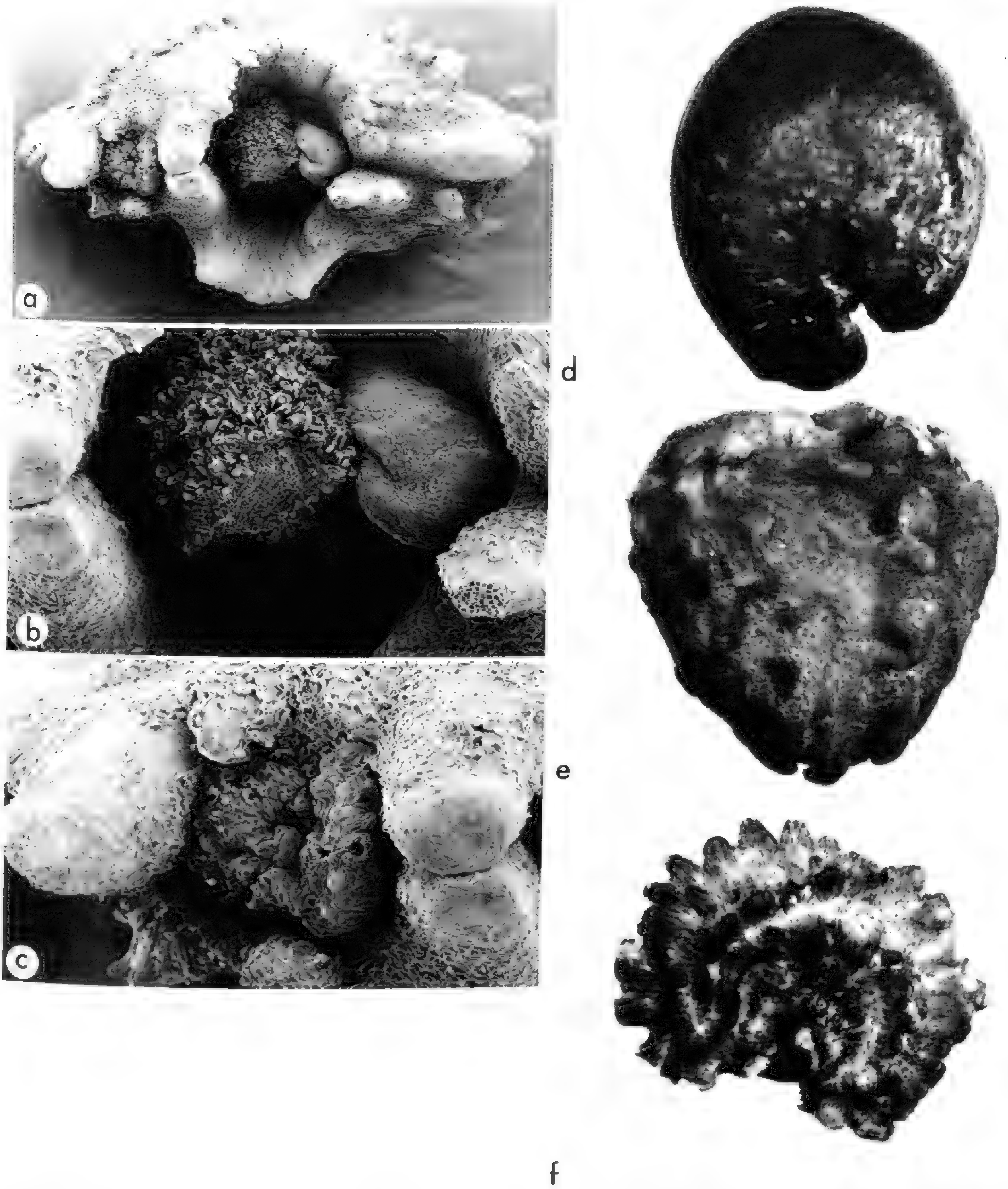

FIGURE 8. Seeds of Lasieae.—a–c. SEM of *Lasiomorpha senegalensis* (*Hay 2701*, FHO).—a. Ventral view.—b. Detail of funicle and strophiole: the locule is filled with mucilage, which may be secreted by the glandular cells covering the funicle.—c. Micropyle: note the operculum with collapsed ovular micropyle. The seed coat appears to be the result of growth in the chalazal region of the ovule. It forms a "new" coat and a "new" micropyle and throws the ovular integuments forward as an operculum. The pattern is typical of all genera except *Anaphyllum*.—d. *Podolasia stipitata* (*King's collector 5324*, K).—e. *Lasia spinosa* (*Nicolson 1651*, K).—f. *Urospatha sagittifolia* (*Bogner 580*, K). See Figure 9 for scale.

epidermis of the tepals, as is often the case in *Anthurium* (Hay, 1988a, 1990).

Lasiomorpha Schott, Bonplandia 5: 127. 1857. TYPE: *Lasiomorpha senegalensis* Schott (syn. *Cyrtosperma senegalense* (Schott) Engl.). [Type: Senegal: *Perrotet 763* (lectotype, P, selected by Knecht, 1983).]

Robust and sometimes massive colony-forming herb to 3.5 m high; stem a short dense rhizome to 12 cm diam. bearing slender, sometimes branching stolons to 3 m long. Leaves several together,

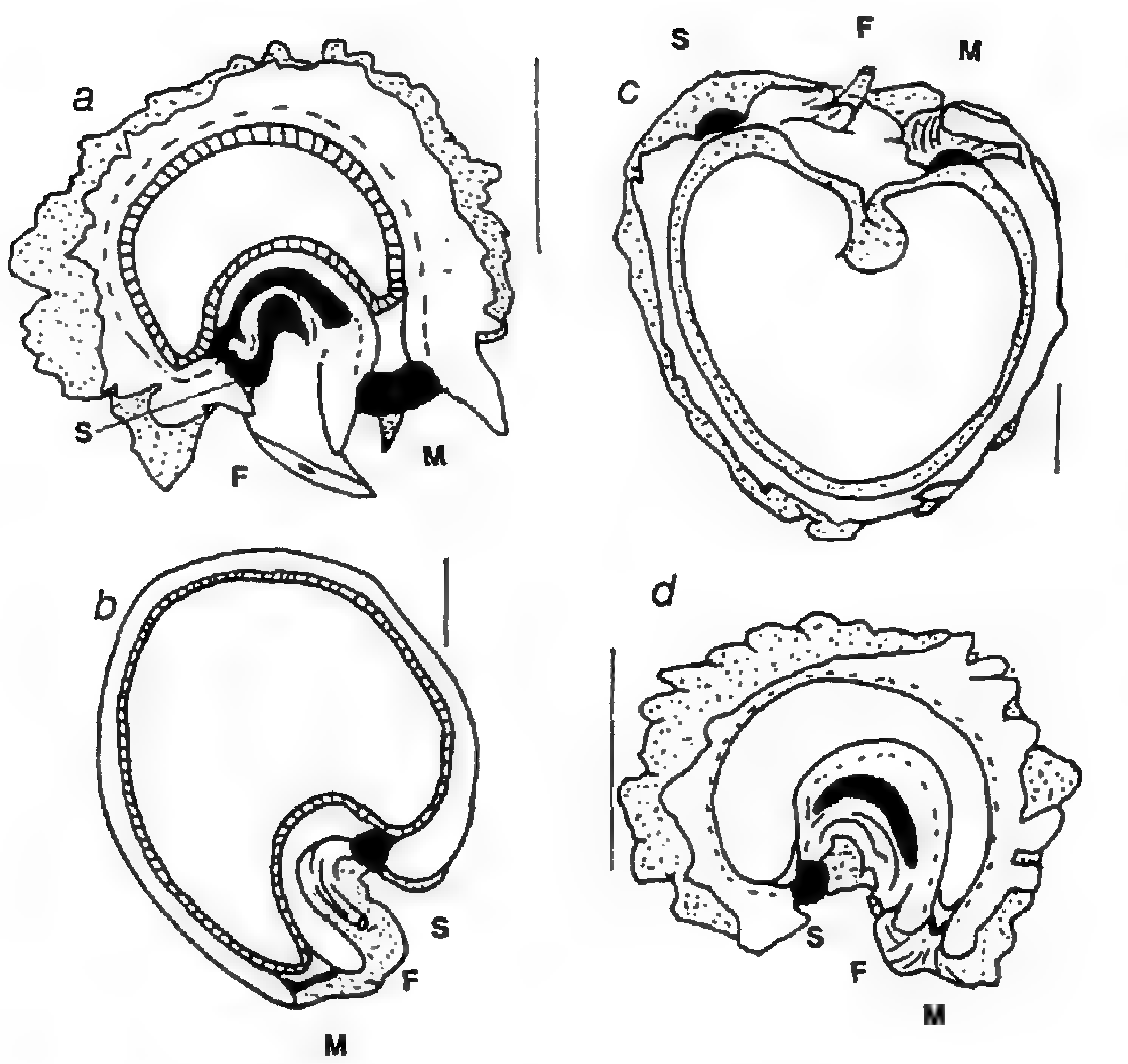

FIGURE 9. Seeds of Lasieae drawn from specimens in Figure 8.—a. *Lasiomorpha senegalensis.*—b. *Podolasia stipitata.*—c. *Lasia spinosa.*—d. *Urospatha sagittifolia.* F = funicle, M = micropyle, S = strophiole. Scale bar = 2 mm.

on petioles angular in cross section and armed in vertical rows along the edges; sheath short, persistent; geniculum absent or very weakly differentiated; blade hastate to sagittate, unarmed, leathery, to 1.2 m long. Inflorescence solitary on a peduncle similar to and about equaling the petioles, without a geniculum; spathe ovate, to ca. 40 cm long, convolute in the lower portion, erect, brownish green without, purple streaked with yellow within, after anthesis becoming green, persistent; spadix shorter than the spathe, ± sessile. Flowers 4-tepalate and -staminate; filaments united into a short tube; ovary slightly inferior; pollination drops present; ovary unilocular, 4–6-ovulate, with a rather prominent basal and parietal placenta. Seeds to 5 × 5 mm, strongly campylotropous, with rudimentary aril, several per fruit; coat hard, brown, warty and spiny (Figs. 8a, b, c, 9a).

Distribution. A single Tropical West African species from Senegal to Chad to Angola, in ditches, swamps, ponds, and swamp-forest gaps; often very common.

Engler (1879, 1911) included *Lasiomorpha senegalensis* and *Cyrtosperma giganteum* in his section *Lasiomorpha* of *Cyrtosperma* because of the multiovulate, unilocular ovary, and endospermous seed. *Lasiomorpha senegalensis* differs from *Cyrtosperma* sensu stricto by having persistent spathes (a feature shared with *Urospatha*), angular petioles (similar to the unarmed ones of *Urospatha loefgreniana* Engl.), stolons (occurring otherwise only in *Lasia*), more elaborate fruits with tough red inner and outer epidermis and white mesocarp, filaments united into a tube (a previously overlooked feature), somewhat inferior ovaries, and absence of (or weakly differentiated) genicula on the petioles and peduncles. These distinguishing characters are matched by its isolated geographical position (Hay, 1988a).

Schott recognized a second species, *L. afzelii*, based on a monstrosity with a ± spherical spadix (Brown, 1902).

Podolasia N. E. Br., Gard. Chron. New Ser. 18(2): 70. 1882. TYPE: *P. stipitata* N. E. Br. [Type: cult. in Hort. Veitch ex Borneo, *Curtis s.n.* (holotype, K).]

Rhizomatous herbs, solitary or forming small clumps by branching of the rhizome; stem erect to decumbent, short, to ca. 2.5 cm diam., with distinct, unarmed, green internodes to ca. 2 cm long, rooting between the persistent leaf bases. Leaves several together, hastate to sagittate, with long petioles armed with mostly down-pointing, stout spines. Inflorescence solitary; peduncle similar to and about equaling the petioles; spathe ovate-lanceolate, purple-brown, open to the base; spadix usually stipitate, the stipe growing considerably after the spathe has opened. Flowers hermaphrodite throughout, 4–6-tepalate and staminate; filaments free; ovary unilocular, uniovulate with parietal to basal placentation; receptive stigmas wet. Fruit red, smooth, large, ca. 1.2 cm diam., thicker than the spadix. Seed strongly campylotropous, ± spherical in outline; coat thin, hard, smooth, dark brown; endosperm very sparse (Figs. 8d, 9b).

Distribution. One west Malesian species chiefly confined to peaty soils.

The genus appears intermediate between *Cyrtosperma* and *Lasia* in its photosynthetic, rather elongated stem and in the venation of the posterior lobes, which is more similar to that of hastate leaves of *Lasia spinosa* than it is to *Cyrtosperma*. *Podolasia* agrees with *Cyrtosperma* in placentation and fruit.

Podolasia stipitata was introduced from Borneo by the nurseryman Veitch and described from cultivated material.

Lasia Lour., Fl. Cochinch. 81. 1790. Not "*Lasia*" P. Beauv. (1804), which is *Forsstroemia* Lindberg (Musci—Cryphaeaceae). TYPE of *Lasia*:

L. aculeata Lour. [Type: Vietnam, nr. Hanoi, *Loureiro s.n.* (holotype, BM).] = *L. spinosa* (L.) Thwaites.

[*Lasius* Hassk., Cat. Bog. 59. 1844. sphalm.]

Clump and colony-forming (rhizomatous or) suffruticose stoloniferous herbs; stems orthotropic to decumbent, to ca. 1.5 m long/tall, with distinct prickly green internodes (or condensed and unarmed). Leaves several; petioles prickly, drying spongy, not or faintly mottled; blades (4×-)pinnatifid to hastate. Inflorescence solitary, on peduncles similar to and usually shorter than the petioles; spathe narrowly lanceolate (rarely ovate), convolute at base often long acuminate and spirally twisted, caducous (or marcescent), purplish brown to greenish; insertion annular, not oblique; spadix sessile. Flowers 4(–6)-tepalate and -staminate; filaments free; ovary unilocular, uniovulate, with apical placentation. Fruit green, minutely spiny in apical part or spines absent. Seed large, ± pyramidal, ca. 1 cm diam., seed coat thin, brown, hard, with a few appressed spines; endosperm absent (or residual) (Figs. 8e, 9c).

Distribution. The full range of the genus is occupied by *L. spinosa* (L.) Thwaites, from India and Sri Lanka to Nepal, China, Indochina, and Malesia; not recorded from Sulawesi, Moluccas, or Australia; in moist forests and open swamps and ditches, to 350 m.

A second species is known only from cultivation: *Lasia concinna* Alderw. was described from a single individual said to have come from Borneo and is still growing at Bogor. It differs from *L. spinosa* in the 3–4× dissected leaves, ovate-lanceolate marcescent spathe, and massive condensed rhizome. This plant may be a hybrid with *Cyrtosperma merkusii* (Hay, 1988c).

In spite of the wide range of *L. spinosa,* there is no obvious dispersal mechanism. The fruits remain green, and though spiny in their top part, there is no tendency to form hooks; in some individuals spines are lacking. Apparently the infructescences disintegrate, and the fruits get washed along. It is therefore of interest that *Lasia* occurs on both sides of Wallace's Line and is absent from Sulawesi. The seeds and fruits show no apparent adaptation to enable them to survive long inundation in salt water. Geography of the Lasiinae is discussed at the end of this paper.

Urospatha Schott, Aroideae 3, figs. 8–10. 1853 & Gen. Aroid. 86. 1858. LECTOTYPE: *U. sagittifolia* (Rudge) Schott, selected by Nicolson (1967). [Basionym: *Pothos sagittifolium* Rudge, Pl. Gui. 24, t. 34. 1805. Type: "Guiana," *Martin s.n.* in Herb. Rudge (holotype, BM).]

Urospathella Bunting, Phytologia 65: 391. 1988. TYPE: *Urospathella wurdackii* (Bunting) Bunting. [Basionym: *Cyrtosperma wurdackii* Bunting, Acta Bot. Venez. 10: 285. 1975 [1977] = *Urospatha wurdackii* (Bunting) A. Hay, Blumea 33: 457. 1988. Type: Venezuela. Territorio Federal Amazonas: Río Guainía, sabanita, 1 km above Pimichín, *Maguire & Wurdack 36384* (holotype, NY).]

Unarmed herbs, robust to slender, solitary or clump-forming, with condensed rhizomes. Leaves several together, on smooth to rough, sometimes angular petioles; blades sagittate, hastate, sometimes lanceolate with the posterior lobes absent or reduced to auricles; venation of the anterior lobe pinnate or curvinerved (when the anterior lobe much reduced and slender, then the primary veins reduced to 2 submarginal veins and the secondaries pinnately arranged along the midrib). Inflorescence solitary on peduncles similar to the petioles; spathe erect, usually convolute in lower part, mostly with a twisted acuminate upper portion, sometimes ± flat; spadix with hermaphrodite flowers throughout, sessile or stipitate. Flowers 4–6-tepalate and -staminate; filaments free; ovary usually bilocular with axile placentation or unilocular with basal-parietal placentation; receptive stigmas wet. Seed campylotropous, smooth to heavily warted, pachychalazal; seed coat hard, brown; endosperm usually absent (Figs. 8f, 9d).

Distribution. About twelve species from Central America and tropical South America, mostly in open habitats including wet places in savanna vegetation.

The genus is in need of revision. It is apparently one of the larger genera of Lasieae. However, a number of the "species" may be referable to *U. sagittifolia* in addition to those already suggested for merging by Jonker-Verhoef & Jonker (1953). The "species" seem to be rather characterless in the herbarium, and more photographs and living material would prove useful. For example, the angular petioles of *U. loefgreniana* Engler, from Brazil, become more or less indistinguishable from cylindrical petioles when dried. Leaf shape and venation are extremely variable within species of *Cyrtosperma, Lasia, Lasiomorpha,* and *Podolasia.* No doubt this is the case in this genus. Likewise it is highly probable that flowering takes place before the plants have reached full size, so that the inflorescences can be expected to be phenotypically variable as well. Seeds may prove to be useful in species delimitation.

This genus and *Dracontium* show the parallel reduction series to the unilocular condition already completed in other genera. Since Engler's monograph (1911), in which he considered *Urospatha* characteristically to have bilocular ovaries, two Venezuelan species with unilocular ovaries have been described: *U. savannarum* Steyermark and *U. wurdackii* (Bunting) A. Hay. The latter was first described as a species of *Cyrtosperma* (see above). Bunting (1988) recently erected the genus *Urospathella* for the latter species, giving no adequate grounds for not recognizing the species in *Urospatha.* He argued that the unilocular ovary sets it aside from *Urospatha* sensu stricto and took the stance that the unilocular ovary described for *Urospatha savannarum* Steyerm. is yet to be verified. However, Steyermark showed in his figure of *Urospatha savannarum* a unilocular ovary (Steyermark, 1951, fig. 15). In his diagnosis of *Urospathella* Bunting (1988) described the locule as biovulate, as it often is in bilocular species of *Urospatha.* He noted that the ovules are basifixed, where they are centrally placed on the partition of the ovary in the bilocular species. Clearly in unilocular species the ovules cannot occupy the position they occupy in the bilocular species, so that in this case the position of the ovules can carry very little weight. He also reported that the ovule form is also distinctive "having the funiculus inserted at the center of the ovule, nearly perpendicular to its axis." If it is to be understood from this that the funicle is inserted about midway along the length of the ovule, this is normal for the tribe.

He further distinguished *Urospathella* from *Urospatha* on the basis of the twisted spathe of the latter. The spathe is not twisted in *Urospatha savannarum* (Bogner, pers. comm.), and species with twisted and untwisted spathes occur in *Lasia, Cyrtosperma,* and *Anaphyllum.* This distinction in spathe form concerns only the distal portion of the spathe limb and is trivial compared with distinctions in spathe form affecting the body of the spathe, such as between *Dracontioides* and *Anaphyllopsis.*

Bunting (1988) further reported seed form and leaf shape as distinguishing features of *Urospathella.* Verrucose exalbuminous seeds occur in *Urospatha wurdackii* and in other species of *Urospatha* (Bogner, pers. comm., see also Figs. 8f and 9d). More recently, Bunting (1989) has published anatomical evidence that the seed of "*Urospathella wurdackii*" is albuminous, supporting the segregation of this species in a genus of its own. However, it now seems that the status of the endosperm in mature seeds of *Urospatha* species is something of a gray area, with small amounts of endosperm sometimes being found in the seeds of *U. sagittifolia* (Bogner, pers. comm.). In effect, this finding removes the only reason for segregating *Urospathella* that carries significant weight. The lanceolate leaf is a distinctive feature of this species, and, in Bunting's (1988, 1989) view, of the genus *Urospathella.* The seedling leaves of *Urospatha sagittifolia* are ovate to lanceolate (Bogner, pers. comm.) as they are in *Cyrtosperma.* A putative case of neoteny in the foliage leaf blade is an inadequate basis for a genus, especially in a family where diversity of leaf form characterizes so many genera. Even taken together, the suite of characters Bunting used to erect *Urospathella* can only be seen as those distinguishing "*Urospathella wurdackii*" from other species of *Urospatha.*

The Englerian concept of *Urospatha* (bilocular ovaries; exalbuminous seeds) is no longer tenable. At this point it remains only to say that *Urospatha* sens. lat. seems homogeneous in both aspect and geography, but that it requires a monograph for its characterization to be established.

Urospatha friedrichsthalii Schott, from Nicaragua, an illustration of which accompanies the generic protologue (Schott, 1853, fig. 7), is a *Sagittaria* (possibly *S. montevidensis* Cham. & Schlecht.) in the Alismataceae.

GEOGRAPHY OF THE TRIBE

In the absence of fossil evidence earlier than the Miocene for seeds attributed to *Urospatha* from Germany and the Urals (Mai & Gregor, 1982; Gregor & Bogner, 1984), interpretation of the distribution of the Lasieae with reference to their age and origin is problematic. Distributions of the tribe and the subtribes are shown in Figures 10–13.

The distribution of the Dracontiinae (Fig. 10) suggests that this group is Gondwanan in origin and that *Dracontium* has extended northward into Central America and southern North America. *Anaphyllopsis* and *Dracontioides* have relict distributions in South America and are confined to areas coinciding exactly with Pleistocene forest refugia proposed by Prance (1982). *Anaphyllopsis* has three species confined one to each of three refugia in the Guianas, western Venezuela, and Pará, Brazil

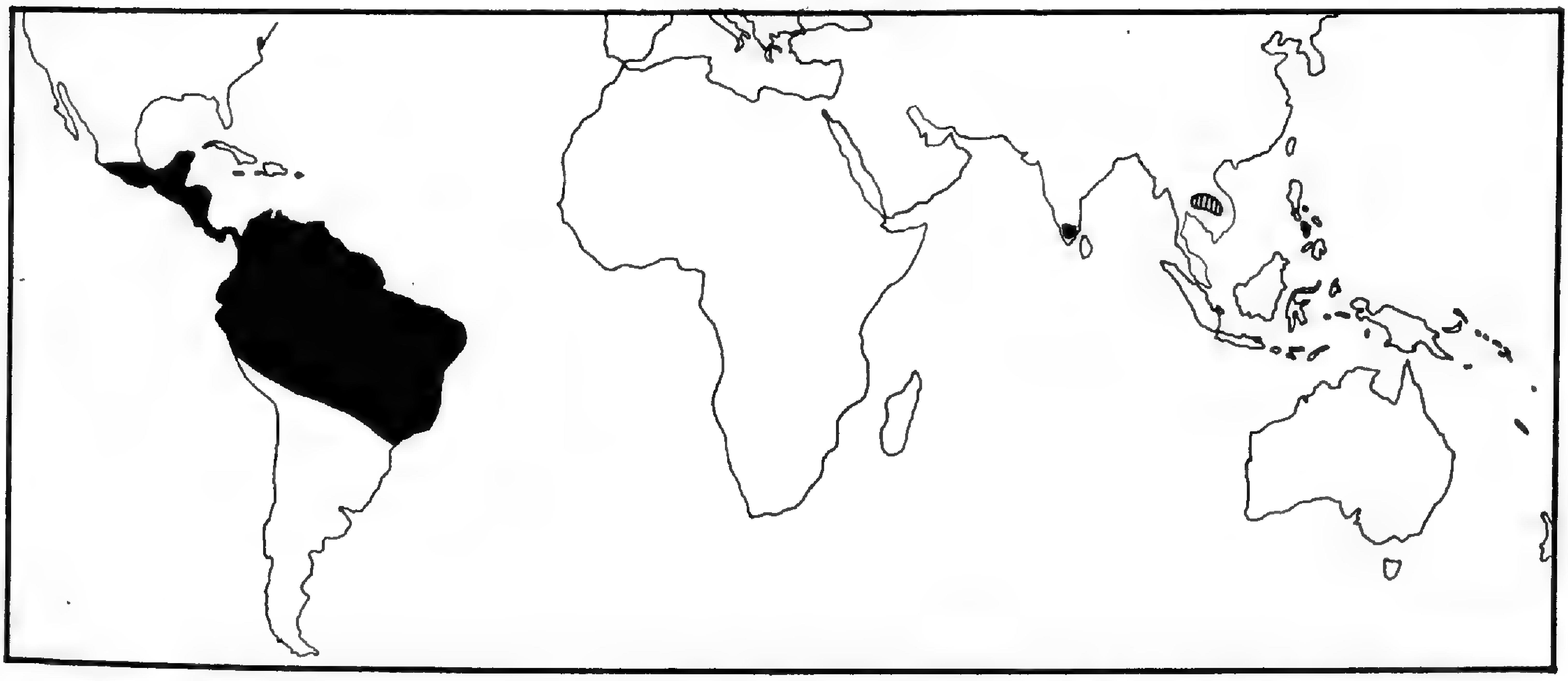

FIGURE 10. World distribution of Lasieae subtribes Dracontiinae (black, New World), Anaphyllinae (black, India), and Pycnospathinae (vertical hatching).

(Hay, 1988b) and the monotypic *Dracontioides* is confined to two refugia in eastern Brazil (Fig. 11). By contrast, Pycnospathinae (Fig. 10), considered here and by Bogner (1973) to be closest to Dracontiinae, are isolated relictually in Laurasian Indochina. Anaphyllinae (Fig. 10) are restricted to and relictual in Gondwanan India, though one cannot discount the possibility of *Anaphyllum* having migrated into India from a Tertiary tropical Laurasian flora such as postulated by Wolfe (1975).

The Lasiinae (Fig. 12), whose distribution almost covers that of the whole tribe, are similarly equivocal. *Lasiomorpha* and *Urospatha* show close austral amphi-Atlantic affinity, suggesting Gondwanan origin. However, in the East (Fig. 13), there is a center of generic diversity in Laurasian West Malesia (one species each of *Lasia*, *Podolasia*, and *Cyrtosperma*), and *Lasia spinosa* and eleven species of *Cyrtosperma* in Gondwanan Papuasia, with no representatives in Sulawesi, Halmahera, or Australia.

The Papuasian representatives of *Cyrtosperma* are almost certainly *originally* Papuasian. The species are few, uncommon, and mostly well differentiated at specific and supraspecific levels, and thus the genus does not appear to be a new arrival undergoing speciation. However, *Cyrtosperma merkusii*, which is evidently wild only west of Wallace's Line, a biogeographic demarcation reflecting a line of contact between the Australian plate and Laurasia, has its closest relatives in the Solomon Islands and the Lousiade Archipelago, except for *C. giganteum*, which is known only from a single locality on the New Guinea mainland. It can be suggested that, since the collision of the Australian plate with the Indonesian Archipelago some 15 million years ago (Whitmore, 1973), a *Cyrtosperma* crossed Wallace's Line and *C. merkusii* subsequently evolved in West Malesia. However, the absence of the genus from Sulawesi and Halmahera, and the confinement of most of the nearest relatives of *C. merkusii* to eastern Papuasia militate against this suggestion. Furthermore, although *Cyrtosperma* is probably bird-dispersed, there are no species common to long-separated islands (except in the eastern part of the range of *C. merkusii*, where human agency is suspected), indicating that migration across open ocean is highly improbable.

A similar though reversed picture is presented by *Lasia spinosa*. (The second species of *Lasia*, *L. concinna*, is of doubtful status and origin and is ignored here.) *Lasia spinosa* is found from Sri Lanka to southern China and West Malesia, where it is restricted to areas bounded by the Sunda Shelf. It is absent from the Philippines, Sulawesi, and Halmahera, and then reappears on the Sahul Shelf as a rare plant throughout lowland New Guinea and in the Bismarck Archipelago (Hay, 1981, 1988a), though it is absent from Australia. It has no evident means of traversing open ocean: the fruit wall is thin, fleshy, unpalatable, and inconspicuous; though minutely thorny, it is not hooked or sticky. The seed coat, although hard, is thin and the micropyle is large; neither the seed nor the fruit seem likely to survive more than a short period of inundation in salt water. *Lasia spinosa* is a freshwater swamp plant occurring mostly in open habitats in seasonal and aseasonal climates. If *Cyrtosperma*, *Lasiomorpha*, and *Urospatha* originated in Gondwanaland, it seems reasonable to

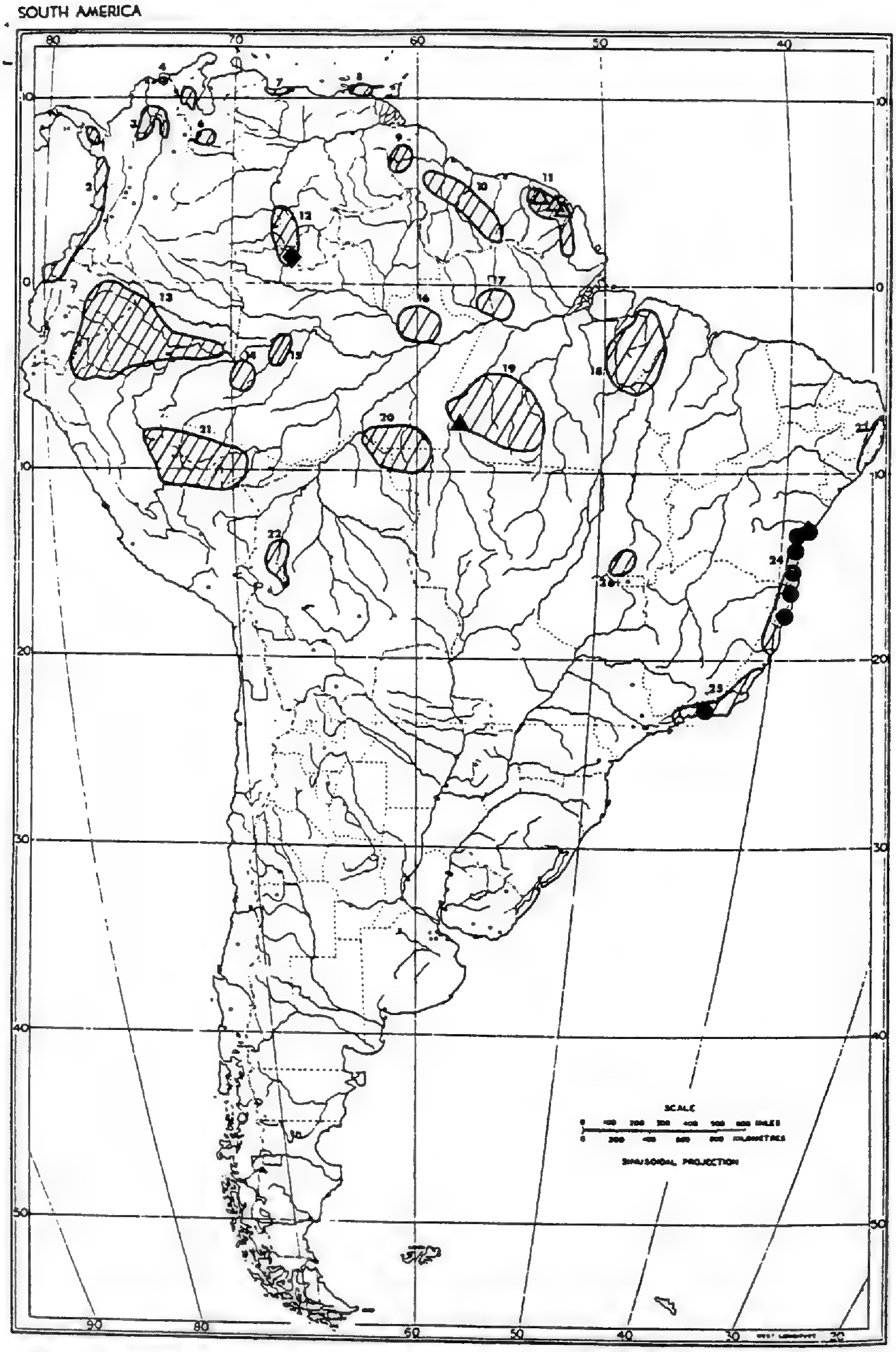

FIGURE 11. The distribution of *Anaphyllopsis* and *Dracontioides* species mapped over Prance's (1982) proposed Pleistocene refugia in South America. ▲ = *Anaphyllopsis cururuana.* △ = *Anaphyllopsis americana.* ◆ = *Anaphyllopsis pinnata* A. Hay. ● = *Dracontioides desciscens.*

surmise that *Lasia* did also, and that it was rafted on India and migrated through Southeast Asia after India reached its present position in the late Tertiary (Axelrod, 1970). However, it is difficult to envisage its migration to New Guinea, both for the morphological reasons above, and on account of its absence from Philippines, Sulawesi, and Halmahera, where there are suitable habitats. The suggestion of migration in the opposite direction involves similar objections.

If, however, trans-Wallacean migration is proposed, it seems clear that *Lasia* must have migrated from west to east, while *Cyrtosperma* must have gone from east to west. If that was the case, the Lasiinae arrived in Malesia twice, *Lasia* and *Podolasia* via India, *Cyrtosperma* on the leading

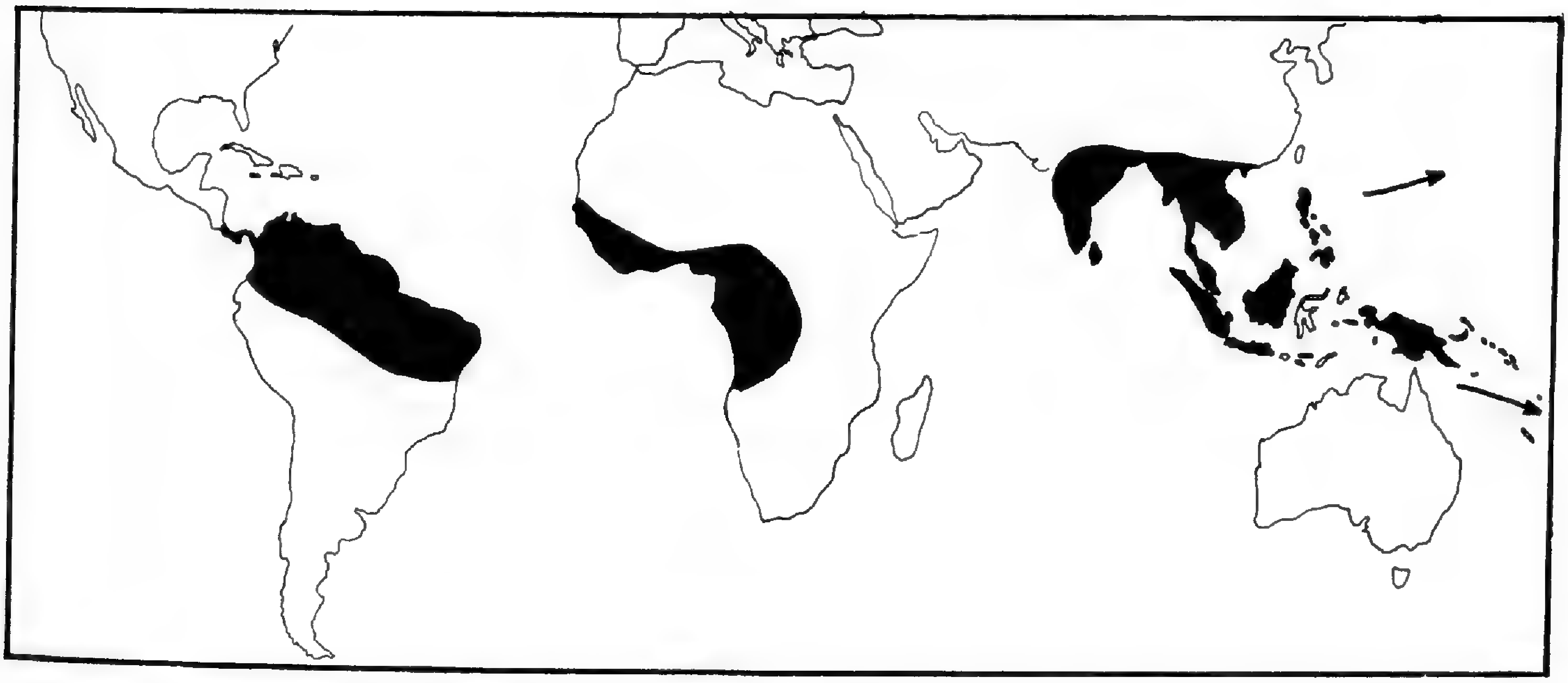

FIGURE 12. World distribution of Lasieae subtribe Lasiinae. Arrows indicate direction of extension of *Cyrtosperma* into Oceania.

edge of the Australian plate. This (and the distribution of *Lasiomorpha* and *Urospatha*) requires that proto-Lasiina predated the breakup of Gondwanaland. Bearing in mind that these genera are very closely related, it is not difficult to modify this hypothesis such that it is suggested that *Lasia* and *Cyrtosperma* had themselves already differentiated before the breakup of Gondwanaland.

Then it is argued that *Cyrtosperma* and *Lasia* have both reached Malesia twice, and that neither of them has undergone long-distance dispersal over sea. It is suggested that, already differentiated by the time Gondwana began to fragment in the late Jurassic/lower Cretaceous, the genera of Lasiinae were distributed such that *Urospatha* rafted off on South America, and *Lasiomorpha* on Africa. In the east, the ranges of *Cyrtosperma* and *Lasia* must have straddled the Indian and Australian plates and were split as India broke away some 140–120 mya (Audley-Charles et al., 1981). Moving east and later north, the aging soils and drying climate of Australia may have provided fewer habitats for this group, which became confined to the poor archipelagic flora of the leading edge of the Aus-

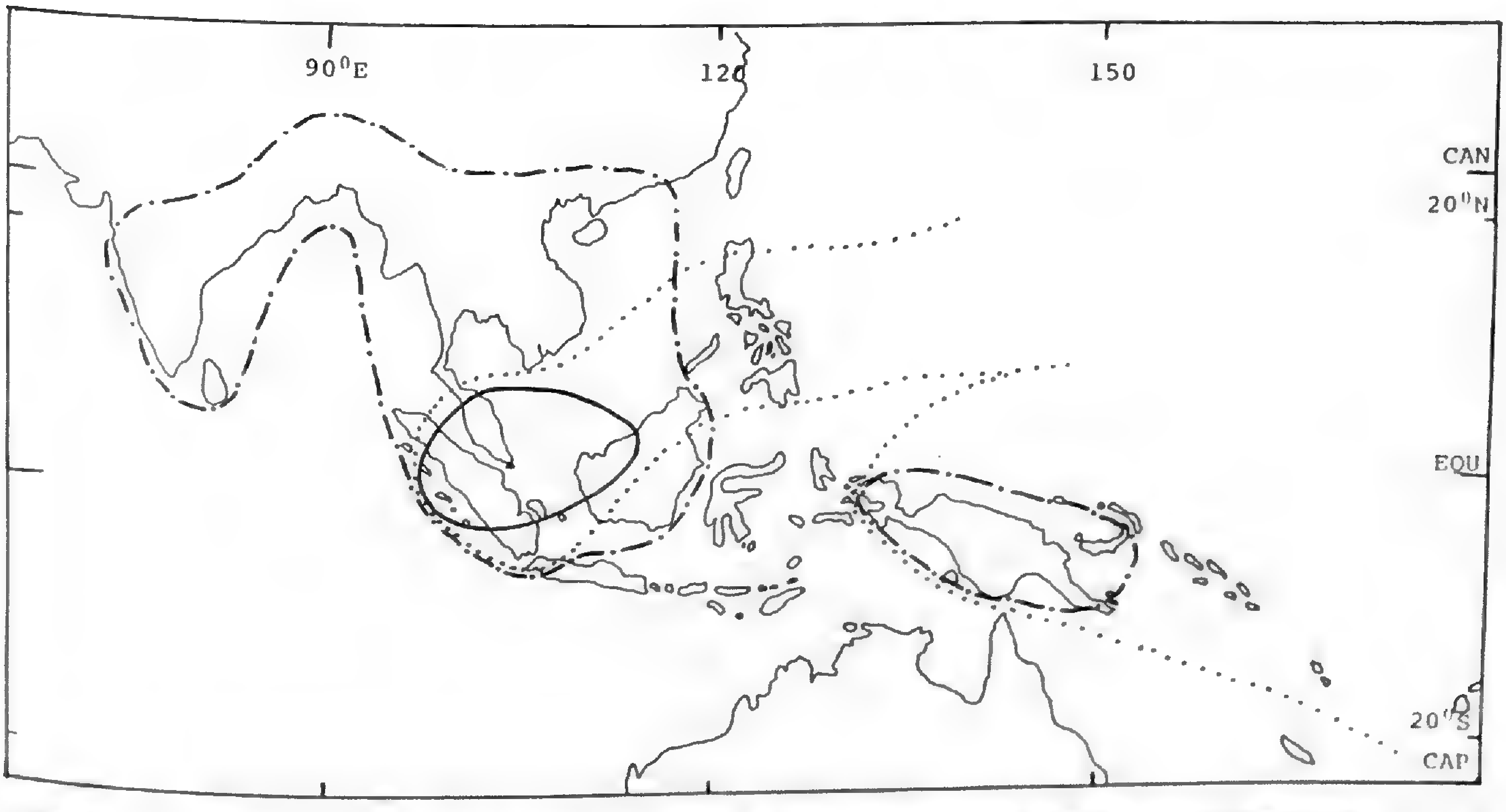

FIGURE 13. Distribution of Lasieae subtribe Lasiinae in Indomalesia. ·-·-· = *Lasia*. —— = *Podolasia*. ····· = *Cyrtosperma*.

tralian plate until the Miocene collision with Laurasia and orogeny in New Guinea (van Steenis, 1979). Meanwhile, after 80–100 my of isolation on India, *Cyrtosperma* and *Lasia* (and *Podolasia*) migrated into West Malesia when the Indian plate collided with Laurasia (Audley-Charles et al., 1981).

Dual arrivals in Malesia have been postulated for other plant groups of fairly low taxonomic rank: Dransfield (1981) used this hypothesis to explain the disjunct distribution of the *Clinostigma* alliance of palms, especially the genus *Rhopaloblaste*, and possibly also for the coryphoid genera *Livistona* and *Licuala*. Whitmore (1981) cited the bamboo genus *Nastus* as another example. Invoked here for the Lasieae, it is necessary to apply the hypothesis to a species—*Lasia spinosa*. As *L. spinosa* shows little tendency even to raciate over its enormous range, a period of stasis in excess of 100 my seems possible for this relict. For *Anaphyllum* and *Pycnospatha*, then, a Gondwanan origin, followed in the latter by migration and contraction in a 40-my-period seems plausible.

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Cover illustration. *Sparaxis villosa* (Burman f.) Goldblatt, by M. L. Branch.

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PHYLOGENY OF ASTERIDAE: AN INTRODUCTION[1]

Larry Hufford[2]

This issue of the *Annals of the Missouri Botanical Garden* includes papers from the symposium "Phylogeny of Asteridae." The symposium was jointly sponsored by the American Society of Plant Taxonomists and the Botanical Society of America and was held at their annual meeting, 7 August 1991, in Richmond, Virginia. As with most higher level plant groups, the monophyly, sister group (or groups), and patterns of relationship of Asteridae are unclear, and few explicit hypotheses address these problems in detail. This symposium was organized to summarize our current understanding and discuss new research on the phylogeny of Asteridae.

The angiosperm subclass Asteridae was first circumscribed by Takhtajan (1964) and subsequently adopted in Cronquist's (1968, 1981, 1988) classifications. The Asteridae of Takhtajan (1964, 1980) and Cronquist (1968, 1981, 1988) are largely limited to taxa with sympetalous corollas and haplostemonous androecia. In this issue of the *Annals*, Wagenitz traces the formal taxonomic recognition of the group based on sympetalous corollas from de Jussieu and de Candolle. Wagenitz discusses characters that support orders and ordinal complexes and outlines problems with our current understanding of Asteridae.

Some investigators (e.g., Dahlgren, 1927; Wunderlich, 1959; Philipson, 1974) have questioned the narrow circumscription of Asteridae and the similar earlier Sympetalae and Gamopetalae to include only taxa with a sympetalous corolla and haplostemonous androecium because most of these taxa share tenuinucellate, unitegmic ovules and endosperm haustoria with a set of choripetalous and often polystemonous taxa. Recently, phytochemical data have been used to question the monophyly of Asteridae. For example, Jensen et al. (1975) hypothesized that Asteridae are polyphyletic and outlined three separate asterid lineages. Jensen's investigations of iridoid chemistry in Rosidae and Asteridae have been particularly important in recent phylogenetic hypotheses and classifications (see especially Dahlgren, 1977, 1983; Takhtajan 1987). Jensen (this issue) discusses two different biosynthetic pathways for iridoids among Asteridae and hypothesizes that taxa with these separate pathways may not be monophyletic. The

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question of monophyly is further addressed in this issue by Downie and Palmer, Hufford, and Olmstead et al. (all of whom conclude that an expanded Asteridae is monophyletic). Hufford, addressing the placement of Asteridae, suggests that they are rooted among taxa circumscribed as Corniflorae by Dahlgren (1983) with Ericales as their sister group.

The relationships among Asteridae were addressed by many symposium participants. Downie and Palmer, using chloroplast DNA (cpDNA) restriction site data, and Olmstead et al., using *rbc*L sequence data, discuss relationships among major asterid clades. Carlquist surveys the implications and limitations of wood anatomy for understanding relationships within Asteridae. Donoghue's phylogenetic analysis of Dipsacales using *rbc*L sequence data provides support for the monophyly of Caprifoliaceae sens. str. (without *Adoxa*, *Sambucus*, and *Viburnum*), Valerianaceae, and Dipsacaceae. Lammers uses results from recent cpDNA restriction site and *rbc*L sequence studies as a basis for refining the circumscription of Campanulales and their families.

The evolution of four large and economically important families of Asteridae is also addressed. Brigitta Bremer uses both morphological and cpDNA restriction site data in a phylogenetic analysis of Rubiaceae and explores the evolution of biotic and abiotic seed dispersal on the basis of her results. Olmstead and Palmer present a phylogenetic analysis of Solanaceae using cpDNA restriction sites. Cantino presents a morphology-based cladistic analysis of Labiatae and suggests a polyphyletic origin among Verbenaceae. The symposium closed with talks on Asteraceae by K. Bremer (emphasizing morphological data) and R. Jansen (emphasizing cpDNA restriction site data). Several issues raised by K. Bremer are discussed in the paper by Karis et al. The talk by Jansen focused on results in papers published since the symposium (Jansen et al., 1990, 1991). The Kim et al. paper in this issue discusses recent investigations of Asteraceae in Jansen's laboratory using *rbc*L sequence data.

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THE ASTERIDAE: EVOLUTION OF A CONCEPT AND ITS PRESENT STATUS[1]

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ABSTRACT

The concept of Asteridae can be traced back to the Monopetalae of Tournefort (1694) and de Jussieu (1789). This group, later better known as the Sympetalae, was essentially based on a single character, the united petals. A closer look at the floral morphology and the study of embryology (especially of the ovules) by Van Tieghem and Warming led to the exclusion of some families (e.g., the Cucurbitaceae). Moreover, it became clear that only the "Tetracyclicae" (with one series of stamina alternating with the petals) may probably form a coherent group. Formal recognition of this group as a subclass was proposed by Takhtajan in 1964 and has been accepted by Cronquist (1968). Recent studies have emphasized chemical characters, although embryology is still important.

Because of a combination of characters, the following orders are good candidates for monophyletic groups: Gentianales (including Rubiaceae, but excluding Retziaceae, Buddlejaceae, and probably Menyanthaceae), Dipsacales, and Scrophulariales (including Plantaginaceae, Lamiales). Still controversial is the circumscription of the Solanales and Campanulales sens. lat. There have been some "imports" of families with strongly reduced flowers (mostly wind-pollinated water plants) formerly placed in orders outside the Asteridae: Hippuridaceae, Callitrichaceae, and Hydrostachyaceae. In these groups, flower morphology alone has been misleading in determining the proper taxonomic position. The position of the Dialypetalanthaceae and Loasaceae, with some characters pointing to an Asteridae affinity but with polyandry, is not clear. More important and much more controversial is the question of the nearest allies outside this group. Several orders in the Rosidae (Rosales, Geraniales, Cornales, Apiales) have been named as probable relatives for part of the Asteridae or for the whole group. However, the evidence is unequivocal neither from morphology nor from phytochemistry.

At the beginning of scientific botany the flower was identified with the corolla as its most showy part. Botanists must have noted very early that in some groups this consisted of several separate parts, the petals, whereas in others it was shed as a whole and formed a single tube or funnel. Linnaeus (1751) called the botanists using criteria of the corolla for the primary division of the system "Corollistae," and the most important of these was Tournefort (1694, 1700). He maintained the old-fashioned division in Arbores and Herbae, and in each of these we find classes defined by the term "flore monopetalo." The Monopetalae were accepted as one of the main divisions of the Dicotyledones by de Jussieu (1789), who can rightly be named the father of the natural systems of the nineteenth century. His Monopetalae are nearly identical with the Sympetalae of later systems.

In 1813, A. P. de Candolle coined the new term gamopetalous ("gamopétale"), which led to the replacement of Monopetalae by Gamopetalae. This meant that the corolla was seen as a product of the fusion of several petals. This is not an ontogenetically visible process and thus can be termed idealistic morphology, but it has in fact later been interpreted phylogenetically. Reichenbach (1828 in Mössler's *Handbuch der Gewächskunde*) seems to have been the first to use the alternative term Sympetalae ("Synpetalae") instead of Gamopetalae. In the systems of the nineteenth century, for example, by Bartling (1830), Endlicher (1836–1840), Bentham & Hooker (1873–1876), Eichler (1876), and Engler (1924), the Gamopetalae or Sympetalae can be found in nearly identical circumscription. An important step to the shaping of the Asteridae was the insight that two groups can be distinguished. A core group (the "Tetracyclicae," a name first used by Warming in 1879) with

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invariably only one series of stamens alternating with the corolla lobes, and a more variable group (the "Heteromerae" of Bentham & Hooker, 1873–1876, or "Pentacyclicae" of Warming, 1879) with two series of stamens or one with stamens superimposed to the lobes of the corolla. The Pentacyclicae comprise the orders Ericales, Diapensiales, Ebenales, and Primulales of modern systems. These are placed in the Dilleniidae in the systems of Takhtajan and Cronquist.

The "Tetracyclicae" are the immediate "ancestors" of the Asteridae. They can be found as a group without a name in Cronquist's (1957) system and were christened by Takhtajan in 1964.

This is the history of the formal concept of the Asteridae. Let us now look at the additional characters used for shaping the group, for the exclusion of some families and the addition of others, for the various attempts to subdivide the group into orders, and for tying the Asteridae to other subclasses. The molecular data that have recently become available have not influenced this overview.

SYSTEMATICS OF THE ASTERIDAE

Besides floral morphology, embryology and, in more recent times, phytochemistry have been of foremost importance in classifying groups. In the second half of the nineteenth century data on at least some embryological features accumulated. Very important was the distinction between ovules with one and two integuments and those with a massive or a very thin nucellus. The first to note this character was Warming in 1878. Van Tieghem (1897) even proposed to base a system on these characters. The Cucurbitaceae are a family that has been excluded at an early date from the Sympetalae by many authors based on this character (and the morphological similarities to families in the "Parietales"). Yamazaki (1974) created a system of the "Gamopetalae" using the embryogeny as the decisive character.

The characters shared by the Asteridae can be enumerated as follows: sympetalous corolla, stamens as many as or fewer than the corolla lobes and alternate with them, and unitegmic, tenuinucellate ovules. The sieve-element plastids are from the S-type (starch-containing), with the notable exception of part of the Acanthaceae (Behnke, 1986). Very characteristic is the constancy in the number of floral parts in most families in Asteridae as compared with other subclasses. This has been shown impressively in a publication by Endress (1990). According to Cronquist (1968), this subclass is "highly natural." The question is: are these characters "shared-derived characters," i.e., are they synapomorphies in the sense of Hennig? We need not argue much about the status as derived characters; this is fairly evident, but it is not enough. Can we be reasonably sure that these characters are not due to parallel evolution originating from different phyletic lines? Of course we cannot be sure, and this is the point where the discussion begins. Before proceeding, however, I will address the larger groups (orders) within the Asteridae.

Good candidates for monophyletic groups are, in my opinion, the Gentianales, Dipsacales, Scrophulariales (including the Lamiales), and probably the Campanulales–Asterales.

The families of the Gentianales (Loganiaceae, Rubiaceae, Apocynaceae, Asclepiadaceae, Gentianaceae) are tied together by a combination of vegetative, floral, and phytochemical characters (Wagenitz, 1959). The group contains basically woody plants with opposite, entire leaves often with stipules (otherwise lacking in the Asteridae), and with colleters, a special type of multicellular glandular hair located on the stipules or the base of the leaves and even inside the calyx (other names for these structures in the calyx are: Intrasepaldrüsen (Glück, 1919), squamellae (Woodson & Moore, 1938), and squamae intravaginales (Vijayaraghavan & Padmanaban, 1969)). An important anatomical character is the occurrence of internal phloem (lacking in the Rubiaceae). The flowers are nearly always regular with an isomerous androecium; contorted aestivation is widespread but is not a common character. Endosperm formation is nuclear with very few exceptions. Indolealkaloids of a special type occur in three families (although not in all genera): The Loganiaceae (excluding the Retziaceae and Buddlejaceae), Rubiaceae, and Apocynaceae constitute a coherent group on the basis of this character (Kisakürek, 1980). The Asclepiadaceae, which are morphologically close to the Apocynaceae, are linked to those Apocynaceae without alkaloids by the presence of cardenolides in both groups. Brewbaker (1967) and Mathew & Philip (1986) have stressed that all the families of Gentianales contain species with binucleate and trinucleate pollen, a fact difficult to evaluate. *Buddleja* and allied genera (Buddlejaceae) and the monotypic Retziaceae differ in many characters from the Loganiaceae and should be placed in the Scrophulariales sens. lat. (Bendre, 1973, 1975; Maldonado de Magnano, 1986a, b; Carlquist, 1986; Engell, 1987; Hegnauer, 1989). Still controversial is the position of the Menyanthaceae (Bohm et al., 1986; Vijayaraghavan & Padmanaban, 1969), which have been assigned to the Solanales (Cronquist, 1988), the Cornales (G. Dahlgren, 1989b), and the Asteranae (Yamazaki, 1974, because of the development of the embryo according to the Asterad type).

The Dipsacales (Caprifoliaceae, Valerianaceae, Triplostegiaceae, Morinaceae, Dipsacaceae) have a combination of the following characters: opposite leaves without stipules, inferior ovary, a strong tendency toward zygomorphy with reductions in the numbers of the stamens and carpels. Several families possess an epicalyx (Hofmann & Göttmann, 1990). The most distinctive character is the type of nectary consisting of a region of unicellular hairs on the corolla or sometimes on a massive structure at its base (Wagenitz & Laing, 1984). This character is not present in *Viburnum*, *Sambucus*, the Adoxaceae, and Calyceraceae, and their position in the order remains questionable, especially because there are other considerable differences (Donoghue, 1983; Troll & Weberling, 1966; Weberling, 1977; Weberling & Hildenbrand, 1982, 1986). Recently an interesting character has been worked out by Stabbetorp (1989) for *Sambucus*, which may connect the genus with the Caprifoliaceae sens. str.: the occurrence of sterile ovules in which megasporogenesis occurs. This should be reinvestigated in other genera. The presence of some special iridoids is a common character of *Sambucus*, *Viburnum*, and the Valerianaceae (Hegnauer, 1989).

It is more difficult to characterize the Scrophulariales, but the core families of this group are closely tied together by a common set of characters. Some of these characters may be lacking in some families but present in others. It has long been known that Scrophulariaceae, Orobanchaceae, Globulariaceae, Pedaliaceae, Martyniaceae, Lentibulariaceae, Gesneriaceae, Acanthaceae, Bignoniaceae, and Myoporaceae form a closely related group. In several cases there are genera or groups of genera that have been shifted from one family to another in this complex (e.g., *Paulownia* from Bignoniaceae to Scrophulariaceae (Armstrong, 1985; Raman, 1989) and *Charadrophila* from Gesneriaceae to Scrophulariaceae (Weber, 1989)). Some authors have included the Martyniaceae in the Pedaliaceae, but pollen morphology does not support this view (Bretting & Nilsson, 1988; cf. Ihlenfeldt, 1967). It is now generally accepted that Plantaginaceae, although rather different in habit and floral construction, belong to this group. Labiatae and Verbenaceae, two families notoriously difficult to delimit (see El-Gazzar & Watson, 1970; Raj, 1983; Hegnauer, 1989), are apparently close to this complex of families too (Cantino, 1982; Dahlgren in G. Dahlgren (1989b) united Scrophulariales and Lamiales under the last-mentioned name). The close affinity between these families is also shown by the difficulties of the recent cladistic analysis by Lu (1990), the purpose of which is to resolve relationships in the group.

In the Scrophulariales flowers are nearly always zygomorphic, with a strong tendency toward reduction in the number of stamens, and with two carpels possessing numerous to few ovules. Endosperm formation is cellular, and endosperm haustoria are common (see Rauh & Jäger-Zürn (1966) and Di Fulvio (1979) for more detailed analyses of the embryological characters). Pollen tube callose (present in the Polemoniales) is absent (Prósperi & Cocucci, 1979; Cocucci, 1983). Occurrence of iridoid substances and the use of stachyose and other oligosaccharides as storing substances are characteristic (Hegnauer, 1989). A micromorphological character that has been emphasized only recently (although basically known since at least 1893) is the occurrence of protein crystals in the nuclei. This is not a feature restricted to this group, but it is otherwise remarkably rare (Speta, 1977, 1979; Bigazzi, 1984, 1986, 1989a, b), and the different types of these inclusions may prove to be of similar interest to those in the sieve-tube plastids in other groups. The "placentoid" in the anthers (a parenchymatous outgrowth from the connective into the locule), present with few exceptions, is an interesting morphological feature connecting the Scrophulariales with part of the Solanales and should be investigated further (Warming, 1873; Hartl, 1964; Huber, 1980; Bernardello, 1987). It may occur outside these groups, for example, in part of the genus *Exacum* (Gentianaceae; Klackenberg, 1985) and in a few cases in the Rosidae (Endress & Stumpf, 1991), but remains a rather rare feature.

The Solanales–Boraginales–Polemoniales complex of families has many features in common with the Scrophulariales. Differences that I tabulated in my 1977 publication are still valid. A closer inspection reveals that most of the characters of the Solanales (sens. lat.) represent the plesiomorphic state, while the Scrophulariales show apomorphic character states. This makes the distinction less certain, and additional characters must be sought. The recent systems show a rather conspicuously different division of this group.

Asterales and Campanulales have long been connected on the basis of morphological characters and the similar pollen-presentation mechanism. The especially striking similarity in this respect between Lobeliaceae and Compositae is probably due to parallelism, but the detailed investigations of the floral development in Goodeniaceae, Brunoniaceae, and Campanulaceae by Leins and Erbar (Erbar & Leins, 1988, 1989; Leins & Erbar, 1987, 1989) have revealed common characters and trends. Together with the occurrence of polyacetylenes in Goodeniaceae, Campanulaceae, and Compositae (Ferreira & Gottlieb, 1982), this speaks for the unity of this group. The screening of 210 dicotyledonous families by Pollard & Amuti (1981) found inulin alone to be the stored substance in all families of Campanulales in the broad sense, in the Asterales, the Calyceraceae, Boraginaceae, and Menyanthaceae. In view of other differences (especially the occurrence of iridoids in the Goodeniaceae and Stylidiaceae; Jensen et al., 1975), however, opinions are diverse about the delimitation of the Campanulales (Carolin, 1978). The Stylidiaceae have been put into the Rosales by Thorne (1983) and in a separate order near the Ericales by Dahlgren (in G. Dahlgren, 1989a, b), and the Goodeniaceae in a separate order Goodeniales near the Campanulales by Vijayaraghavan & Malik (1972).

ASTERIDAE WITH REDUCED FLOWERS

In this section we will look at some families or genera with very simple flowers, in which the perianth is reduced or lacking, that nevertheless have been considered to belong to the Asteridae because of a combination of embryological and phytochemical characters.

1. *Hippuris*. The embryology of this water plant was studied by Juel in 1911. It has unitegmic ovules with a reduced nucellus similar to those found in the Asteridae. Warming (1913) placed *Hippuris* near the Cornaceae (which can have the same type of ovule; see also Leins & Erbar, 1990), but the chemical data are clearly in line with a placement in or near the Scrophulariales (Hegnauer, 1969) as first proposed by Pulle (1938).

2. *Callitriche*. The single genus of this family has for a long time been placed near the Euphorbiaceae or the Haloragaceae, families with simple flowers. As in the case of *Hippuris*, embryological investigations (Samuelsson, 1913; Jørgensen, 1923, 1925) were decisive for the now prevailing opinion: The tenuinucellate and unitegmic ovule, formation of micropylar and chalazal haustoria, and cellular endosperm point to a position in the Scrophulariales-Lamiales complex. Taking into account the opposite leaves, the structure of the ovary, and the chemical characters, most modern systems include Callitriche in the Lamiales (or with these in the Scrophulariales).

3. *Hydrostachys*. This genus constitutes the family Hydrostachyaceae, which traditionally has been associated with the Rosales. Only in the 1960s did the painstaking studies by Jäger-Zürn (1965) and Rauh & Jäger-Zürn (1966, 1967) show that these reduced water plants seem to be derived from the Asteridae, especially the Scrophulariales. Embryological characters and the structure of the gynoecium were the characters showing this, while pollen morphology was not helpful in this respect (Straka, 1988). Recently, Leins & Erbar (1990) have shown that the male flowers can also be interpreted to conform with this view.

All these plants have some deviating character combinations besides the reduced flowers otherwise not known in the Scrophulariales: *Hippuris*: inferior, apparently monocarpellary gynoecium; *Callitriche*: transverse (not median) position of the carpels, free styles; *Hydrostachys*: transverse position of the carpels, median stipules, free styles.

Not many systematists follow Cronquist (1983) in uniting these diverse elements in one order. Although the cladistic analysis by Lu (1990) groups the three families together, the author himself considers the position of *Hydrostachys* uncertain. Additional evidence for the position of these genera is thus still welcome (Leins & Erbar, 1988, 1990).

POLYANDROUS ASTERIDAE

Another puzzle is posed by groups that show some connections with families of the Asteridae but are polyandrous. I will briefly discuss two of these: the Dialypetalanthaceae and Loasaceae. The genus *Dialypetalanthus* has been described as a member of Rubiaceae despite its polyandry, and most recent authors (Hutchinson, 1973; Takhtajan, 1959, 1987; Dahlgren & Thorne, 1985) have accepted a position in the order Rubiales. Others place the family in the Myrtales. The data base is clearly too limited, however. To my knowledge, the embryology and phytochemistry of the Dialypetalanthaceae are totally unknown. If living material is available, once these two types of study have been completed, deciding where to place this family should not be difficult. On the other hand, the Loasaceae have been rather extensively investigated. There are several characters pointing to placement in the Asteridae in embryology or phytochemistry, but these characters are not unequivocal, because they occur in some choripetalous groups too. The combination of an inferior ovary with polyandry (in most genera) makes it difficult to find a close alliance to any family of the Asteridae. Recently, Hufford (1990) has supported

Dahlgren's suggestion that "the family shares an ancestry with Cornales and woody saxifrages." As Cronquist (1988) remarked, this is surely a case where we are eagerly awaiting the results from molecular methods.

POSITION OF ASTERIDAE WITHIN ANGIOSPERMS

After a discussion of the circumscription of the Asteridae, the question remains: Where is the root (or the roots) of this group? In other words, can we find a sister group in the Choripetalae for the Asteridae as a whole or for their subgroups? Bessey (1897, 1915), Hallier (1912), and Wernham (1913) were the first to try an answer. In the earlier discussions of this problem the authors often tried to "derive" (German "ableiten") one recent group from another. This is especially clear from the graphic representations of the systems of Bessey and Hallier, although Cronquist and Takhtajan have used this model too. There are, however, problems with this system. In a strictly phylogenetic system, at least, no extant group can be the ancestor of another (special cases like allopolyploid species excepted); moreover, even if interpreted as meaning "derived from the ancestors of a present group," this is prone to misinterpretations. These difficulties have led many authors to another type of graphic representation: the famous "bubbles" of Dahlgren (1975; also Dahlgren, 1977, 1980; Dahlgren et al., 1981; G. Dahlgren, 1989a, b), which have forerunners in Linnaeus (in Giseke, 1792) and Pulle (1938). A similar scheme has been used by Stebbins (1974) and Thorne (1976, 1981, 1983). These taxonomists avoid discussing the derivation of one group from another, instead, they speak of a common origin or the relatively nearest group.

What is the result of the search for an ancestor or near relative among the nonsympetalous dicotyledons? We cannot go into details here, but I want to give some examples of the reasoning of different authors. Let us analyze how Wernham (1913) tackled the problem. In the search for an ancestor of the "Contortae" (Gentianales, not including the Rubiaceae), he looked for a group with the tendency to an isomerous androecium, a bicarpellate gynoecium, and without a tendency to epigyny. He found this in the Geraniales. From his "apocynal stock" he then derived the "Tubiflorae." Rubiaceae and Dipsacales were associated with the Umbelliferae mainly because of the common occurrence of an inferior ovary with two (or three) carpels and an "umbellifloral" inflorescence of Umbelliferae and Rubiaceae. At that time, presumed affinities rested solely on characters of floral morphology. For us today these arguments alone are not convincing. In past decades embryology and phytochemistry have been used extensively as mentioned before, but difficulties remain.

Two groups of authors may be distinguished. Cronquist (1957–1988) and Takhtajan in his earlier systems (from 1959 to 1980) accepted the Asteridae as a monophyletic group and pointed to a "Rosalean" ancestry (Cronquist from 1981 onward). In the systems by Thorne and Dahlgren the Asteridae are not a monophyletic group (there are remarkable differences among the systems of Thorne from 1976 to 1982, which I cannot dwell upon), and in his most recent system Takhtajan (1987) has accepted a twofold origin too (splitting his old Asteridae into Asteridae and Lamiidae). For Dahlgren, who has been more explicit in his reasoning, chemical characters rank high. Two connections are supposed (see Kubitzki & Gottlieb, 1984):

1. The iridoid-containing groups Gentianales–Scrophulariales (sens. lat.) are linked with the Cornales in a broad sense (including the woody Saxifragales). Besides the chemical character, the occurrence of unitegmic-tenuinucellate ovules in several families of the Cornales can be regarded as a hint to some degree of affinity (Philipson, 1974).

2. The Asterales–Campanulales show several chemical correlations with the Apiales (and Rutales). The impressive list of chemical correspondences between the Compositae and Umbelliferae is tabulated by Hegnauer (1977), and it is interesting that butterflies of the genus *Papilio* fed exclusively on these two families (Richard & Guédès, 1983). Holub et al. (1987) have doubted that the sesquiterpenelactones must be accepted as a sign of a common ancestry because there are differences in the stereostructure (Holub & Buděšínský, 1986). To me, however, it seems improbable that all these different classes of substances (some of them rather rare in plants) have evolved totally independently, especially if other characters (e.g., floral development, Erbar, 1988) are taken into account. As stressed above, the circumscription of the Campanulales is still a problem.

The Solanales and Boraginales, which lack both iridoids and sesquiterpenelactones, are problematic. Most taxonomists place them rather close to the Scrophulariales complex.

Although there has been some convergence between the different systems published in recent times, there are many discrepancies, and admittedly some families are placed by the authors in an order without clear evidence only to dispose of them. Even if we do not mention several families that are still poorly known, there remain a lot of questions, e.g., the placement and delimitation of the Solanales and Boraginales, the position of the Lennoaceae (Yatskievych & Mason, 1986), Hoplestigmataceae (Nowicke & Miller, 1989), Calyceraceae, and the Oleales. Furthermore, the idea of the connection of a larger part of the Asteridae with the "Cornales" or "Cornanae" is somewhat vague because authors differ widely in the circumscription of these groups.

Taxonomists will look at the forthcoming molecular data with great interest, although they will not expect a quick solution of all problems. Molecular taxonomists should bear in mind that without the work of many generations of botanists using classical methods, no one would know what the questions are, where the plants grow, and which of them are the most interesting to analyze.

Finally, it should be noted that the results of recent molecular investigations have deliberately not been taken into account. This should avoid any bias in comparing the different approaches.

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ROSIDAE AND THEIR RELATIONSHIPS TO OTHER NONMAGNOLIID DICOTYLEDONS: A PHYLOGENETIC ANALYSIS USING MORPHOLOGICAL AND CHEMICAL DATA[1]

Larry Hufford[2]

ABSTRACT

Parsimony analysis was used to develop phylogenetic hypotheses for Rosidae and other nonmagnoliid dicotyledons, especially Asteridae. Rosidae were placed among "lower" Hamamelidae as the sister group of *Platanus* and Hamamelidaceae. "Higher" Hamamelidae (Fagales, Juglandales, and Casuarinaceae), Dilleniidae, and Asteridae nest within a paraphyletic Rosidae. With some expansion, the traditional Asteridae are monophyletic. For example, the problematic *Columellia* was placed among Asteridae as the sister group of Caprifoliaceae. Asteridae were placed as the sister group of Ericales among rosids circumscribed as Corniflorae in recent classifications of Dahlgren. Special attention was given to problematic groups that have been allied variously with Asteridae, Dilleniidae, and Rosidae. For example, Actinidiaceae and Fouquieriaceae were placed among Ericales. Loasaceae and Sarraceniaceae formed the sister group of Hydrangeaceae in the Corniflorae grade of Rosidae. Dilleniidae were not monophyletic. For example, *Paeonia* was placed as the sister taxon of the rest of the Rosidae (including dilleniids and asterids), and Ochnaceae as the sister taxon of Linales. Dilleniaceae and Theaceae form a monophyletic group with *Paracryphia* placed as the sister group of Rhizophoraceae and Anisophylleaceae.

Rosidae are central to understanding phylogenetic patterns among nonmagnoliid dicotyledons. As circumscribed by Takhtajan (1969, 1980, 1987) and Cronquist (1981, 1988), Rosidae may be paraphyletic with respect to Asteridae, Dilleniidae, and some Hamamelidae. To understand better the evolution and diversification of nonmagnoliid dicotyledons, more precise and viable hypotheses of relationships among these major groups are necessry.

Rosidae have been considered "more advanced" than Magnoliidae and "less advanced" than Asteridae (Cronquist, 1981). Cunoniaceae, Rosaceae, and other members of the broadly circumscribed Rosales of Cronquist (1981; or Rosanae of Takhtajan, 1987) have been considered primitive Rosidae because their morphological, anatomical, and chemical attributes are similar to those of many Hamamelidae. Hamamelidae (sensu Takhtajan, 1980, 1987; Cronquist, 1981), however, may be polyphyletic (Crane & Blackmore, 1989). Rosidae may be nested, or positioned, among Hamamelidae, particularly among the so-called "lower" hamamelids, such as Hamamelidaceae and Platanaceae (Hufford & Crane, 1989). Certain so-called "higher" hamamelids, such as Fagales and Juglandales, have been suggested to be more closely related to Rosidae than to "lower" Hamamelidae (Wolfe, 1973, 1989, Hickey & Wolfe, 1975; Hickey & Doyle, 1977; Thorne, 1976; Nixon, 1989).

Our understanding of rosid phylogeny may be complicated by the systematic treatment of Dilleniidae. Takhtajan (1980, 1987) and Cronquist (1981) presented Dilleniidae as a monophyletic group rooted among Magnoliidae. Character analyses of putatively primitive Dilleniidae and Rosidae have called attention to the similarities shared by these two groups (e.g., Bate-Smith, 1973; Walker & Doyle, 1975; Cronquist, 1981; Wolfe, 1989), and uncertainty often surrounds the placement of particular taxa in one or the other. These character similarities and the uncertain placement of taxa highlight the possibility of Rosidae and Dilleniidae

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composing part of a more inclusive monophyletic group that is nested among Hamamelidae (cf. Ehrendorfer, 1989).

A monophyletic Rosidae may include taxa circumscribed as Asteridae (sensu Cronquist, 1981). Recent discussions of the origin of Asteridae have focused on alternative placements among Rosidae, but no consensus has emerged about their rosid sister group. Cronquist (1988: 414; see also 1981) suggested that the origin of Asteridae "very probably lies in the order Rosales." The similarly circumscribed Asteridae in Takhtajan (1980) were illustrated to be the sister group of a branch including Cornales and Araliales; these groups together were shown to originate among Saxifragales. The placement of Asteridae also depends upon their monophyly, which has been questioned repeatedly (Dahlgren, 1927; Wunderlich, 1959; Philipson, 1974, 1975, 1977; Dahlgren, 1975, 1977). Jensen et al. (1975) allied the iridoid-containing asterids with Cornales and Ericales and the noniridoid-containing asterids with Araliales and Rutales. Hickey & Wolfe (1975) used leaf architectural data to suggest that some asterid taxa were most similar to Dilleniidae and others to Rosidae. Takhtajan (1987) circumscribed asterids in three groups, Dipsacales, Lamiidae, and Asteridae sens. str., which he envisioned to have separate origins in or near Cornanae.

Numerous problematic taxa may have important ramifications for our understanding of the evolution of nonmagnoliid dicotyledons. The systematic placement of Ericales, Actinidiaceae, Fouquieriaceae, Loasaceae, and Sarraceniaceae has been questioned repeatedly. They share iridoid compounds and embryological characteristics with some Asteridae and Rosidae, but Cronquist (1981, 1988) has placed them all in Dilleniidae. Similarly, Takhtajan (1987) placed all of these taxa, except Loasaceae, among Dilleniidae. In contrast, Dahlgren (1977, 1980, 1983) circumscribed all of these taxa, except Loasaceae, in his superorder Corniflorae. He placed Loasaceae in a monotypic superorder allied with Corniflorae. If Dahlgren's Corniflorae and associated groups, such as Loasaceae, are the rosid groups most closely related to asterids, then the traditional placement of these problematic taxa among Dilleniidae may have limited our understanding of Asteridae evolution.

Broadly based cladistic analyses of rosids and potentially related groups may begin to resolve the problems outlined above. Large-scale studies of higher taxa are important because they include the mosaic distribution of character states at this level and provide accurate tests of prior hypotheses of relationship for problematic groups suggested to have a range of alliances. Large-scale cladistic analyses of higher-level taxa provide more precise hypotheses about relationships than current classifications and, thus, critically set the stage for subsequent, smaller-scale studies by narrowing the set of ingroup and outgroup taxa that must be considered. This preliminary, exploratory investigation of Rosidae and allied groups focuses on: (1) testing hypotheses of monophyly for Asteridae and providing hypotheses about potential sister groups of asterids; (2) testing the placement of the problematic Ericales, Actinidiaceae, Fouquieriaceae, Loasaceae, and Sarraceniaceae that have been allied with Dilleniidae, Rosidae, and Asteridae; and (3) developing hypotheses about relationships among rosid groups, giving special consideration to the placement of Dilleniidae and Hamamelidae.

MATERIALS AND METHODS

TAXA

Eighty-five taxa (Table 1), including commonly accepted (e.g., in Takhtajan, 1969, 1980, 1987; Cronquist, 1981, 1988) members of the Hamamelidae, Dilleniidae, Asteridae, and Rosidae as well as numerous problematic taxa of uncertain systematic placement, were investigated. Winteraceae served as the outgroup for polarizing character states and rooting cladograms.

Families of Cronquist's (1981) Rosales are represented by one or more taxa because this order may be paraphyletic and includes groups suggested to be basal in the subclass. Place-holders represent most other orders of Cronquist's (1981) Rosidae. The orders Haloragales, Podostemales, Rafflesiales, and Santalales are not included because they (1) are considered to be most closely related to or nested within one of the other included groups; (2) have exceptionally derived traits that are not critical for understanding basal Rosidae and Asteridae or other problems outlined above; and (3) have not been implicated in the relationship of Rosidae to Hamamelidae, Dilleniidae, or Asteridae.

Hamamelidae in the study include the "lower" hamamelids (except *Eucommia*) investigated by Hufford & Crane (1989); a set of "higher" hamamelids, such as Fagales and Juglandales, suggested recently to be more closely related to Rosidae than to "lower" hamamelids (Wolfe, 1973, 1989; Hickey & Wolfe, 1975; Hickey & Doyle, 1977; Thorne, 1976; Nixon, 1989); and the problematic Buxaceae and Casuarinaceae.

Sampling Dilleniidae is difficult because their monophyly is questionable; thus, the subclass may

TABLE 1. Taxa used in the phylogenetic analysis. When particular taxa served as a basis for coding higher level groups they are indicated in parentheses.

Actinidiaceae (*Actinidia* Lindley)
Alangiaceae (*Alangium* sect. *Conostigma* Bloemb.)
Alseuosmiaceae (*Alseuosmia* Cunn.)
Anisophylleaceae (*Anisophyllea* R. Br. ex Sabine)
Anodopetalum A. Cunn. ex Endl.
Apiaceae
Araliaceae
Asteraceae
Bauera Banks ex Andrews
Betulaceae (*Betula* L.)
Brunellia Ruíz & Pavón
Bruniaceae
Buxaceae (*Buxus* L. and *Pachysandra* Siebold & Zucc.)
Campanulaceae
Caprifoliaceae
Casuarinaceae
Celastrales (Celastraceae)
Cercidiphyllum Siebold & Zucc.
Clethraceae (*Clethra* L.)
Columellia Ruíz & Pavón
Connaraceae (*Cnestis* Juss.)
Cornaceae
Crassulaceae
Crossosomataceae (*Crossosoma* Nutt.)
Deutzia Thunb.
Davidsonia F. Muell.
Dilleniaceae (*Dillenia* L.)
Ericaceae
Escalloniaceae (*Escallonia* Mutis ex L.)
Eucryphia Cav.
Euphorbiales (Euphorbiaceae)
Euptelea Siebold & Zucc.
Fabaceae (Mimosoideae)
Fagaceae (*Fagus* L.)
Fouquieriaceae
Garryaceae
Geraniales (Oxalidaceae)
Hamamelidaceae subfamily Altingioideae
Hamamelidaceae subfamily Disanthoideae
Hamamelidaceae subfamily Exbucklandoideae
Hamamelidaceae subfamily Hamamelidoideae
Hamamelidaceae subfamily Rhodoleioideae
Hydrangea L.
Juglandaceae (*Engelhardia* Leschen. ex Blume)
Linales (Linaceae)
Loasaceae (*Mentzelia* L.)
Loganiaceae
Myricaceae (*Myrica* L.)
Myrothamnus Welw.
Myrtales (Lythraceae)
Nepenthaceae
Nyssaceae (*Nyssa* L.)
Ochnaceae
Paeonia L.
Paracryphia Baker
Penthorum L.
Philadelphus L.
Pittosporaceae
Platanus L.
Polemoniaceae (tropical genera emphasized in coding decisions)
Polygalales (Malphighiaceae)
Proteales (Proteaceae)
Rhamnales (Rhamnaceae)
Rhizophoraceae (*Crossostylis* Forster & Forster)
Rhoiptelea Diels & Hand.-Mazz.
Rosaceae (tribes Quillajeae and Spiraeeae)
Rubiaceae
Sapindaceae
Sarraceniaceae (*Heliamphora* Benth.)
Saxifragaceae
Scrophulariaceae
Solanaceae
Spiraeanthemum A. Gray
Staphyleaceae
Tetracarpaea Hook.
Tetracentron Oliver
Theaceae
Trochodendron Siebold & Zucc.
Viburnum L.
Winteraceae

not be represented adequately by a few place-holder taxa. Selecting putatively primitive Dilleniidae as place-holders is problematic because prior phylogenetic hypotheses for the subclass may have been influenced heavily by suggestions that it originated among Magnoliidae rather than among Hamamelidae or Rosidae. Dilleniaceae, Theaceae, Ochnaceae, and *Paeonia* are included to represent putatively basal dilleniid groups.

In order to test hypotheses of monophyly and systematic placement for Asteridae, nine representatives of its major orders (sensu Takhtajan, 1969, 1980, 1987; Cronquist, 1981, 1988) are included. The representatives include divergent groups identified in treatments by Takhtajan (1987), Dahlgren (1980, 1983), Dahlgren et al. (1981), and Thorne (1976, 1981, 1983) in which asterids are not monophyletic.

I accept provisionally the monophyly of certain families and orders discussed by Cronquist (1981). For example, Rosaceae are included despite their potential paraphyly; if higher rosid families and orders actually nested within it also are included as terminal taxa, then misleading results may occur. The higher rosid orders, Celastrales, Geraniales, Linales, Myrtales, Polygalales, Proteales, and Rhamnales, may be nested within other terminal taxa in the analysis. Prior phylogenetic hypotheses for these groups are not sufficiently precise to determine their relationship with other terminal taxa. Hence, I opt to include various higher rosid families and orders to examine the composition of major clades. This analysis may serve subsequently as the basis for more detailed analyses of major rosid clades.

CHARACTERS AND STATE CODING

Structural and chemical data (Table 2) were obtained largely from the literature (sources in Appendix 1). Few characters with over 10% missing data are included, and these are attributes (e.g., stomatal pattern) emphasized in prior systematic discussions of the taxa. Bruniaceae, *Columellia*, *Paracryphia*, *Rhoiptelea*, and *Tetracarpaea*, taxa that have proven difficult to place in traditional systematic treatments, are included, despite relatively extensive missing data, to provide provisional hypotheses about sister groups. Characters are coded as missing (unknown) when no single state or pair of states could be reasonably hypothesized to be plesiomorphic for a particular taxon. Wood characters for Saxifragaceae and Crassulaceae are coded as missing because these groups are hypothesized to be primitively herbaceous, and, thus, wood characters are not applicable. Numerous taxa are coded as polymorphic for certain characters primarily because of variability in the genera and higher-level groups in the analysis. Multistate characters compose 47% of the total.

DATA ANALYSIS

Wagner parsimony was used to search for most parsimonious trees with PAUP (version 3.0, Swofford, 1989). Multistate characters were treated as unordered to provide the least biased approach possible for state evolution. Different taxon addition sequences, including simple, closest, and random (see Swofford, 1989, for details), were used to initiate trees for branch-swapping procedures, although the most parsimonious trees were consistently found using simple sequences. To minimize computer run times, heuristic search procedures were performed using a sequential regime of branch-swapping options, beginning with nearest-neighbor interchanges, followed by subtree pruning-regrafting, and concluded with tree bisection-reconnection (Swofford, 1989). All of the trees saved from a prior swapping procedure were used to initiate a subsequent swapping procedure. A consensus tree was formed using the strict option in PAUP (Swofford, 1989). MacClade (version 2.97c+, Maddison & Maddison, 1989) was used in conjunction with PAUP to explore character state evolution and alternative topologies.

RESULTS AND DISCUSSION

Fifty-six equally most parsimonious trees (consistency index = 0.18) with 682 character state changes were identified. The strict consensus tree (Fig. 1) shows that variation among the 56 equally most parsimonious trees is restricted to four regions: (1) among subfamilies of Hamamelidaceae; (2) among *Hydrangea*, *Deutzia*, and *Philadelphus*, representative genera of Hydrangeaceae; (3) among Fabaceae, Rhamnaceae, and Sapindaceae; and (4) among *Rhoiptelea*, Betulaceae, and the Casuarinaceae–Juglandaceae–Myricaceae clade. One of the 56 equally most parsimonious trees (Fig. 2) is used to discuss character state evolution.

The Hamamelidae of Takhtajan (1980, 1987) and Cronquist (1981, 1988) are shown to be polyphyletic (Fig. 2). "Lower" Hamamelidae (sensu Endress, 1986, 1989a; Hufford & Crane, 1989) are a paraphyletic assemblage at the base of Rosidae, and "higher" Hamamelidae (i.e., Fagales, Juglandales, and Casuarinaceae) are nested among Rosidae. Patterns of relationship among "lower" hamamelids reflect those shown by Hufford & Crane (1989). Buxaceae, a family sometimes placed in Rosidae (Scholz, 1964; Cronquist, 1981, 1988), form the sister taxon of *Cercidiphyllum* and *Myrothamnus*, with which they share a decussate leaf arrangement, unisexual flowers, and pollen with a papillate secondary tectal sculpturing. Drinnan et al. (1991) discussed the similarities of the Mid-Cretaceous fossil *Spanomera* with Buxaceae and *Myrothamnus*, and it may form part of the monophyletic group that includes those taxa and *Cercidiphyllum*.

Rosids are placed among "lower" Hamamelidae as the sister group of *Platanus* and Hamamelidaceae. Derived features shared by rosids include flowers with a disc nectary, anthers with unbifurcated stomia, and pollen with endoapertures (although all three attributes occur as parallelisms among Hamamelidaceae). The rosid group includes taxa circumscribed as Asteridae and Dilleniidae in recent treatments by Takhtajan (1980, 1987) and Cronquist (1981, 1988).

Paeonia, often placed among dilleniids (e.g., Thorne, 1976; Cronquist, 1981; Takhtajan, 1980; Dahlgren, 1983), is a basal branch of Rosidae in my results (Fig. 2). In recent classifications, Thorne (1983) and Takhtajan (1987) transferred *Paeonia* from a position near Dilleniaceae to one near Glaucidiaceae (near Berberidales and Nelumbonales).

TABLE 2. Character state assignments for taxa used in the phylogenetic analysis. Question marks indicate missing data. Characters and character states are listed in Appendix 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Winteraceae	0	0	0	0	0	0	0	0/2	0	0	?	?	?	?	?	0	0	0	0	0
Trochodendron	2	0	0	0	0	1	0	1	0	0	?	?	?	?	?	0	0	0/1	0	0
Tetracentron	0	0	0	0	1	1	0	1	1	0	?	?	?	?	?	0	0	1	0	0
Euptelea	1	0	0	0	0	2	1	0	0	1	0	1	0	1	0	0	1	1	0	0
Cercidiphyllum	0	1	0	0	1	1	0	0	1	1	0	0	0	1	1	0	0	2	0	0
Myrothamnus	0	1	0	0	1	1	1	0	0	1	0	2	0	2	1	0	1	6	0	0
Platanus	2	0	0	0	1	1	1	?	0	1	?	1	1	2	1	0	0	7	0	0
Hamamelidoideae	0	0	0	0	1	2	0	?	0	1	0	0	0	1	0	0	0	0/1	0	1
Disanthoideae	0	0	0	0	1	1	0	?	0	1	1	0	0	1	0	0	0	0/1	0	1
Exbucklandoideae	0	0	0	0	1	1	0	?	0	1	0	0	0	1	0	0	0	3	0	1
Rhodoleioideae	0	0	0	0	1	2	0	?	0	1	0	0	0	1	0	0	0	0/1	0	1
Altingioideae	0	0	0	0	1	1	0	?	0	1	0	0	0	1	0	0	0	0/1	0	1
Juglandaceae	0	0	1	0	0	0	2	0	0	1	1	1	2	4	1	2	1	1/2	0	0
Myricaceae	0/1	0	0	0	0	0	1	0	0	1	1	1	1	2	1	0	1	1/2	0	0
Fagaceae	0	0	0	0	1	0	1	0	0	1	?	1/2	1	3	?	4	1	7	0	0
Casuarinaceae	1	2	0	0	0	?	?	2	0	1	2	2	1	2	1	2	1	7	0	0
Buxaceae	1	1	0	0	0	0	0	3	0	1	0	2	0	2	1	0	1	1	0	0
Rhoipteleaceae	0	0	1	0	1	0	2	0	0	1	1	1	1	4	1	2	1	0	0	0
Bauera	?	1	0	0	1	0	?	?	0	1	2	2	0	2	1	2	1	2	0	0
Anodopetalum	0	1	0	0	1	0	2	0	0	1	2	1	0	2	1	2	1	1	0	0
Spiraeanthemum	0	1	0	0	1	0	0	2	0	1	0	1	0	1	0	2	0/1	1	0	0
Brunellia	0	1	1	0	1	0	1	0	0	1	1	0/1	0	1	1	2	?	0/3	0	0
Eucryphia	0	1	0/1	0	1	0	1	2	0	1	1	1	0	1	1	2	1	1/7	0	0
Davidsonia	0	0	1	0	1	0	1	2	0	1	?	1	1	1	1	2	0	7	0	0
Connaraceae	0	0	1	0	0	0	?	?	0	1	2	1	1	4	1	4	1	6	0	0
Tetracarpaea	1	0	0	0	0	0	1	0	0	1	1	2	0	1	1	0	2	2	0	0
Pittosporaceae	0	0	0	0	0	0	2	2	0	1	2	1/2	0	?	2	3	1	1	0	0
Nepenthaceae	?	0	0	1	0	0	?	0	0	1	2	2	2	4	0	0	2	4	0	0
Sarraceniaceae	?	0	0	1	0	?	?	0	0	1	0	2	0	0	1	0	1	4	0	0
Crossosomataceae	0	0	0	0	0	0	?	0	0	1	2	2	0	4	0	0	1	4	0	0
Sapindaceae	0	0	1	0	0	0	2	0	0	1	2	2	1	4	2	4	1	7	0	0
Fabaceae	0	0	1	0	1	0	0	2	0	1	2	2	2	4	1	4	1	4/6	0	1
Bruniaceae	?	0	0	0	0	?	?	?	0	1	0	0	0	1	1	0	1	1/4	0	0
Alseuosmiaceae	0	0	0	0	0	0	0/2	0	0	1	0	1	0	3	1	4	1	?	0	0
Rosaceae	0	0	0	0	0	0	2	0	0	1	2	1	0	4	1	0	1	5	0	0

TABLE 2. *Continued.*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Anisophylleaceae	?	0	0	0	0	0	0	?	0	1	2	1	2	4	1	2	0	1	0	0
Rhizophoraceae	0	1	0	0	1	0	0	?	0	1	2	1	2	4	1	2	0	1	0	0
Saxifragaceae	0	0	0	0	0	0	2	0	0	1	?	?	?	?	?	?	?	?	?	?
Crassulaceae	0/1	0	0	0	0	0	2	?	0	1	?	?	?	?	?	?	?	?	?	?
Penthorum	1	0	0	0	0	0	2	0	0	1	0	1	0	4	1	2	1	4	0	0
Columellia	1	1	0	0	0	?	?	0	0	1	1	1	0	4	0	0	1	6	0	0
Hydrangea	0	1	0	0	0	2	0	2	0	1	0	1	0	0	1	1	1	0	0	0
Deutzia	0	1	0	0	0	2	2	?	0	1	0	1	0	3	1	1	1	0	0	0
Philadelphus	0	1	0	0	0	1	0/2	0	0	1	0	1	0	3	1	1	1	0	0	0
Escalloniaceae	1	0	0	0	1	0	0/2	0	0	1	0	2	0	1	1	0	1	0	0	0
Alangiaceae	0	0	0	0	0	1	3	0	0	1	1	0	2	4	2	4	0	0/1	0	0
Nyssaceae	0	0	0	0	0	1	3	2	0	1	0	0	1	2	1	2	0	0	0	0
Cornaceae	0	1	0	0	0	1	3	0	0	1	0	0	1	2	1	0	0/1	0	0	0
Garryaceae	0	1	0	0	0	1	3	2	0	1	1	2	0	2/4	1	1	1	4	0	0
Loasaceae	0	0	0	0	0	1	2	0	0	1	2	2	1	0	0	2	1/2	4	0	0
Ericaceae	0/1	0/1	0	0	1	0	0	0	0	1	2	1	0	2	0	0	1	1	0	1
Fouquieriaceae	1	0	0	0	0	?	0	0	0	1	2	2	0	4	1	2	1	4	0	0
Actinidiaceae	1	0	0	0	0	0	1	0	0	1	2	1	?	2	0/1	0	?	0	0	0
Clethraceae	1	0	0	0	0	0	0	?	0	1	0	0	0	2	0	2	0/1	0	0	0
Staphyleaceae	0	0/1	1	0	1	0	2	?	0	1	0	0/1	1/2	1	1	1	0	0/1	0	0
Geraniales	0	0	1	0	0	0	3	2	0	1	2	2	2	4	1	4	1	0/6	0	0
Celastrales	1	0/1	0	0	0/1	0	0	1/2	0	1	?	1	1/2	4	1	5	0/1	?	0	0
Euphorbiales	?	0	0	0	1	2	2	2	0	1	2	0/1	?	4	2	4	?	0	0	0
Rhamnales	0	0	0	0	1	0	2	0	0	1	2	2	1	4	2	4	1	?	0	1
Linales	0	0/1	0	0	1	0	?	2	0	1	2	2	0	4	1	1	0/1	?	0	0
Polygalales	0	1	0	0	1	0	0	2	0	1	2	0/1	0/2	4	2	4	0/1	0/1	0	0
Proteales	0	0	0/1	0	0	0	2	2	0	1	2	2	1/2	4	1	1	0	4	0	0
Myrtales	1	1	0	0	0	0	0	0	0	1	2	2	1	4	1	4	1	?	0	1
Betulaceae	0	0	0	0	1	0	1	0	0	1	?	1	1	4	2	1	0/1	7	0	0
Apiaceae	2	0	1	0	0	0	?	?	0	1	2	2	1	3	1	4	?	2	1	0
Araliaceae	2	0	1	0	0	0	?	2	0	1	?	1	1	?	2	4	1	1/2	1	0
Dilleniaceae	0	0	0	0	?	0	2	?	0	1	0	0	2	3	1	1	0	0/1	?	0
Paeonia	0	0	1	0	0	?	?	0	0	1	1	2	0	3	1	1	1	1/2	0	0
Loganiaceae	1	1	0	0	1	0	0	?	0	1	2	1	1	4	2	1	0/1	1/5	0	0
Solanaceae	1	0	0	0	0	0	0	0	0	1	2	2	?	?	2	1	1	4/5	0	0

TABLE 2. Continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Rubiaceae	1	1	0	0	1	0	0	2	0	1	2	1	1	4	1	1	0/1	4	0	0
Campanulaceae	1	0	0	0	0	0	?	0	0	1	2	2	1	4	1	4	?	5	0	0
Viburnum	?	1	0	0	1	0	2	0	0	1	0	1	1	4	0	0	0/1	4	0	0
Caprifoliaceae	?	1	0	0	0	0	2	0	0	1	2	1	1	4	0	0	0/1	0	0	0
Polemoniaceae	1	0/1	0	0	1	0	0	0	0	1	2	2	0	4	2	2	2	1	0	0
Asteraceae	0	0	0	0	1	0	0	0	0	1	2	2	1	4	2	4	1	1/2	0	0
Scrophulariaceae	1	0/1	0	0	1	0	2	0	0	1	2	2	1	4	2	3	1	0/4	0	0
Theaceae	1	0	0	0	0	0	0	?	0	1	0	0	1	1	0	1	0	0	0	0
Ochnaceae	0	0	0	0	1	0	0	0/2	0	1	2	1	1	4	1	2	1	0	0	1
Paracryphia	0	2	0	0	1	0	0	0	0	1	0	0	0	0/1	1	2	0	0	0	0

TABLE 2. Continued.

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Winteraceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trochodendron	0	0	0	0	0	0	1	0	0	0	1	0	2	0	1	0	0	0	0	0
Tetracentron	0	0	2	0	0	0	1	1	0	0	1	2	2	0	1	0	0	0	0	0
Euptelea	0	?	?	?	?	0	0	?	0	0	1	0	0	1	0	2	0	0	1	0
Cercidiphyllum	2	?	?	?	?	0	0	0	0	0	1	5	0	1	?	2	0	0	0	0
Myrothamnus	2	0	2	0	0	0	?	1	0	0	1	2/3	0	0	1	0	0	0	0	0
Platanus	1	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	2	1
Hamamelidoideae	0	1	1	0	0	0	2	1	0	0	1	4	2	0	2	1	0	0	2	0
Disanthoideae	0	1	1	0	0	0	3	1	0	0	0	4	1	0	2	1	1	0	1	0
Exbucklandoideae	0	1	1	0	0	0	?	2/4	0	0	1	4	2	0	2	1	0	0	1	0
Rhodoleioideae	0	1	3	0	0	0	2	2	0	0	1	4	2	0	2	1	0	0	0	0
Altingioideae	1	?	?	?	?	0	0	1/2	0	0	1	4	3	0	2	1	0	0	0	0
Juglandaceae	1	0	2	0	0	0	0	1/2	0	1	?	4	3	0	2	1	0	2	4	1
Myricaceae	1	?	?	?	?	0	0	1/4	0	1	0	4	0	0	2	1	0	2	4	1
Fagaceae	1	0	3	0	0	0	0	1/2	0	1	0	3	3	0	2	1	0	0	3	0

TABLE 2. *Continued.*

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Casuarinaceae	1/2	?	?	?	?	0	0	?	0	0	0	4	0	0	2	1	0	3	3	0
Buxaceae	1	0	2	0	0	0	1	1	0	1	0	2/3	1	0	2	0	0	1	3	0
Rhoipteleaceae	0	0	2	0	0	0	?	?	0	1	?	4	0	0	2	1	0	2	2	0
Bauera	0	1	1/2	0	0	0	?	2	0	1	0	4	2	0	3	1	1	0	1	0
Anodopetalum	1	1	2	?	0	0	2	4	0	1	0	4	1	0	2	1	1	0	?	0
Spiraeanthemum	2	0	2	1	0	0	2	4	0	1	0	6	1	0	1	1	1	0	3	0
Brunellia	0/2	0	1	0	0	0	2	4	0	1	0	0	1	0	1	1	0	0	3	0
Eucryphia	0	1	2	0	0	0	2	3	0	1	0	0	0	0	2	1	1	0	0	0
Davidsonia	0	1	1	1	0	0	2	4	0	1	0	4	0	0	2	1	1	1	1	0
Connaraceae	0	1	1/2	0/1	0/1	0	2	4	0	1	0	1	1	0	1	1	1	0	3	0
Tetracarpaea	0	1	2	0	0	0	0	1/4	0	0	0	1/2	0	1	0	1	1	0	0	0
Pittosporaceae	0	1	1	0/1	0/1	0	2	1	0	?	0	4	0	0	3	1	1	3	0	0
Nepenthaceae	2	1	2	0	0	0	3	2/4	0	?	0	2	0	0	2	1	1	0	0	0
Sarraceniaceae	0	1	1	0	0	0	2	2/4	0	0	0	3	0	0	3	1	1	0	0	0
Crossosomataceae	0	1	1/2	0	0	0	2	3	0	0	0	6	0	1	0	1	1	0	1	0
Sapindaceae	0	1	1/2	0/1	0	0	?	1/4	0	1	0	3	0	0	3	1	1	0	2	0
Fabaceae	0	1	1	1	0/1	0	?	2/4	0	1	0	5	0	1	?	1	1	0	2	0
Bruniaceae	0	1	1	0	0	0	2	1	0	1	0	4	3	0	2	1	1	0	2/3	0
Alseuosmiaceae	0	1	1	0	1	1	2	1	0/1	1	0	4	3	0	3	1	1	0	1	0
Rosaceae	0	1	1	1	0	1	2	3	0	1	0	1	0	?	0	1	1	0	0/1	0
Anisophylleaceae	0	1	2	0	0	?	2	4	0	1	0	2	3	0	2	1	1	0	2	0
Rhizophoraceae	0	1	2	?	?	?	2	3	0	?	0	0	3	0	3	1	1	1	?	0
Saxifragaceae	0	1	1	1	0	0	2	4	0	0	0	3/4	1/2	0	1	1	1	0	0	0
Crassulaceae	0	1	1/2	0/1	0/1	0	2	4	0/1	?	0	1/2	2	0	0	1	1	0	0	0
Penthorum	0	1	1	1	0	0	?	4	0	0	0	0/1	2	0	1	1	1	0	0	0
Columellia	0	1	1	1	1	0	2	1	1	1	0	4	3	0	3	1	1	0/3	0	0
Hydrangea	0	1	1/2	1	0	1	2	4	0	1	0	6	3	0	2	1	1	0/3	1	0
Deutzia	0	1	1	1	0	0	2	4	0	?	0	2	3	0	2	1	1	0	0	0
Philadelphus	0	1	2	1	0	0	2	4	0	0	0	2	3	0	2	1	1	0	0	0
Escalloniaceae	0	1	1	1	0/1	0	2	1	0	1	0	4	3	0	3	1	1	0/3	0	0
Alangiaceae	0	1	1/2	1	1	0	2	1	0	0	0	4	3	0	3	1	1	3	2	0
Nyssaceae	0	1	1	0	0	0	2	4	0	0	0	4	3	0	3	1	0	1	2	0
Cornaceae	0	1	2	1	0	0	2	1	0	1	0	4	3	0	3	1	1	0	2	0
Garryaceae	2	0	2	?	0	0	0	1	0	0	0	4	3	0	2	1	1	3	2	0
Loasaceae	0	1	1	0	0	0	2	3	0	0	0	3	3	0	3	1	1	3	0	0
Ericaceae	0	1	1	0	1	0	2	4	0	1	0	1	0	0	3	1	1	0	0	0

TABLE 2. Continued.

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Fouquieriaceae	0	1	1	1	1	0	2	2/4	0	1	0	3	0	0	3	1	1	0	1	0
Actinidiaceae	2	1	1/2	1	0	0	0	3	0	1	0	0	0	0	2	1	1	0	0	0
Clethraceae	0	1	1	1	1	0	2	4	0	1	0	3	0	0	3	1	1	0	0	0
Staphyleaceae	0	1	1	0	0	1	2	1	0	1	0	3	0/2	0	2	1	1	0	1	0
Geraniales	0	1	1	0	1	0	2	4	0	1	0	1	0	0	2	1	1	0	1	0
Celastrales	0	1	1/2	1	0	0	2	1/4	0	?	?	6	0/2	0	3	1	1	0	3	0
Euphorbiales	1/2	1	1	0	0	0	2	1/2	0	?	0	3	0	0	2	?	0	1	2/3	0
Rhamnales	0	1	1/2	0	0	1	2	1	0	1	0	4/5	2/3	0	3	1	1	2	2	0
Linales	0	1	1	0/1	0	0	2	1	0	0	0	6	0	0	3	1	1	1	3	0
Polygalales	0	1	1	0/1	0	0	0	4	0	1	0	3	0	0	2	1	1	0	2	0
Proteales	0	1	2	1	?	0	2	1	0	0	0	5	0/2	0/1	?	1	1	0	2/3	0
Myrtales	0	1	2	0	0	1	2	4	0	1	0	6	0	0	3	1	1	0	1	0
Betulaceae	0	0	3	0	0	0	0	1	0	1	0	4	2	0	2	1	1	0	2/3	0
Apiaceae	0	1	1	0	0	0	2	1	0	1	0	4	3	0	2	1	1	1	2	0
Araliaceae	0	1	1	0	0	0	2	2	0	1	0	6	3	0	2	1	1	1	2	0
Dilleniaceae	0	1	1	0	0	0	0/2	5	0	0	0	0/6	0	0/1	0/1	1	1	0	1	0
Paeonia	0	1	1	0	0	0	2	5	0	0	0	6	0	0	0	0	0	0	0	0
Loganiaceae	0	1	1/2	1	1	0	0/2	1	1	1	0	3/4	0	0	3	1	1	0	0	0
Solanaceae	0	1	1	1	1	0	2	1	1	1	0	4	0	0	3	1	1	0	0	0
Rubiaceae	0	1	1/2	1	1	0	2	1	1	1	0	4	3	0	3	1	1	0	1	0
Campanulaceae	0	1	1	1	1	0	2	1	0	?	0	6	3	0	3	1	1	0	0	0
Viburnum	0	1	1	1	1	0	2	1	1	1	0	3	3	0	3	1	1	0	1	0
Caprifoliaceae	0	1	1	1	1	0	2	1	1	1	0	6	3	0	3	1	1	0/3	1	0
Polemoniaceae	0	1	1	1	1	0	2	1	1	1	0	3	0	0	3	1	1	0	0/1	0
Asteraceae	0/1	?	1	?	1	0	2	1	1	1	0	4	3	0	3	1	1	2	4	0
Scrophulariaceae	0	1	1	1	1	0	2	1	1	1	0	4	0	0	3	1	1	0	0	0
Theaceae	0	1	1	0/1	0/1	0	2	5	0	1	0	6	0	0	2/3	1	1	0	0	0
Ochnaceae	0	1	1	0	0	0	0/2	?	0	0	0	0/6	0	0	3	1	1	0	0/1	0
Paracryphia	0	0	2	0	0	0	?	4	0	0	0	0	0	0	2	1	0	0	1	0

TABLE 2. Continued.

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Winteraceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Trochodendron	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0
Tetracentron	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Euptelea	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	3	1	0	0	2
Cercidiphyllum	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	3	1	0	0	0
Myrothamnus	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	2	1	0	?	0
Platanus	0	0	0	1	1	0	0	1	0	0	1	?	2	1	0	0	0	0	0	2
Hamamelidoideae	0	0	0	1	1	0	0	1	1	0	1	0	2	1	0	0	0	0	0	0
Disanthoideae	0	0	0	1	1	0	0	0	1	0	1	0	2	1	0	0	0	0	0	0
Exbucklandoideae	0	0	0	1	1	0	0	1	?	0	1	0	2	1	0	3	0	0	0	0
Rhodoleioideae	0	0	0	1	1	0	0	?	?	0	1	0	2	1	1	3	0	0	0	0
Altingioideae	0	0	0	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0
Juglandaceae	1	0	1	1	2	0	0	1	1	0	1	?	0	0	1	4	0	1	2	2
Myricaceae	1	0	?	1	2	0	0	1	1	0	1	0	0	0	1	4	0	1	2	3
Fagaceae	0	0	1	1	2	0	?	1	1	0	1	0	2	1	1	5	0	0	1	2
Casuarinaceae	0	0	1	1	2	0	?	1	1	0	1	0	0	0	1	4	0	1	2	2
Buxaceae	0	0	?	0	0	0	?	0	0	0	1	0	2	0	1	3	1	0	0	1
Rhoipteleaceae	0	0	?	1	2	?	?	1	?	?	1	0	2	0	1	4	0	1	2	2
Bauera	0	0	0	1	0	?	0	1	?	?	1	1	2	1	1	0	0	0	0	0
Anodopetalum	0	0	0	1	0	0	0	1	0	0	1	1	2	1	1	8	0	0	1	4
Spiraeanthemum	0	0	0	1	0	0	0	1	0	0	1	1	2	1	1	8	0	0	1	0
Brunellia	0	0	0	?	0	?	0	1	?	?	1	1	2	1	1	8	0	0	1	0
Eucryphia	0	0	0	?	0	0	0	1	0	0	1	1	2	1	1	8	0	0	1	0
Davidsonia	0	0	0	?	2	0	0	1	0	0	1	1	2	1	1	8	0	0	1	2
Connaraceae	0	0	0	1	0/1	0	0	1	0	0	1	0	2	1	1	8	0	0	1	0
Tetracarpaea	0	0	0	1	0	?	0	0	?	0	1	1	2	1	1	5	0	0	1	0
Pittosporaceae	1	1	0	1	0	0	1	0	0	0	1	0	2	1	1	0	0	0	0	1
Nepenthaceae	0	0	0	?	0	0	0	0	0	0	1	1	?	?	?	4	0	?	?	1
Sarraceniaceae	1	1	0	0	0	1	0	0	0	0	1	0	2	1	1	7	0	?	1	1
Crossosomataceae	0	0	0	1	0/1	0	0	?	1	1	1	0	2	1	1	0	0	0	0	0
Sapindaceae	0	0	0	1	2	0	1	1	0	0	1	0	2	1	1	1	0	0	1	?
Fabaceae	0	0	0	?	2	0	1	1	0	0	1	0	2	1	1	8	0	0	1	0
Bruniaceae	1	0	0	?	0	0	0	1	0	0	1	0	2	1	1	0	0	0	0	2
Alseuosmiaceae	1	1	0	?	0	0	0	0	?	?	1	0	2	1	1	6	0	0	2	4
Rosaceae	0	0	0	1	1/2	0	0	1	0	0	1	0	2	1	1	1	0	0	1	0
Anisophylleaceae	1	0	0	1	2	0	0	0	?	?	1	0	2	1	1	8	0	0	1	2

TABLE 2. Continued.

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Rhizophoraceae	0	0	0	1	0/1	0	0	?	1	0	1	1	2	1	1	6	0	0	1	2
Saxifragaceae	0	0	0	0	0	0	0	1	0	0	1	?	2	1	1	0/1	0	0	1	0
Crassulaceae	0	0	0	0	0	0	0	1	0	0	1	?	2	1	1	1	0	0	1	0
Penthorum	0	0	0	0	0	?	0	0	1	0	1	1	2	1	1	1	0	0	1	0
Columellia	1	1	0	?	0	0	0	0	?	0	1	0	2	1	1	0	0	0	?	0
Hydrangea	1	1	0	0	0	1	0	1	0	0	1	1	2	0	1	0	0	0	0	1
Deutzia	1	1	0	0	0	1	0	0	0	0	1	1	2	0	1	0	0	0	0	1
Philadelphus	1	1	0	0	0	0	0	0	0	0	1	1	2	?	1	8	0	0	1	1
Escalloniaceae	1	1	0	1	?	1	0	0	0	0	1	1	2	1	1	3	0	0	1	0
Alangiaceae	1	0	0	0/1	0	1	0	0	0	1	1	0	2	1	1	0/3	0	0	1	3
Nyssaceae	1	1	0	0	0	1	0	0	1	1	1	0	2	1	1	8	0	0	1	3
Cornaceae	1	0	0	0	0	1	0	0	1	0	1	0	2	1	1	8	0	0	1	3
Garryaceae	1	0	0	0	0	1	0	0	0	1	1	0	2	1	1	0	1	0	0	3
Loasaceae	1	1	0	0	0	1	0	0	0	1	1	?	2	1	1	1	0	0	1	1
Ericaceae	1	1	0	0	0	1	0	1	1	1	1	0	2	1	1	6	0	0	2	0/1
Fouquieriaceae	0	1	0	0	1	1	0	0	1	0	1	0	2	1	1	0	0	0	0	1
Actinidiaceae	1	1	0	0	0	1	0	0	?	0	1	1	2	1	1	6/7	0	0	2	1/4
Clethraceae	1	1	0	0	0	1	0	0	0	0	1	0	2	1	1	6	0	0	2	1
Staphyleaceae	0	0	0	1	0	0	0	0	0	0	1	0	2	1	1	0	0	0	1	0
Geraniales	0	1	0	1	0	?	0	0	0	0	1	0	2	1	1	0	0	0	1	1
Celastrales	0	0	0	1	0	0	0	0/1	0	0	1	?	2	1	1	0	0	0	0	?
Euphorbiales	0	0	0	1	0	0	1	0	1	0	1	?	2	1	1	0	0	0	0	4
Rhamnales	0	0	0	1	1/2	0	0	0	0	0	1	0	2	1	1	8	0	0	1	3
Linales	0	0	0	1	1	0	0	0	0	1	1	0	2	1	1	4/7	0	0	1	0
Polygalales	0	0	0	1	2	0/1	0	0	0	0	1	0	2	1	1	0	0	0	1/2	2/4
Proteales	0	0	0	1	2	0	0	1	0	0	1	0	0/1	0/1	1	?	0	0	1	?
Myrtales	0	0	0	1	2	0	0	1	1	1	1	0	2	1	1	1/3	0	0	1	0
Betulaceae	1	0	1	1	1/2	0	0	1	1	0	1	0	0	0	1	4	0	1	2	2
Apiaceae	1	1	0	1	0	0	1	1	0	1	1	0	2	1	1	1/3	0	0/1	1	4
Araliaceae	1	0	0	1	0	0	1	0	0	1	1	0	2	1	1	0	0	0/1	0	3/4
Dilleniaceae	0	0	0	1	0	0	0	1	1	0	1	0	2	1	0/1	8	0	0	1	0
Paeonia	0	0	0	1	0	0	0	0	0	1	1	0	2	1	1	0	0	0	0	0
Loganiaceae	1	1	0	1	0	1	0	0	0	1	1	0	2	1	1	0	0	0	0	0
Solanaceae	1	1	0	0/1	0	0	0	0/1	0	1	1	0	1	1	1	1/4	0	0	1	0/4
Rubiaceae	1	1	0	0/1	0/2	1	0	1	0	0	1	0	2	1	1	0	1	0	0	0/4
Campanulaceae	1	1	0	0	0	0	1	0	0	1	1	0	2	1	1	6/8	0	0	1	0

TABLE 2. Continued.

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Viburnum	1	0	0	0	0	1	0	0	?	?	1	?	2	1	1	0	0	0	0	3
Caprifoliaceae	1	1	0	0	0	1	0	0	1	0	1	0	2	1	1	4	0	0	2	4
Polemoniaceae	1	1	0	1	0	0	0	0/1	0	1	1	0	0	0	1	0/1	0	0	0	1
Asteraceae	1	1	0	0/1	2	0	1	0	0	1	1	0	0/1	0/1	1	0/4	0	0	0	2
Scrophulariaceae	1	1	0	0	0	1	0	0	0	0	1	0	2	1	1	0	0	0	1	0
Theaceae	0	1	0	1	0	0	0	1	1	0	1	0	2	1	1	4	0	0	1	0
Ochnaceae	0	1	0	1	0/2	0	0	0	0	0	1	0	2	1	1	6/7	0	0	1	0
Paracryphia	1	0	0	?	0	?	0	?	?	?	1	0	2	1	1	3	0	0	1	0

Worsdell (1908) earlier suggested a relationship between *Paeonia* and Ranunculaceae, and Sawada (1971) argued that floral structure implied a position among magnoliids. This cladistic analysis is not sufficiently inclusive to evaluate the placement of *Paeonia* among groups such as Ranunculaceae, Berberidales, and Nelumbonales. Extensive attention has been given to the distinctive coenocytic proembryo of *Paeonia* (Cave et al., 1961; Murgai, 1959; Yakovlev & Yoffe, 1957), but this autapomorphy currently has no bearing on our understanding of its sister group relationship. The nectarial disc surrounding the base of the apocarpous gynoecium of *Paeonia* (Hiepko, 1965, 1966) is a derived feature shared by the rosid group (including dilleniids and asterids) but not by Magnoliidae (including Ranunculaceae, Berberidales, and Nelumbonales). Corner (1946) was among the first to suggest that *Paeonia* was more closely related to Dilleniaceae than to Ranunculaceae or other Magnoliidae. Corner (and more recently others), however, emphasized attributes such as centrifugal androecial development, arillate seeds with a hard testa, and exstipulate leaves, which are present among rosids as well as Dilleniales and Theales (sensu Cronquist, 1981).

The sister group of *Paeonia* comprises two groups (Fig. 2): (1) Crossosomataceae and their sister group (treated as the "core rosid group") and (2) Bruniaceae and their sister group (treated as the "Corniflorae–asterid group").

THE CORE ROSID GROUP

Crossosomataceae, placed as the sister taxon of the rest of the core rosid group, have been allied with *Paeonia*, Ranunculaceae, Dilleniaceae, Rosaceae, and Fabaceae. Kapil & Vani (1963) treated *Crossosoma* as more closely related to Dilleniaceae and Rosaceae than to *Paeonia* and Ranunculaceae. Richardson (1970) and DeBuhr (1978) used leaf and wood structure to ally Crossosomataceae more closely with Rosaceae than Dilleniaceae. Similarity indices based on chemical attributes showed Crossosomataceae to be equally similar to *Paeonia*, Dilleniaceae, and rosids (Tatsuno & Scogin, 1978). Crossosomataceae appear to have diverged little from the basic character states of the core rosid group, although its stipitate carpels and polystemony are parallelisms with those of other rosids.

The Rosaceae–Crassulaceae–Saxifragaceae clade is supported by striate pollen and five-carpellate gynoecia (although the carpel number for both Crassulaceae and Saxifragaceae was coded as polymorphic). Missing data may have influenced

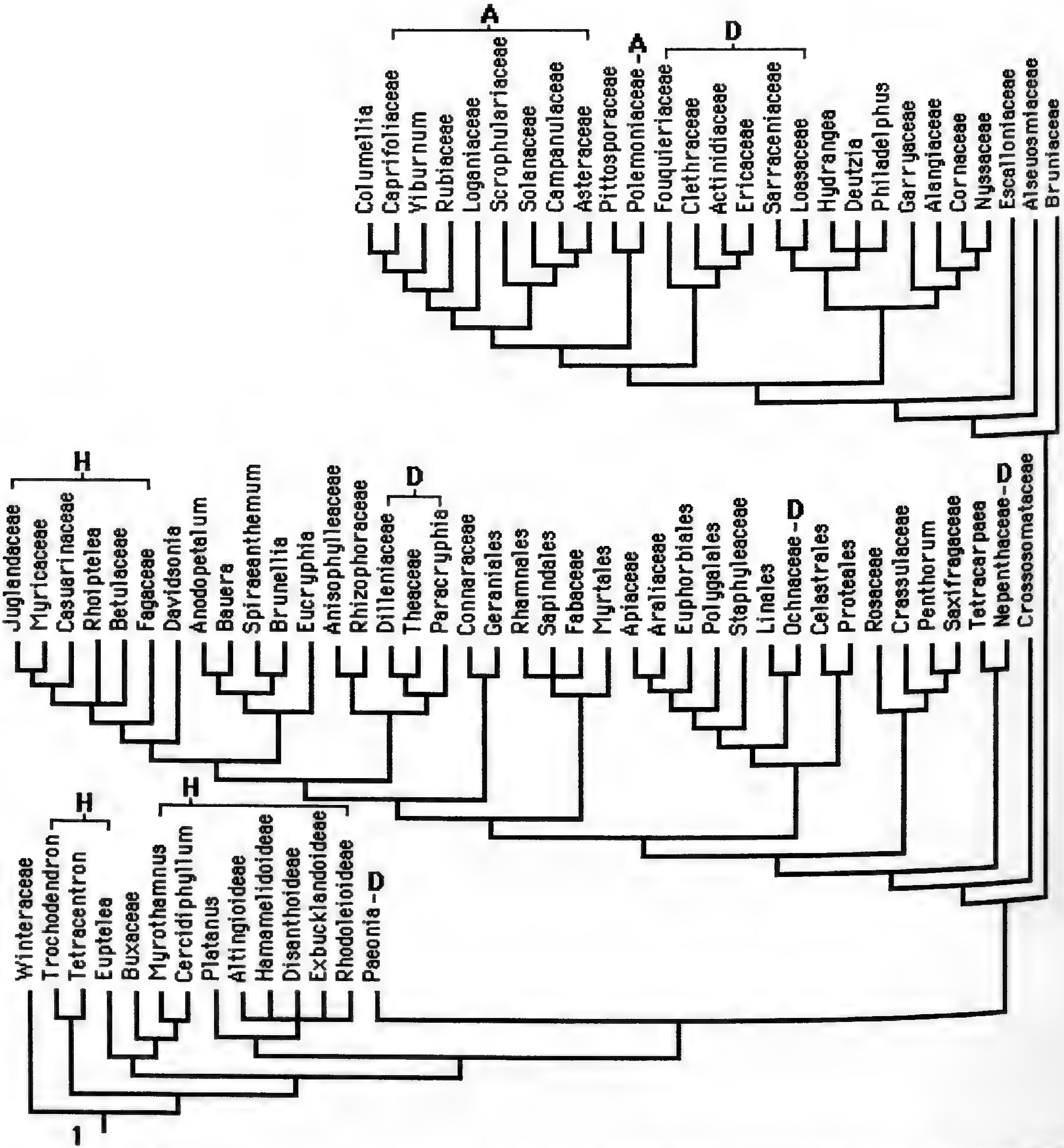


FIGURE 1. A strict consensus tree based on the set of 56 equally most parsimonious trees. Groups circumscribed by Cronquist (1981) as Asteridae, Dilleniidae, and Hamamelidae are indicated. (Key: A, Asteridae; D, Dilleniidae; H, Hamamelidae.)

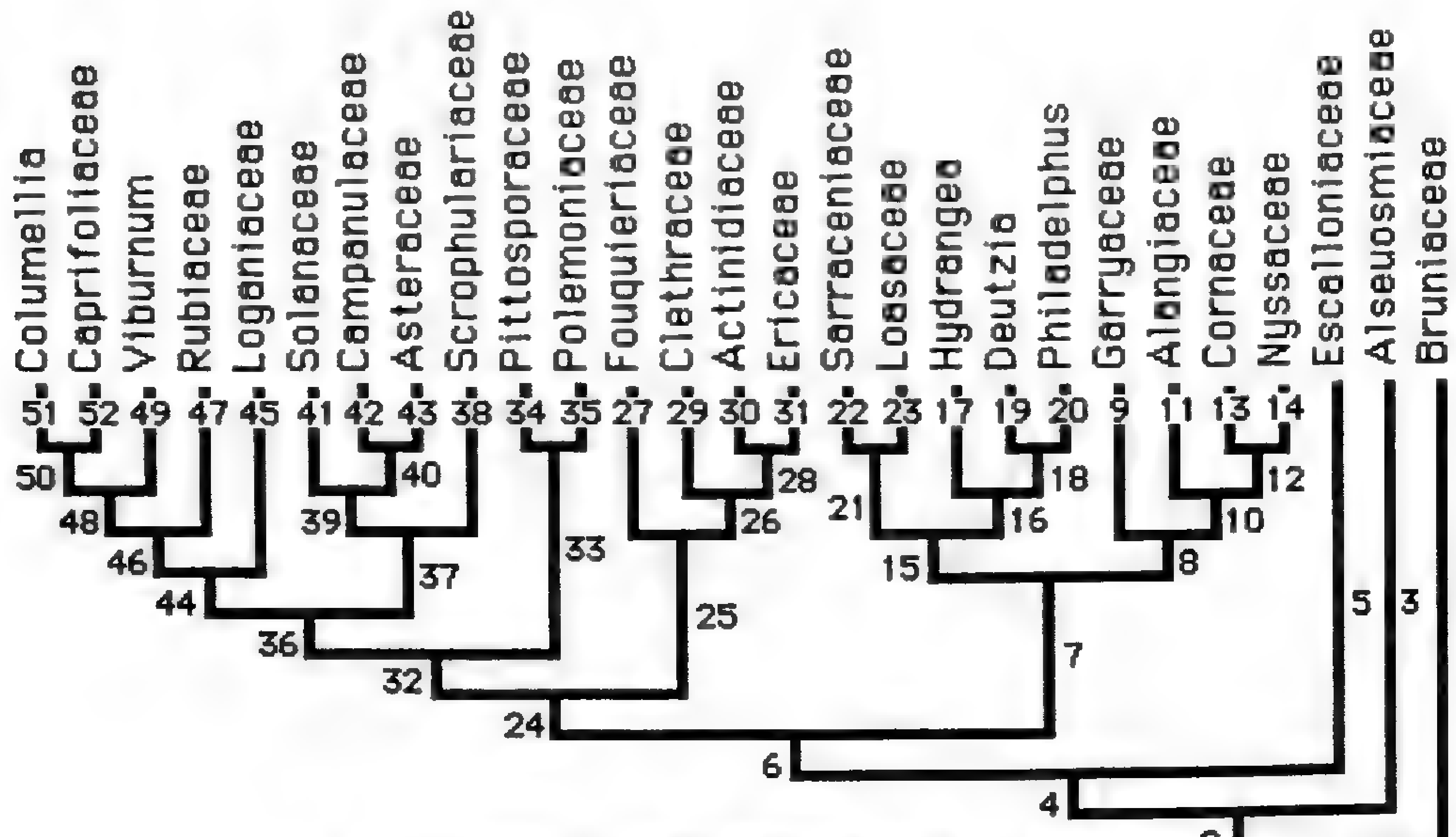
the placement of the Crassulaceae–Saxifragaceae group (including *Penthorum*). Crassulaceae and Saxifragaceae were considered primitively herbaceous (see Hart & Koek-Noorman, 1989), and all wood characters were coded as nonapplicable (i.e., missing) for these taxa. Engler (1930) broadly circumscribed Saxifragaceae to include the so-called "woody saxifrages," groups such as Escalloniaceae and Hydrangeaceae. My results show that "woody" saxifrages are more closely related to certain members of the Corniflorae–asterid group than to Saxifragaceae sens. str. (the "herbaceous" saxifrages). This is supported by chloroplast DNA data (Downie & Palmer, 1992; Olmstead et al., 1992). Saxifragaceae sens. str. lack the iridoid chemistry and some embryological states that help to define the Corniflorae–asterid group. The Crassulaceae–Saxifragaceae group demonstrates evolution of ab initio cellular endosperm and the formation of endosperm haustoria parallel with members of the Corniflorae–asterid group. This may help to explain its previous alliance with groups such as Escalloniaceae and Hydrangeaceae. *Penthorum* has been treated as intermediate between Saxifragaceae and Crassulaceae (e.g., Agababian, 1961; Huber, 1963; Hideux & Ferguson, 1976; Grund & Jensen, 1981; Haskins & Hayden, 1987; Spongberg, 1972), although my results are consistent with suggestions (Dahlgren, 1930; Jay, 1970; Wakabayashi, 1970) that it is more closely related to the former.

Some "higher" rosid orders and Dilleniidae are placed in the core rosid group between Cunoniaceae and Rosaceae, taxa hypothesized to be among the most primitive Rosidae (Dickison, 1989a). This result might be expected, given that "higher" rosids often are suggested to "originate" among Rosales (e.g., Cronquist, 1981). Two caveats are needed with regard to the placement of "higher" rosid orders. First, the "higher" rosid orders actually may nest within one of the represented terminal taxa. For example, Rosaceae may be a paraphyletic group with other recognized "families" or "orders" nesting within it. Including paraphyletic terminal taxa in addition to monophyletic segregates may have caused misleading results. It is particularly important that the monophyly of putatively primitive rosids such as Rosaceae and Cunoniaceae (see Hufford & Dickison, in press) be more rigorously assessed. Second, additional core rosid taxa, especially those sharing derived characters with "higher" rosid orders, should be included to assess more reasonably the sister group relationships of higher rosids.

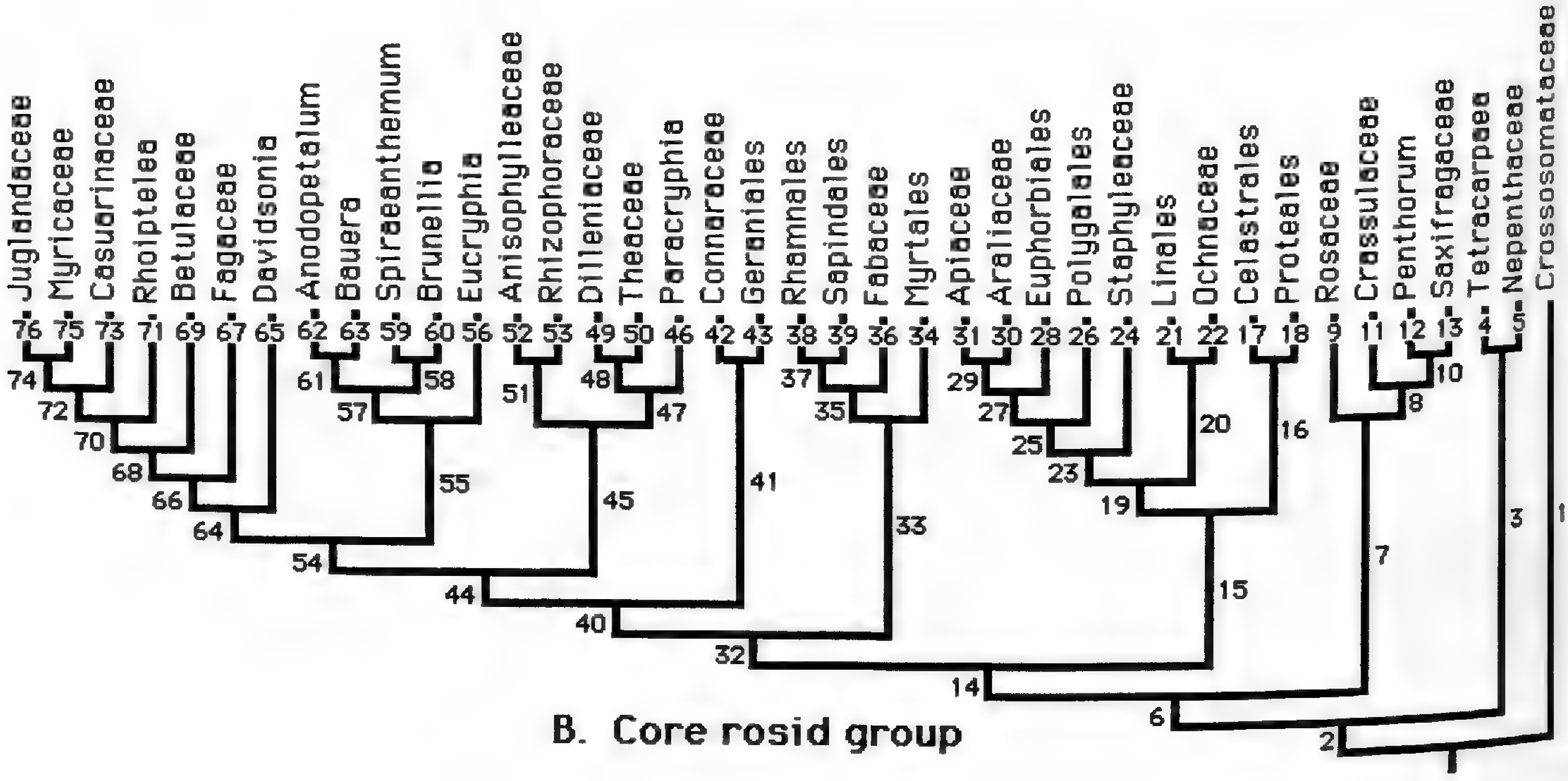
The Euphorbiales are included to determine their placement when considered to be part of the rosid group. Euphorbiales have been allied with Celastrales (Cronquist, 1981) and Geraniales (reviewed by Webster, 1987) among Rosidae, although they are perhaps most often placed among Dilleniidae near Malvales (Dahlgren, 1983; Dahlgren et al., 1981; Takhtajan, 1980, 1987; Thorne, 1981, 1983). My results place Euphorbiales as the sister group of Araliales (the Araliaceae–Apiaceae clade), a relationship supported by the presence of polyacetylenes. If Euphorbiales are actually more closely related to higher dilleniids, then their inclusion in the analysis may have influenced the placement of Araliales. For example, Dahlgren et al. (1981) allied Araliales with Pittosporaceae, and they are often suggested (e.g., Huber, 1963) to be related to Cornales. Altering the cladogram topology to place Pittosporaceae as the sister group of Araliales in the core rosid group adds only one character state change to the total number required for the most parsimonious trees. Changing the topology to place a Pittosporaceae–Araliales clade in various positions in the Corniflorae–asterid group adds five or more character state changes. For example, placing the Pittosporaceae–Araliales clade as the sister group of the Cornales adds seven character state changes. Bate-Smith et al. (1975) and Lee & Fairbrothers (1978) suggested, however, that Araliales are only "remotely" related to Cornales. Restriction site mapping of the cpDNA inverted repeat (Downie & Palmer, 1992) and *rbc*L sequence data (Olmstead et al., 1992) support the placement of Araliales among Asteridae.

Recent investigations of Rhizophoraceae have segregated *Anisophyllea* R. Br. ex Sabine, *Combretocarpus* Hook. f., *Poga* Pierre, and *Polygonanthus* Ducke as the separate family Anisophylleaceae (Cronquist, 1981; Behnke, 1988; Juncosa & Tomlinson, 1988a, b; Tobe & Raven, 1987, 1988a, b), although Vliet (1976, using wood anatomy) and Vezey et al. (1988, using pollen structure) identified three divergent groups in Rhizophoraceae sens. lat. Tobe & Raven (1988a) hypothesized monophyly for Rhizophoraceae sens. str. on the basis of subdermally initiated laticifers in the gynoecial walls and colleters. Rhizophoraceae sens. str. have been allied with Celastraceae and Elaeocarpaceae (Juncosa & Tomlinson, 1988a; Tobe & Raven, 1988b) and Anisophylleaceae with Myrtales (Tobe & Raven, 1988a). Anisophylleaceae, however, lack intraxylary phloem and vestured pits, which are derived features of Myrtales. Many characters (including crassinucellate ovules, micropyles formed by both integuments, nuclear endosperm formation, exalbuminous seeds, and pollen two-celled at "maturity") used by Tobe & Raven (1988a) to ally Anisophylleaceae with Myrtales appear to be symplesiomorphies for the core rosid group. Dahlgren (1980, 1983) placed Anisophylleaceae in Corniflorae (largely equivalent to the non-Asteridae portion of the Corniflorae–asterid group in my results). The unilacunar nodes, exstipulate leaves, and unitegmic ovules of Anisophylleaceae are present in some members of the Corniflorae–asterid group; however, it is more parsimonious to place the family as the sister group of Rhizophoraceae sens. str. in the core rosid group. My results demonstrate that it still may be reasonable to hypothesize monophyly for Anisophylleaceae and Rhizophoraceae sens. str.

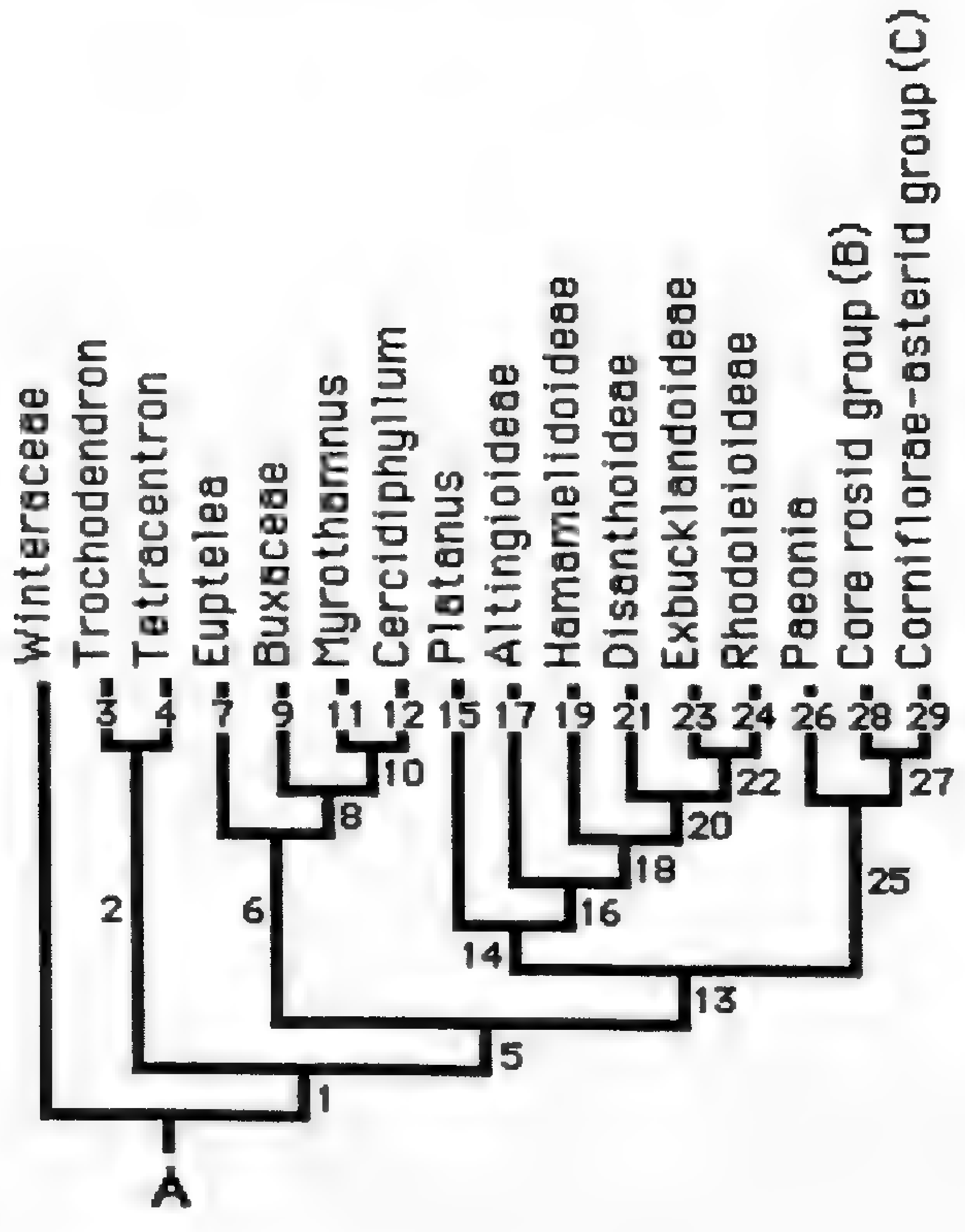
Anisophylleaceae and Rhizophoraceae are placed as the sister taxa of *Paracryphia*, Dilleniaceae, and Theaceae, although this relationship is weakly supported by a reversal to long imperforate elements in wood. The bitegmic, tenuinucellate ovules of Theales (sensu Cronquist, 1981), such as Theaceae, Scytopetalaceae, Medusagynaceae, and Clusiaceae, parallel those of some Rhizophoraceae sens. str. (e.g., *Gynotroches* Blume and *Pellacalyx* Korth; Juncosa & Tobe, 1988), and the unitegmic,



C. Corniflorae-asterid group



B. Core rosid group



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crassinucellate ovules of other Theales, such as *Paracryphia*, Oncothecaceae, and some Caryocaraceae, parallel those of some Anisophylleaceae (e.g., *Anisophyllea* and *Combretocarpus*; Tobe & Raven, 1987).

Dilleniaceae, Theaceae, and Ochnaceae are included as place-holders to represent Dilleniidae (sensu Takhtajan, 1980, 1987; Cronquist, 1981, 1988). The Dilleniaceae–Theaceae clade is supported by basally connate ovaries and centrifugal polystemony (a parallelism with *Paeonia*). *Paracryphia* is placed as the sister taxon of Dilleniaceae and Theaceae on the basis of wood with long vessel elements and heterogeneous type I rays. Ochnaceae appear to be more closely related to Linales than to these dilleniids (Fig. 1). Experimentally placing Ochnaceae as the sister group of the *Paracyphia*–Dilleniaceae–Theaceae clade adds five character state changes. My results do not support the placement of Actinidiaceae, Fouquieriaceae, Loasaceae, Sarraceniaceae, and Ericales in Dilleniidae as they are treated by Takhtajan (1980, 1987) and Cronquist (1981). The chemical, ovular, and endosperm attributes of these problematic taxa sup-

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FIGURE 2. One of the set of equally most parsimonious cladograms requiring 689 character state changes. Clades B (core rosid group) and C (Corniflorae–asterid group) are sister groups positioned at the indicated points on clade A. The character state changes for each branch of A, B, and C are indicated below as follows: clade letter and branch number: character number-apomorphic state.

A1: 6-1; 18-1; 23-2; 28-1; 31-1; 53-1; A2: 8-1; 27-1; 33-2; 35-1; 56-1; A3: 1-2; 23-0; 28-0; 48-1; A4: 5-1; 9-1; 32-2; A5: 10-1; 17-1; 51-1; A6: 1-1; 56-3; 57-1; A7: 6-2; 7-1; 15-0; 34-1; 36-2; 39-1; 48-1; 60-2; A8: 2-1; 12-2; 14-2; 21-1; 32-2; 35-1; A9: 6-0; 8-3; 27-1; 30-1; 31-0; 33-1; 35-2; 38-1; 39-3; 53-2; 55-1; 60-1; A10: 1-0; 5-1; 18-2; 21-2; 49-1; A11: 7-1; 18-6; 44-1; 56-2; A12: 9-1; 12-0; 14-1; 17-0; 28-0; 32-5; 34-1; 36-2; 45-1; A13: 22-1; 23-1; 44-1; 53-2; 54-1; A14: 5-0; 17-0; 21-1; 39-2; 45-1; 48-1; A15: 1-2; 7-1; 13-1; 14-2; 18-7; 22-0; 40-1; 60-2; A16: 12-0; 15-0; 20-1; 32-4; 33-2; 35-2; 36-1; 49-1; A17: 33-3; 39-0; 46-1; 53-0; 54-0; A18: 21-0; 27-2; A19: 6-2; A20: 39-1; A21: 11-1; 27-3; 31-0; 33-1; 37-1; 48-0; A22: 28-2; 56-3; A23: 18-3; A24: 6-2; 23-3; 39-0; 55-1; A25: 6-0; 12-2; 27-2; 31-0; 32-6; 55-1; A26: 3-1; 11-1; 14-3; 16-1; 28-5; 50-1; A27: 18-4; 36-1; 37-1; A28: 11-2; 14-4; 28-4; A29: 30-1; 32-4; 33-3; 35-2; 41-1.

B1: 15-0; 28-3; 34-1; 39-1; 49-1; 50-1; B2: 59-1; B3: 1-1; 7-1; 17-2; 23-2; 27-0; 32-2; 52-1; 56-4; B4: 11-1; 14-1; 18-2; 34-1; 56-5; B5:4-1; 13-2; 15-0; 21-2; 27-3; 35-2; 60-1; B6: 12-1; 48-1; B7: 7-2; 24-1; 32-1; 56-1; B8: 11-0; 16-2; 33-2; 44-0; 52-1; B9: 18-5; 26-1; 28-3; 30-1; 45-1/2; B10: 35-1; B11: no changes; B12: 1-1; 48-0; 49-1; B13: 32-3/4; B14: 13-1; 16-1; 35-3; 39-1; B15: 8-2; 28-1; B16: 17-0; 23-2; 24-1; 39-3; B17: 1-1; 16-5; 59-0; B18: 7-2; 12-2; 32-5; 45-2; 53-0/1; B19: 5-1; 18-0; 48-0; B20: 56-7; B21: 12-2; 13-0; 38-1; 39-3; 45-1; 50-1; B22: 16-2; 20-1; 42-1; B23: 7-2; 30-1; 32-3; 35-2; B24: 3-1; 11-0; 14-1; 17-0; 26-1; B25: 15-2; 16-4; 39-2; 60-4; B26: 2-1; 7-0; 13-0/2; 27-0; 28-4; 45-2; B27: 1-2; 38-1; 47-1; 59-0; B28: 6-2; 21-1/2, 37-0; 49-1; B29: 3-1; 5-0; 14-3; 18-2; 19-1; 32-4; 33-3; 41-1; 50-1; B30: 28-2; 32-6; B31: 12-2; 15-1; 42-1; 48-1; 56-1/3; 59-1; B32: 16-4; 18-6; 30-1; 56-8; B33: 12-2; 20-1; 45-2; B34: 1-1; 2-1; 23-2; 26-1; 49-1; 50-1; 56-1/3; B35: 3-1; 5-1; 32-5; 39-2; 47-1; B36: 8-2; 13-2; 24-1; 34-1; B37: 7-2; 15-2; 18-7; 28-1; 60-3; B38: 3-0; 26-1; 33-2/3; 38-2; 47-0; 48-0; B39: 5-0; 20-0; 32-3; 56-1; B40: 32-1; 35-2; B41: 3-1; 7-3; 8-2; 25-1; B42: 33-1; 35-1; 39-3; B43: 12-2; 13-2; 42-1; 48-0; 56-0; 60-1; B44: 14-1; 16-2; 18-1; 23-2; 32-0; B45: 13-2; 17-0; 49-1; B46: 2-2; 13-0; 22-0; 37-0; 41-1; 56-3; B47: 11-0; 12-0; 18-0; 30-0; B48: 16-1; 23-1; 28-5; 32-6; B49: 7-2; 14-3; 35-0/1; B50: 1-1; 13-1; 15-0; 30-1; 39-0; 42-1; 56-4; B51: 14-4; 33-3; 39-2; 48-0; 60-2; B52: 32-2; 41-1; 45-2; B53: 2-1; 5-1; 28-3; 35-3; 38-1; 52-1; 56-6; B54: 5-1; 7-1; 11-1; 52-1; B55: 2-1; 13-0; B56: 8-2; 28-3; 39-0; B57: 33-1; B58: 21-2; 22-0; 35-1; 39-3; B59: 7-0; 8-2; 11-0; 15-0; 24-1; 32-6; B60: 3-1; 18-0/3; 23-1; 37-0; B61: 7-2; 11-2; 14-2; 32-4; B62: 21-1; 60-4; B63: 12-2; 18-2; 28-2; 33-2; 35-3; 56-0; 59-0; B64: 18-7; 23-1; 32-4; 45-2; 60-2; B65: 3-1; 8-2; 17-0; 24-1; 38-1; B66: 14-3; 22-0; 23-3; 27-0; 28-1; 37-0; 39-3; 43-1; 49-1; 52-0; 56-4; B67: 16-4; 21-1; 32-3; 33-3; 56-5; B68: 14-4; 53-0; 54-0; 58-1; 59-2; B69: 15-2; 16-1; 33-2; 37-1; 41-1; B70: 7-2; 23-2; 38-2; B71: 3-1; 18-0; 39-2; 53-2; B72: 5-0; 14-2; 21-1; B73: 1-1; 2-2; 8-2; 11-2; 12-2; 30-0; 38-3; B74: 18-1; 39-4; 40-1; 41-1; B75: 7-1; 16-0; 60-3; B76: 3-1; 13-2; 14-4; 33-3.

C1: 12-0; 39-2/3; 48-1; 60-2; C2: 25-1; 35-3; 42-1; C3: 12-1; 14-3; 16-4; 26-1; 39-1; 56-6; 59-2; 60-4; C4: 1-1; 24-1; C5: 5-1; 18-0; 52-1; 56-3; 59-1; C6: 14-4; 16-2; 44-0; 60-1; C7: 1-0; 6-1; 7-2; 25-0; 30-0; C8: 7-3; 11-1; 23-2; 38-3; 39-2; 42-0; 50-1; 60-3; C9: 2-1; 8-2; 16-1; 21-2; 22-0; 27-0; 35-2; 44-1; 57-1; C10: 12-0; 13-1; 17-0; 18-0; 59-1; C11: 13-2; 15-2; 16-4; 25-1; C12: 11-0; 14-2; 38-0; 49-1; 56-8; C13: 2-1; 16-0; 30-1; 50-0; C14: 8-2; 23-1; 24-0; 28-4; 37-0; 38-1; 42-1; C15: 14-0; 28-4; 32-2; C16: 2-1; 6-2; 12-1; 16-1; 18-0; 35-2; 52-1; 54-0; C17: 7-0; 8-2; 26-1; 30-1; 32-6; 39-1; 48-1; C18: 14-3; C19: no changes; C20: 6-1; 23-2; 46-0; 56-8; 59-1; C21: 24-0; 32-3; 56-1; 59-1; C22: 4-1; 16-0; 33-0; 56-7; C23: 11-2; 13-1; 15-0; 28-3; 38-3; 50-1; C24: 11-2; 33-0; C25: 28-4; 32-3; 49-1; C26: 12-0; 14-2; 15-0; 18-0; 56-6; 59-2; C27: 39-1; 41-0; 45-1; C28: 12-1; 16-0; 32-1; C29: 11-0; 49-0; C30: 7-1; 21-2; 25-0; 27-0; 28-3; 32-0; 35-2; 52-1; C31: 18-1; 20-1; 24-0; 48-1; 50-1; C32: 15-2; 29-1; C33: 18-1; 44-1; 46-0; C34: 1-0; 7-2; 8-2; 16-3; 29-0; 38-3; 47-1; C35: 17-2; 32-3; 50-1; 53-0; 54-0; C36: 13-1; 16-1; 60-0; C37: 59-1; C38: 7-2; 16-3; C39: 18-5; 46-0; 50-1; 53-1; 56-4; C40: 16-4; 33-3; 47-1; C41: no changes; C42: 15-1; 29-0; 32-6; 53-2; 56-6/8; C43: 1-0; 18-1/2; 38-2; 39-4; 45-2; 59-0; 60-2; C44: 2-1; 5-1; 12-1; C45: 18-1/5, 44-1; 50-1; C46: 15-0; 33-3; 39-1; C47: 8-2; 15-1; 48-1; 57-1; C48: 7-2; 16-0; 49-1; C49: 11-0; 32-3; 42-0; 60-3; C50: 5-0; 18-0; 59-2; C51: 11-1; 13-0; 18-6; 39-0; 46-0; C52: 32-6; 56-4; 60-4.

port their placement in the Corniflorae–asterid group. Marcgraviaceae, although not included in my investigation, also may be more closely related to members of the Corniflorae–asterid clade than to Theales, among which it is commonly placed (e.g., Cronquist, 1981; Dahlgren, 1983; Thorne, 1983; Takhtajan, 1987). The bitegmic, tenuinucellate ovules of Marcgraviaceae are compatible with those of Theales and the Corniflorae–asterid group, but its integumentary endothelium, cellular endosperm, and endosperm haustoria (Mauritzon, 1939; Swamy, 1948a) are attributes generally found in combination only in the latter. Marcgraviaceae warrant examination for iridoid compounds, which might help to support a hypothesis of relationship to the Corniflorae–asterid group.

Core Cunoniaceae, represented by *Anodopetalum* and *Spiraeanthemum,* form a monophyletic group along with *Bauera* and *Brunellia,* supporting the results of a phylogenetic analysis of the family by Hufford & Dickison (in press). The more inclusive analysis by Hufford & Dickison has shown *Eucryphia* to be nested within Cunoniaceae and not its sister group as might be interpreted from these results (Fig. 1). The Cunoniaceae clade, including *Bauera, Brunellia,* and *Eucryphia,* is supported by small pollen grains.

The close placement of Rhizophoraceae and Cunoniaceae is interesting, given the interpetiolar stipules (often enclosing the terminal bud and sometimes associated with colleters) in both groups. *Dialypetalanthus* Kuhlm., generally placed in the monotypic Dialypetalanthaceae allied with Myrtales and Rubiaceae (Cronquist, 1981; Rizzini & Occhioni, 1949), has interpetiolar stipules and other attributes similar to Cunoniaceae and Rhizophoraceae. Although Juncosa & Tomlinson (1988a) regarded suggestions of relationship for Rhizophoraceae sens. str., Cunoniaceae, and Dialypetalanthaceae as "indefensible," this warrants testing in a broadly based phylogenetic analysis that includes Myrtales and Rubiaceae.

Cunoniaceae are placed as the sister group of a clade consisting of *Davidsonia,* Fagaceae, and other taxa often considered to be "higher" Hamamelidae (Fig. 1). This result supports contentions that "higher" hamamelids are more closely related to rosids than to "lower" hamamelids (Wolfe, 1973, 1989; Hickey & Wolfe, 1975; Hickey & Doyle, 1977; Nixon, 1989). Although Fagaceae–Betulaceae, Juglandaceae–Myricaceae–Rhoipteleaceae, and Casuarinaceae are commonly discussed as three separate monophyletic groups (e.g., Cronquist, 1981), they are seldom placed in a single group as shown by my results (although, see Stone & Broome, 1971, 1975; Zavada & Dilcher, 1986; Kedves, 1989; Nixon, 1989). Fagaceae and their sister group are defined by chalazalogamy (not present in all Fagaceae) and nonpersistent endosperm. Betulaceae and their sister group share pollen traits, including poroid apertures and poorly developed columellae ("granular" columellae sensu Zavada & Dilcher, 1986). Zavada & Dilcher (1986) identified other pollen characteristics, including a microchanneled tectum and thin footlayer, that may help define this group (these attributes are not included in this analysis because of insufficient sampling among other rosids).

THE CORNIFLORAE–ASTERID GROUP

Ovular traits are important for developing hypotheses about relationships in the Corniflorae–asterid group as emphasized by Dahlgren (1975). The Corniflorae–asterid group, consisting of Bruniaceae and their sister group (Fig. 2), shares unitegmic ovules. Although Bruniaceae retain crassinucellate ovules, their sister group is defined by tenuinucellate ovules. Among Cornales, Garryaceae, Alangiaceae, and Cornaceae have a reversal to crassinucellate ovules. *Fouquieria* has a reversal to bitegmic ovules but has retained its single-layered nucellus.

Dahlgren (1975) also used endosperm attributes to circumscribe Corniflorae (a group corresponding largely to the nonasterid members of the Corniflorae–asterid group of Fig. 2). The presence of ab initio cellular endosperm defines the sister group of *Escallonia,* although reversals to nuclear endosperm occur in some members of this group (e.g., Garryaceae, Loganiaceae, Pittosporaceae, and Polemoniaceae). Some of the taxa in this group are polymorphic for endosperm formation (e.g., Asteraceae, Solanaceae, Rubiaceae, and Alangiaceae). The ab initio cellular endosperm of the Corniflorae–asterid group is a reversal to a trait present among "lower" hamamelids (which may have retained it from Magnoliidae; cf. Dahlgren, 1975). The formation of endosperm haustoria was not used as a character because of limited data availability, but mapping its occurrence on the cladogram indicates numerous parallel origins are likely. Although lost in *Actinidia,* endosperm haustoria are shared by most members of the ericalean clade, including *Fouquieria.*

The placement of Alseuosmiaceae (Fig. 1) reflects Takhtajan's (1980) classification in which they are listed between Bruniaceae and Pterostemonaceae. Airy Shaw (1973) and Gardner (1978) noted affinities between them and Escalloniaceae.

Many members of the Corniflorae–asterid group retain a suite of wood attributes generally considered to be "primitive," but Alseuosmiaceae have derived tendencies toward raylessness and scarcity of axial parenchyma (Dickison, 1986c). Other members of the Corniflorae–asterid group, such as Loasaceae, Polemoniaceae, and Scrophulariaceae (Carlquist, 1988, 1992), also have trends toward raylessness and/or scarcity of axial parenchyma, which have been associated with paedomorphic wood evolution (Carlquist, 1962). Paedomorphosis must have occurred numerous times in wood of the Corniflorae–asterid group.

The Cornales (represented by Garryaceae, Alangiaceae, Nyssaceae, and Cornaceae) are defined by uniovulate carpels (parallel with some core rosids), fleshy (berry- to drupelike) fruits, and camptodromous secondary venation in leaves. A reversal to crassinucellate ovules also supports the clade, although Nyssaceae are secondarily tenuinucellate. Among Nyssaceae, *Nyssa* and *Camptotheca* are tenuinucellate, and *Davidia* is crassinucellate (Mohana Rao, 1972a; Schmid, 1978a; Tandon & Herr, 1971). Based on Eyde's (1988) phylogenetic hypothesis for Nyssaceae, the thick nucellus of *Davidia* is a parallelism with that of other Cornales. Two additional features, endosperm with hemicellulose and the formation of a nucellar cap, also may support the hypothesis of monophyly for Cornales, but neither was used in this analysis because of limited data availability.

My results support Eyde's (1988) placement of Cornaceae and Nyssaceae as sister groups on the basis of shared foveolate pollen exine. Alangiaceae share with Cornaceae and Nyssaceae reversals to long vessel and imperforate elements in their wood (Adams, 1949; Titman, 1949; Metcalfe & Chalk, 1950; Li & Chao, 1954, report shorter measurements for Alangiaceae than other authors). *Garrya* diverges from other Cornales in floral attributes. The dioecy, loss of a nectary, and other floral simplifications probably are associated with the evolution of wind pollination in *Garrya* (see Dahling, 1978). Dahling (1978) suggested that pollen of *Garrya* strongly resembles that of Cornaceae, but it differs in having a papillate secondary tectal sculpture that parallels that of *Euptelea, Buxaceae, Cercidiphyllum*, and *Myrothamnus*. Paliwal & Kakkar (1970) noted that *Garrya* diverged from Cornaceae in unique leaf features.

Actinodromous leaf venation and basifixed anthers support the monophyly of Cornales, Hydrangeaceae (represented by *Hydrangea, Deutzia*, and *Philadelphus*), Loasaceae, and Sarraceniaceae (Fig. 2). The Hydrangeaceae–Loasaceae–Sarraceniaceae group is supported by diplostemonous androecia, although Loasaceae are coded as polystemonous. Diplostemony is present among Loasaceae only in *Schismocarpus* (Hufford, 1989, 1990). A generic-level cladistic analysis of Loasaceae, however, has shown polystemony to be plesiomorphic for the family even when the outgroup is coded as diplostemonous (Hufford, unpublished results). Among Sarraceniaceae, only *Heliamphora* includes diplostemonous members (Maguire, 1978). Both *Darlingtonia* and *Sarracenia* are polystemonous (Maguire, 1978). Based on Thanikaimoni & Vasanthy's (1972) and Maguire's (1978) hypothesis that *Heliamphora* is the most primitive member of Sarraceniaceae, the family was coded using it. The Loasaceae–Sarraceniaceae clade is supported by tricarpellate gynoecia. Coding for gynoecial states is based on *Mentzelia* for Loasaceae and *Heliamphora* for Sarraceniaceae, although both families have variation in gynoecial merosity, with five carpels being the most common in each.

Loasaceae have been placed in Dilleniidae in some treatments (e.g., Gilg, 1925; Cronquist, 1981) largely on the basis of their parietal placentation and putatively centrifugally developing polystemonous androecia. Various androecial developmental patterns are present among Loasaceae, but none are strictly centrifugal (Hufford, 1990). Those Loasaceae with a centrifugal phase during androecial development actually begin with centripetal development and have complex androecia that are probably derived within the family. Emphasis has been given to trichomes in taxonomic studies of Loasaceae, although they have not been used to develop hypotheses of relationship for the family because of their presumed uniqueness. Among Loasaceae, the tuberculate trichomes with and without a prominent pedestal of basal cells may be homologous with similar tuberculate trichomes, including some with distinct basal cells, of Hydrangeaceae (Hardin & Pilatowski, 1981). Loasaceae and Hydrangeaceae are among the few groups found to possess 10-carboxyl (and 10-decarboxylated) iridoids (Dahlgren et al., 1981). Other groups with these iridoid forms include Ericaceae, Oleaceae, Retziaceae, Stilbaceae, and Verbenaceae. Seco-iridoids are present in Loasaceae and Sarraceniaceae as well as in Hydrangeaceae, Gentianales, Dipsacales, and a few other members of the Corniflorae–asterid group (Dahlgren et al., 1981).

Sarraceniaceae have been allied with magnoliids, such as Ranunculaceae and Papaveraceae (Lindley, 1847; Thanikaimoni & Vasanthy, 1972;

Takhtajan, 1980), or dilleniids, such as Theales and Parietales (Markgraf, 1955; DeBuhr, 1977). This analysis does not test the placement of Sarraceniaceae among magnoliids, but its evolution among them seems unlikely given its derived features. Sarraceniaceae have been allied with Nepenthaceae in some classifications (e.g., Cronquist's, 1981, Nepenthales) on the basis of shared ascidiate leaves involved in insectivory. My results, which place Nepenthaceae in the core rosid group, are not consistent with those classifications.

Although Sarraceniaceae are placed as the sister taxon of Loasaceae in these results, I call attention to their potential evolution among Ericales. DeCandolle (1873) noted similarities among Sarraceniaceae and Monotropoideae and Pyroloideae of Ericaceae. Jensen et al. (1975) more recently called attention to similarities between Sarraceniaceae and Ericales. For example, the placentation of Sarraceniaceae, Monotropoideae, and Pyroloideae is axile in the lower part of the gynoecium and parietal in the upper (Abbott, 1936; Maguire, 1978; Hufford, unpublished obs.). Inversion of the anthers is common among Ericales, although it has not been described for Cyrillaceae. Anther inversion occurs relatively early during stamen development among most Ericales, although in *Clethra* and some Ericaceae it occurs at anthesis. In Sarraceniaceae, anther inversion at anthesis occurs in *Heliamphora* (Maguire, 1978), although it is unknown in *Darlingtonia* and *Sarracenia*. The umbrellalike stigma of Sarraceniaceae may represent an elaboration of the capitate stigma common among Ericales. Numerous cells of the flowers of Sarraceniaceae and Ericales are tanniferous (Hufford, unpublished obs.). These attributes are notably not shared by Sarraceniaceae and Loasaceae, but may be derived states shared by the former and some Ericales. Within Sarraceniaceae, Loasaceae, and Ericales, gynoecia with three to five carpels are present.

The clade composed of Ericales (with Fouquieriaceae) and Asteridae (with Pittosporaceae and *Columellia*) is supported by unilacunar nodes and sympetally (Fig. 2). Unilacunar nodes and sympetaly were used historically to hypothesize monophyly of Asteridae. Both traits occur as parallelisms in *Escallonia*.

The core ericalean groups, Clethraceae and Ericaceae, form part of a monophyletic group including *Actinidia* and Fouquieriaceae. Fouquieriaceae have been allied primarily with parietalean dilleniids (Bentham & Hooker, 1862; Niedenzu, 1895; Behnke, 1976; Cronquist, 1981; Takhtajan, 1980, 1987). Various chemical compounds, including ellagitannins and iridoids, in Fouquieriaceae do not support their placement in Dilleniidae (Bate-Smith, 1964; Scogin, 1977, 1978, Jensen & Nielsen, 1982). Dahlgren et al. (1976) used the chemical profile, polyandrous flowers, and tricarpellate gynoecia of Fouquieriaceae to suggest they were more closely related to Ericales (as part of Dahlgren's Corniflorae) than to dilleniids, which is consistent with my results and those of Olmstead et al. (1992).

Nash (1903), Henrickson (1967), Thorne (1977, 1981, 1983) and Downie & Palmer (1992) allied Fouquieriaceae with Polemoniaceae, which is especially interesting when the former is compared with *Acanthogilia* [*Gilia*] *gloriosa*. Nash (1903) suggested that Fouquieriaceae were similar to *Gilia* located in the same area. *Acanthogilia* is a basally branched shrub of north-central Baja California (Day & Moran, 1986). It is similar to Fouquieriaceae not only in its overall shoot morphology but also in its long shoot/short shoot dimorphism and leaf development. Leaves on long shoots of *Acanthogilia* sclerify as spines. Short shoots arise in the axils of spinose leaves. The leaves formed on short shoots have deciduous blades but persistent bases reminiscent of Fouquieriaceae. The pollen of both *Fouquieria* and *Acanthogilia* is colporate with a reticulate exine. Neither of these genera has the specialized pollen characteristics of many Polemoniaceae. Day & Moran (1986: 125) suggested that *Acanthogilia* is most closely related to *Cantua* in being a "specialized desert descendant of a diploid line also ancestral to *Cantua*," although it shares numerous derived features with *Fouquieria*.

My results place Polemoniaceae and Pittosporaceae as the sister group of the rest of Asteridae and Fouquieriaceae as the sister group of the rest of Ericales (Fig. 1). Chloroplast DNA sequence data (Olmstead et al., 1992) currently support the hypothesis that Fouquieriaceae and Polemoniaceae are part of a monophyletic Ericales. Polemoniaceae and asterids have distinctly epipetalous stamens. Epipetalous stamens are derived in some ericalean groups, but none were coded with this state in my analysis. The tricarpellate gynoecia and loculicidal capsules of Polemoniaceae are characteristic of Ericales, such as Clethraceae, but not of asterids, which tend to have bicarpellate gynoecia and septicidal capsules. Iridoid compounds have been lost among Ericales (e.g., in Cyrillaceae and Clethraceae) and asterids. Some of the specialized pollen of Polemoniaceae and the ericalean Epacridaceae are quite similar. Asterids that lack iridoids generally synthesize polyacetylenes and/or tropane alkaloids (Dahlgren et al., 1981; Gershenzon & Mabry, 1983), but this is not true of Polemoniaceae. Polemoniaceae, Clethraceae, and the Monotropoideae and Pyroloideae of the Ericaceae were the only groups to form both ketose and isoketose oligosaccharides in a broad survey by Pollard & Amuti (1981). Isoketose oligosaccharides were found in various asterids, possibly indicating this trait is shared by all members of the asterid–ericalean monophyletic group.

Actinidia has been allied with Dilleniaceae and Theaceae (Hutchinson, 1959; Dickison, 1972b; Schmid, 1978b; Cronquist, 1981). Its unitegmic, tenuinucellate ovules, and iridoid compounds are derived features shared with members of the Corniflorae–asterid group but not with Dilleniaceae. Some Theales share ovular characteristics with *Actinidia* but not its cellular endosperm and iridoids. Heel (1987) has shown that androecial development in *Actinidia* is not strictly centrifugal as among some dilleniids, although the putative presence of this attribute has been used to place it in Dilleniidae. Hallier (1905), Hunter (1966), and Takhtajan (1969) allied *Actinidia* with Ericales; this is supported by my results. The branch (Fig. 2) with Clethraceae, Ericaceae, and *Actinidia* is corroborated by the occurrence of 600–1,000-μm-long vessel elements, opposite intervessel pitting, and imperforate pollen tectum in all three taxa. Like other Ericales, the anthers of *Actinidia* become inverted.

The present study significantly demonstrates the placement of Asteridae as the sister group of Ericales among taxa recognized by Dahlgren (1980, 1983) as Corniflorae. Epipetalous stamens may be a derived feature shared by all Asteridae, although the placement of Pittosporaceae as the sister group of Polemoniaceae makes this equivocal. Haplostemony is commonly used to support the hypothesis of monophyly of Asteridae, but my results show that it originates with "lower" hamamelids and is retained in the Corniflorae–asterid group. Diplostemony and polystemony are derived variously in the Corniflorae–asterid group as well as among the core rosids. Corolla connation (sympetaly) unites the asterid and ericalean groups, but it also occurs in other members of the Corniflorae–asterid group, including Alangiaceae, Alseuosmiaceae, Escalloniaceae, and Loasaceae.

Columellia has been allied with a wide variety of groups (see Stern et al., 1969), ranging from asterids (including Gesneriaceae, Loganiaceae, and Rubiaceae), "woody saxifrages" (such as *Philadelphus* and *Escallonia*), and dilleniids (Cucurbitaceae). My results place *Columellia* as the sister group of Caprifoliaceae. Stern et al. (1969) suggested that most attributes of *Columellia* were shared by Escalloniaceae, and experimentally placing *Columellia* as the sister group of Escalloniaceae adds three character state changes. Including *Columellia* in more inclusive studies with Dipsacales and Escalloniaceae may lead to more decisive hypotheses about its placement.

My results are not consistent with hypotheses that *Viburnum* is more closely related to groups other than Caprifoliaceae nor with those (e.g., Dahlgren, 1983; Takhtajan, 1987) suggesting that Dipsacales, such as Caprifoliaceae, are more closely related to rosids of the Corniflorae grade than to asterids. The monophyly of *Columellia*, Caprifoliaceae, and *Viburnum* is supported by reversals in wood attributes, such as a solitary distribution of vessels and only true tracheids as imperforate elements. Chloroplast DNA data (Donoghue, 1992; Downie & Palmer, 1992; Olmstead et al., 1992) do support a placement for *Viburnum* and *Sambucus* separate from other Caprifoliaceae (with both placed among Asteridae).

The monophyly of Asteridae as traditionally circumscribed (e.g., Cronquist, 1981) is largely supported. The results do not support the Jensen et al. (1975) hypothesis of a separate rosid origin for asterids with iridoid compounds from those without iridoids. The asterids without iridoids of the Solanales, Campanulales, and Asterales are placed as a monophyletic group nested among the asterids with iridoid compounds. The results also do not support Takhtajan's (1987) classification, in which asterids are circumscribed in three groups (Dipsacales, Lamiidae, and Asteridae sens. str.) with separate origins among the rosid Cornanae.

CONCLUSIONS AND PROBLEMS FOR FURTHER RESEARCH

This preliminary, exploratory analysis has pertinent results for understanding the phylogeny of nonmagnoliid dicotyledons. These include: (1) Hamamelidae (sensu Takhtajan, 1980, 1987; Cronquist, 1981, 1988) are polyphyletic; (2) "lower" Hamamelidae (e.g., Trochodendrales and Hamamelidales) are a grade at the base of the nonmagnoliid dicotyledons; (3) Rosidae (sensu Takhtajan, 1980, 1987; Cronquist, 1981, 1988) are paraphyletic with respect to Asteridae, Dilleniidae, and "higher" Hamamelidae (e.g., Fagales, Juglandales, and Casuarinaceae); (4) "higher" Hamamelidae appear most closely related to *Davidsonia* and Cunoniaceae; (5) monophyly of Dilleniidae is not supported; and (6) Dahlgren's (1980, 1983) Corniflorae are the rosid grade in which Asteridae are rooted.

Rosidae are central to understanding the phylogeny of nonmagnoliid dicotyledons, and they require extensive investigation. Identification of monophyletic groups among basal rosids and ascertaining their relationship to higher rosid orders are crucial. A key step will involve investigating the monophyly of Rosaceae by analyzing their relationships with Chrysobalanaceae, Connaraceae, Fabaceae, Rhabdodendraceae, and Surianaceae, as well as higher rosid orders. Ascertaining the relationships of Engler's (1930) Saxifragaceae also is critical for understanding early evolution in both the core rosid group and the Corniflorae–asterid group (see Soltis et al., 1990). Additional analyses centered on Cunoniaceae (see Hufford & Dickison, in press) will be important for better understanding relationships of *Davidsonia* and "higher" Hamamelidae on one hand and Rhizophoraceae, Dilleniales, and Theales on the other. Monophyletic groups in Dilleniidae and their relations with rosids remain virtually unexplored, but their identification will lead to better understanding of the diversification of nonmagnoliid dicotyledons. More detailed analyses of the Corniflorae (sensu Dahlgren, 1983) grade of Rosidae will be crucial for understanding the relationships of problematic taxa (including major groups such as Ericales and, possibly, Ebenales) and the evolution of character suites present among Asteridae. Defining a monophyletic Asteridae and understanding relationships among their major clades also will be contingent on more fully developed hypotheses of relationships among taxa of the Corniflorae grade. Large, broadly based cladistic analyses will be critical for developing hypotheses of relationship for higher level taxa and, especially, problematic groups.

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APPENDIX 1. Characters and character states used in the cladistic analysis. Literature sources of data used in the analysis are indicated for each broad group of characters.

Nodes and leaves (Bausch, 1938; Cronquist, 1981; Dahling, 1978; Dickison, 1975a, b, 1978, 1980, 1987b, 1989a, b; Dickison & Rutishauser, 1990; Elias, 1971; Endress, 1989c; Eyde, 1966; Haskins & Hayden, 1987; Henrickson, 1972; Hickey & Wolfe, 1975; Hils et al., 1988; Hoogland, 1979; Hufford, 1989; Hutchinson, 1959; Johnson & Wilson, 1989; Keng, 1962; Kohler & Bruckner, 1989; Kohler & Schirarend, 1989; Leeuwenberg & Leenhouts, 1980; Manning, 1978; Metcalfe & Chalk, 1950; Pillans, 1947; Puff, 1978a, b; Richardson, 1970; Robertson, 1972, 1974; Rutishauser & Dickison, 1989; Spongberg, 1972; Stern, 1974, 1978; Styer & Stern, 1979a, b; Swamy, 1954; Varghese, 1969; Weberling, 1976; Withner, 1941; Wolfe, 1973, 1989).

1. Nodes: trilacunar (0), unilacunar (1), multilacunar (2). *Myrothamnus* has the so-called "split lateral" nodal condition (Howard, 1970, 1979) in conjunction with its opposite leaves. In this analysis, the split lateral condition of *Myrothamnus* is homologized with the more conventional unilacunar, one-trace nodes.

2. Leaf arrangement: alternate (0), opposite (1), whorls (2).

3. Leaf morphology: simple (0), compound (1).

4. Ascidiate leaves: absent (0), present (1).

5. Stipules: absent (0), present (1).

6. Venation: pinnate (0), actinodromous (1), pinnate but with basal concentration of laterals (2).

7. Secondary veins: brochidodromous (0), craspedodromous (1), semicraspedodromous (2), camptodromous (3).

8. Stomates: anomocytic (0), laterocytic (1), paracytic (2), encyclocytic (3). Connaraceae and Platanaceae are coded as question marks because of stomatal variability.

9. Reproductive short shoots with only a single leaf: absent (0), present (1).

Wood (Baas & Zweypfennig, 1979; Bailey & Nast, 1945; Brush, 1917; Carlquist, 1964, 1966, 1969, 1976, 1978, 1981a, b, 1982a, b, 1984; Carlquist & Hoekman, 1985; Carlquist et al., 1984; Cronquist, 1981; DeBuhr, 1977, 1978; Dickison, 1967a, 1972a, 1978, 1980, 1986c; Dickison & Baas, 1977; Giebel & Dickison, 1976; Hall, 1952; Haskins & Hayden, 1987; Heimsch, 1942; Heimsch & Wetmore, 1939; Heimsch & Tschabold, 1972; Hils et al., 1988; Ingle & Dadswell, 1986; Keefe & Moseley, 1978; Keng, 1962; Koek-Noorman, 1969; Marco, 1935; Metcalfe & Chalk, 1950; Moseley, 1948; Moseley & Beeks, 1955; Nast & Bailey, 1946; Patel, 1973; Record, 1938a, b, 1942; Stern, 1974, 1978; Stern et al., 1969; Styer & Stern, 1979a, b; Swamy & Bailey, 1949; Tang, 1932; Tippo, 1938; Vliet, 1976).

10. Conducting elements: only tracheids (0), vessels or vessels and tracheids (1).

11. Vessel element perforations: all scalariform with many bars (>20) (0), all or most scalariform with few bars (<20)(1), all or most simple and those that are scalariform with few bars (2).

12. Vessel element length: long (most >1,000 μm) (0), moderate (600–1,000 μm), (1), short (most <600 μm) (2).

13. Vessel element diameter: narrow (most <60 μm) (0), moderate (60–100 μm) (1), wide (most >100 μm) (2).

14. Intervessel pitting: scalariform (0), scalariform-opposite (1), opposite (2), opposite-alternate (3), alternate (4).

15. Vessel distribution: solitary (0), mostly solitary with some clusters and some pairs and/or radial multiples (1), mostly radial multiples and clusters with few solitary (2).

16. Imperforate elements: only true tracheids (0), true tracheids and fiber-tracheids (1), only fiber-tracheids (2).

fiber-tracheids and libriform fibers (3), only libriform fibers (4), variable with true tracheids, fiber-tracheids and libriform fibers (5). Character state definitions follow Carlquist (1988). Coding for *Alseuosmia* is based on Dickison's (1986c) characterization of the pits as "indistinctly bordered or simple" rather than on Carlquist (1988), who described the imperforate elements as true tracheids.

17. Imperforate element length: long (most >1,500 μm) (0), moderate (most 500–1,500 μm) (1), short (most <500 μm) (2).

18. Type of rays: heterogeneous type I (0), heterogeneous type IIA (1), heterogeneous type IIB (2), heterogeneous type III (3), paedomorphic type I (4), paedomorphic type II (5), paedomorphic type III (6), homogeneous type I (7). Character states based on definitions in Carlquist (1988). Linales, Celastrales, Rhamnales, and Myrtales are coded as question marks because of variability.

19. Rays with secretory canals: absent (0), present (1).

20. Ray cells with gum deposits: absent (0), present (1).

Flowers (Bange, 1952; Beamish & Lin, 1965; Bensel & Palser, 1975a, b, c; Bhandari, 1971; Bogle, 1986, 1989; Brizicky, 1961; Brouwer, 1924; Burkett, 1932; Chapman, 1953; Cronquist, 1981; Cuatrecasas, 1970; Dahlgren, 1975; Dahling, 1978; Daumann, 1974; Davis, 1966; Dickison, 1968, 1970, 1971, 1972b, 1975a, c, 1978, 1986a; Dnyansagar, 1955; Elias, 1971; Endress, 1969, 1977, 1986, 1989a, b, c; Eyde, 1964, 1968, 1988; Eyde & Tseng, 1971; Flores & Moseley, 1982; Gardner, 1978; Gaumann, 1919; Graham et al., 1987; Gusejnova, 1976; Harms, 1930; Heel, 1987; Herr & Dowd, 1968; Hils et al., 1988; Hjelmquist, 1948, 1957; Hufford & Endress, 1989; Hutchinson, 1927, 1959; Jäger-Zürn, 1966; Johansen, 1936; Juncosa & Tobe, 1988; Kapil & Vani, 1963; Kaul & Kapil, 1974; Kavaljian, 1952; Keng, 1962; Klopfer, 1973; Langdon, 1939; Lawrence, 1951; Leeuwenberg, 1969; Manning, 1978; Maguire, 1978; Mauritzon, 1936; Mohana Rao, 1972a, b; Mohrbutter, 1936; Moore, 1948; Morf, 1950; Nagaraja Rao, 1957; Nair & Abraham, 1962; Nair & Sarma, 1961; Narayana, 1975; Narayana & Radhakrishnaiah, 1976; Narayana & Rao, 1971; Narayana & Sundari, 1972; Nast & Bailey, 1945; Palser et al., 1989; Philipson, 1970; Pillans, 1947; Prakash & McAlister, 1977; Puff & Robbrecht, 1989; Robertson, 1972, 1974; Sastri, 1958; Schlechter, 1920; Schmid, 1978b; Shreve, 1906; Singh, 1959, 1961; Sleumer, 1968; Small & Rydberg, 1905; Souèges, 1936; Spongberg, 1971, 1972, 1978; Stern et al., 1969; Subra Rao, 1941; Swamy, 1948b; Swamy & Bailey, 1949; Szyszylowicz, 1895; Tandon & Herr, 1971; Tieghem, 1903; Tobe & Raven, 1983, 1987, 1988a; Uhl, 1964; Wiggins, 1959; Wilkinson, 1944, 1948a, b, c, 1949; Wilson, 1965, 1973; Wunderlich, 1959).

21. Plant sex distribution: bisexual (0), monoecious (1), dioecious (2).

22. Floral phyllomes: unicyclic (0), bicyclic (1). *Euptelea*, *Cercidiphyllum*, Myricaceae, and Casuarinaceae are coded as question marks because floral phyllomes are absent. Hamamelidaceae subfamily Altingioideae and Asteraceae are coded as question marks because of the ambiguous homology of the floral phyllomes.

23. Perianth merosity: numerous and helical (0), pentamerous (1), tetramerous (2), few and irregular (3).

24. Calyx connation: absent (0), present (1).

25. Corolla connation: absent (0), present (1).

26. Hypanthium: absent (0), present (1).

27. Nectary: absent (0), abaxial gynoecial surface (1), disc (2), perianth (3).

28. Androecial pattern and merosity: helical polyandry (0), haplostemony (1), complex polyandry with 11–20 stamens (2), complex polyandry with >20 stamens (3), diplostemony (4), centrifugal polyandry (5).

29. Epipetalous stamens: absent (0), present (1).

30. Anther insertion: basifixed (0), dorsifixed (1).

31. Stomial pattern: no bifurcations ("linear") (0), bifurcated proximally and/or distally (1). Pores are considered to be derived from unbifurcated stomia.

32. Carpel number: > five (0), five (1), four (2), three (3), two (4), one (5), variable one–five (6).

33. Carpel insertion: superior (0), only extreme base inferior (1), basal half inferior (2), mostly to completely inferior (3).

34. Carpel stipitation: absent (0), present (1).

35. Carpel connation: distinct (0), base of ovaries connate (1), ovaries completely connate and base of styles may be connate (2), ovaries and styles completely connate (3).

36. Style: eccentric peak of ovary (0), intercalated (1), absent (2).

37. Stigma position: decurrent (0), localized on stylar apex (1).

38. Placentation: marginal and/or axile (0), axile-apical (1), axile-basal (2), parietal (3).

39. Ovules per carpel: many (>10) (0), few and variable (1–10) (1), strictly one (2), strictly two (3), one per gynoecium (with more than one carpel) (4).

40. Orthotropous ovules: absent (0), present (1).

41. Integument number: two (0), one (1).

42. Nucellus: crassinucellate (0), tenuinucellate (1).

43. Entrance of pollen tube: porogamy (0), chalazalogamy (1).

44. Endosperm formation: ab initio cellular (0), nuclear (1).

45. Endosperm persistance: persists and copious (0), persists but scanty (1), does not persist (2).

Chemistry (Bate-Smith, 1973, 1977; Bohlmann et al., 1973; Challice, 1981; Cronquist, 1981; Crowden, 1969; Dahlgren et al., 1976; Elsworth & Martin, 1971; Gershenzon & Mabry, 1983; Giannasi, 1986; Gornall et al., 1979; Jay, 1967, 1968a, b, 1969; Jay & Lebreton, 1972; Jensen et al., 1975; Lebreton & Bouchez, 1967; Romeike, 1978; Sainty et al., 1981; Smith et al., 1977; Sorenson, 1977; Tatsuno & Scogin, 1978).

46. Iridoids: absent (0), present (1).

47. Polyacetylenes: absent (0), present (1).

48. Myricetin: absent (0), present (1).

49. Ellagic acid: absent (0), present (1).

50. Proanthocyanins: absent (0), present (1).

51. Oil cells: absent (0), present (1).

Pollen (Avetisian, 1975; Basak & Subramanyan, 1966; Bremer, 1987; Chao, 1954; Crepet, 1989; Cronquist, 1981; Dahling, 1978; Dickison, 1967b, 1979, 1987a; Dickison & Baas, 1977; Donoghue, 1985; Endress, 1986; Erdtman, 1952; Franks & Watson, 1963; Ham, 1988; Ham & Heuven, 1989; Henrickson, 1967; Hideux & Ferguson, 1976; Huynh, 1969; Kohler, 1980; Kohler & Bruckner, 1989, 1990; Maguire, 1978; Mason, 1975; Muller, 1969; Nixon, 1989; Nowicke, 1966; Puff & Robbrecht, 1989; Punt, 1978; Reitsma, 1966, 1970; Robertson, 1974; Robbrecht & Puff, 1986; Saad, 1961, 1962; Schmid, 1978a; Shoup & Tseng, 1977; Sohma, 1963, 1967; Stone & Broome, 1971, 1975; Stuchlik, 1967; Taylor & Levin, 1975; Thanikaimoni & Vasanthy, 1972; Tseng & Shoup, 1978; Venkata Rao, 1965; Vezey et al., 1988; Walker, 1976a, b; Whitehead, 1965; Yang, 1952; Zavada & Dilcher, 1986).

52. Pollen size: most 20–30 μm or >30 μm (0), most <20 μm (1).

53. Aperture length : width ratio: 1 : 1 (0), ⅔ : 1 (1), >3 : 1 (2). Apertures with a length : width ratio of 1 : 2 appear to be derived within Juglandaceae and Myricaceae.

54. Ectoaperture termini: rounded (0), pointed (1).

55. Endoaperture: absent (0), present (1).

56. Primary tectal sculpture: reticulate (0), striate (1), clavate (2), rugate (3), spinulose/scabrate (4), vermiform (5), psilate (6), verruculate (7), foveolate (8).

57. Secondary tectal sculpture: smooth (0), papillate (1).

58. Tectal structure: columellate (0), granular (poorly developed columellae) (1).

59. Tectal perforations: semitectate (0), tectate perforate (1), imperforate (2). The intectate *Myrothamnus* was coded as a question mark.

Fruit (Cronquist, 1981, 1988; Cuatrecasas, 1970; Dickison, 1984; Endress, 1989a; Gilg, 1895a, b; Hils et al., 1988; Hoogland, 1952; Hutchinson, 1959; Keng, 1962; Sleumer, 1968; Urban & Gilg, 1900).

60. Fruit type: follicle or septicidal capsule (0), loculicidal capsule (1), nut or samaroid nutlet (achene) (2), fleshy (berry) (3).

MONOPHYLY OF THE ASTERIDAE AND IDENTIFICATION OF THEIR MAJOR LINEAGES INFERRED FROM DNA SEQUENCES OF *rbc*L[1]

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ABSTRACT

A parsimony analysis of 57 angiosperm *rbc*L sequences was conducted to test the monophyly of the Asteridae and to identify major lineages within the Asteridae. Three major clades, the Caryophyllidae, the Rosidae plus Dilleniidae, and the Asteridae sensu lato, emerge from an unresolved radiation in the "higher" dicots. The Asteridae sens. lat. include the Ericales, Cornales, and Apiales in addition to the Asteridae sens. str. Two major lineages within the Asteridae sens. lat. are identified: the Dipsacales, Apiales, Asterales, and Campanulales in one, and the Gentianales, Scrophulariales, Lamiales, Boraginales, and Solanales in the other. This analysis demonstrates the utility of molecular phylogenies to help place problematic taxa, such as the Menyanthaceae, Oleaceae, and Callitrichaceae, within the Asteridae. Implications from this phylogenetic analysis and evidence from the fossil record lead to the suggestion that the origin and diversification of the major higher-dicot lineages occurred during a relatively short period of time about 80–95 million years ago.

The modern concept of the Asteridae, sensu Takhtajan (1980) and Cronquist (1981), is derived from the ancestral Monopetalae (de Jussieu, 1789) and Gamopetalae (de Candolle, 1813) by the elimination of many groups of plants bearing the original defining feature of fused corollas (Wagenitz, 1992). Cronquist (1981: 852) stated that "the Asteridae are the most advanced subclass of dicotyledons." This statement puts into words a generally held perception, based on traditional assumptions regarding trends in character evolution in the angiosperms, that the subclass is of relatively recent origin compared to other major groups of dicots (Sporne, 1969, 1975; Stebbins, 1974).

There is no consensus of opinion concerning the monophyly of the Asteridae. Whereas a combination of floral and embryological characters seems to define a natural group, portrayed as monophyletic in the treatments of Cronquist (1981) and Takhtajan (1980, but not 1987), chemical characters suggest two separate asterid lineages, each derived independently from ancestors in the Rosidae (Dahlgren, 1980). As Wagenitz (1977) pointed out, no division of the Asteridae into separate lineages can be constructed without having to postulate parallel evolution in morphology, embryology, and phytochemistry. Parsimony-based methods of phylogeny reconstruction offer a means of assessing phylogenetic information in which parallelisms exist, by establishing objective criteria for accepting one hypothesis of relationships (i.e., tree) over another hypothesis. Parsimony-based phylogeny reconstructions among major groups in the dicots are few. Donoghue & Doyle (1989), in their analysis of basal angiosperm lineages, identified a "higher"-dicot clade (i.e., derived relative to the basal dicots). This clade, to which all Asteridae, Rosidae, Dilleniidae, Caryophyllidae, and Hamamelidae, as well as certain members of the Magnoliidae, belong is characterized by the presence of tricolpate pollen. Hamby & Zimmer (1991) conducted a parsimony analysis of nuclear ribosomal RNA sequences in angiosperms and other seed plant groups, but found little resolution among

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TABLE 1. Sources of *rbc*L sequences. Arrangement follows Cronquist (1981).

Family	Species	Source/voucher[a]
Monocots		
Liliidae		
Burmanniaceae	*Burmannia biflora*	MWC (unpublished)
Liliaceae	*Lilium superbum*	MWC (unpublished)
Orchidaceae	*Oncidium excavatum*	MWC (unpublished)
Commelinidae		
Poaceae	*Cenchrus setigerus*	Doebley et al. (1990)
	Puccinellia distans	Doebley et al. (1990)
Dicots		
Magnoliidae		
Lauraceae	*Persea americana*	Golenberg et al. (1990)
Magnoliaceae	*M. macrophylla*	Golenberg et al. (1990)
Nelumbonaceae	*Nelumbo lutea*	Les et al. (1991)
Nymphaeaceae	*Nuphar variegata*	Les et al. (1991)
	Nymphaea odorata	Les et al. (1991)
Hamamelidae		
Cercidiphyllaceae	*Cercidiphyllum japonica*[b]	*RGO s.n.*
Platanaceae	*Platanus racemosa*	EMG (unpublished)
Caryophyllidae		
Amaranthaceae	*Amaranthus hypochondriacus*	Michalowski et al. (1990)
Caryophyllaceae	*Stellaria media*	JHR, JRM & HDW (unpublished)
Chenopodiaceae	*Spinacia oleracea*	Zurawski et al. (1981)
Phytolacaceae	*Phytolacca americana*	JHR, JRM & HDW (unpublished)
Plumbaginaceae	*Plumbago capensis*	DEG et al. (unpublished)
Polygonaceae	*Rheum ×cultorum*	DEG et al. (unpublished)
Dilleniidae		
Brassicaceae	*Brassica campestris*	JMN (unpublished)
Ericaceae	*Rhododendron hippophaeoides*	MWC & KK (unpublished)
Fouquieriaceae	*Fouquieria splendens*[b]	*Matthaei BG 860162*
Malvaceae	*Gossypium hirtum*	Gulov et al. (1990)
Violaceae	*Viola soraria*[b]	RGO (no voucher)
Rosidae		
Apiaceae	*Coriandrum sativum*[b]	JDP (no voucher)
Araliaceae	*Hedera helix*[b]	*RKJ s.n.*
Cornaceae	*Cornus mas*	Donoghue et al. (1992)
Fabaceae	*Medicago sativa*	Aldrich et al. (1986)
Grossulariaceae	*Brexia madagascarensis*	Soltis et al. (1990)
Hydrangeaceae	*Carpenteria californica*	Soltis et al. (1990)
Linaceae	*Linum perenne*	MWC (unpublished)
Onagraceae	*Clarkia xantiana*	KJS & EC (unpublished)
Polygalaceae	*Securidaca diversifolia*	MWC (unpublished)
Saxifragaceae	*Heuchera micrantha*	Soltis et al. (1990)
	Parnassia fimbriata	Soltis et al. (1990)
	Penthorum sedoides	Soltis et al. (1990)
Vochysiaceae	*Qualea* sp.	MWC (unpublished)
Asteridae		
Apocynaceae	*Apocynum cannabinum*[b]	RGO (no voucher)
Asteraceae	*Barnadesia caryophylla*	Michaels et al. (in prep.)
Bignoniaceae	*Catalpa* sp.[b]	*CWD s.n.*
Boraginaceae	*Borago officinalis*[b]	RGO (no voucher)
Callitrichaceae	*Callitriche heterophylla*[b]	*TCP 2152*
Calyceraceae	*Boopis anthemoides*	Michaels et al. (in prep.)

TABLE 1. Continued.

Family	Species	Source/voucher[a]
Campanulaceae	*Campanula ramosa*	Michaels et al. (in prep.)
Caprifoliaceae	*Symphoricarpos albus*[b]	*RGO s.n.*
	Viburnum acerifolia	Michaels et al. (in prep.)
Convolvulaceae	*Convolvulus tricolor*[b]	RGO (no voucher)
Dipsacaceae	*Dipsacus sativus*	Michaels et al. (in prep.)
Gentianaceae	*Exacum affine*[b]	*Matthaei BG s.n.*
Hydrophyllaceae	*Hydrophyllum virginiana*[b]	RGO (no voucher)
Lamiaceae	*Lamium purpureum*[b]	RGO (no voucher)
Menyanthaceae	*Villarsia calthifolia*[b]	*RO 9726*
Oleaceae	*Ligustrum vulgare*[b]	*RGO s.n.*
Polemoniaceae	*Polemonium reptans*[b]	*BBG s.n.*
Scrophulariaceae	*Antirrhinum majus*[b]	*CWD s.n.*
Solanaceae	*Nicotiana tabacum*	Lin et al. (1986)
Valerianaceae	*Valeriana officinalis*	Michaels et al. (in prep.)
Verbenaceae	*Clerodendrum fragrans*[b]	*Matthaei BG 840210*

[a] BBG = Beal Botanical Garden, Michigan State University, CWD = Claude dePamphilis, DEG = David Giannasi, EC = Elena Conti, EMG Ed Golenberg, HDW = High Wilson, JDP = Jeffrey Palmer, JMN = Jackie Nugent, JHR = Jeff Rettig, JRM = James Manhart, KJS = Ken Sytsma, KK = Kathy Kron, Matthaei BG = Matthaei Botanic Garden, University of Michigan, MWC = Mark Chase, RKJ = Robert Jansen, RGO = Richard Olmstead, RO = Robert Ornduff, TCP = Thomas Philbrick.

[b] Sequences determined for this study.

the higher dicots. The higher dicots (sensu Donoghue & Doyle, 1989) are currently the subject of a morphology-based parsimony analysis aimed at identifying the relatives of the Asteridae (Hufford, 1992), and the Asteridae are the subject of a parsimony analysis of restriction sites in the cpDNA inverted repeat (Downie & Palmer, 1992).

The conceptual basis of our research into the phylogeny of the Asteridae is to develop a molecular data set derived from cpDNA sequences to address questions relating to the origin and diversification of the Asteridae. To do so requires sampling in sufficient depth among the entire higher dicots, as well as including representative outgroups from the "lower" dicots and monocots to root the resulting tree. Parsimony analysis of DNA sequence data is sensitive to taxonomic sampling. To prevent the attraction of distantly related branches on a parsimony tree, adequate sampling is necessary (see below). The choice of the chloroplast gene *rbc*L for our phylogenetic analysis of the Asteridae is based on prior studies (Palmer et al., 1988; Soltis et al., 1990; Golenberg et al., 1990; Doebley et al., 1990; Olmstead et al., 1990; Michaels et al., in prep.; Kim et al., 1992), which have revealed an appropriate amount of sequence variability at this phylogenetic level. Our analysis also benefits from the fact that *rbc*L is presently being sequenced in numerous groups of angiosperms, so that representative sequences outside the Asteridae are available as outgroups.

We undertook the study of Asteridae phylogeny with several goals in mind: (1) to test the monophyly of the Asteridae; (2) to identify major lineages of the Asteridae; (3) to evaluate ordinal circumscriptions; (4) to determine relationships among orders and among families within orders; (5) to help place taxa that are placed ambiguously in existing classifications; (6) to provide a basis for interpreting character evolution within the Asteridae; and (7) to provide a basis, along with a reassessment of traditional taxonomic characters, for a revised classification of the Asteridae. The present analysis will focus on the first two of these goals and will demonstrate the potential of molecular phylogenies for resolving ambiguously placed taxa. A second analysis, currently underway with greater sampling in the Asteridae, emphasizes familial and ordinal relationships. Suggestions for taxonomic revisions will await its outcome. The value of this *rbc*L-based phylogeny of the Asteridae for identifying family-level sister groups to aid in phylogenetic studies of specific families or orders is demonstrated elsewhere in this volume (Donoghue et al., 1992; Olmstead & Palmer, 1992).

MATERIALS AND METHODS

Plant material was either field-collected or obtained as fresh leaf material or seed from various sources (Table 1). DNA was isolated from fresh leaf material as either total cellular DNA following the modified CTAB procedure (Doyle & Doyle, 1987), or as purified chloroplast DNA (cpDNA)

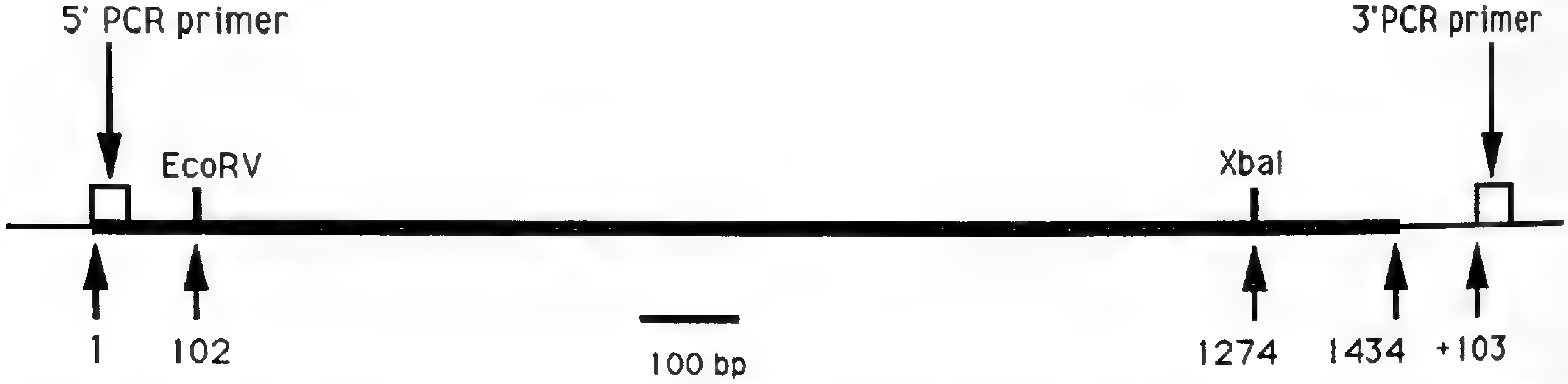

FIGURE 1. Cloning and PCR amplification strategy for *rbc*L. Length of the coding sequence (1434 bp) and position of the 3′ PCR primer (beginning +103 bp from termination of coding region), shown here as in *Nicotiana tabacum*, are variable among species examined.

by the sucrose gradient method (Palmer, 1986). All cpDNAs and most total DNAs were further purified by CsCl/ethidium bromide gradient centrifugation.

An approximately 1550 bp segment of double-stranded DNA containing the complete coding sequence for the chloroplast gene *rbc*L was amplified using the Taq polymerase-mediated polymerase chain reaction (PCR). Two synthetic oligonucleotides were designed for use as amplification primers. The 5′ primer is based on the first 26 nucleotide positions of the *rbc*L coding sequence and is two-fold degenerate at position 18 to account for the only difference between the maize and tobacco sequences in this region. The 3′ primer is based on a 24 bp sequence that contains part of a stem-loop structure beginning 103 bp beyond the coding sequence termination for *rbc*L in tobacco (Fig. 1).

The sequence for *rbc*L was obtained following cloning of the PCR product for most of the species examined. However, the sequence for *Cercidiphyllum japonicum* and portions of several other sequences were obtained by direct sequencing of the PCR product following amplification with one biotin-labeled primer and strand separation on a streptavidin-agarose column (Mitchell & Merril, 1989). A cloning strategy was adopted that made use of highly conserved EcoRV and Xbal restriction sites (recognition sites at nucleotide positions 103–108 and 1269–1274, respectively) and the residual activity of the thermostable Taq polymerase in the PCR mixture (Fig. 1). Crude PCR product was digested with the two enzymes for two hours at 37°C and ligated into the plasmid cloning vector BlueScript Sk+ (Stratagene, Inc.), which had been digested previously with EcoRV to enable the cloning of blunt-end double-stranded DNA fragments. The residual Taq polymerase activity and nucleotide pool in the crude PCR product allow the filling-in of the four-base, 5′ overhang at the Xbal restriction site at the same time that the restriction digest is occurring. Following transformation, clones were selected with inserts of approximately 1200 bp (EcoRV-Xbal fragments) and 300 bp (Xbal-3′ PCR primer fragments). Sequencing was accomplished using the dideoxy method with primers provided by G. Zurawski. For most taxa at least two independent clones of each fragment were sequenced to minimize possible errors introduced by misincorporation during PCR. Estimated rates of misincorporation in independent clones from the same PCR reaction ranged from 0 to 0.3%. This figure is in accord with published rates of PCR misincorporation (Saiki et al., 1988). Positions at which misincorporation was detected for a specific taxon were entered as unknown in the sequence for that taxon in the phylogenetic analysis.

A total of 1305 bp of sequence was compared beginning at position 103 and ending at position 1407. In the first 1407 bp of sequence, no insertions or deletions were observed in any of the sequences studied. Alignment of sequences was done by comparison to the sequence for *Nicotiana tabacum*. Beyond position 1407 sequence divergence becomes great, and small insertions and deletions make the alignment of homologous positions uncertain. Additional sequences were obtained from published and unpublished sources (Table 1). All sequences are complete for the 1305 bp region being compared with the exception of *Nelumbo*, *Nuphar*, and *Nymphaea* (1053 bp each) and *Platanus* (1163 bp). Of the 1305 bp compared, 612 positions are variable and 415 of these are phylogenetically informative. Parsimony analyses were performed using PAUP version 3.0n (Swofford, 1989) on a Macintosh IIfx computer using the heuristic search option with global branch swapping, MULPARS, and ten replicate runs with random order of taxon entry to search for the shortest trees. A bootstrap analysis (Felsenstein, 1985) of 100 replicates was performed using global branch swapping, MULPARS, and the CLOSEST addition sequence to assess the relative support of clades identified by the parsimony analysis. To facilitate the bootstrap analysis of such a large data set, the topological constraint option in PAUP was used to constrain certain taxonomic groupings that had been identified as monophyletic by preliminary analyses. This approach effectively reduces the number of terminal taxa in the analysis, while maintaining all of the sequences, thereby enabling the optimal assessment of character state transformations over the tree. Internal nodes on the tree, where branching pattern is critical to the questions addressed by this analysis, were left unconstrained. Portions of the tree that were constrained in the bootstrap analysis are indicated in Figure 3.

RESULTS

Sequences were obtained for 57 taxa (Table 1), including 15 published sequences, 23 unpublished sequences (provided by M. Chase, D. Les, K. Sytsma, E. Golenberg, H. Michaels, J. Nugent, J. Manhart & D. Gianassi), and 19 sequences generated for this study. All sequences generated as part of this study are deposited with Genbank and are available upon request from the authors (direct requests to R. Olmstead). Sampling focused on the Asteridae, with additional sequences obtained for taxa selected because they are putatively closely related to the Asteridae and because they fill gaps among other dicot lineages. Outgroup sampling reflects to a great degree the diversity of groups presently being examined for *rbc*L sequences.

A Wagner parsimony analysis, in which all inferred nucleotide substitutions are equally weighted, yielded 16 minimum length trees of 2,638 steps and a consistency index (CI) of 0.29 (Kluge & Farris, 1969), from which a strict consensus tree was constructed (Fig. 2). The monocots and "lower" dicots (i.e., Magnoliideae with nontricolpate pollen) provide a good selection of outgroup taxa with which to root the portion of the tree representing the higher dicots, even though no outgroup for the angiosperms as a whole was included in the analysis.

The strict consensus tree (Fig. 2) is rooted arbitrarily using the woody Magnoliidae taxa, *Magnolia* and *Persea*, as outgroups. The tree shows three clusters of taxa among the lower dicots and monocots: (1) woody Magnoliidae (if rooted elsewhere among the lower angiosperms, these taxa form a clade), (2) monocots, and (3) Nymphaeales (minus *Nelumbo*). Two of these groups have been proposed recently to represent the basal branches of angiosperm phylogeny (woody Magnoliidae—Donoghue & Doyle, 1989; Nymphaeales—Hamby & Zimmer, 1991). Rooting the *rbc*L tree with the woody magnoliids (Fig. 2) agrees with traditional angiosperm classification (Cronquist, 1981) and has been suggested by Donoghue & Doyle (1989) on the basis of a phylogenetic analysis using conventional taxonomic characters. Rooting the *rbc*L tree with the Nymphaeales (*Nuphar* and *Nymphaea*), as suggested by Hamby & Zimmer (1991) on the basis of rRNA sequence data, yields a tree (not shown) in which monocots and the woody Magnoliidae form a clade and the remaining dicots form another. Using either rooting, the higher dicots form a group corresponding to the "tricolpate" clade of Donoghue & Doyle (1989).

Five major clades are identified among the higher dicots (Figs. 2, 3). The basal branch consists of *Nelumbo* (Magnoliidae) and *Platanus* (Hamamelidae). The separation of *Nelumbo* from the rest of the water lilies (e.g., Nymphaeales) has been suggested by Donoghue & Doyle (1989) based on morphology, and by Les et al. (1991) based on *rbc*L sequences. The remaining taxa fall into four recognizable groups, but with only weak bootstrap support for any specific branching order among them (Figs. 3, 4). One group consists of the Saxifragaceae sens. str., represented by *Heuchera* and *Penthorum*. The majority rule consensus tree and bootstrap analysis (Fig. 3) suggest that *Cercidiphyllum* falls within or near this group. The most strongly supported group among the higher dicots is the Caryophyllidae, which occurred in 97% of the bootstrap replicates (Fig. 3). The remaining taxa form two main clades, one comprising most of the representatives of the Rosidae and Dilleniidae and the other predominantly of Asteridae. A bootstrap analysis (Fig. 3) provides relative estimates of support for the groupings in the critical region of the tree where the higher-dicot clades diverge.

Within the asterid clade, two main lineages are shown. One includes the orders Gentianales, Solanales, Boraginales, Scrophulariales, and Lamiales, while the other includes the Asterales, Campanulales, Dipsacales, Goodeniales, Apiales, and Menyanthaceae, all Asteridae sensu Cronquist (1981) except the Apiales (Rosidae). Two smaller clades are associated with the Asteridae near the base of the two main lineages. One of these clades consists of *Cornus* and *Carpenteria*, and the other includes *Fouquieria*, *Polemonium*, and *Rhododendron*.

In addition to the analysis of 57 *rbc*L sequences (Figs. 2–4), a larger preliminary analysis of 92 sequences, some of which were incomplete at the time of the analysis, was conducted (results not shown). This global analysis differed only slightly

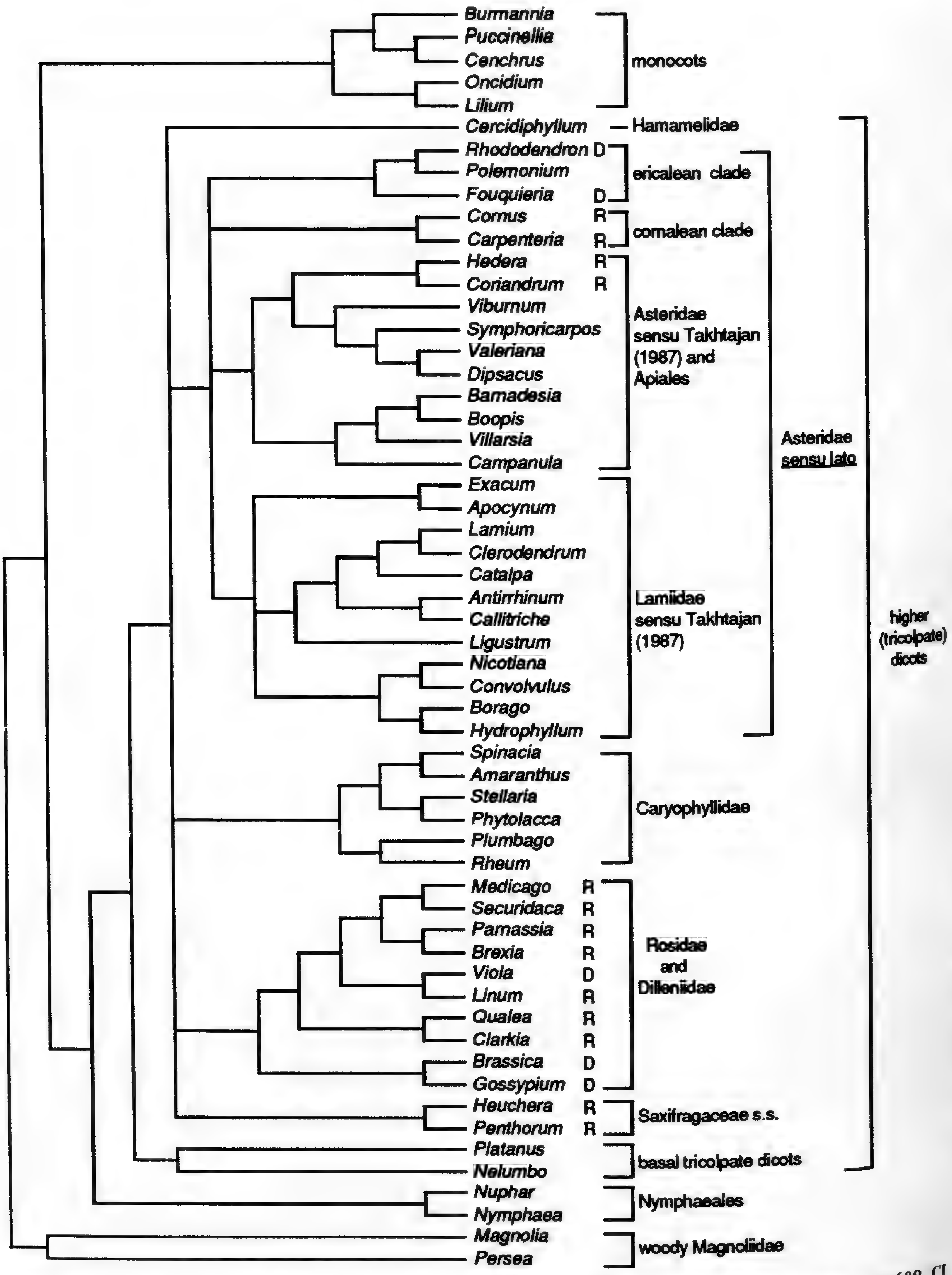

FIGURE 2. Strict consensus of 16 minimum length Wagner trees based on *rbc*L sequences (length = 2,638, CI = 0.29). The tree is arbitrarily rooted using the woody Magnoliidae as the outgroup. Representatives of the Rosidae (R) and Dilleniidae (D) are identified.

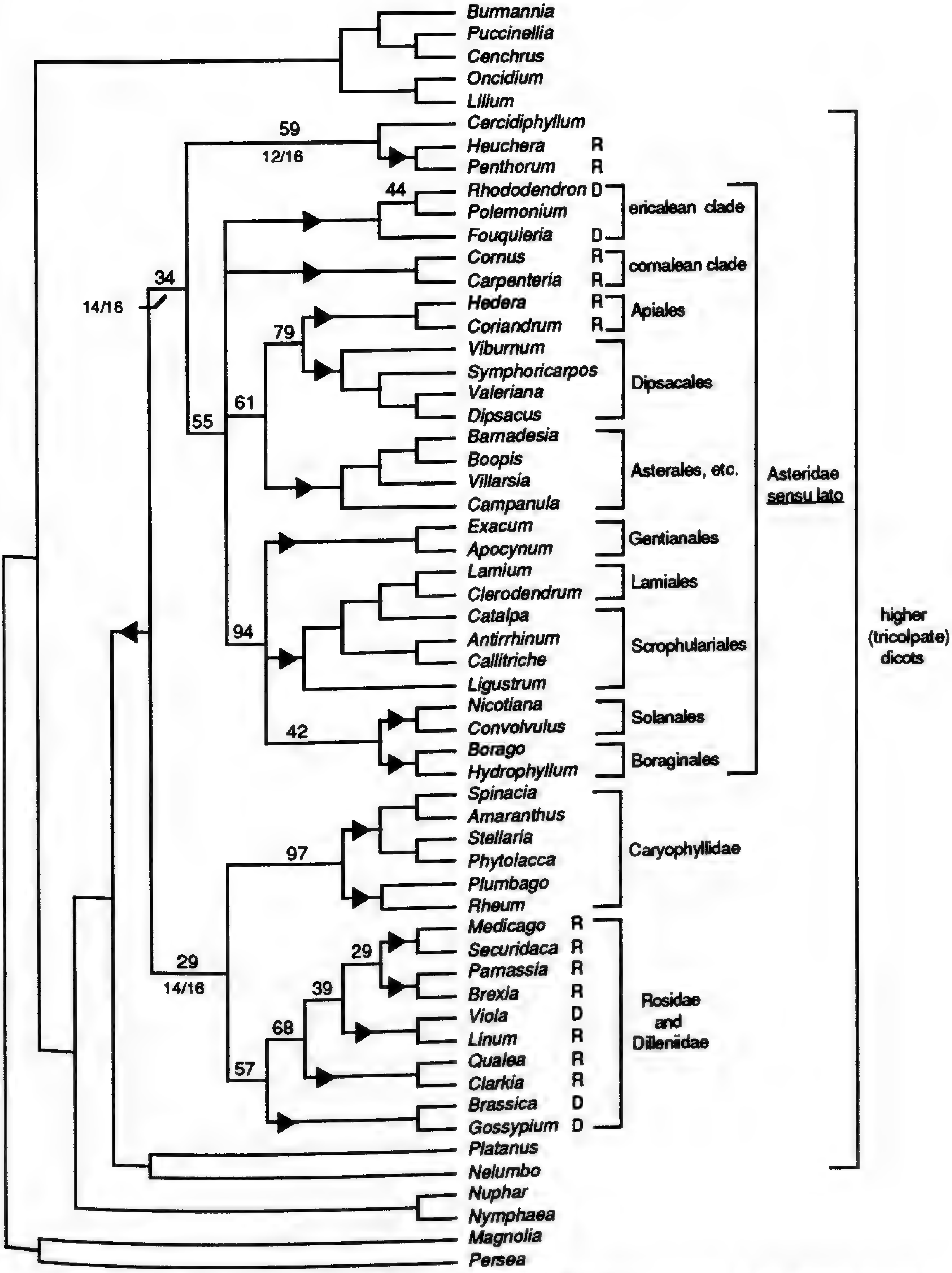

FIGURE 3. Results of a bootstrap analysis. Branching order in clades distal to arrows, in the direction arrows are pointing, is constrained topologically (except the ericalean clade, in which order was unconstrained). Major groups in the Asteridae sens. lat. are identified. Numbers above internodes of unconstrained portions of the tree indicate the percentage of bootstrap replicates supporting the distal clade. Fractions below internodes indicate the number of the 16 equally most parsimonious trees exhibiting that branch; all other clades are found in all 16 trees. Representatives of the Rosidae (R) and Dilleniidae (D) are identified.

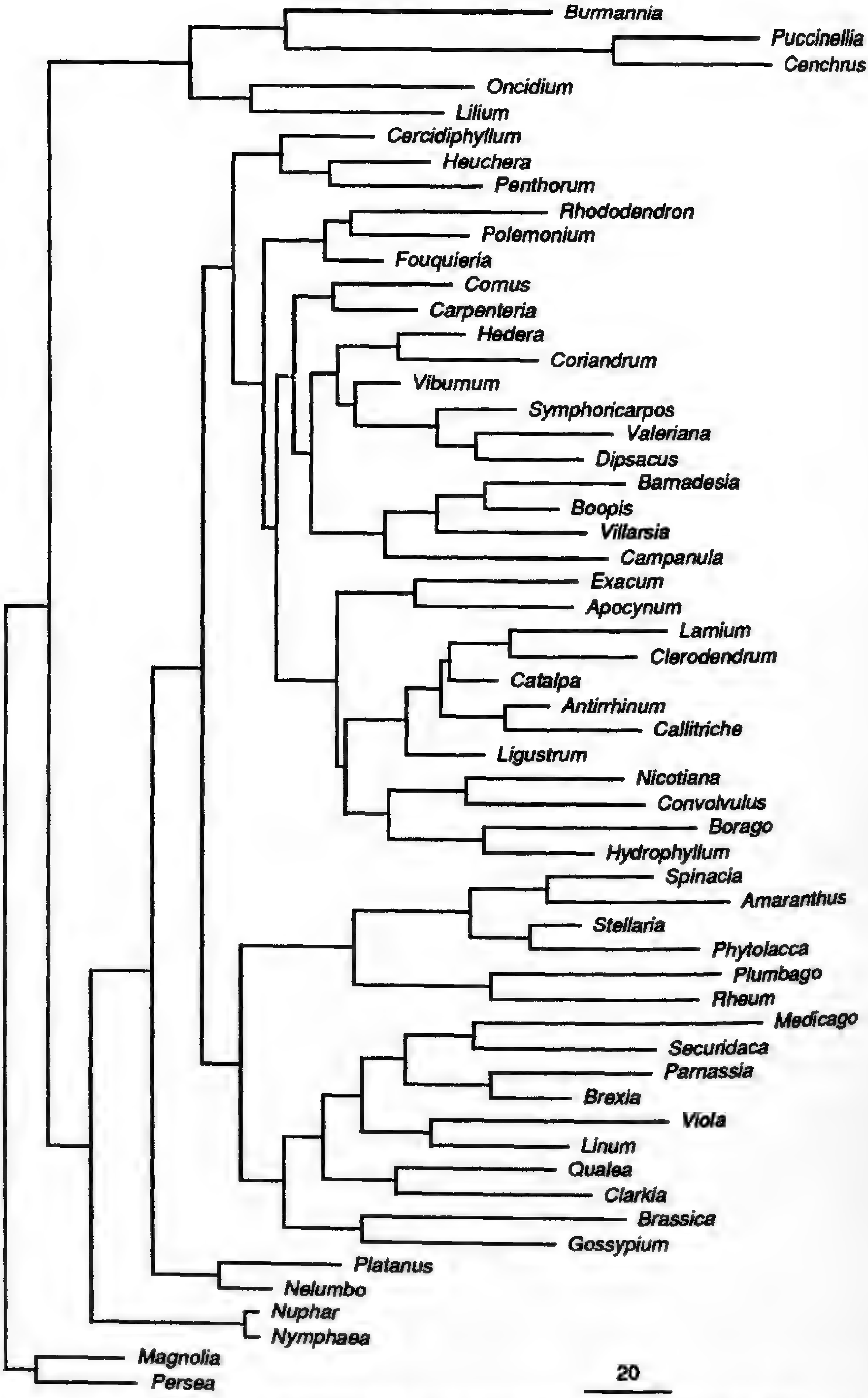

FIGURE 4. One of the 16 equally parsimonious Wagner trees based on *rbc*L sequences (length = 2,638, CI = 0.29). This tree is the one most similar to the preliminary analysis of 92 *rbc*L sequences (see text). Branch lengths are proportional to the number of inferred nucleotide substitutions (note scale at bottom).

from the results of the more detailed analysis of 57 sequences shown here. A complete report including more detailed sampling within the Asteridae will await completion of the data acquisition and analysis. Out of the 16 equally parsimonious trees resulting from the present analysis, the one that is in closest agreement with the global analysis is shown in Figure 4, with the branch lengths proportional to the number of nucleotide substitutions.

DISCUSSION

PHYLOGENETIC IMPLICATIONS

Our goals of determining family and ordinal-level relationships within the Asteridae depend in large part on the resolution of questions of higher-level relationships and monophyly of the entire subclass Asteridae. Preliminary analyses with extensive sampling within the Asteridae, but with limited outgroup sampling (e.g., *Spinacia*, *Heuchera*, and *Magnolia* alternatively and in combination), yielded contradictory hypotheses of basal relationships within the Asteridae. These results suggested that the origin and early diversification of the Asteridae lie deep within the higher dicots and that greater sampling among the higher dicots and outgroups in the lower dicots and monocots would be necessary to resolve the question of monophyly of the Asteridae and the relationships among major lineages of Asteridae. Therefore, it became necessary to address the question of monophyly of the Asteridae first, by sampling more broadly among the angiosperms, before turning our attention to relationships among families and orders within the Asteridae.

An initial attempt to root the resulting angiosperm tree was made using *Welsitschia* (*rbc*L sequence courtesy of G. Furnier), a member of the Gnetales, the putative sister group to the angiosperms (Doyle & Donoghue, 1986). However, the inclusion of such a remote outgroup introduced a systematic error in the form of a very long outgroup branch attaching along a very long ingroup branch (Swofford & Olsen, 1990). This long ingroup branch led to the grasses *Puccinellia* and *Cenchrus* (Fig. 4), an unlikely place to root an angiosperm tree. This result suggests that the much longer internode distances among seed plant groups, relative to those within the angiosperms, may require using some form of a priori weighting of *rbc*L sequences among seed plant lineages (e.g., weighting first and second codon positions more than third positions or weighting transversions over transitions). In contrast, within the more closely related and more densely sampled angiosperms, an equally weighted Wagner parsimony analysis should be sufficient to infer relationships.

Our approach was to restrict our sampling to angiosperms on the assumption that adequate taxonomic sampling within the angiosperms would enable a Wagner parsimony analysis to produce a better estimate of branching topology than would be produced when one or more very long outgroup branches were added. By this approach, the pattern of branching among the higher dicots should be most accurately estimated, regardless of the position of the root among the lower dicots or monocots. The resulting tree can still provide insight into the basal relationships within the angiosperms by examining trees rooted on the basis of hypotheses generated by other lines of evidence. If the tree is rooted by the branch connecting the woody magnoliids to the rest of the tree (Donoghue & Doyle, 1989), then the monocots and the remaining dicots each form monophyletic groups (Fig. 2). If the tree is rooted by the branch connecting the Nymphaeales to the rest of the tree (Hamby & Zimmer, 1991), then the woody magnoliids and the monocots form a clade and the remainder of the dicots forms a clade (tree not shown). Neither of these rootings imply relationships among the basal angiosperms that are in complete agreement with the other hypotheses of relationship cited above, perhaps because sampling among the basal angiosperm lineages is incomplete. However, the higher-dicot clade characterized by the presence of tricolpate pollen, which was identified by Donoghue & Doyle (1989), is supported by the *rbc*L sequence analysis. Because the focus of this study is on the higher dicots, the Asteridae in particular, sampling among the basal lineages is sporadic and far from representative of the important basal angiosperm groups. However, sampling among the basal angiosperms should be sufficient to provide outgroup comparison to assess relationships among the higher dicots where sampling is more complete, especially within the Asteridae.

Relationships among the higher (i.e., tricolpate) dicots implied by the *rbc*L tree include an initial branch consisting of *Nelumbo* and *Platanus*. This is an unexpected pairing, but many other potentially closely related taxa in the Hamamelidae and Magnoliidae are not included and both of these sequences are incomplete (*Nelumbo* lacks 252 bp; *Platanus* lacks 142 bp). Nevertheless, their placement near the base of the tricolpate dicots is consistent with other evidence (Donoghue & Doyle, 1989).

Perhaps the most striking implication of the *rbc*L tree is that the major higher-dicot lineages, including the Caryophyllidae, Rosidae/Dilleniidae, and the "advanced" subclass Asteridae, trace to an apparent radiation point early in the evolution of the higher dicots. The lack of resolution among the major higher-dicot lineages is due to the small number of nucleotide substitutions between branch points relative to the total length of time since the lineages diverged. The observation of few substitutions between branch points, combined with an assumption of relative constancy of substitution rate, implies a rapid radiation of major higher-dicot groups. The lack of resolution also stems, in part, from homoplasy at nucleotide positions that are informative regarding relationships at that level. There is hope that sufficient information does exist in the *rbc*L sequences to offer greater resolution than this study provides, by sampling additional taxa near the critical juncture of the higher-dicot radiation (see discussion on sampling below).

Three major higher-dicot lineages are identified which coincide, more or less, with the taxonomic level of subclass in the classifications of Cronquist (1981) and Takhtajan (1980). In addition, a fourth smaller group is identified comprising several members of the Saxifragaceae sens. str. (Rosidae) and *Cercidiphyllum* (Hamamelidae). The Saxifragaceae sens. lat. were the subject of a recent *rbc*L sequence analysis (Soltis et al., 1990), in which it was concluded that the traditional, broadly defined Saxifragaceae are a heterogeneous group of more or less distantly related taxa. However, the restricted sampling of that study (see discussion below) limited its ability to interpret which taxa belong together in a more narrowly defined Saxifragaceae. By including representatives of the Soltis et al. (1990) study in the larger analysis reported here, Saxifragaceae sens. str. represented by *Heuchera* and *Penthorum* (Fig. 2), along with *Astilbe* and *Itea* (results not shown), are identified. The association of *Cercidiphyllum* with this group of Saxifragaceae, either as separate lineages connected at the same unresolved node on the main higher-dicot lineage (Fig. 2) or together as a clade (Figs. 3, 4), suggests an association between the woody Hamamelidae (e.g., *Cercidiphyllum*) and basal Rosidae (e.g., Saxifragaceae). This association may be a key to understanding higher-dicot diversification, but much greater sampling of taxa in these groups is needed before a clear picture can emerge.

The Caryophyllidae, including Polygonaceae and Plumbaginaceae, appear as a strongly supported, monophyletic group, whose circumscription in traditional classifications coincides completely with the molecular evidence presented here and in the more detailed analysis of the Caryophyllales of Rettig et al. (in prep.). Our results indicate that the Polygonaceae and Plumbaginaceae form a clade that is the sister group to the Caryophyllales as has been suggested by Rodman et al. (1984). The Caryophyllidae are consistently supported by numerous synapomorphies on all the equally parsimonious trees and are supported by the highest bootstrap value (97%) of any of the major higher-dicot lineages identified by this analysis (Fig. 3).

The Dilleniidae and Rosidae form a second major lineage of higher dicots (with several important exclusions). The results of this analysis suggest that neither subclass, sensu Takhtajan (1980) and Cronquist (1981), is a monophyletic group (Figs. 2, 3). In addition, representatives of each of these subclasses occur in the third major higher-dicot lineage, which consists primarily of the Asteridae, and several members of the Saxifragaceae sens. lat. (Rosidae) form a distinct lineage at or near the base of the higher-dicot diversification. The ten taxa that form the Rosidae/Dilleniidae clade in our analysis are a dramatic underrepresentation of the diversity in these two subclasses. However, the existence of this clade, as well as the lack of any clear distinction between the representatives of these two subclasses in the *rbc*L tree, is supported by preliminary evidence from other workers sequencing *rbc*L in the Rosidae and Dilleniidae (M. Chase, pers. comm.; R. Price, pers. comm.).

The third major clade of higher dicots is the Asteridae sensu lato, which include several taxa traditionally placed in the Rosidae or Dilleniidae. Two minor clades at the base of the Asteridae (*Cornus* and *Carpenteria* in one, and *Rhododendron*, *Fouquieria*, and *Polemonium* in the other) are unresolved with respect to the divergence of the two main lineages of Asteridae. The presence of these two clades reflects a grade in the evolution of the Asteridae recognized by many previous treatments (although evidence from the preliminary analysis with more taxa suggests that one of these small groups, *Cornus* and *Carpenteria*, may belong with the Dipsacales and Asterales). Cronquist (1981) and Takhtajan (1980) recognized a narrowly defined Cornales, placed in the Rosidae, but suggested that the Asteridae may have arisen from a cornalean ancestor or share a close common ancestor with the Cornales. Thorne (1983) and Dahlgren (1980) recognized the more inclusive superorder, Corniflorae, comprising the Cornales and Dipsacales, and including either the Apiales (Thorne, 1983) or the Ericales and Fouquieriaceae (Dahlgren, 1980). In both of their treatments this group is placed in a position of lesser "advancement" relative to the rest of the orders of the Asteridae.

None of the above-mentioned recent treatments of angiosperm classification place the Polemoniaceae with the Ericaceae and Fouquieriaceae, although Thorne (1983) placed the Fouquieriaceae near the Polemoniaceae and each of the other treatments cited above have placed the Fouquieriaceae near the Ericaceae. It is clear from the *rbc*L tree that the Cornales, Ericales, and Fouquieriaceae arose at an early period in the diversification that gave rise to the Asteridae sensu Cronquist (1981), after the separation of the entire lineage from the one leading to most other Rosidae and Dilleniidae. Additional molecular support for the inclusion of these two lineages in the Asteridae sens. lat. comes from the analysis of restriction site mapping of the cpDNA inverted repeat (Downie & Palmer, 1992) and further taxonomic sampling of *rbc*L sequences in the Ericales and related taxa (K. Kron & M. Chase, pers. comm.).

Two primary lineages emerge from the unresolved basal portion of the Asteridae. One corresponds to Takhtajan's (1987) subclass Lamiidae, including the orders Gentianales, Lamiales, Scrophulariales, Solanales, and Boraginales. This lineage is one of the most strongly supported clades in the higher dicots with a bootstrap value of 94% (Fig. 3) and is identified in the study of Downie & Palmer (1992). Four of these orders, Gentianales, Lamiales, Solanales, and Boraginales, appear to be monophyletic groups based on the limited sampling presented here. This tentative conclusion is supported by a preliminary analysis of a larger number of taxa within this clade (results not shown). The Lamiales form a monophyletic group with the Scrophulariales as suggested by Wagenitz (1992) and are not close to the Boraginaceae, in agreement with Cantino (1982). The Oleaceae, represented in this study by *Ligustrum*, have been placed alternately with the Gentianales (Dahlgren, 1980; Takhtajan, 1987) and the Scrophulariales (Cronquist, 1981) and are identified as one of several families of questionable placement in the Asteridae by Wagenitz (1992). This study suggests that the Oleaceae represent a basal branch of the clade leading to the Scrophulariales and Lamiales.

Although groups corresponding to orders can be identified within this primary lineage, relationships among these groups remain unclear. The association of the Lamiales with the Scrophulariales appears to be well supported, but the suggested relationship between the Solanales and the Boraginales is weakly supported by the bootstrap analysis (Fig. 3). In the preliminary analysis of 92 sequences (not shown), including greater sampling within this lineage, the Boraginales come out with the Scrophulariales/Lamiales rather than with the Solanales. More extensive taxonomic sampling and more phylogenetically informative data may be necessary to resolve ordinal relationships within this lineage.

The second primary lineage of Asteridae to emerge from the early diversification of the subclass corresponds closely to the Asteridae sensu stricto of Takhtajan (1987), but with the inclusion of the Apiales. The bootstrap value of 61% (Fig. 3) indicates moderate support for this clade and reflects some support in the data for inclusion of the Cornales. Two clades are recognized within this lineage, one comprising the Apiales and Dipsacales and the other comprising representatives of the Asterales, Campanulales, Goodeniales, and Menyanthaceae (*Villarsia*). The close molecular association between the Apiales and the Dipsacales was predicted only by the classification of Thorne (1983) among recent angiosperm classifications, although a similarity in secondary chemistry between the Apiales and Asterales also has been noted (Hegnauer, 1977). The placement of an order of Rosidae (i.e., Apiales) sensu Cronquist (1981) well within the Asteridae will surprise many observers. Nevertheless, a bootstrap value of 79% (Fig. 3) shows relatively strong support for a sister-group relationship between the Apiales and Dipsacales. This relationship is supported also by the work of Downie & Palmer (1992) and of Hamby & Zimmer (pers. comm.) using rRNA sequences. In the Dipsacales, the Caprifoliaceae sens. lat. (represented by *Viburnum* and *Symphoricarpos*) appear to form a paraphyletic group from which the Valerianaceae and Dipsacaceae are derived. Wagenitz (1992) identifies the Dipsacales and the Campanulales/Asterales (including Goodeniaceae) as "good candidates" for monophyletic groups, and the *rbc*L analysis provides additional support for his view. More detailed analyses of both of these monophyletic groups based on *rbc*L data are reported elsewhere (Campanulales/Asterales—Michaels et al., in prep.; Dipsacales—Donoghue et al., 1992).

The placement of the Menyanthaceae in the Campanulales/Asterales clade is an unanticipated result, but one that illustrates a strength of molecular approaches to phylogeny reconstruction. The Menyanthaceae have been placed alternately in the Gentianales (e.g., Takhtajan, 1987) and Solanales (e.g., Cronquist, 1981), but Bohm et al. (1986) could not find support for either placement on the basis of flavonoid data. Pollard & Amuti (1981) recognized a similarity between the Menyanthaceae and the Campanulales/Asterales on the basis of a primary reliance on inulin as a storage compound, but also included other more distantly related families (e.g., Boraginaceae). Considering these conflicting hypotheses, it is not surprising that Wagenitz (1992) considers the placement of the Menyanthaceae to be "still controversial." The *rbc*L sequence data place the Menyanthaceae (represented here by *Villarsia*) squarely in the Campanulales/Asterales clade, a placement confirmed by sequencing a second member of the family, *Menyanthes* (unpublished data) and by the cpDNA restriction site analysis of Downie & Palmer (1992).

Another controversially placed taxon included in this analysis is the aquatic plant *Callitriche*. With its very reduced flowers and modifications associated with the aquatic habit, *Callitriche* has been assigned to a position, based on gynoecial and embryological characters, in or near the Lamiales in most recent treatments (Dahlgren, 1980; Thorne, 1983; Takhtajan, 1987; but see Cronquist, 1981). The analysis of *rbc*L sequence data suggests that *Callitriche* belongs in the Scrophulariales/Lamiales clade, but more closely related to the Scrophulariaceae than to the Lamiales.

The uncertain placement of some taxa in classifications based on conventional sources of data (e.g., morphology, anatomy, and secondary chemistry) is often the result of divergent evolution in these characters. This obscures relationships because derived characters shared between close relatives may no longer be apparent. In these circumstances cpDNA sequence data may have their greatest influence on classifications, because the stochastic nature of nucleotide substitutions in cpDNA is not expected to be coupled with differing rates of evolution of conventional characters. Therefore, taxa ambiguously placed in traditional classifications should resolve on an *rbc*L tree as confidently as any other taxa. This does not imply that cpDNA sequence divergence cannot be unpredictably variable and that this variability cannot introduce error or uncertainty into phylogenetic analysis of cpDNA sequence data (Doebley et al., 1990; Swofford & Olsen, 1990).

FLORAL EVOLUTION AND THE FOSSIL RECORD

The reconstruction of a framework phylogeny of the higher dicots, the identification of a monophyletic Asteridae sens. lat., and the delineation of primary lines of descent within the Asteridae enable one to begin to evaluate hypotheses of character evolution within the higher dicots and Asteridae. The results of our *rbc*L sequence analysis concur with the phylogenetic analysis based on conventional characters by Donoghue & Doyle (1989) in the identification of a clade of higher dicots characterized by the presence of tricolpate pollen. Whereas our sampling is more representative of the higher dicots and that of Donoghue & Doyle is more representative of the lower dicots and monocots, it is heartening to observe the concordance in results at the point where the two studies converge.

Among the higher, tricolpate dicots, evolution of floral morphology has proceeded from ancestors with numerous parts spirally arranged to a reduced, fixed number of floral segments arranged in whorl. The evolution of whorled floral appendages has probably occurred more than once in dicots and certainly arose independently in dicots and monocots, but our analysis of *rbc*L sequence data suggests that a single origin of this floral arrangement may be sufficient to explain its presence in the major groups of higher dicots (e.g., Caryophyllidae, Dilleniidae, Rosidae, Asteridae). More extensive sampling of cpDNA sequences among the early tricolpate dicot lineages (e.g., Ranunculales, Hamamelidales) will be needed to determine whether a single origin is, in reality, sufficient to explain the distribution of this character among the higher dicots.

The lack of resolution of relationships among the major lineages of higher dicots suggests that the origin and divergence of these groups occurred close together in time and probably soon after the evolution of whorled floral appendages. Flowers with all parts in whorls are known by the Cenomanian age, approximately 95 million years ago (Friis & Crepet, 1987). By the middle Late Cretaceous (Santonian–Campanian), whorled flowers "usually with the perianth and androecium in whorls of five, and gynoecium of two or three carpels" were dominant (Friis & Crepet, 1987) and the first sympetalous flowers are known (Friis, 1985). The fossil record, notoriously incomplete when it comes to flowers, is entirely consistent with a nearly simultaneous (in geologic terms) origin of the major higher-dicot groups. Even though no fossils of clearly asterid affinity, sensu Cronquist or Takhtajan, are known until the Tertiary, one implication of our phylogenetic analysis is that the origin of the Asteridae sens. lat. was close in time to the appearance of other higher-dicot groups in the Late Cretaceous (Doyle & Donoghue, 1986; Hennig, 1966; Marshall, 1990). Fossil fruits assignable to the extant genus *Cornus* (E. M. Friis, unpublished data, cited in Eyde, 1988) and fossil flowers and fruits referable to the Ericales (Friis, 1985) are known from the Late Cretaceous. Both of these fossils belong to orders, Cornales and Ericales, respectively, identified by the *rbc*L analysis to belong to the Asteridae sensu lato. Therefore, claims that fossils of asterid affinity do not appear until the Tertiary (Mueller, 1981; Cronquist, 1981) reflect our misconception of asterid affinity rather than a lack of fossil evidence.

The identification of a clade comprising the Asteridae sens. lat. that originated early in the diversification of the higher dicots and which is characterized (in large part) by the fusion of perianth parts suggests that the innovation of perianth fusion occurred soon after the evolution of whorled floral appendages. This implication of our analysis may seem strikingly at odds with the traditional concept of floral evolution, namely, many, spirally arranged parts *to* few, whorled parts *to* fused parts, with a phylogenetic diversification at each stage. However, there is no contradiction with this traditional concept of floral evolution; the only difference is that the transition from the second to the third stages occurred in rapid succession and that the phylogenetic radiation within each of these two floral plans occurred *after* that transition.

The interpretation of floral evolution within the Asteridae sens. lat. poses interesting hypotheses concerning the evolution of perianth fusion. If the two lineages that do not exhibit perianth fusion (*Cornus/Carpenteria* and *Hedera/Coriandrum*) represent the retention of the ancestral state of free floral parts, then the fusion of floral parts must have occurred at least three times during the evolution of the Asteridae sens. lat.: (1) Dipsacales, (2) Asterales/Campanulales, and (3) a clade comprising the ericalean group and the Lamiales/Scrophulariales/Gentianales/Boraginales/Solanales (evidence from phylogenetic studies in the Ericales suggests a separate origin of perianth fusion in that order (Kron & Chase, pers. comm.)). Alternatively, if a single origin of perianth fusion is postulated to have occurred in the Asteridae sens. lat., then either two reversals would be necessary to explain the distribution of free perianths, if the Cornales belong on the lineage leading to the Dipsacales, Apiales, Campanulales, and Asterales, or only one reversal, if the Cornales belong at the base of the entire clade. A simple parsimony argument, in which reversals and parallel evolution are equally likely, would favor a single origin of perianth fusion in the Asteridae sens. lat. By implication, the Apiales and possibly the Cornales would represent groups in which the existence of a free perianth is derived from an ancestrally fused perianth. It is noteworthy that the only putative cases of reversal in perianth fusion (e.g., Cornales and Apiales) are postulated to have occurred early in the diversification of the Asteridae, perhaps before subsequent floral evolution acted to constrain the development of the perianth to be obligately fused (Donoghue, 1989). Some recent evidence from studies of corolla development in the Asteridae and the Apiales (Erbar, 1988, 1991) is consistent with the hypothesis presented here that the polypetalous condition in the Apiales may represent a reversal from an ancestral sympetalous state. Erbar (1991) identified two developmental patterns leading to sympetaly in the Asteridae. In early sympetaly the corolla is initiated as a ring from which petal lobes later develop, whereas in late sympetaly the corolla is initiated as distinct petals, which fuse later in development. Corolla is of the late type in the families of the Lamiidae and the early type in the orders Asterales sens. lat. and Dipsacales. Corolla development in the Apiales is initiated as a ring, as in the Dipsacales and Asterales, but its development ceases when petal lobes are initiated, resulting in a corolla of apparently free petals (a correlation between ring formation and inferior ovary may present an alternate explanation, L. Hufford, pers. comm.). Comparable observations on corolla development in the Cornales is unavailable.

SAMPLING

Sampling is a critical issue that often is given insufficient attention in molecular phylogenetic studies. Sampling can affect both the resolution of a phylogenetic analysis and the effectiveness of statistical evaluation of the results (e.g., bootstrap analysis). Both the number of characters (e.g., nucleotides) and the number of taxa are factors that influence the resolution and reliability of an analysis. Of these two sampling considerations, we perceive the issue of taxonomic sampling to be the more critical. An insufficient number of characters often will result in a lack of resolution, rather than incorrect topology, whereas insufficient taxonomic sampling may lead to incorrect topology. This is particularly likely when unequal rates of nucleotide substitution exist within a clade or when the amount of substitution in the sequences being compared is high relative to the phylogenetic distance between sampled taxa (Felsenstein, 1978; Swofford & Olsen, 1990). In a parsimony analysis, an uneven sampling of taxa within a clade can have the same effect as unequal rates among lineages within the clade. Likewise, too few taxa sampled in a clade, even if evenly distributed, can have the effect of raising the effective rate of substitution for the sequence being compared (i.e., substitutions per internode length on a cladogram). Swofford & Ol-

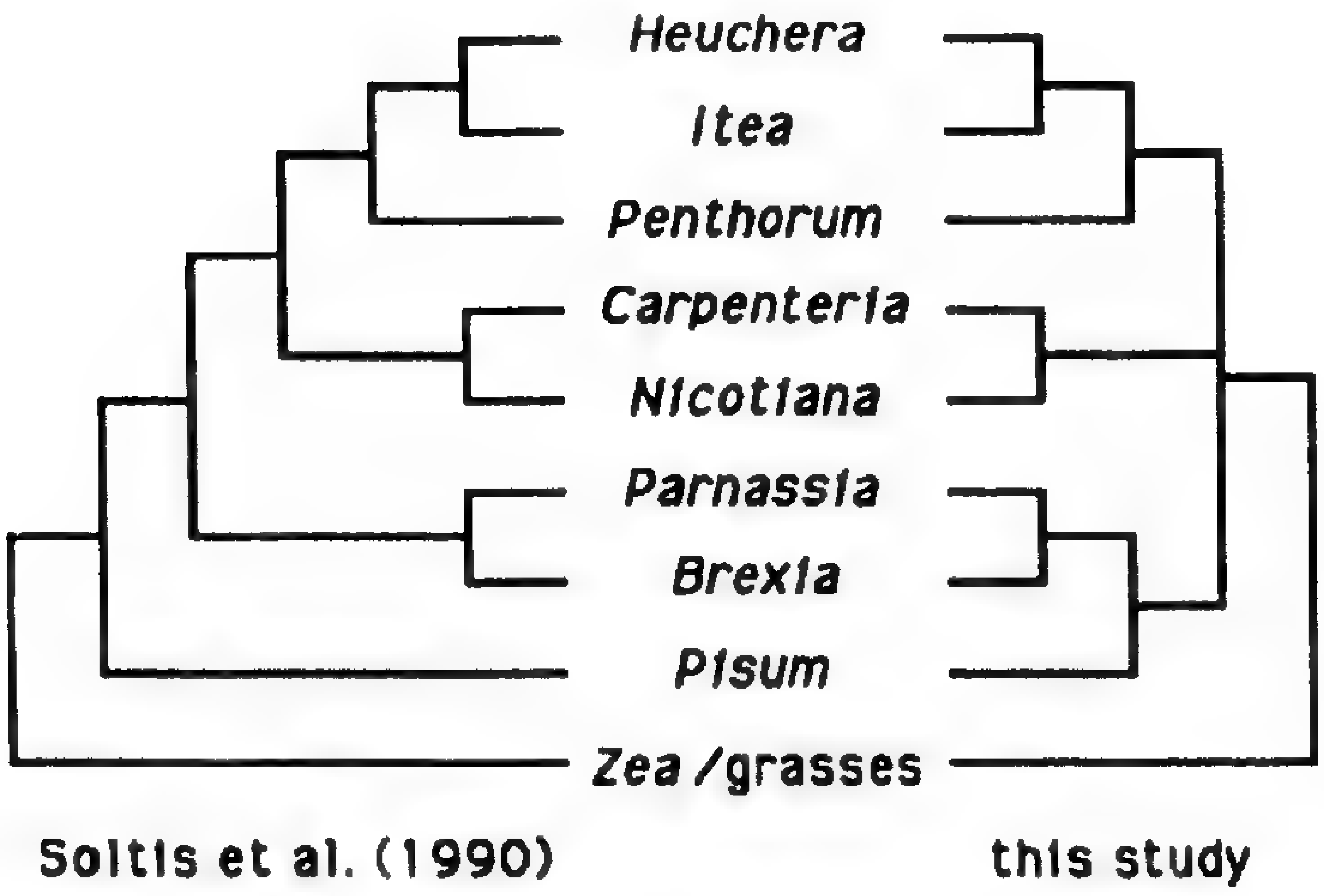

FIGURE 5. A comparison of the results of Soltis et al. (1990) and this study for taxa shared between the two studies.

sen (1990: 497) recommended that taxonomic sampling be carried out "so as to divide long branches reasonably evenly" and go on to point out that "long branches (sparse regions) within the ingroup can contribute to systematic errors," because in a parsimony analysis, "multiple substitutions are more easily detected in dense[ly sampled] regions."

Although increasing the taxonomic sampling density has the beneficial consequence of increasing the effectiveness of a parsimony analysis, it also has the paradoxical effect of reducing the apparent support for the resulting tree by the most commonly used means of evaluating tree branching patterns, the bootstrap (Felsenstein, 1985, and pers. comm.). The bootstrap approach provides a quantitative value for the occurrence of specific clades given the available data. Low bootsrap values can occur for two reasons: (1) when high levels of homoplasy exist in the data, making alternative groupings of taxa nearly equally likely; and (2) when there are few characters to support each branch point. Increasing the number of taxa without increasing the number of characters can increase the level of homoplasy in an analysis (Archie, 1989; Sanderson & Donoghue, 1989), and by splitting branches, will reduce the number of characters supporting each branch point, thereby reducing the bootstrap values on the resulting tree. Other methods of evaluating trees in a parsimony analysis, including decay analysis and comparing the distribution of all possible trees (Donoghue et al., 1992), are made more difficult, or rendered impossible, by increasing the number of taxa included in an analysis.

It is our concern that studies involving a small number of taxa drawn from a large and heterogeneous taxonomic class may show support for topologies that do not reflect phylogeny as accurately as studies involving a greater sampling within the same taxonomic class. To illustrate this point, we offer two examples of studies involving small numbers of taxa drawn from the same taxonomic distribution as our analysis of 57 taxa reported here. First, anecdotal evidence from our analysis of *rbc*L sequences comes from the behavior of the sequence for *Spinacia*. In preliminary analyses with varying sets of taxa, but with no other members of the Caryophyllidae included, the sequence for *Spinacia* came out either within the Asteridae, within the Rosidae, or on a branch by itself at the base of the higher-dicot radiation. Only with the inclusion of other sequences from the Caryophyllidae (provided by D. Giannasi, J. Rettig & J. Manhart) did the position of *Spinacia* and the rest of the Caryophyllidae consistently come out near the base of the higher-dicot radiation (Fig. 2), regardless of which other taxa representing other clades were included in the analysis.

Soltis et al. (1990) employed *rbc*L sequence data to address the question of phylogenetic relationships within the Saxifragaceae sens. lat. and to determine if they represent an assemblage of relatively unrelated taxa. In addition to eight members of the Saxifragaceae sens. lat., three other diverse angiosperms, *Nicotiana* (Asteridae), *Pisum* (Rosidae), and *Zea* (monocot), were included in their analysis. Our analysis included five of their sequences from the Saxifragaceae sens. lat. as well as *Nicotiana*, *Medicago* (a close relative of *Pisum*), and two grass species in the same family as *Zea* (a sixth member of the Saxifragaceae sens. lat. and *Pisum* were also included in our preliminary analysis of 92 taxa). The topologies for the comparable portions of the tree from Soltis et al. (1990) and from our analysis differ primarily in the placement of the root (Fig. 5). In our view, the tree of Soltis et al. (1990) is rooted artifactually by the attraction of two long-branch lineages, *Pisum* and *Zea*. The resulting tree, otherwise topologically congruent with our tree, implies putatively erroneous conclusions concerning relationships within the Saxifragaceae sens. lat. and their position within the higher dicots. The source of the apparent error in their tree stems from: (1) the coincidence of including members of the Fabaceae (*Pisum*) and Poaceae (*Zea*), both fast-rate lineages for *rbc*L sequence evolution (note long branches in Fig. 4); and (2) rooting their analysis using the remote outgroup *Zea*, which has been shown to be diverging at a fast rate even when compared to other grasses (Doebley et al., 1990). This is not meant as a criticism of the study of Soltis et al. (1990), which was one of the first to use *rbc*L sequences in a phylogenetic analysis, but rather as an example to illustrate the potential pitfall of inadequate taxonomic sampling.

SUMMARY AND PROSPECT

It is remarkable how many *rbc*L sequences have been acquired in the short time since the gene was first suggested for use in phylogenetic studies (Zurawski & Clegg, 1987; Ritland & Clegg, 1987; Palmer et al., 1988). Several recent studies (Golenberg et al., 1990; Soltis et al., 1990; Doebley et al., 1990; Michaels et al., in prep.; Les et al., 1991; Donoghue et al., 1992; Kim et al., 1992) and additional studies currently in progress (D. Giannasi, pers. comm.; J. Rettig & J. Manhart, pers. comm.; D. Clark, pers. comm.; M. Chase, pers. comm.) atest to the mushrooming interest in the application of *rbc*L sequences to phylogenetic studies in flowering plants. A recent survey of researchers (conducted in July 1990 by J. Palmer) revealed that over 200 *rbc*L genes had been sequenced; by the time this study is published, that number will have been greatly eclipsed. Much credit is owed to the generosity of G. Zurawski for providing sequencing primers to all interested researchers and to the open exchange of information on techniques and of sequences among researchers. The prospect in the near future for a comprehensive angiosperm phylogeny based on *rbc*L sequences is great.

The Asteridae sens. lat. have been the focus of the most extensive sampling for *rbc*L sequences, with more than 40 families and over 100 species sampled (Michaels et al., in prep.; Olmstead et al., this study, and unpublished; Kim et al., 1992; Donoghue et al., 1992; K. Kron & M. Chase, pers. comm.; D. Soltis, pers. comm.). The Asteridae provide an exemplary case study of how cpDNA sequence data can address systematic questions at a variety of levels, from the identification of a monophyletic, higher-order group, the Asteridae sensu lato (this study), to the circumscription of orders and relationship among families within orders (Michaels et al., in prep; Donoghue et al., 1992; Olmstead et al., unpublished), through to the study of tribal relationships within a large and diverse family, the Asteraceae (Kim et al., 1992).

The expanding body of evidence from *rbc*L studies does not mean that avenues for additional work are narrowing. To the contrary, *rbc*L sequence studies have identified many problems where the simple solution of increased taxonomic sampling will not suffice. The prospects for future research lie in several directions: (1) A slowly evolving gene such as *rbc*L has a lower limit of effective resolution in phylogenetic studies (Doebley et al., 1990; Kim et al., 1992). Many problems within orders, families, or even large genera may be addressed more effectively by applying the techniques used in current *rbc*L studies to more rapidly evolving chloroplast genes, as well as by continuing the now widely used approach of cpDNA restriction site analysis. The former approach is currently underway in studies of the Asteraceae (R. Jansen, pers. comm.), Polemoniaceae (K. Steele, pers. comm.), and the Lamiales/Scrophulariales (R. Olmstead, unpublished). (2) Problems of ancient radiations (e.g., the higher-dicot radiation discussed above) may remain unresolved with *rbc*L sequences and will require additional data, perhaps 3–5 times as much cpDNA sequence to achieve resolution. (3) It should be noted that data from *rbc*L sequences are all derived from a single gene and may be subject to unknown evolutionary constraints. Phylogenetic reconstructions derived independently from chloroplast genes of differing functions (i.e., genes not involved in photosynthesis) or from mitochondrial or nuclear genes (e.g., rDNA genes) need to be conducted on the same taxa to confirm results and to test the underlying assumption that the nucleotide substitutions sampled from one gene represent a random sample. Overall, the prospect is bright that significant advances in our understanding of plant systematics will be forthcoming from continued studies of chloroplast and other DNA sequences.

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RESTRICTION SITE MAPPING OF THE CHLOROPLAST DNA INVERTED REPEAT: A MOLECULAR PHYLOGENY OF THE ASTERIDAE[1]

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ABSTRACT

By focusing exclusively on the highly conserved inverted repeat region of the chloroplast genome, we extend comparative restriction site mapping to greater evolutionary depths than those to which it has been applied previously. A cladistic analysis of inverted repeat restriction site data is presented in order to enhance understanding of relationships within the Asteridae and to test the possible monophyly of the Asteridae. A total of 114 species, representing 33 families of Asteridae and eight families of Rosidae and Dilleniidae (sensu Cronquist) was examined, of which 99 species exhibited restriction maps of sufficient colinearity to be included in the phylogenetic analysis. Analysis with four restriction endonucleases identified a total of 77 restriction sites, 55 of which were phylogenetically informative. Parsimony analysis identified six major groups that broadly correspond to traditionally recognized orders in the Asteridae: Asterales, Boraginales, Dipsacales, Gentianales, Scrophulariales plus Lamiales, and Solanales. The results further suggest that the Asteridae, as traditionally circumscribed, are not monophyletic. The Apiaceae, Araliaceae, Cornaceae, Hydrangeaceae, Loasaceae, and possibly the Fouquieriaceae, all placed previously by Cronquist in subclasses Dilleniidae and Rosidae, should be included in a broadly defined Asteridae. The Cornaceae, Hydrangeaceae and Loasaceae appear closely related. Unexpected results include a probable sister-group relationship between the Apiales and Dipsacales, and the placement of the Menyanthaceae in the Asterales. Familial relationships within several orders and interordinal relationships remain poorly resolved.

The Asteridae, comprising about a third of all dicot species, are the second largest subclass of dicots and are thought to be of relatively recent origin compared to other dicot subclasses (Cronquist, 1981). Most members are characterized by derived features of floral morphology (e.g., sympetalous flowers), embryology, and chemistry. Although the concept of Asteridae can be traced back to the late seventeenth and early eighteenth centuries (de Jussieu, 1789; de Candolle, 1813), the present circumscription of this group as a subclass was described initially by Takhtajan (1964). Phylogenetic relationships within recent classifications of the subclass (sensu Cronquist, 1981, and Takhtajan, 1980) have remained unclear despite intensive morphological, anatomical, and phytochemical analyses. Substantial disagreement exists regarding interfamilial and interordinal relationships, with many genera and families of uncertain familial or ordinal placement. Moreover, the monophyly of the subclass itself has been disputed (Dahlgren, 1983; Thorne, 1983; Takhtajan, 1987). To date, very few cladistic studies that treat taxa above the family level have been put forth for the Asteridae (Cantino, 1982; Lu, 1990; Olmstead et al., 1990; Michaels et al., in prep.; other studies in this volume).

Although phylogenetic analysis of restriction site variation in chloroplast genomes has been used to construct explicit hypotheses of relationships in a number of plant groups (reviewed in Palmer, 1987; Palmer et al., 1988), it has never been applied at taxonomic levels higher than the rank of family. In fact, restriction site analysis has generally been viewed as inappropriate at these levels. As phylogenetic distance and molecular divergence increase, so does the proportion of homoplastic site changes. Additionally, the accumulation of inser-

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tions and deletions prevents alignment of restriction maps and assessment of site homology. Higher-level relationships have been studied previously by chloroplast gene sequencing (e.g., Soltis et al., 1990b; Olmstead et al., 1992) and by the distribution of major structural rearrangements in the chloroplast genome (e.g., Jansen & Palmer, 1987; Downie et al., 1991).

While investigating chloroplast genome structural variation in a wide array of angiosperms (Downie & Palmer, 1991), we noticed that the chloroplast DNA (cpDNA) of many species possessed restriction fragments in their large inverted repeat (IR) that were similar in size. In a typical angiosperm chloroplast genome of 150 kb, each of the two IR copies is about 25 kb in size. The remarkable conservation in size of IR restriction fragments across most dicot lineages lead us to believe that it might be possible to analyze restriction sites in this region for phylogenetic purposes. Preliminary mapping studies revealed that many restriction sites were indeed conserved across major lineages of Asteridae.

The first evidence that IR sequences in cpDNA have lower mutation rates than single-copy sequences came from restriction site analyses at the intrafamilial level (Palmer & Zamir, 1982; Palmer et al., 1983a, b; Clegg et al., 1984; Sytsma & Schaal, 1985; Jansen & Palmer, 1987). A detailed examination of gene sequences confirmed this inference and demonstrated that rates of nucleotide substitution at silent (synonymous) sites and in noncoding sequences in the IR are 4–6 times lower than those in the large and small single-copy regions (Wolfe et al., 1987; K. Wolfe, unpublished). The rate of insertions and deletions also appears to be suppressed in the IR compared to single-copy regions (Doebley et al., 1987; Jansen & Palmer, 1988; Schilling & Jansen, 1989; Wallace & Jansen, 1990; Soltis et al., 1990b; K. Wolfe, C. Morden & J. Palmer, unpublished). The evolutionary processes and molecular mechanisms responsible for mutation rates in the IR are not understood.

Here we present results from a cladistic analysis of cpDNA IR restriction site variation within the Asteridae. Since the study presented here was not designed to sample restriction site changes comprehensively, but rather to look for phylogenetically useful structural changes, only four restriction enzymes were used instead of the 10–25 that typify such studies. Nevertheless, a substantial number of restriction site mutations was obtained in this pilot study. Our goal in presenting this study is twofold: (1) to demonstrate, by focusing exclusively on the highly conserved IR region of the chloroplast chromosome, that comparative restriction site mapping can be extended to taxonomic levels higher than previously considered possible, and (2) to formulate more precise hypotheses about relationships among the diverse clades comprising the Asteridae and to test their monophyly and origins relative to putatively ancestral groups in the Rosidae and Dilleniidae.

MATERIALS AND METHODS

Material of 114 species, representing 103 species of Asteridae, 2 species of Dilleniidae, and 9 species of Rosidae (sensu Cronquist, 1981), was field collected or obtained from various sources, either as fresh leaf material or DNA. A list of sources and voucher information for all taxa examined herein is available upon request. The 114 species represent 33 of 49 families of Asteridae (sensu Cronquist), two families of Dilleniidae, and six families of Rosidae (Table 1). The remaining families treated by Cronquist in subclass Asteridae were omitted from the analysis because material was unavailable for study. The isolation of cpDNA or total cellular DNA from leaf material was accomplished using the sucrose gradient technique of Palmer (1986) or the modified CTAB procedure of Doyle & Doyle (1987), respectively. All cpDNAs and most total DNAs were further purified by centrifugation in cesium chloride/ethidium bromide gradients.

All DNAs were digested singly with each of four restriction endonucleases: *Bam*HI, *Bgl*II, *Eco*RV, and *Hin*dIII. DNA digests for 75 of the 114 species listed in Table 1 were separated electrophoretically in 1.0% agarose gels in which the bromophenol blue dye marker was run 6 cm. In this way four 20-cm-wide filters could be placed on a standard 20 × 25-cm x-ray film. For the remaining 39 species, which were analyzed at a later date, the dye marker was run 12 cm. The resulting cpDNA fragments were bidirectionally transferred to nylon filters (Zetabind, AMF Cuno), and visualized by filter hybridizations using ^{32}P-labeled probes (described below) and autoradiography (Palmer, 1986; Palmer et al., 1988; Downie & Palmer, 1991). Size markers used were equimolar mixtures of phage lambda DNA digested with *Eco*RI and *Hin*dIII and with *Hin*dIII alone. Filters were washed in 2× SSC, 0.5% SDS twice for 5–10 minutes at room temperature and 2–3 times for 60 minutes at 65°C prior to autoradiography. Twenty-six subclones of a *Nicotiana tabacum* cpDNA library (Sugiura et al., 1986; Fig. 1) were used as hybridization probes. These probes span the entire *N. tabacum* cpDNA

TABLE 1. Taxa scored for inverted repeat restriction site variation. System of classification follows that of Cronquist (1981). Asterisks denote plants that are not included in the cladistic analysis because their chloroplast genomes are rearranged or extremely divergent in base sequence relative to *Nicotiana tabacum*.

- DILLENIIDAE
  - Violales
    - Fouquieriaceae
      - *Fouquieria splendens*
    - Loasaceae
      - *Eucnide hirta*

- ROSIDAE
  - Apiales
    - Apiaceae
      - *Coriandrum sativum*
    - Araliaceae
      - *Hedera helix*
      - *Trevesia sundaica*
  - Cornales
    - Cornaceae
      - *Aucuba japonica*
      - *Cornus mas*
      - *Cornus kousa*
  - Rosales
    - Grossulariaceae
      - *Ribes americanum*
    - Hydrangeaceae
      - *Hydrangea* sp.
    - Rosaceae
      - *Spiraea nipponica*

- ASTERIDAE
  - Asterales
    - Asteraceae
      - *Barnadesia caryophylla*
      - *Lactuca sativa*
  - Callitrichales
    - Callitrichaceae
      - *Callitriche heterophylla*
  - Calycerales
    - Calyceraceae
      - *Boopis graminea*
      - *Gamocarpha poeppigii*
  - Campanulales
    - Campanulaceae
      - *Campanula garganica**
      - *Campanula ramosa**
      - *Hippobroma longiflora**
      - *Jasione montana**
      - *Lobelia erinus**
      - *Lobelia laxiflora**
      - *Monopsis lutea**
      - *Platycodon grandiflorus**
      - *Sclerotheca jayorum**
    - Goodeniaceae
      - *Goodenia ovata**
      - *Scaevola taccada**
  - Dipsacales
    - Caprifoliaceae
      - *Kolkwitzia amabilis*
      - *Lonicera subsessilis*
      - *Sambucus canadensis*
      - *Symphoricarpos albus*
      - *Viburnum acerifolium*
      - *Weigela hortensis*
    - Dipsacaceae
      - *Cephalaria leucantha*
      - *Dipsacus sativus*
      - *Scabiosa ochroleuca*
    - Valerianaceae
      - *Valeriana* sp.
  - Gentianales
    - Apocynaceae
      - *Apocynum cannabinum*
      - *Acokanthera oblongifolia*
      - *Ochrosia eliptica*
      - *Prestonia acutifolia*
      - *Vinca minor*
    - Ascelpiadaceae
      - *Asclepias curassavica*
      - *Asclepias exaltata*
      - *Periploca sepium*
    - Gentianaceae
      - *Exacum affine*
      - *Gentiana dahurica*
      - *Lisianthus skinneri*
      - *Obolaria virginica*
    - Loganiaceae
      - *Fagraea zeylanica*
      - *Spigelia marilandica*
      - *Strychnos spinosa*
  - Lamiales
    - Boraginaceae
      - *Borago officinalis*
      - *Heliotropium arborescens*
      - *Mertensia virginica*
    - Lamiaceae
      - *Comanthosphace stellipila*
      - *Melissa officinalis*
      - *Pogostemon patchulii*
      - *Prasium majus*
      - *Prostanthera nivea*
      - *Salvia divinorum*
      - *Scutellaria bolanderi*
      - *Stachys officinalis*
      - *Teucrium canadense*
    - Verbenaceae
      - *Callicarpa dichotoma*
      - *Caryopteris clandonensis*
      - *Clerodendrum fragrans*
      - *Clerodendrum ugandense*
      - *Phyla scaberrima*
      - *Phryma leptostachya*
      - *Premna japonica*
      - *Verbena bonariensis*
  - Rubiales
    - Rubiaceae
      - *Pentas lanceolata*

TABLE 1. Continued.

Scrophulariales
Acanthaceae
Graptophyllum pictum
Justicia carnea
Pachystachys lutea
Bignoniaceae
Campsis radicans
Catalpa bignonioides
Clytostoma callistegioides
Buddlejaceae
Buddleja davidii
Gesneriaceae
Alsobia dianthiflora
Nematanthus hirsutus
Globulariaceae
Globularia salicinus
Myoporaceae
Eremophila maculata
Myoporum sandwicense
Oleaceae
Forysthia sp.
Ligustrum sinensis
Syringa vulgaris
Orobanchaceae
*Conopholis americana**
*Epifagus virginiana**
Pedaliaceae
Proboscidea louisianica
Sesamum indicum
Scrophulariaceae
Antirrhinum majus
Digitalis parviflorum
Paulownia tomentosa
*Striga asiatica**
Verbascum thapsus
Solanales
Convolvulaceae
Calonyction aculeatum
Convolvulus tricolor
Ipomoea pes-caprae
Cuscutaceae
Cuscuta sp.*
Hydrophyllaceae
Eriodictyon californica
Hydrophyllum virginiana
Menyanthaceae
Fauria crista-galli
Menyanthes trifoliata
Nymphoides peltata
Villarsia calthifolia
Nolanaceae
Nolana spathulata
Polemoniaceae
Phlox 'Pinafore Pink'
Polemonium reptans
Solanaceae
Iochroma cyaneum
Nicotiana tabacum
Schizanthus pinnatus
Solandra grandiflora

IR and adjacent portions of the single-copy regions, and range in size from 0.2 to 3.3 kb (averaging approximately 1 kb).

Unambiguous restriction site maps for each of the four enzymes were constructed for *Nicotiana tabacum* by computer analysis of its completely known cpDNA sequence (Shinozaki et al., 1986; Fig. 1). Because many restriction sites and fragment sizes among the taxa examined coincided with those known in *N. tabacum*, mapping efforts were greatly facilitated by scoring our data against these maps. The inclusion of one lane of *N. tabacum* cpDNA on all filters permitted a comparison between the expected size of a particular fragment in *N. tabacum* (as ascertained from the computer-generated map) and the observed size in other taxa.

Parsimony analyses of the restriction site data were conducted using PAUP version 3.0k- (Swofford, 1990) on a Macintosh IIfx computer. All three branch-swapping algorithms and the three sequences of taxon addition (simple, closest, and random) used by PAUP were employed in an attempt to find the most parsimonious trees. The data matrix is available upon request.

To assess the circumscription and possible monophyly of the Asteridae, a number of outgroups were chosen from putatively related taxa in Rosidae and Dilleniidae sensu Cronquist. These taxa included representatives from the Apiaceae, Araliaceae, Cornaceae, Fouquieriaceae, Grossulariaceae, Hydrangeaceae, Loasaceae, and Rosaceae (Table 1). Among current classifications, a consensus exists favoring a "Rosalean" ancestry for the Asteridae (e.g., Cronquist, 1981; Takhtajan, 1987); however, the exact boundaries between the Rosidae and Asteridae are subject to some dispute. Results from a concurrent phylogenetic analysis of *rbc*L sequence data (Olmstead et al., 1992) indicate that the Apiaceae, Araliaceae, Cornaceae, and Hydrangeaceae should all be included in a broadly defined Asteridae. Other evidence suggests the same for the Loasaceae (Takhtajan, 1980) and Fouquieriaceae (Thorne, 1977). Consequently, *Spiraea nipponica* (Rosaceae, Rosidae) was ultimately

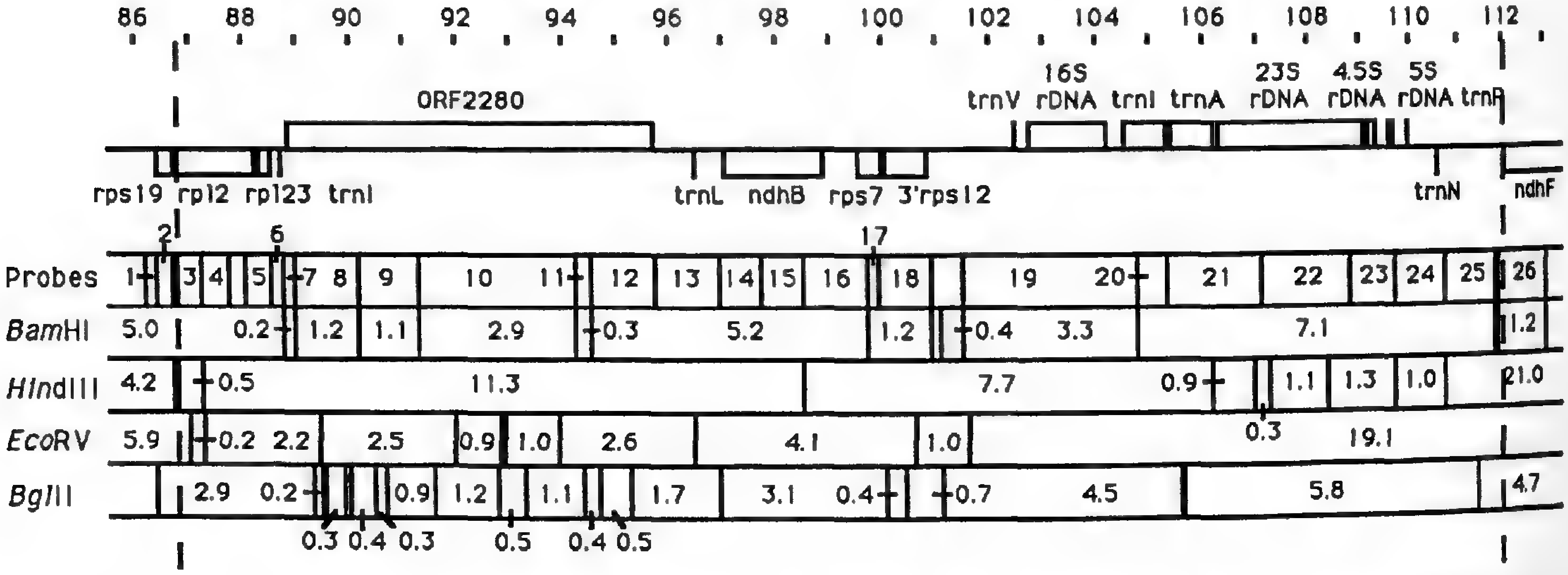

FIGURE 1. Gene and restriction site maps of the inverted repeat (IR) and adjacent single-copy regions of *Nicotiana tabacum* cpDNA. Cleavage sites, gene locations, and sequence coordinates in kb (scale on top) are modified from Shinozaki et al. (1986). Restriction fragment sizes are indicated in kb. The subclones used as hybridization probes are numbered from 1 to 26. Probe 3 spans the junction (sequence coordinate 86685) between the IR and the large single-copy region; probe 26 spans the junction (sequence coordinate 112023) between the IR and the small single-copy region. The boundaries of the *N. tabacum* IR are indicated by vertical dashed lines. Restriction site data from 114 species of dicotyledonous plants were scored against these maps.

chosen as the outgroup in this analysis, because the Rosaceae are clearly excluded from the Asteridae in all modern systems of classification. The trees computed by PAUP were rooted by positioning the root along the branch connecting *Spiraea* to the rest of the network (see simultaneous resolution procedure, Maddison et al., 1984).

RESULTS AND DISCUSSION

(1) RESTRICTION SITE VARIATION

Restriction site maps of IR sequences for each of 114 species (Table 1) were constructed for four enzymes using 26 hybridization probes from *Nicotiana tabacum* (Fig. 1). The maps reveal that the IR of 99 of these cpDNAs is both colinear in gene arrangement and readily aligned with that of *N. tabacum* (and, thereby, also with the IR of the majority of angiosperms so far examined). In contrast, at the interfamilial level, little or no alignment of restriction sites was possible in adjacent single-copy regions. Restriction site maps of the IR for 15 species (Table 1) could not be aligned with the computer-generated base maps of *N. tabacum*. Consequently, these taxa were excluded from the cladistic analysis. Excluded were two parasitic asterid genera, *Conopholis* (Orobanchaceae) and *Striga* (Scrophulariaceae), which have each lost one entire segment of their cpDNA IR. Increased sequence divergence in those regions that are contained within an IR in most angiosperms made the assessment of site homology difficult. Except for *Conopholis* and *Striga*, variation in size of the IR was minimal and did not confound interpretation. The 13 other excluded species, from the Campanulaceae (including Lobeliaceae), Goodeniaceae, Cuscutaceae, and Orobanchaceae (Table 1), all possessed a large IR but were otherwise too rearranged and divergent in sequence relative to *N. tabacum* to be included in the analysis.

Comparison of the 99 alignable restriction site maps, representing 37 families of dicots, revealed low levels of restriction site divergence. Fifty-five (71.5%) of the 77 restriction sites identified among 99 taxa were shared by two or more taxa and were thus informative for phylogenetic analysis; 17 (22%) of the remaining sites were unvarying, and five (6.5%) were unique to individual taxa and, therefore, provided no phylogenetic information. The 77 restriction sites examined represent 462 bp or 1.8% of the entire IR and 0.3% of the entire chloroplast genome. The occurrence of many invariant restriction sites and of readily identifiable homologous sites across 37 families belonging to

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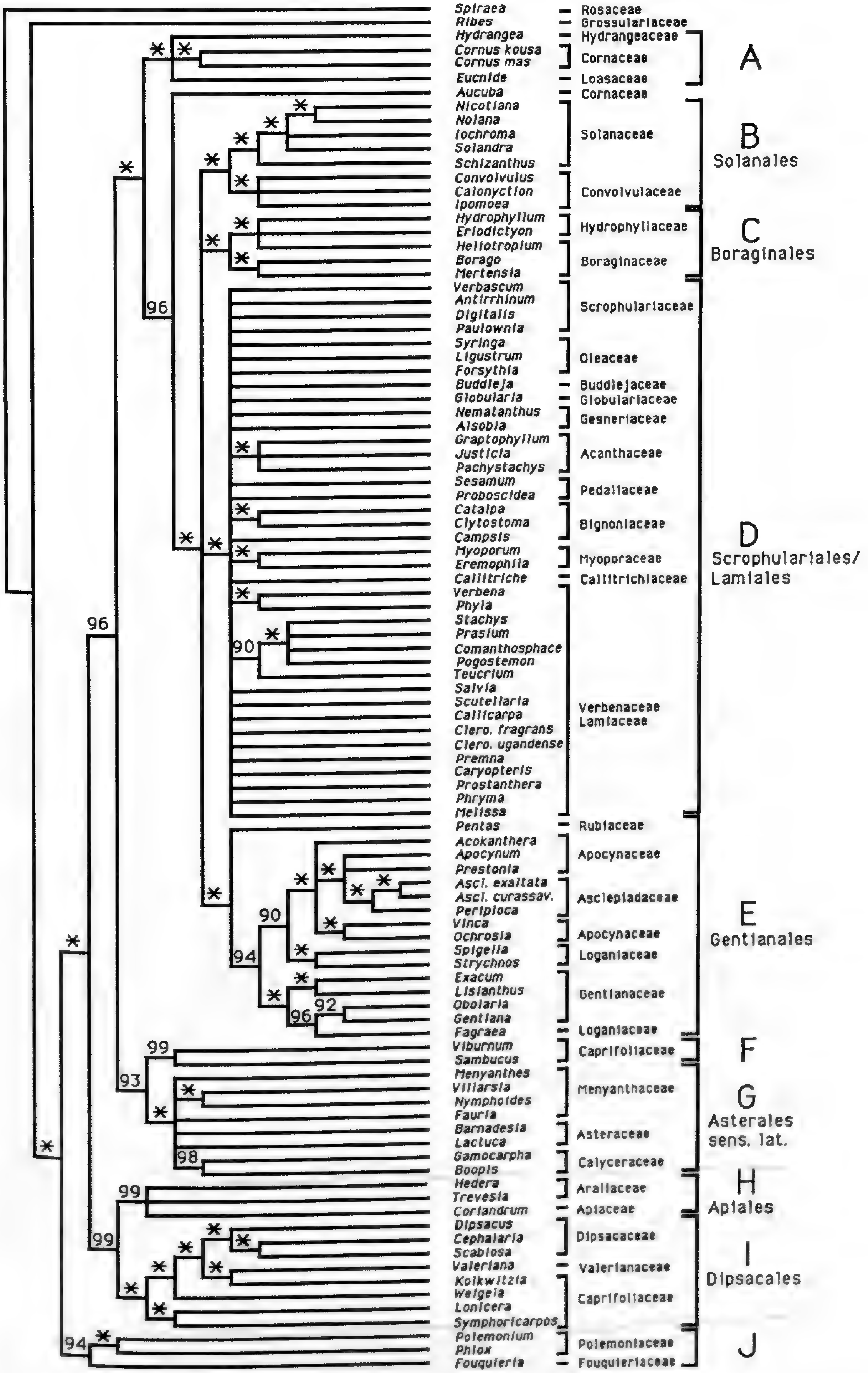
FIGURE 2. Majority-rule consensus tree consistent with 90% of 5,000 equally parsimonious 159-step trees derived from Wagner parsimony. Asterisks denote clades that are consistent with 100% of the equally parsimonious trees. Complete names of all taxa are provided in Table 1. Taxa are divided into ten groups (A to J) and are discussed in the text. Familial designations follow Cronquist (1981).


Spiraea - Rosaceae
Ribes - Grossulariaceae
Hydrangea - Hydrangeaceae
Cornus kousa
Cornus mas
Cornaceae
Eucnide - Loasaceae
A
Aucuba - Cornaceae
Nicotiana
Nolana
Iochroma
Solandra
Schizanthus
Solanaceae
Convolvulus
Calonyction
Ipomoea
Convolvulaceae
B
Solanales
Hydrophyllum
Eriodictyon
Hydrophyllaceae
Heliotropium
Borago
Mertensia
Boraginaceae
C
Boraginales
Verbascum
Antirrhinum
Digitalis
Paulownia
Scrophulariaceae
Syringa
Ligustrum
Forsythia
Oleaceae
Buddleja - Buddlejaceae
Globularia - Globulariaceae
Nematanthus
Alsobia
Gesneriaceae
Graptophyllum
Justicia
Pachystachys
Acanthaceae
Sesamum
Proboscidea
Pedaliaceae
Catalpa
Clytostoma
Campsis
Bignoniaceae
Myoporum
Eremophila
Myoporaceae
Callitriche - Callitrichaceae
Verbena
Phyla
Stachys
Prasium
Comanthosphace
Pogostemon
Teucrium
Salvia
Scutellaria
Callicarpa
Clero. fragrans
Clero. ugandense
Premna
Caryopteris
Prostanthera
Phryma
Melissa
Verbenaceae
Lamiaceae
D
Scrophulariales/
Lamiales
Pentas - Rubiaceae
Acokanthera
Apocynum
Prestonia
Apocynaceae
Ascl. exaltata
Ascl. curassav.
Periploca
Asclepiadaceae
Vinca
Ochrosia
Apocynaceae
Spigelia
Strychnos
Loganiaceae
Exacum
Lisianthus
Obolaria
Gentiana
Gentianaceae
Fagraea - Loganiaceae
E
Gentianales
Viburnum
Sambucus
Caprifoliaceae
F
Menyanthes
Villarsia
Nymphoides
Fauria
Menyanthaceae
Barnadesia
Lactuca
Asteraceae
Gamocarpha
Boopis
Calyceraceae
G
Asterales
sens. lat.
Hedera
Trevesia
Araliaceae
Coriandrum - Apiaceae
H
Apiales
Dipsacus
Cephalaria
Scabiosa
Dipsacaceae
Valeriana - Valerianaceae
Kolkwitzia
Weigela
Lonicera
Symphoricarpos
Caprifoliaceae
I
Dipsacales
Polemonium
Phlox
Polemoniaceae
Fouquieria - Fouquieriaceae
J
96
96
90
90
94
96
92
99
93
98
99
99
94

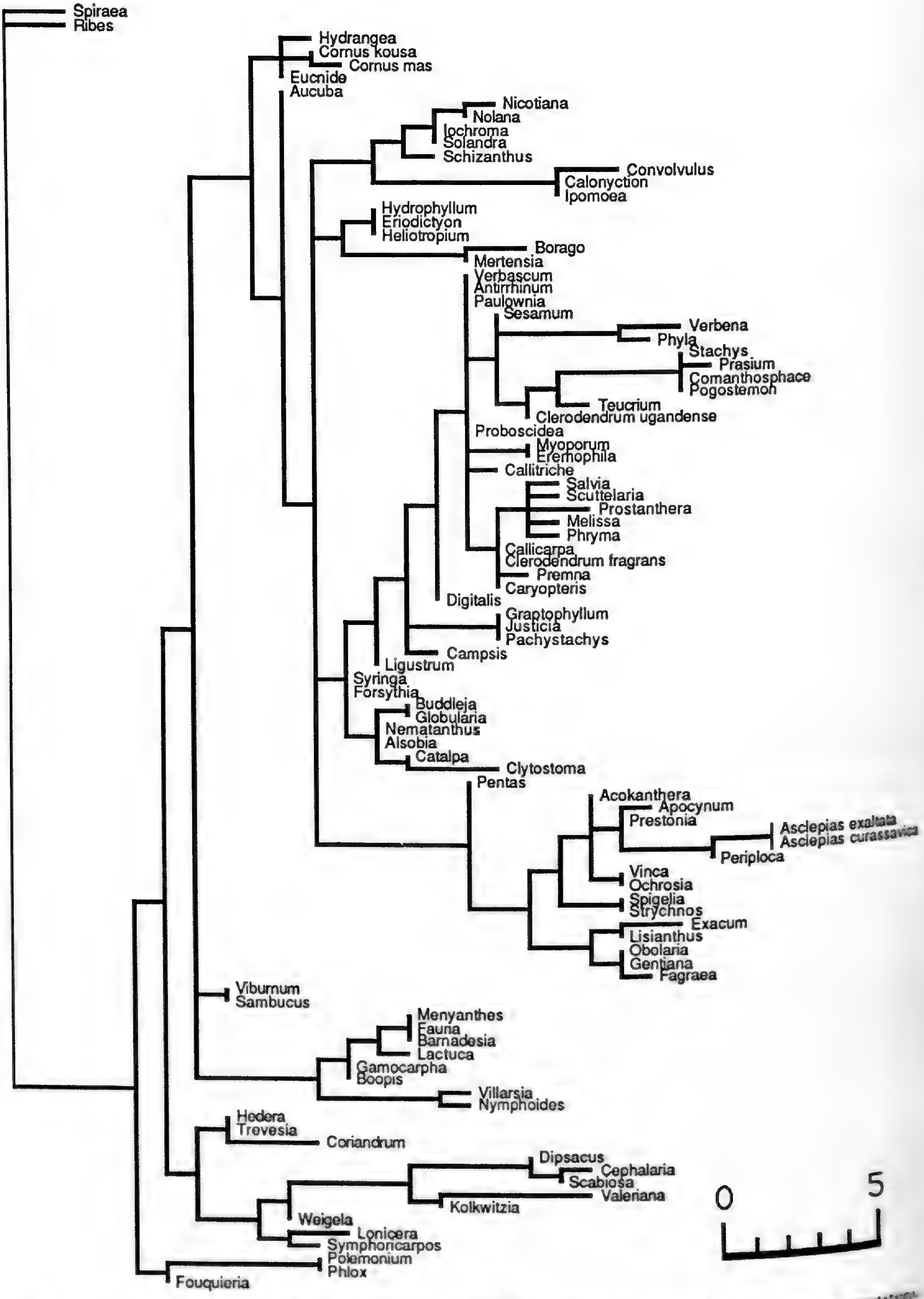


FIGURE 3. One of 5,000 equally parsimonious Wagner trees based on cpDNA IR restriction site mutations. Branch lengths are proportional to the number of inferred mutations.

three subclasses of dicotyledons (sensu Cronquist, 1981) is notable. Even more remarkable is the observation that several of these restriction sites were found to be conserved among representatives from all dicot subclasses and from some monocot subclasses as well (S. Downie & J. Palmer, unpublished). Monocots and dicots represent angiosperm lineages that may have diverged on the order of 200 million years ago (Wolfe et al., 1989).

The largest number of site changes between any pair of DNAs as inferred from the tree in Figure 3 is 21, for *Nicotiana* and *Valeriana* and for *Borago* and *Valeriana* (Table 3). In contrast, several of the DNAs are identical in all 77 restriction sites compared. Sequence divergence values were calculated among the outgroup species, *Spiraea nipponica*, and one (or two, as in the case of Group D) representative species within each of the 10 major groups identified in Figure 2. Estimates of nucleotide substitution per site (100 × *P*) between pairs of taxa range between 0.7 and 8.5 with an average of 4.5 (Brown et al., 1979; Table 3). This range of nucleotide divergence among species belonging to at least two subclasses and ten orders of dicotyledons is similar to those reported for intergeneric studies where the entire chloroplast genome was examined (e.g., Palmer et al., 1983a; Jansen & Palmer, 1987, 1988).

(2) RESTRICTION FRAGMENT LENGTH VARIATION

Three deletions, one insertion, and one nonpolarizable length variant were detected in cpDNAs of 27 of the 99 species (Table 2). We have greatly underestimated the actual extent of restriction fragment length variation in the 99 species examined because most cpDNA length mutations (for the entire genome) are 1–10 bp in size (Palmer, 1985). We could not detect length variants smaller than 300 bp for those gels where the bromophenol blue dye marker was run 6 cm and length variants smaller than 200 bp for those gels where the dye marker was run 12 cm (see methods section).

The first length variant in Table 2 corresponds to the loss of an intron from the *rpl2* gene. It has been shown previously that the *rpl2* intron has been lost at least six times in the dicots, including at least twice in the Asteridae, once in the ancestral Convolvulaceae and once in the ancestral Menyanthaceae (Downie et al., 1991). The four other length variants occur within the gene ORF2280 (Fig. 1). This gene is absent in the grasses, and major deletions within the gene are known in several other nonasterid taxa (Hiratsuka et al., 1989; Downie & Palmer, 1991, and unpublished). The absence of any detectable length variation in intergenic spacers is surprising, as these comprise 23% of the *Nicotiana tabacum* IR and presumably could easily accommodate the disruptive effects of insertions and deletions. The rarity of length variation within the IR relative to single-copy sequences has been reported previously (Doebley et al., 1987; Jansen & Palmer, 1988; Schilling & Jansen, 1989; Wallace & Jansen, 1990; Soltis et al., 1990a; K. Wolfe, C. Morden & J. Palmer, unpublished).

Four of these length variants were shared by two or more taxa and, thus, are phylogenetically informative. Although length mutations were not used in the phylogenetic analysis, the phylogeny constructed from IR restriction site mutations (see below; Figs. 2 and 3) implies that the second, third, and fourth length mutations described in Table 2 have occurred independently eight, one, and three times, respectively. For those taxa possessing deletions, restriction sites in these regions were scored as missing data.

(3) PHYLOGENETIC ANALYSIS OF INVERTED REPEAT RESTRICTION SITE MUTATIONS

A phylogenetic analysis using Wagner parsimony and 99 taxa resulted in many shortest trees of 159 steps, with a consistency index (CI) of 0.36 (excluding uninformative characters). Sanderson & Donoghue (1989) found CI to be inversely correlated with the number of taxa included in an analysis. The largest data sets analyzed in their study included 65–68 taxa and had CI values of 0.32–0.37. Although there was no data set in their study comparable in number of taxa to ours, a CI value of 0.36 for 99 taxa appears to be higher than expected.

The exact number of minimum length trees could not be determined. PAUP found 9,000 159-step trees before the computer's memory was exhausted and the analysis terminated. Subsequently, the maximum number of trees saved by PAUP was arbitrarily set to 5,000, and from these a 90% majority rule consensus tree was derived (Fig. 2). Given the exploratory nature of this study, a 90% majority rule consensus tree was chosen over a strict consensus tree in order to offer greater resolution among the clades. However, it is stressed that the percentage values presented in Figure 2 do not measure the robustness of the clades, but rather indicate how many times particular groups of plants fall out together as monophyletic in the 5,000 shortest trees examined. The large number of taxa (99) relative to the number of informative characters (55) resulted in few synapomorphies

TABLE 2. Chloroplast DNA restriction-fragment length variation[a] in the inverted repeat region in Asteridae and related genera.

Probe[b]	Variation[c]	Size (bp)	Species
4	Deletion	600	Convolvulaceae
			Calonyction aculeatum
			Convolvulus tricolor
			Ipomoea pes-caprae
			Menyanthaceae
			Fauria crista-galli
			Menyanthes trifoliata
			Nymphoides peltata
			Villarsia calthifolia
8	Deletion	400	Apiaceae
			Coriandrum sativum
			Araliaceae
			Hedera helix
			Trevesia sundaica
			Asclepiadaceae
			Asclepias curassavica
			Asclepias exaltata
			Periploca sepium
			Bignoniaceae
			Catalpa bignonioides
			Clytostoma callistegioides
			Caprifoliaceae
			Kolkwitzia amabilis
			Lonicera subsessilis
			Symphoricarpos albus
			Weigela hortensis
			Convolvulaceae
			Calonyction aculeatum
			Convolvulus tricolor
			Ipomoea pes-caprae
			Dipsacaceae
			Cephalaria leucantha
			Dipsacus sativus
			Scabiosa ochroleuca
			Oleaceae
			Ligustrum sinensis
			Pedaliaceae
			Sesamum indicum
			Solanaceae
			Schizanthus pinnatus
			Valerianaceae
			Valeriana sp.
10	Insertion	500	Caprifoliaceae
			Kolkwitzia amabilis
			Lonicera subsessilis
			Symphoricarpos albus
			Weigela hortensis
			Dipsacaceae
			Cephalaria leucantha
			Dipsacus sativus
			Scabiosa ochroleuca
			Valerianaceae
			Valeriana sp.
12–13	Deletion	500	Bignoniaceae
			Clytostoma callistegioides

TABLE 2. Continued.

Probe[b]	Variation[c]	Size (bp)	Species
			Convolvulaceae
			Calonyction aculeatum
			Convolvulus tricolor
			Ipomoea pes-caprae
			Solanaceae
			Schizanthus pinnatus
12–13	Nonpolarizable	500	Rosaceae
			Spiraea nipponica

[a] Only length variants greater than 200–300 bp were detected (see text).
[b] See Figure 1 for map coordinates in kb and region of gene deletion/insertion.
[c] Restriction-fragment length variation relative to *Nicotiana tabacum*.

supporting each clade in the most parsimonious trees. The distribution of character support in one of these 5,000 equally parsimonious trees (chosen because of its similarity with the consensus tree) is illustrated in Figure 3, with nearly two-thirds of the nonterminal branches supported by only one character change. This, combined with the great length of time for the computer analyses, suggests that a bootstrap analysis (Felsenstein, 1985) to provide a quantitative measure of support for the clades identified in the consensus tree would be both inappropriate and impractical. Among 99 taxa and 77 restriction sites compared, the number of mutations for each site inferred from the tree in Figure 3 ranged from 0 to 8 with a mean of 2.1. Consequently, many of the single-length branches are characterized by homoplasious mutations. In spite of the low ratio of characters to taxa and the large number of equally parsimonious trees, a high degree of resolution is attained in some portions of the cladogram. The clades identified by an asterisk in Figure 2 were consistent with 100% of the equally parsimonious trees. The distribution of homoplasy is such that it effectively increases the number of characters supporting many branches.

(4) PHYLOGENETIC IMPLICATIONS OF CHLOROPLAST DNA MUTATIONS

Ten groups are identified that either coincide with orders recognized traditionally in the subclass or present novel relationships. These ten groups, identified from top to bottom in Figure 2, are: (A) a clade consisting of *Cornus*, Hydrangeaceae, and Loasaceae; (B) Solanales; (C) Boraginales; (D) Scrophulariales plus Lamiales; (E) Gentianales; (F) a clade consisting of *Viburnum* and *Sambucus*; (G) a clade consisting of Asterales, Calyceraceae, and Menyanthaceae; (H) Apiales; (I) Dipsacales (minus *Viburnum* and *Sambucus*); and (J) a basal

TABLE 3. Estimated nucleotide sequence divergence of the cpDNA IR among species of Asteridae and related genera. Complete names of species and their ordinal placement are presented in Table 1. The upper right portion of the matrix indicates the number of IR restriction site mutations between the two taxa as determined by direct pairwise comparisons. Pairwise nucleotide sequence divergence estimates are expressed by 100 × p in the lower left portion of the matrix (Brown et al., 1979). The number of restriction sites examined for each species ranged from 37 to 48.

Species	1	2	3	4	5	6	7	8	9	10	11	12
1. *Spiraea*	—	8	16	10	11	11	17	9	12	10	17	7
2. *Hydrangea*	3.0	—	10	9	7	5	17	5	10	8	17	5
3. *Nicotiana*	6.4	4.4	—	13	7	5	19	11	16	12	21	11
4. *Borago*	4.1	3.0	4.7	—	10	8	18	11	16	14	21	12
5. *Verbascum*	4.4	2.6	2.7	4.3	—	2	16	8	13	9	16	6
6. *Syringa*	4.4	1.8	1.9	3.5	0.7	—	14	6	11	9	16	6
7. *Asclepias*	7.5	6.8	8.0	8.2	6.8	5.9	—	18	19	17	19	16
8. *Viburnum*	3.5	1.8	4.0	4.1	3.0	2.2	7.3	—	7	7	12	4
9. *Lactuca*	4.9	3.7	6.3	6.4	5.1	4.3	8.2	2.6	—	12	17	7
10. *Coriandrum*	3.3	2.3	3.2	6.6	2.8	2.8	6.6	1.9	4.1	—	13	7
11. *Valeriana*	6.9	6.3	8.2	8.4	7.1	6.3	8.5	4.5	6.8	4.4	—	14
12. *Fouquieria*	2.8	1.8	4.1	5.0	2.3	2.3	6.6	1.5	2.7	2.0	5.3	—

branch consisting of *Fouquieria* and Polemoniaceae.

The major clade comprising groups B, C, D, and E is consistent with the subclass Lamiidae as recognized by Takhtajan (1987), but with the exclusion of the Menyanthaceae and Loasaceae. For the most part, relationships among the ten groups are poorly resolved.

Monophyly of the Asteridae. Disagreement prevails as to whether or not the Asteridae are monophyletic. Cronquist (1981), Stebbins (1974), Takhtajan (1980), and Wagenitz (1977) consider the Asteridae to be a natural group, implying that they are monophyletic, whereas Philipson (1977), Dahlgren (1983), Throne (1983), and Takhtajan (1987) view the Asteridae (sensu Cronquist) as unnatural. Our results indicate that the Asteridae, as traditionally circumscribed, are not monophyletic. The Apiaceae, Araliaceae, Cornaceae, Hydrangeaceae, Loasaceae, and possibly the Fouquieriaceae, all traditionally placed in the Rosidae or Dilleniidae (e.g., Cronquist, 1981), should, in our view, be included within a broadly defined Asteridae. Additional molecular support for the inclusion of the Apiaceae, Araliaceae, Cornaceae, and Hydrangeaceae in Asteridae sens. lat. comes from *rbc*L sequence data (Olmstead et al., 1992, and unpublished). Olmstead et al. (1992) have shown that the origin and diversification of the Asteridae sens. lat. lie deep within the "higher" dicots, i.e., that the subclass is not of recent origin as argued by Cronquist (1981). Our results, using *Spiraea* as an outgroup, are generally in accord with those obtained from the *rbc*L analysis, in which representatives from the Magnoliidae were used as outgroups (Olmstead et al., 1992).

These results indicate that the subclass does not entirely correspond to its usual circumscription as a primarily sympetalous group. The occurrence of distinct petals in *Aucuba* (Cornaceae), the Apiales, and the clade consisting of *Cornus* (Cornaceae), *Hydrangea* (Hydrangeaceae), and *Eucnide* (Loasaceae) suggests that at least two reversals are necessary to generate polypetally in these taxa from putatively sympetalous ancestors. Alternatively, these taxa may represent the retention of the ancestral state of polypetally with sympetally arising at least four times during evolution of the Asteridae.

Phylogenetic Relationships Within the Asteridae. Below we discuss the ten major groups of Asteridae sens. lat. seen in the cladogram (Fig. 2). Our results, although preliminary, are generally consistent with traditional morphological groupings and with the results obtained from *rbc*L sequence data (Olmstead et al., 1992). The results of our analysis regarding representatives of the Rosidae (Apiaceae, Araliaceae, Cornaceae, Hydrangeaceae) and Dilleniidae (Fouquieriaceae, Loasaceae) sensu Cronquist in the Asteridae sens. lat. suggest that neither of these subclasses are monophyletic and that their higher-level relationships are in need of further study.

(A) *Hydrangeaceae, Cornaceae, and Loasaceae.* The traditional association of Hydrangeaceae with the Saxifragaceae and its allied woody families has been disputed by Dahlgren (1980, 1983), Takhtajan (1987), and Soltis et al. (1990b). Dahlgren considered the Hydrangeaceae to be closely allied to Cornaceae and treated them along with the Caprifoliaceae in his Cornales, an order he described as closely related to the Dipsacales, Fouquieriales, and Ericales. On the basis of morphological and chemical data, Hufford (1992) showed that the "woody saxifrages" (e.g., Hydrangeaceae) are more closely related to members of the Cornaceae and Loasaceae than to the "herbaceous saxifrages" (e.g., Saxifragaceae sens. str.). Our results indicate that *Hydrangea, Cornus*, and *Eucnide* (Loasaceae) belong to a monophyletic group, with the relationships among the genera unresolved.

Historically, the affinities of the Loasaceae have been obscure. Takhtajan (1969) initially considered the Loasaceae to be related to the Boraginaceae and Hydrophyllaceae. Subsequent treatments either placed Loasaceae in a separate order, Loasales, related to the Dipsacales and the Polemoniales (Takhtajan, 1980), or to the Gentianales (Takhtajan, 1987). Hufford (1990, 1992) provided evidence against the hypothesis that the Loasaceae share a common ancestry with members of the Dilleniidae, a position favored by Cronquist (1981), and instead supported Dahlgren's (1983) suggestion that the family shares an ancestry with the Dipsacales, Cornales, and the "woody saxifrages." On the basis of wood anatomy, Carlquist (1992) believes that Loasales are not far from such orders as the Dipsacales or Cornales. The results presented here support, in part, the hypotheses presented by Hufford, Dahlgren, and Carlquist, attesting to a common ancestry for Loasaceae and Cornales.

The systematic position of *Aucuba* is unclear. This genus is placed in the Cornaceae by Cronquist (1981), whereas Takhtajan (1980) placed it in the closely related family Aucubaceae. *Aucuba* differs from all other cornaceous taxa in its chemistry, floral anatomy, embryology, and pollen structure (Rodriguez, 1971; Takhtajan, 1980). Our results place *Aucuba* outside of Group A and suggest that if the Cornaceae are circumscribed to include this taxon, the family would be polyphyletic. However, by imposing the constraint on the cladistic analysis that *Aucuba* and *Cornus* species form a monophyletic group, shortest trees one step longer than the most parsimonious trees were found. Consequently, the putative polyphyly exhibited by this group must be regarded as tentative.

(B) *Solanales.* The clade designated as Solanales in this analysis comprises three families (sensu Cronquist): Solanaceae, Nolanaceae, and Convolvulaceae. It is widely agreed that the Solanaceae and Nolanaceae are closely related. In the past, Nolanaceae have either been treated at the subfamilial level within the Solanaceae (D'Arcy, 1979) or as a closely related segregate family derived from the Solanaceae (Cronquist, 1981; Takhtajan, 1987). Our results are consistent with those of Thorne (1968), D'Arcy (1979), and Olmstead & Palmer (1992), affirming the submersion of *Nolana* within the Solanaceae. The position of the morphologically distinct *Schizanthus* as the earliest diverging lineage in the Solanaceae is also supported by the more extensive restriction site analysis of Olmstead & Palmer (1992). Our results differ from those of Olmstead & Palmer in the relationships among *Nicotiana, Nolana,* and *Solandra.* Our results place *Nicotiana* and *Nolana* as sister taxa, with *Solandra* basal to this group (Fig. 2). Olmstead & Palmer show that *Nolana* and *Solandra* are more closely related to each other than either is to *Nicotiana.*

The Solanaceae and Convolvulaceae emerge as sister groups in our analysis. Anatomical and phytochemical similarities between these two families have suggested a close relationship in the past (Cronquist, 1981; Thorne, 1983). Moreover, a phylogenetic analysis of *rbc*L sequence data (Olmstead et al., 1992) corroborates this relationship.

(C) *Boraginales.* The clade designated as the Boraginales is represented by two families in this analysis: Boraginaceae and Hydrophyllaceae. The close morphological relationship between these families has long been evident (e.g., Dahlgren, 1983; Takhtajan, 1987), in spite of Cronquist's (1981) treatment to the contrary, wherein the Boraginaceae are placed alongside the Lamiaceae and Verbenaceae in his Lamiales, and the Hydrophyllaceae are placed in his Solanales. Cronquist does, however, acknowledge the strong similarity between them. The division of this clade into two distinct lineages, with *Heliotropium* (Boraginaceae) placed in a clade with *Hydrophyllum* and *Eriodictyon* (Hydrophyllaceae), raises questions about the circumscription and generic relationships of the two families.

(D) *Scrophulariales plus Lamiales.* The largest group recognized in the analysis is composed of families that have traditionally been considered in the Scrophulariales and Lamiales. They are treated here together, owing to the lack of resolution within the clade. Included here are representatives from 12 families, Scrophulariaceae, Globulariaceae, Gesneriaceae, Acanthaceae, Pedaliaceae, Bignoniaceae, Myoporaceae, Lamiaceae, Verbenaceae, Callitrichaceae, Buddlejaceae, and Oleaceae. It is widely agreed that the first seven families are closely related. The Lamiaceae and Verbenaceae form a closely related pair (Cantino, 1992) and are often treated in the separate order Lamiales; however, based on our data, the distinction between this order and the Scrophulariales is weak. The association of Lamiaceae and Verbenaceae with the Scrophulariales suggested by cpDNA restriction site data (Fig. 2) and *rbc*L sequence data (Olmstead et al., 1992) is in accordance with several previous treatments (Wagenitz, 1977; Cantino, 1982; Dahlgren, 1983), but disagrees with hypotheses by Takhtajan (1980) and Cronquist (1981), who suggested that the Boraginales are the extant group most closely related to these two families.

Our results further suggest that Buddlejaceae, frequently regarded as a tribe in the Loganiaceae (Gentianales), are misplaced and should be considered within the Scrophulariales plus Lamiales. Callitrichaceae, often included either in the Lamiales (Dahlgren, 1983; Thorne, 1983; Takhtajan, 1987) or in their own order near the Scrophulariales (Cronquist, 1981), lie within the Scrophulariales plus Lamiales clade. These results are consistent with those of *rbc*L sequence analysis (Olmstead et al., 1992, and unpublished).

The affinities of the Oleaceae have also been disputed. The family has been placed either in its own order (Oleales) near the Gentianales (Dahlgren, 1983; Thorne, 1983; Takhtajan, 1987), within the Gentianales (Stebbins, 1974), or in the Scrophulariales (Cronquist, 1981). Disparities in floral symmetry, phytochemistry, embryology, and anatomy between the Oleaceae and either the Gentianales or the Scrophulariales have precluded a satisfactory placement in either order. Our results suggest that the Oleaceae (as represented by *Forsythia, Ligustrum,* and *Syringa*) are more closely related to the Scrophulariales than to the Gentianales. This is consistent with the *rbc*L analysis of Olmstead et al. (1992), which placed the family in a basal position in the Scrophulariales.

Of the seven scrophularialean families for which more than one species was examined, only two, Acanthaceae and Myoporaceae, emerge as monophyletic. The gynobasic-styled Lamiaceae (*Stachys*, *Prasium*, *Comanthosphace*, and *Pogostemon*) also emerge as distinct in agreement with Cantino (1992), but their relationship with other mints and the Verbenaceae is not resolved.

The lack of resolution within and among the families that constitute the Scrophulariales is likely due to two factors. First, the low number of informative restriction sites within these taxa presents a problem. Of the 55 phylogenetically informative characters used in the cladistic analysis, only 10 provide information on relationships among the 22 species from nine families that make up the Scrophulariales (Table 1). Several of these DNAs are identical in all 77 restriction sites compared. The estimated pairwise percent sequence divergence (Brown et al., 1979) between *Syringa* (Oleaceae) and *Verbascum* (Scrophulariaceae), which may represent extremes within the order (see above), is 0.7% (Table 3). Data from only four restriction enzymes were available; as data from more restriction enzymes and from gene sequencing are included in subsequent phylogenetic analyses, greater resolution among the families is expected. A study of this nature is currently in progress (C. Morden, C. dePamphilis & J. Palmer, unpublished).

Second, the Scrophulariales are a relatively homogeneous order, with the morphological similarities among its constituent families emphasized by many. Several families are connected by genera thought to be transitional or of uncertain placement (Armstrong, 1985); consequently, precise circumscriptions of some families are ambiguous. Moreover, some members of the order are considered to be specialized derivatives of the Scrophulariaceae, the largest and putatively central family in the order (Cronquist, 1981). Cladistic analyses using primarily morphological characters (Lu, 1990) and *rbc*L sequence data (Olmstead et al., 1992) offered little resolution among the families comprising the orders Scrophulariales and Lamiales. Diversification of the Scrophulariales into families and perhaps even genera may have occurred rapidly relative to other orders within the subclass.

(E) *Gentianales.* The Apocynaceae, Asclepiadaceae, Loganiaceae, Gentianaceae, and Rubiaceae are representatives of the Gentianales in this study. Reasonable consensus exists among systematists regarding the circumscription and, to a lesser degree, the infraordinal structure of the Gentianales. The first four families listed above are closely related in all modern taxonomic systems and are relatively homogeneous in wood anatomy (Carlquist, 1992), morphology, and phytochemistry. The Menyanthaceae, Buddlejaceae, and Oleaceae, often included in the Gentianales, are placed elsewhere in our analysis (see Groups D and G).

Although most systematists treat the Apocynaceae and Asclepiadaceae as distinct families, some believe that because few characters clearly differentiate these taxa, it would be more appropriate to treat them as a single family (Hallier, 1905; Demeter, 1922; Stebbins, 1974; Thorne, 1983). Our results support the latter view. The Apocynaceae form a monophyletic group when the Asclepiadaceae (represented by *Asclepias* and *Periploca*) are included within it (Fig. 2).

The Loganiaceae are a morphologically heterogeneous group, with many segregate families recognized by some authors. The family is represented here by three genera: *Fagraea*, *Spigelia*, and *Strychnos*. The latter two genera form a clade in our analysis, whereas *Fagraea* is grouped with the Gentianaceae, suggesting that it might be misplaced in the Loganiaceae (see Jensen, 1992). Alternatively, the Loganiaceae may be a paraphyletic group ancestral to the Apocynaceae and Gentianaceae.

The Rubiaceae, represented here by *Pentas*, are often associated with the Gentianales (Bremer, 1992). In the treatments of Takhtajan (1980, 1987), Thorne (1983), Dahlgren (1983), and Wagenitz (1977), the Rubiaceae are included in the Gentianales. However, their lack of internal phloem (otherwise ubiquitous in the order) and the presence of an inferior ovary (otherwise superior with few exceptions) make the family stand apart from the rest of the order. Cronquist (1981) excluded the Rubiaceae from the Gentianales and considered them in their own order, the Rubiales. Similarly, wood anatomy suggests that the Rubiaceae may not belong within the Gentianales (Carlquist, 1992), but rather in a neighboring monofamilial order. Our data place the Rubiaceae as the most basal branch within the Gentianales (Fig. 2), and are, therefore, consistent with either their inclusion in the Gentianales or their segregation in a separate order.

(F) *Viburnum and Sambucus.* The relationships between *Viburnum* and *Sambucus*, and between these two taxa and other genera traditionally placed within the Caprifoliaceae, have been subject to much speculation. Our data support the close relationship between *Viburnum* and *Sambucus* posited by Donoghue (1983) on the basis of morphological evidence. The separation of *Viburnum* and *Sambucus* (plus *Adoxa*) from the rest of the Caprifoliaceae and from other Dipsacales has been suggested by Donoghue and coworkers on the basis of morphological evidence, *rbc*L sequence data, and preliminary cpDNA restriction site data (Donoghue, 1983, 1990; Donoghue et al., 1992). Our data also agree with this view. The absence of two restriction fragment length variants in *Viburnum* and *Sambucus*, otherwise present in the four other Caprifoliaceae examined (Table 2), further distinguishes them from the Caprifoliaceae sens. str. but is neutral with respect to the controversy concerning their phylogenetic affinities.

The putative sister-group relationship between the clade consisting of *Viburnum* and *Sambucus* and the Asterales, as seen in Figure 2, is complicated by the fact that more than one most parsimonious reconstruction (MPR) exists (Swofford & Maddison, 1987). Because the branch uniting Groups F and G has zero-length under one MPR but a length of one under a different MPR, PAUP retains the zero-length branch (Swofford, 1990). The collapse of this zero-length branch yields an unresolved trichotomy consisting of Groups A through E as one branch, Group G as another branch, and Group F as the third branch (Fig. 3). Given this, the close relationship of *Viburnum* and *Sambucus* to the Asterales in Figure 2 must be regarded as tentative. On the basis of *rbc*L sequence data (Donoghue et al., 1992), the connection between *Viburnum* and *Sambucus* and the Asterales is also unclear.

(G) *Asterales sensu lato.* The clade identified as the Asterales in Figure 2 comprises representatives from the Asteraceae, Calyceraceae, and Menyanthaceae. Material from the allied Campanulales (Goodeniaceae and Campanulaceae) was examined (Table 1), but extensive length and sequence variation in their cpDNAs made comparative mapping and the confirmation of homology of restriction sites impossible. Therefore, these families were not included in the phylogenetic analysis. Sister-group relationships between *Gamocarpha* and *Boopis* (Calyceraceae), and between *Villarsia* and *Nymphoides* (Menyanthaceae), are evident; however, relationships among the Asteraceae, Calyceraceae, and Menyanthaceae are not resolved. Other than the loss of the *rpl*2 intron in the Menyanthaceae (Table 3; Downie et al., 1991), the DNAs of *Menyanthes* and *Fauria* (Menyanthaceae) and *Barnadesia* (Asteraceae) are identical at all restriction fragments compared, with only two character differences separating *Barnadesia* from *Lactuca* (Fig. 3). A closer relationship between *Villarsia* and *Nymphoides* than between these two genera and any other in the Menyanthaceae is also inferred from morphological and flavonoid chemical data (Ornduff, 1973; Bohm et al., 1986).

Affinities between the Asteraceae and Calyceraceae have often been claimed based on floral morphology and wood anatomy (Turner, 1977; Skvarla et al., 1977; Carlquist, 1992). Dahlgren (1983) and Thorne (1983) placed the Calyceraceae in the Dipsacales, whereas Cronquist (1981) placed them in their own order, the Calycerales, which he stated is related to and probably derived from the Dipsacales. Our results strongly indicate that the Calyceraceae belong within the clade designated here as the Asterales and not within the Dipsacales. Phylogenetic analyses of *rbc*L sequence data corroborate these results and indicate further that the families Calyceraceae and Goodeniaceae are the closest living relatives to the Asteraceae (Michaels et al., in prep.; Olmstead et al., 1992).

The presence of Menyanthaceae in the asteralean clade is unexpected. Once relegated to infrafamilial status within the Gentianaceae (Bentham, 1876; Rendle, 1925), the Menyanthaceae are now recognized at the familial level. Discordance between anatomical and chemical characters has precluded a consensus on its ordinal placement. Most modern systematists include the Menyanthaceae within the Gentianales (e.g., Takhtajan, 1987), but Cronquist (1981) viewed their position here as "discordant" and placed them in the Solanales. Our data are in agreement with the strong evidence from *rbc*L sequences (Olmstead et al., 1992) that instead places Menyanthaceae within the Asterales. Although the families differ strikingly in flower and inflorescence morphology, a close relationship between the Menyanthaceae and Asteraceae was posited by Yamazaki (1971) on the basis of similarity in embryo development, and by Pollard & Amuti (1981) on the basis of common possession of inulin.

(H) *Apiales.* Cronquist (1981) placed the Apiales (Apiaceae and Araliaceae) in the subclass Rosidae. The morphological resemblance among the Apiales, Cornaceae, and some genera of Caprifoliaceae has been noted (Thorne, 1983), with the Apiales considered allied to the Cornales and placed in the Rosidae (Cronquist, 1981). Our results agree that the Araliaceae and Apiaceae are closely related (e.g., Takhtajan, 1980; Cronquist, 1981; Thorne, 1983). The placement of the Apiales as sister group to the Dipsacales in our study is variously supported by *rbc*L sequence data. Our data are in close agreement with Olmstead et al. (1992) in placing the Apiales as sister group to the Dipsacales, but differ from Donoghue et al. (1992) in which the position of the Apiales in relation to the Dipsacales (and Asterales) is uncertain.

(I) *Dipsacales.* Included here are taxa belonging to the Caprifoliaceae, Dipsacaceae, and Valerianaceae. *Viburnum* and *Sambucus* are excluded from this clade in our analysis (see above discussion of Group F). The Dipsacaceae emerge as monophyletic and are nested along with Valerianaceae within a paraphyletic Caprifoliaceae (Fig. 2). *Kolkwitzia,* belonging to the tribe Linnaeeae of Caprifoliaceae, and *Valeriana* (Valerianaceae) emerge as sister taxa in our analysis. A close relationship has been proposed between this tribe and the Valerianaceae (Wilkinson, 1949; Donoghue, 1983; Donoghue et al., 1992). *Lonicera* and *Symphoricarpos* also emerge as more closely related to each other than either is to any other member of the Caprifoliaceae. A more detailed analysis of the phylogeny of the Dipsacales based on *rbc*L sequences is presented elsewhere in this volume (Donoghue et al., 1992).

(J) *Fouquieria and Polemoniaceae.* The systematic positions of the Fouquieriaceae and the Polemoniaceae have long been matters of controversy. The Fouquieriaceae have been variously placed in the Violales (Dilleniidae; Cronquist, 1981), the Tamaricales (Dilleniidae; Takhtajan, 1980), or in their own order, the Fouquieriales (Corniflorae, near Ericales and Cornales; Dahlgren, 1983). The Polemoniaceae, once thought to be allied with the Caryophyllales (Caryophyllidae) or with the Geraniales (Rosidae; see review in Dawson, 1936), are often placed in the Asteridae (Cronquist, 1981; Takhtajan, 1980). Henrickson (1967) and Thorne (1977) considered the Polemoniaceae to have affinities with the Fouquieriaceae. Hufford (1992) allied the Polemoniaceae with the Pittosporaceae and treated this clade as sister group to the Asteridae, and placed the Fouquieriaceae as the sister group to the Ericales (Dilleniidae). The latter hypothesis is supported by Olmstead et al. (1992, and unpublished), whose results showed that the Fouquieriaceae and Polemoniaceae are part of a monophyletic Ericales. The placement of the Fouquieriaceae alongside the Polemoniaceae in this study is in agreement with Henrickson's and Thorne's earlier hypotheses: however, their close relationship is not well supported.

Fouquieria possesses a number of distinctive features that make it equally as anomalous in the Dilleniidae as in the Asteridae (Wagenitz, 1977; Cronquist, 1981; Hufford, 1992). The basal position of *Fouquieria* and Polemoniaceae in Figures 2 and 3 is surprising and demands further attention. In this regard, it is noteworthy that some support for this position is also found in a *rbc*L sequence phylogeny (Olmstead et al., 1992, and unpublished).

CONCLUSIONS

Comparative restriction site mapping of IR sequences of chloroplast genomes from 99 species and 37 families of Asteridae and putatively allied taxa in the Rosidae and Dilleniidae allows for phylogenetic inference at high taxonomic levels. This study demonstrates for the first time the potential of this approach for illuminating phylogenetic relationships at the familial and ordinal level. Wolfe et al. (1987) have demonstrated that rates of nucleotide substitutions at silent sites and in noncoding sequences in the IR are 4–6 times lower than those in single-copy regions. Consequently, by focusing exclusively on the highly conserved IR region of the chloroplast genome one can predict that comparative restriction site mapping studies can be extended to evolutionary depths 4–6 times greater than that to which they have been applied previously. Since restriction site variation within the entire chloroplast genome has been used successfully to infer phylogenies for a few large families, it is not surprising that restriction site mapping of the IR works well over the whole Asteridae.

This conservatism in IR restriction site mutations is, however, both a blessing and a curse. At appropriate levels of nucleotide divergence, these data can be used in a cladistic analysis to infer relationships; however, the extreme conservatism of the IR precludes robust hypotheses of relationships among relatively closely related taxa. Also, excessive divergence in restriction sites in several families (Table 1), particularly those that have lost one entire segment of the cpDNA IR, prevents alignment of restriction maps and assessment of site homology. Divergence at the structural level, whether due to inversions or major length variation, also limits the utility of this approach. At deep phylogenetic levels, the approach presented here will yield fewer informative characters than DNA sequencing but is clearly a useful adjunct approach to sequencing. The utility of *rbc*L sequence data in inferring relationships across different subclasses of angiosperms has been demonstrated by Olmstead et al. (1992).

Phylogenetic analysis of cpDNA IR restriction site variation provides a means of reassessing the traditional and largely morphologically based classifications of the Asteridae. The results presented here are preliminary in the sense that the ratio of informative characters to taxa is low and therefore are not a sufficient basis for a new classification of the subclass. Nevertheless, they provide a set of explicit hypotheses about relationships in the Asteridae that can be tested as additional evidence becomes available. These data provide important corroborating evidence for other contemporary studies focusing on cpDNA sequence data (Donoghue et al., 1992; Michaels et al., in prep.; Olmstead et al., 1992). If subsequent analyses support the results presented here, some realignments in the circumscription and classification of the Asteridae will be in order.

The following general conclusions are reached concerning phylogenetic relationships in Asteridae sensu lato. (1) Six distinct clades that broadly correspond to traditionally recognized orders in the Asteridae can be circumscribed: Solanales, Boraginales, Scrophulariales plus Lamiales, Gentianales, Asterales sens. lat. (including Calyceraceae and Menyanthaceae), and Dipsacales (minus *Viburnum* and *Sambucus*). Infraordinal relationships are reasonably well resolved for four of these orders, but not for the Scrophulariales plus Lamiales and Asterales sens. lat. Interordinal relationships remain poorly resolved. (2) The Apiales, included here in the Asteridae sens. lat., may be the sister group to the Dipsacales. Members of Hydrangeaceae, Cornaceae, and Loasaceae emerge as closely allied and also fall within the Asteridae sens. lat. Consequently, the Asteridae as traditionally circumscribed do not form a monophyletic group. (3) The Caprifoliaceae, in any traditional sense, cannot be monophyletic. *Viburnum* and *Sambucus* emerge as a distinct clade, well separated from the four other genera of Caprifoliaceae examined. Dipsacaceae and Valerianaceae arise from within the Caprifoliceae sens. str., with *Kolkwitzia* as a sister group to Valerianaceae. The Caprifoliaceae are, at best, paraphyletic. (4) Some light is shed on the placement of several problematic taxa. Menyanthaceae are placed in the Asterales sens. lat., Buddlejaceae and Callitrichaceae are placed within the Scrophulariales plus Lamiales, *Nolana* is placed within the Solanaceae, and the Rubiaceae are allied to the Gentianales. (5) Asclepiadaceae are derived from Apocynaceae.

Of the 25 families for which more than one species was examined (Table 1), ten (Acanthaceae, Apocynaceae sens. lat., Araliaceae, Asclepiadaceae, Calyceraceae, Convolvulaceae, Dipsacaceae, Myoporaceae, Polemoniaceae, and Solanaceae) constitute monophyletic groups; two (Caprifoliaceae sens. lat. and Cornaceae) may be polyphyletic; two may be paraphyletic (Apocynaceae and Caprifoliaceae sens. str.); and 12 are unresolved with the data at hand.

The results presented here are generally consistent with traditional morphological groupings and are highly congruent with a phylogenetic analysis of *rbc*L sequence data (Olmstead et al., 1992). The lack of resolution in many portions of the consensus tree is primarily due to an insufficient number of characters rather than conflict among characters, for many of the branches are supported by only one character change (Fig. 3). Future analyses should therefore benefit from the use of additional restriction enzymes to increase the number of restriction sites sampled. With more characters, measures of statistical evaluation (e.g., bootstrap sampling) can be applied. Other problematic families, such as the Plantaginaceae, Lentibulariaceae, and Retziaceae, can be included in further analyses.

Phylogenetic relationships based on these molecular data should help to assess the relative importance of traditional characters (e.g., morphological, phytochemical, embryological) currently used in circumscribing orders and families in the Asteridae. The occurrence of unexpected relationships suggests that a reevaluation of characters is in order, particularly in the taxa heretofore included in the Rosidae and Dilleniidae. In the future, the approach presented here should complement DNA sequencing and structural rearrangement studies in elucidating relationships at higher taxonomic levels.

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SYSTEMATIC IMPLICATIONS OF THE DISTRIBUTION OF IRIDOIDS AND OTHER CHEMICAL COMPOUNDS IN THE LOGANIACEAE AND OTHER FAMILIES OF THE ASTERIDAE[1]

Søren Rosendal Jensen[2]

ABSTRACT

The distribution of the chemical compounds iridoids, anthraquinones, and verbascosides is demonstrated in Dahlgrenograms. An analysis of iridoid biosynthesis and structure allows distinction of two main groups of compounds. Thus, the biosynthetic *route I* gives rise to the seco-iridoids and their derivatives, and another (*route II*) to aucubin and similar decarboyxlated iridoid glucosides. Seco-iridoids from *route I* are widely distributed in Cornanae, Loasanae, and Gentiananae but never in Lamianae. Aucubinlike compounds derived by *route II* are commonly found in Lamianae and in three small families in Cornanae, but are not found in Gentiananae. Ericanae contain both groups, but not within the same order. Likewise, two biosynthetically different groups of anthraquinones can be distinguished, one of which is found solely in Gentiananae and in Lamianae, and thus suggests the monophyletic origin of these taxa. The distribution of the verbascosides, a group of caffeic acid esters, and cornoside, a compound that is often vicarious for iridoids, is shown to be limited to Lamianae and Oleaceae (Gentiananae), barring a few exceptions. This, together with other evidence, may suggest that Oleaceae systematically belong close to Scrophulariaceae, despite the presence of seco-iridoids in Oleaceae. The results of an investigation of the family Loganiaceae, as delineated recently by Leeuwenberg, are presented and analyzed in light of the above distributional patterns. The chemical data, combined with a few morphological characters, reveal that the tribes Spigelieae, Loganieae, Strychneae, Gelsemieae, and Antonieae show many similarities and are characterized by containing seco-iridoids (biosynthetic *route I*), by having intraxylary phloem and nuclear endosperm formation, and by lacking verbascosides. The tribe Potalieae share this set of characters, but because of the presence of a unique combination of compounds, elsewhere only found in Gentianaceae, it may fit better in that family. The tribes Plocospermeae, Buddlejeae, and Retzieae, as well as the genus *Polypremum* from Spigelieae, do not belong in the Gentianaceae, because they are all different in the above set of characters. Chemically (and morphologically), they are more closely related to Scrophulariaceae and its allies or, alternatively, Oleaceae. Our studies have revealed nothing conclusive about tribe Desfontainieae.

Chemical characters have been used extensively in only one of the comprehensive angiosperm systems (R. Dahlgren, 1974, 1975a, 1980; G. Dahlgren, 1989). In this classification scheme, data on the distribution of secondary chemical compounds are incorporated in a rational way. Additionally, Dahlgren continued to construct detailed graphical representations of his system, a feature making it more comprehensible for nonspecialists as well as providing a demonstration of the distribution of characters. Such representations have been coined Dahlgrenograms by Mølgård (1985).

Hegnauer, in his *Chemotaxonomie der Pflanzen* (1962–1990), was among the first to realize the full potential of secondary compounds in systematic botany, but he also saw that the main difficulty was the lack of sufficient information. Only a small proportion of the known plants have been investigated chemically, and large gaps in the knowledge of the distribution of secondary compounds are still evident, making the use of them difficult. However, some types of compounds have been fairly comprehensively investigated; the distributions of some are presented in Dahlgrenograms (Dahlgren et al., 1981).

Another difficulty is deciding whether a chemical

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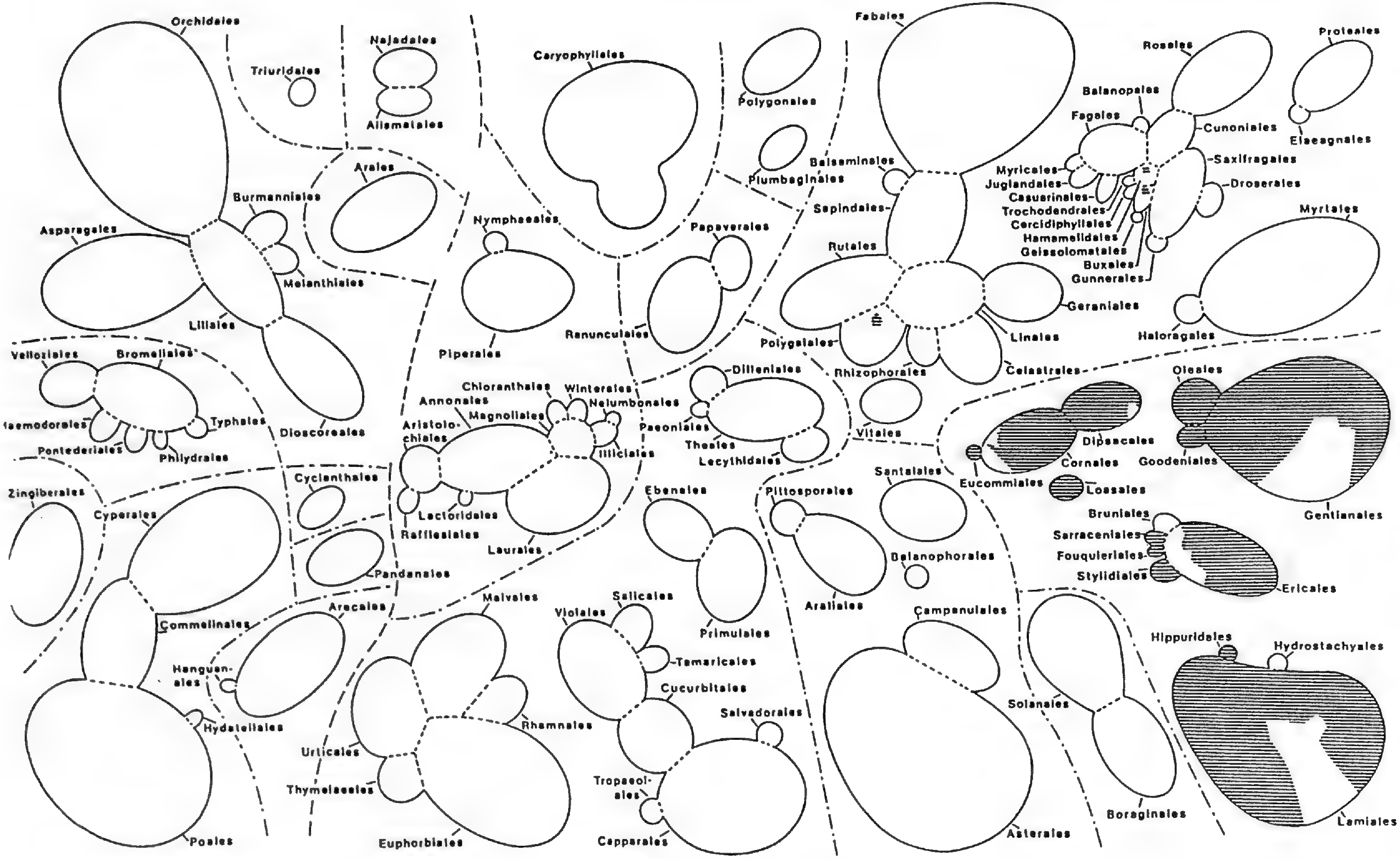


FIGURE 1. Distribution of iridoid compounds (hatched) illustrated in the last Dahlgrenogram (G. Dahlgren, 1989).

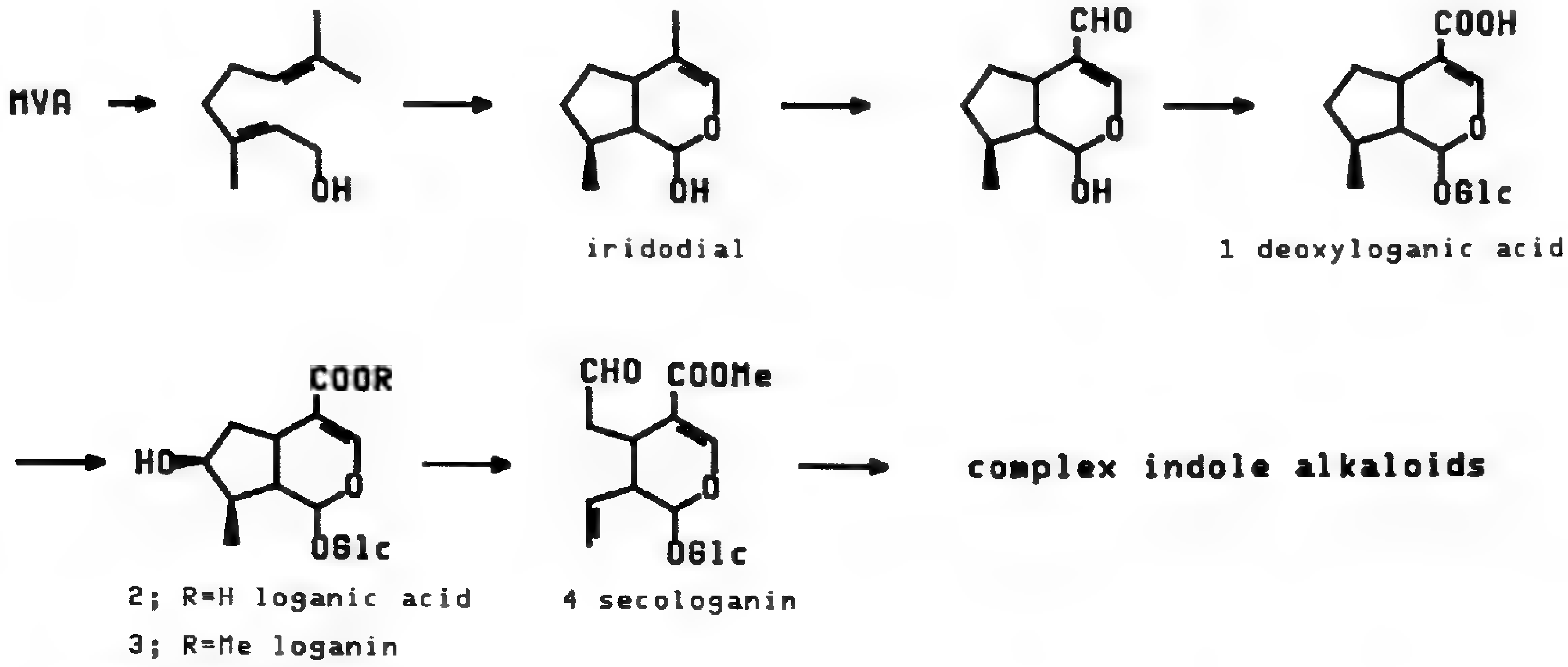


FIGURE 2. Biosynthetic *route I* via iridodial and deoxyloganic acid (1) leading mainly to seco-iridoids and complex indole alkaloids (CIA).

character is systematically relevant. Not only must a number of plants within the families and orders be explored, but also the compounds within a group must be biochemically related and show some structural variation (Gottlieb, 1982). Finally, correlation with other characters is necessary before using the chemical character—a fact that many phytochemists are not aware of.

In the following, I will apply Dahlgrenograms to show the distribution of some chemical characters and demonstrate how they may be used to shed new light on problems of systematic nature within the Asteridae. We have for some years worked on the chemotaxonomy of Loganiaceae in my laboratory. I will present the results and an analysis of them in light of the above chemical evidence combined with a few morphological characters.

I. CHEMICAL CHARACTERS

Dahlgren's system was developed partly in cooperation with me and my colleague Bent J. Nielsen. He put great weight on the iridoids as characters because they showed a surprisingly strong correlation with embryological data (Dahlgren, 1975b). Therefore, it is not strange that the iridoid-containing families appear as a cluster in the system (Fig. 1). Some of the more controversial decisions were the inclusion of Ericales and Loasales as part of the Asteridae. Ericales are usually included in Dilleniidae and Loasaceae often in Violales, although Takhtajan (1980) considered them part of his Lamianae. Traditionally, the Sarraceniaceae have been placed close to Papaveraceae, but Dahlgren (1974) initially placed them in his Cornales, mainly because of the embryology. Only later did we find that iridoids were present (Jensen et al., 1975b).

Recently, with more biosynthetic data available, we have found that at least two distinctive biosynthetic pathways can be tentatively discerned (Jensen, 1991). One group of compounds, including the seco-iridoids and the complex indole alkaloids (CIAs), is derived from iridodial (*route I*; Fig. 2). The other group may be considered more advanced and is biosynthetically formed through epi-iridodial (*route II*; Fig. 3). Only a limited amount of bio-

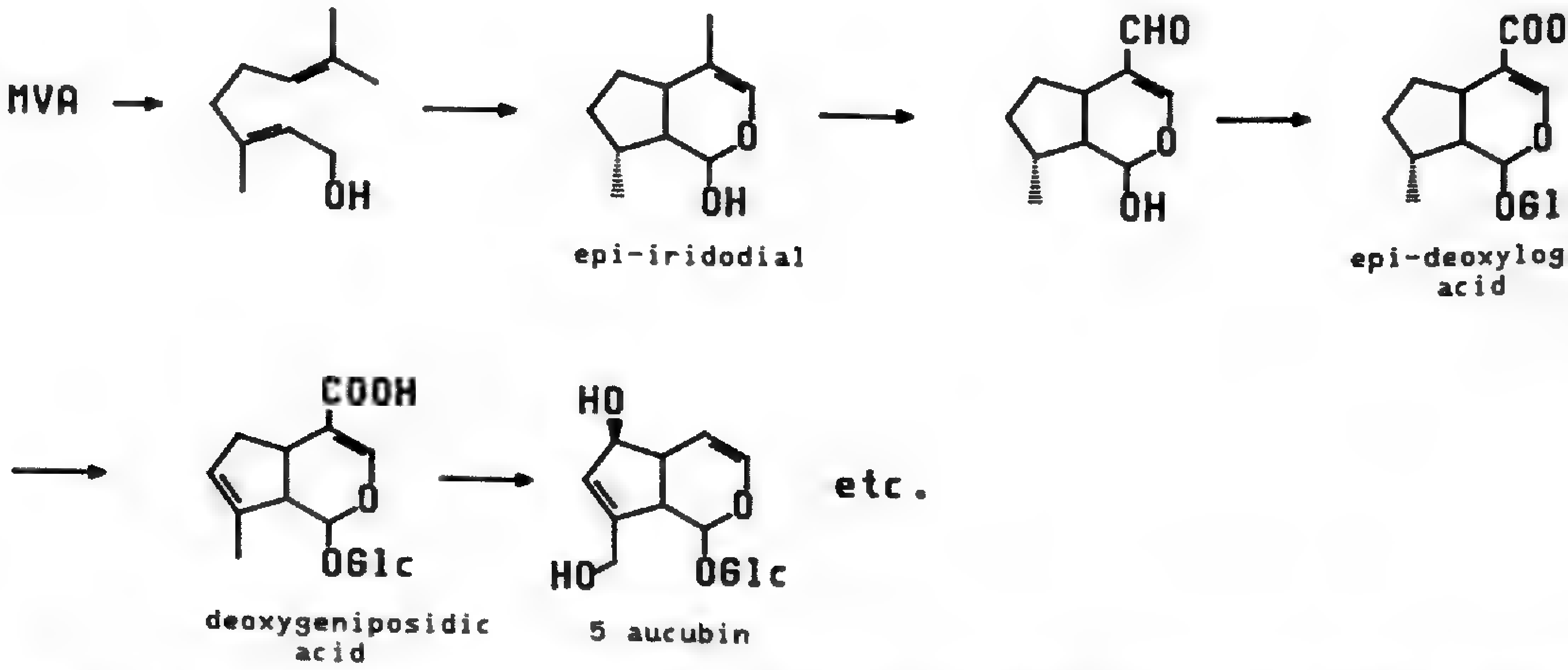


FIGURE 3. Biosynthetic *route II* via epi-iridodial and epi-deoxy-loganic acid leading mainly to aucubin and similar decarboxylated compounds.

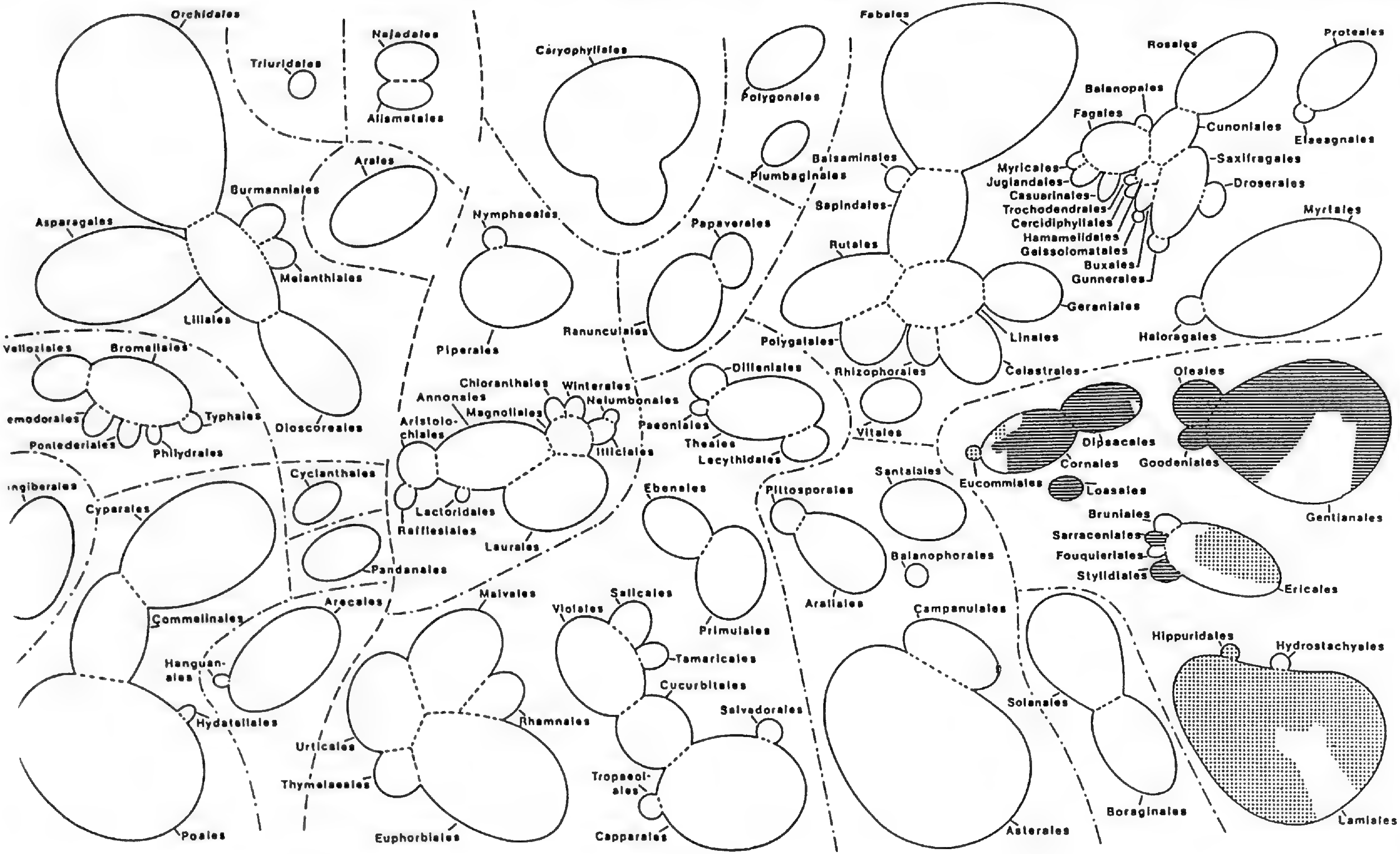


FIGURE 4. Families with seco-iridoids (*route I*—hatched) and with decarboxylated iridoids (*route II*—dotted).

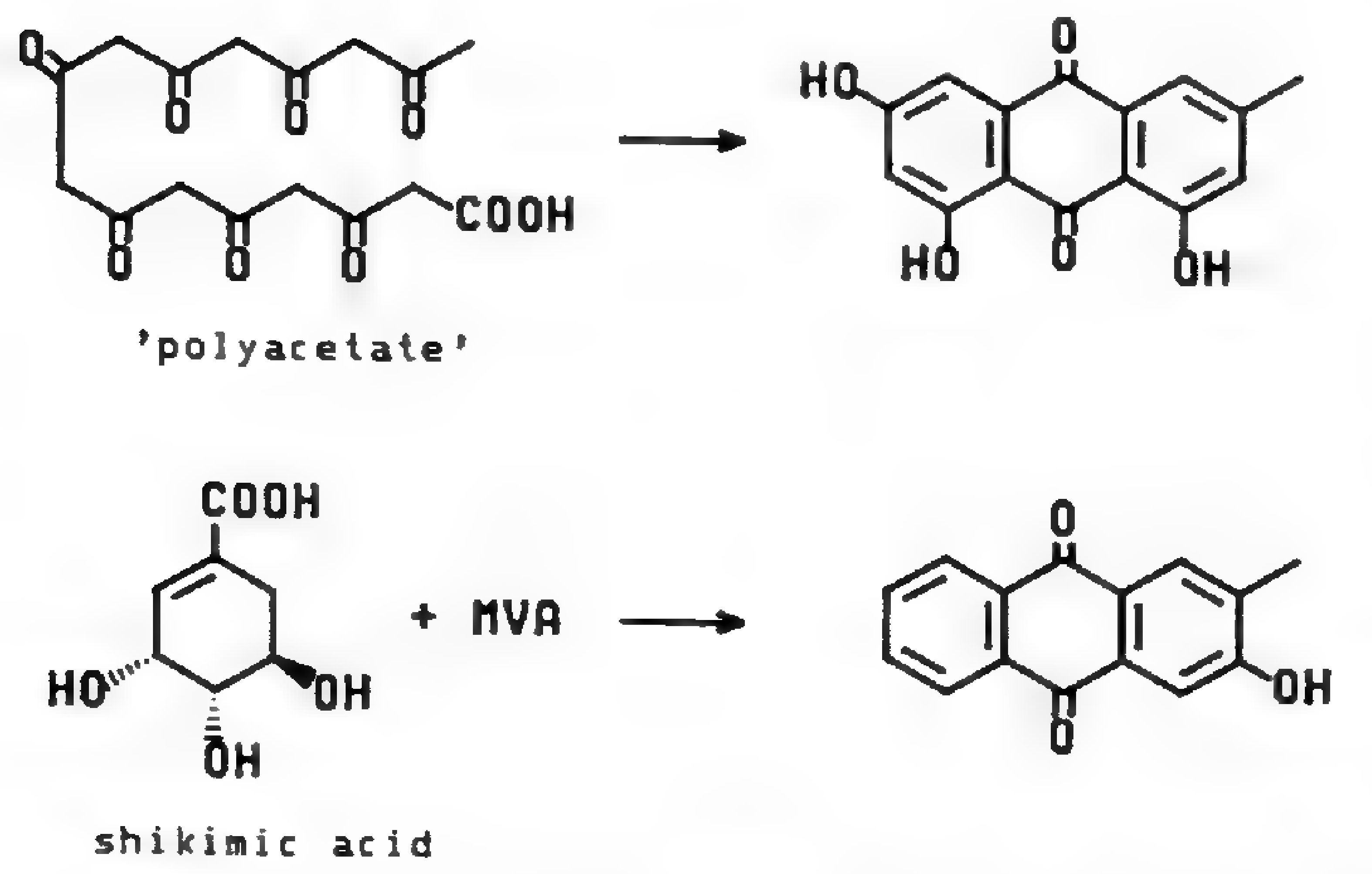


FIGURE 5. The two biosynthetic pathways starting with either "polyacetate" (acet) or shikimic acid (shik) and leading to anthraquinones.

synthetic work has been performed so far, so the above routes are mainly recognized by their products—i.e., the compounds found in the plants. This causes problems with regard to some compounds that can be formed by more than one biosynthetic pathway. Thus, geniposidic acid has been shown to be formed by different routes in *Galium*, *Gardenia*, and *Plantago*, where in each case it is a precursor for other iridoids. However, this problem can usually be overcome by taking accompanying compounds into account (for a detailed discussion, see Jensen, 1991).

The distribution of the two groups of compounds is shown in Figure 4. Note that Dahlgren's system was constructed before we had enough biosynthetic information to make the distinction between the two groups. It is evident from the figure that *route I* is the main pathway in Cornanae, Loasanae, and Gentiananae, with a few scattered occurrences in Ericanae (namely in Stylidiaceae and Sarreniaceae, but perhaps neither belong here). *Route II*, on the other hand, is consistently found in Lamianae except in Lamiaceae–Saturejoideae and Gesneriaceae, where iridoids apparently are lacking. It is found in Cornanae in the monogeneric families Aucubaceae and Garryaceae, as well as in the monotypic family Eucommiaceae (Eucommiales). Finally, compounds apparently belonging to *route II* are also found in Ericaceae (Ericales) and a few closely related families.

This distributional pattern might indicate that the two main groups of taxa characterized by iridoids are not a monophyletic entity. However, based on the chemical evidence, we have demonstrated earlier that information from the distribution of anthraquinones is in agreement with an essentially monophyletic origin of the iridoid-containing taxa (Dahlgren et al., 1981). Anthraquinones are widely scattered in fungi and angiosperms. However, if we take biosynthesis into account, two different main pathways have been demonstrated, and the origin of the compounds is usually easy to see from the oxidation pattern (Fig. 5). In one pathway used by fungi and many angiosperms, anthraquinones are formed by condensation of acetate units to give compounds with the characteristic oxidation pattern seen in Figure 5. The compounds from the alternative pathway are formed by a more complex route, which includes shikimic acid and a terpenoid unit. The oxidation pattern in this case is unpredictable, but apparently usually different from the one above.

An inventory of the two types is listed in Table 1, and the distribution is shown in the next Dahlgrenogram (Fig. 6) together with the iridoids, demonstrating that the advanced pathway is almost solely found in Gentiananae (many genera in Rubiaceae) and Lamianae (some genera in Scrophulariaceae and Bignoniaceae as well as a few finds in Acanthaceae, Gesneriaceae, and Verbenaceae). The normal pathway is much more scattered over the system but is most abundant in Fabales, Polygonales, and Liliales. A possible interpretation of the distribution pattern is that the normal pathway, which is also commonly found in fungi, is either an archaic character, or alternatively, that it is fairly easy to develop *de novo* from readily accessible precursors in the primary metabolism. The advanced pathway is biosynthetically much more complicated and is less likely to have developed several times.

Another type of compound that shows an interesting distribution is caffeic acid, which in plants is usually found in the form of esters (Fig. 7). This character has been investigated extensively by Bate-Smith (1962), who worked with hydrolyzed extracts of plants. Recently, Mølgård (1985) and Mølgård & Ravn (1988) have presented the distribution of such compounds in Dahlgrenograms. The most common ester of caffeic acid is chlorogenic acid, a compound that is widely distributed in the sympetalous families. A less common group of esters of caffeic acid is verbacoside and its homologues, which have a much more limited distribution. I am here introducing the term "verbascosides" for the whole group of compounds. (Harborne (1966), who first demonstrated the taxonomic possibilities, used the name orobanchoside, while Hegnauer (1990, vol. 9: 8) has used the term "verbascosid-ähnliche" for this group of compounds.) In Table 2, I have listed the reported findings of this group of compounds together with some recent (unpublished) results from my own laboratory. Negative results are difficult to deter-

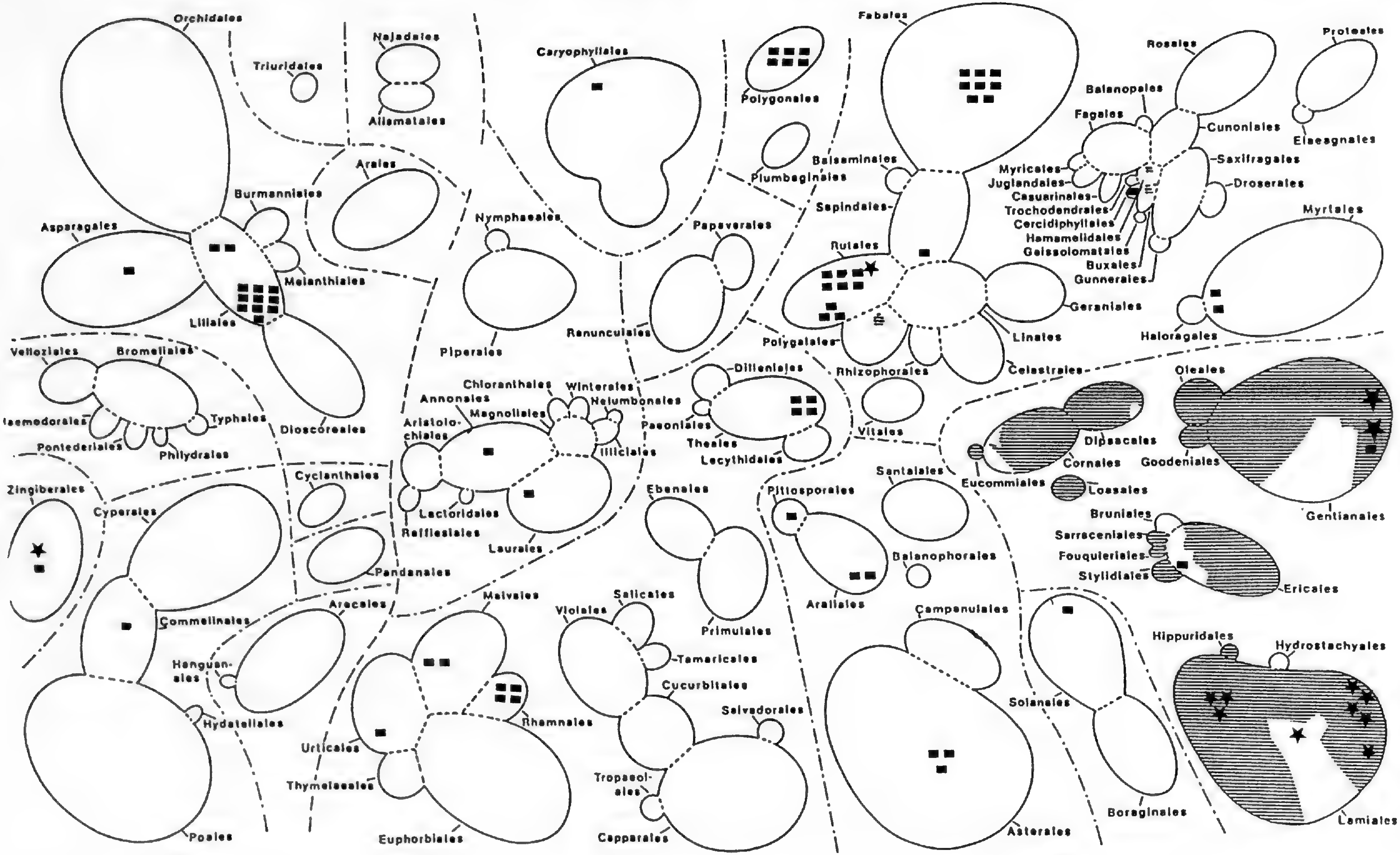


FIGURE 6. Distribution of the two types of anthraquinones. Rectangles: acetate-derived. Stars: shikimic acid-derived. Hatched areas same as for Figure 1.

TABLE 1. Occurrence of Anthraquinones in Angiospermae. (shik = derived from shikimic acid; acet = polyacetate-derived.)

Family	Genus (number)	Type	Reference
Acanthaceae	*Barleria* (1)	shik	Thomson (1987)
Actinidiaceae	*Actinidia* (1)	acet	Zheng & Liang (1985)
Agavaceae	*Phormium* (1)	acet	Harvey & Waring (1987)
Anacardiaceae	*Lannea* (1)	acet	Thomson (1987)
Annonaceae	*Annona* (1)	acet	Wu et al. (1987)
Apiaceae	*Bupleurum* (1)	acet	Choi & Woo (1989)
	Heracleum (1)	acet	Khetwal et al. (1987)
Asteraceae	*Eupatorium* (1)	acet	Talapatra et al. (1985)
	Haplopappus (1)	acet	Thomson (1971)
	Saussurea (1)	acet	Thomson (1987)
Bignoniaceae	*Catalpa* (1)	shik	Thomson (1987)
	Markhamia (1)	shik	Thomson (1987)
	Tabebuia (2)	shik	Thomson (1971)
	Tecomella (1)	shik	Thomson (1987)
Commeliaceae	*Terminalia* (1)	acet	Thomson (1971)
Chenopodiaceae	*Salsola* (3)	acet	Thomson (1987)
Dipterocarpaceae	*Shorea* (?)	acet	Thomson (1987)
	Vatica (1)	acet	Thomson (1987)
Eupteleaceae	*Clutyia* (1)	acet	Thomson (1971)
Fabaceae	*Abrus* (1)	acet	Thomson (1987)
	Cajanus (1)	acet	Thomson (1987)
	Cassia (9)	acet	Thomson (1987)
	Derris (1)	acet	Thomson (1987)
	Desmodium (1)	acet	Thomson (1987)
	Melanoxylon (1)	acet	Thomson (1987)
	Vatairea (2)	acet	Thomson (1971)
	Vataireopsis (1)	acet	Thomson (1971)
Gesneriaceae	*Streptocarpus* (1)	shik	Thomson (1987)
Hernandiaceae	*Illigera* (1)	acet	Yuan et al. (1987)
Hypericaceae	*Harungana* (1)	acet	Thomson (1987)
	Hypericum (sev)	acet	Thomson (1971)
	Psorospermum (3)	acet	Thomson (1987)
	Vismia (6)	acet	Thomson (1987)
Iridaceae	*Gladiolus* (1)	acet	Ali et al. (1989)
	Libertia (2)	acet	Thomson (1971)
Liliaceae	*Aloe* (sev)	acet	Thomson (1987)
	Asphodeline (1)	acet	Thomson (1971)
	Asphodelus (2)	acet	Thomson (1987)
	Bulbine (2)	acet	Thomson (1971)
	Eremurus (3)	acet	Thomson (1971)
	Hemerocallis (1)	acet	Thomson (1987)
	Kniphofia (1)	acet	Thomson (1987)
	Lomandra (1)	acet	Thomson (1987)
	Ruscus (1)	acet	Thomson (1987)
	Simethis (1)	acet	Thomson (1971)
	Xanthorrhorea (1)	acet	Thomson (1987)
Lythraceae	*Wodfordia* (1)	acet	Thomson (1987)
Pittosporaceae	*Pittosporum* (1)	acet	Lin & Wang (1987)
Polygonaceae	*Antigonon* (1)	acet	Thomson (1987)
	Fagopyrum (1)	acet	Thomson (1971)
	Muelenbeckia (1)	acet	Thomson (1971)
	Polygonum (sev)	acet	Thomson (1987)
	Rheum (2)	acet	Thomson (1987)
	Rumex (2)	acet	Thomson (1987)
Rhamnaceae	*Karwinskia* (1)	acet	Thomson (1987)
	Maesopsis (1)	acet	Thomson (1971)

TABLE 1. Continued.

Family	Genus (number)	Type	Reference
	Rhamnus (6)	acet	Thomson (1987)
	Ventilago (3)	acet	Thomson (1987)
Rubiaceae	*Asperula* (1)	acet	Thomson (1971)
	Cinchona (2)	shik	Thomson (1987)
	Coelospermum (2)	shik	Thomson (1971)
	Commitheca (1)	shik	Thomson (1987)
	Coprosma (5)	shik	Thomson (1987)
	Crucianella (1)	shik	Thomson (1971)
	Damnacanthus (1)	shik	Thomson (1971)
	Danais (1)	shik	Thomson (1987)
	Galium (4)	shik	Thomson (1987)
	Hedyotis (2)	shik	Thomson (1987)
	Hymenodictyon (1)	shik	Thomson (1971)
	Knoxia (1)	shik	Thomson (1987)
	Lasianthus (1)	shik	Thomson (1971)
	Morinda (6)	shik	Thomson (1987)
	Oldenlandia (1)	shik	Thomson (1971)
	Plocama (1)	shik	Thomson (1987)
	Prismatomeris (2)	shik	Thomson (1987)
	Putoria (1)	shik	Thomson (1987)
	Relbunium (1)	shik	Thomson (1987)
	Rubia (4)	shik	Thomson (1987)
	Sherardia (1)	shik	Thomson (1971)
Rutaceae	*Clausena* (1)	shik (?)	Thomson (1987)
	Evodia (1)	acet	Thomson (1987)
	Limonia (1)	acet	Musa & Zarga (1986)
	Peganum (1)	acet	Pitre & Srivastava (1987)
	Ruta (1)	acet	Thomson (1987)
	Zanthoxylum (1)	acet	Thomson (1987)
Scrophulariaceae	*Digitalis* (6)	shik	Thomson (1987)
	Isoplexis (1)	shik	Thomson (1987)
	Scrophularia (1)	shik	Thomson (1987)
Simarubaceae	*Alvaradoa* (1)	acet	Thomson (1987)
	Brucea (1)	acet	Yu et al. (1988)
	Picramnia (2)	acet	Thomson (1987)
Solanaceae	*Fabiana* (1)	acet	Thomson (1987)
Sonneratiaceae	*Sonneratia* (1)	acet	Thomson (1971)
Urticaceae	*Boehmeria* (1)	acet	Thomson (1987)
Verbenaceae	*Tectona* (1)	shik	Thomson (1987)
Zingiberaceae	*Aframomum* (1)	acet	Thomson (1987)
	Curcuma (1)	shik	Ogbeide et al. (1985)

mine, since they are usually not reported, but those from our own limited investigation have been included.

The distribution of the verbascosides is shown in Figure 8 together with the iridoids. It is evident that a good correlation with the iridoids of *route II* is found, since the verbascosides are widespread in Lamianae. The only occurrences outside this order are in a single genus of Asteraceae (*Echinacea*), where iridoids have never been found, and in the species *Cassinopsis madagascariensis* from Icacinaceae (Cornales), a family reported to contain iridoids of *route I* only. Verbascosides are also common in Oleaceae (Oleales), a member of Gentiananae, and this is a family that also contains seco-iridoids. I have no explanation for the unexpected finding in Asteraceae, but the two latter exceptions deserve comment. First, we have investigated (Table 2) several members of the Cornales including *Aucuba japonica* and one species of *Garrya*, the two sole sources in the order containing the iridoid aucubin (probably of *route II* origin) and none of these contain verbascosides. However, since proto-Cornalian stock perhaps developed the ability to biosynthesize iridoids of *route II* and verbascosides, and might be imagined to

TABLE 2. Occurrence of verbascosides in Angiospermae.

Family	Genus (number)	Reference
Acanthaceae	*Acanthus* (1)	Mølgård & Ravn (1988)
	Asystasia (1)	Harborne (1966)
	Hygrophila (1)	Henry et al. (1987)
	Pseuderanthemum (1)	Harborne (1966)
	Strobilanthes (1)	Soediro et al. (1983)
Asteraceae	*Echinacea* (3)	Mølgård & Ravn (1988)
Bignoniaceae	*Campsis* (1)	Imakura et al. (1985)
	Catalpa (1)	Harborne (1966)
	Deplanchea (1)	
	Eccremocarpus (1)	Harborne (1966)
	Jacaranda (1)	Gambaro et al. (1988)
	Mussatia (2)	Jimenez et al. (1989)
	Pandorea (1)	Harborne (1966)
	Pawlownia (1)	Mølgård & Ravn (1988)
Buddlejaceae	*Buddleja* (2)	Mølgård & Ravn (1988); Houghton & Hikino (1989)
	Emorya (1)	this work
	Gomphostigma (1)	this work
Callitrichaceae	*Callitriche* (1)	this work
Gesneriaceae	*Conandron* (1)	Mølgård & Ravn (1988)
	Nautilocalyx (1)	this work
	many genera	Harborne (1966); Kvist & Pedersen (1986)
Globulariaceae	*Globularia* (1)	Harborne (1966); this work
	Lytanthus (1)	Harborne (1966)
Hippuridaceae	*Hippuris* (1)	this work
Icacinaceae	*Cassinopsis* (1)	Rasoanaivo et al. (1990)
Lamiaceae	*Ajuga* (3)	Mølgård & Ravn (1988)
	Galeopsis (1)	Mølgård & Ravn (1988)
	Leucoseptrum (1)	Miyase et al. (1982)
	Phlomis (1)	Calis et al. (1990)
	Stachys (3)	Mølgård & Ravn (1988)
	Teucrium (3)	Mølgård & Ravn (1988)
Loganiaceae (?)	*Polypremum* (1)	this work
Martyniaceae	*Martynia* (1)	Mølgård & Ravn (1988)
Myoporaceae	*Eremophila* (6)	Dell et al. (1989)
Oleaceae	*Forsythia* (3)	Kitagawa et al. (1988)
	Olea (1)	Amiot et al. (1986)
	Osmanthus (2)	Kikuchi & Yamauchi (1985)
	Syringa (2)	Kikuchi et al. (1987)
Orobanchaceae	*Cistanche* (2)	Mølgård & Ravn (1988); Yoshizawa et al. (1990)
	Orobanche (2)	Mølgård & Ravn (1988)
Pedaliaceae	*Harpagophytum* (1)	Burger et al. (1987)
	Sesamum (1)	Potterat et al. (1988)
Plantaginaceae	*Plantago* (3)	Mølgård & Ravn (1988)
Plocospermaceae	*Plocosperma* (1)	this work
Retziaceae	*Retzia* (1)	this work
Scrophulariaceae	*Calceolaria* (2)	Nicoletti et al. (1988)
	Castilleja (2)	Gardner et al. (1987)
	Digitalis (2)	Baudouin et al. (1988)
	Eufrasia (1)	Mølgård & Ravn (1988)
	Halleria (1)	Abdullahi et al. (1986)
	Lamourouxia (1)	Jiménez et al. (1988)
	Monochasma (1)	Yahara et al. (1986)
	Pedicularis (1)	this work
	Penstemon (3)	Teborg & Junior (1989)
	Phteirospermum (1)	Takeda (1988)
	Rehmannia (1)	Mølgård & Ravn (1988)

TABLE 2. Continued.

Family	Genus (number)	Reference
	Scrophularia (1)	Mølgård & Ravn (1988)
	Verbascum (6)	Mølgård & Ravn (1988)
	Veronica (2)	Mølgård & Ravn (1988)
Stilbaceae	*Stilbe* (1)	this work
	Eurylobium (1)	this work
	Campylostachys (1)	this work
Verbenaceae	*Verbena* (1)	Mølgård & Ravn (1988)
	Clerodendron (4)	Mølgård & Ravn (1988)
	Lantana (1)	Harborne (1966); this work
	Lippia (1)	Chanh & Koffi (1988)
	Petrea (1)	Garnier et al. (1989)

Species found to be without verbascosides in the present work: Cornanae: *Aucuba japonica*; *Cornus controversa*; *Davidia involucrata*; *Eucommia ulmoides*; *Garrya elliptica*; *Dipsacus sylvestris*; *Morina longifolia*. Gentiananae: *Nerium oleander*; *Rubia peregrina*; *Gardenia jasminoides*; *Theligonum cynocrambe*. Ericanae: *Azalea* sp.; *Rhododendron* (6 spp.); *Mentziesia pilosa*; *Vaccinium* sp.; *Actinidia chinensis*; *Sarracenia* sp. Lamianae: *Lamium album*.

constitute the phylogenetic origin of both Lamianae and Gentiananae, it is perhaps not surprising that a few extant members of Cornales may retain this ability—even if it has been lost by the majority of present-day taxa. Second, the position of Oleaceae in Gentiananae in Dahlgren's system is perhaps one of the more problematic, and most other botanists consider them more closely related to Scrophulariaceae (Lamianae). Recent molecular data (*rbc*L-sequences (Olmstead et al., 1992) and restriction site mapping of the chloroplast (Downie & Palmer, 1992) presented at this symposium) seem to agree with such a view. It may have been the presence of seco-iridoids, which never occur in Lamianae, that was decisive for Dahlgren's removal of Oleaceae from this superorder. However, the type of seco-iridoids in Oleaceae is unique when compared to those found in other seco-iridoid-containing taxa. Furthermore, the biosynthesis, which has not yet been fully investigated, may prove to be different from that found for other seco-iridoids. Thus, the presence of seco-iridoids alone may not be justification for keeping Oleaceae in Gentiananae.

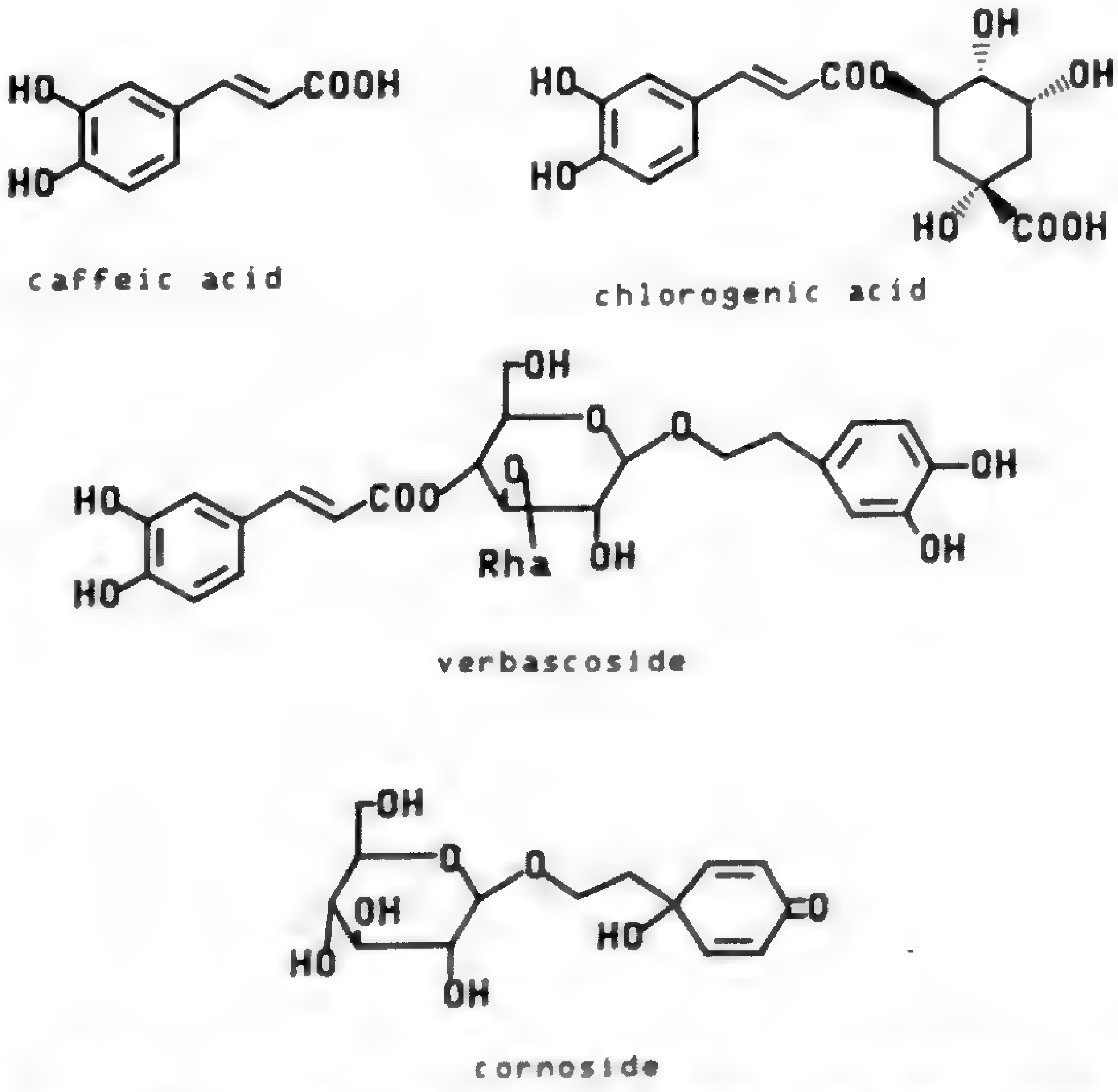
The compound cornoside (Fig. 7), first described by Jensen et al. (1973), has an even more limited distribution, but it seems to some degree to co-occur with the verbascosides. A peculiarity of this compound is that it is often vicarious for iridoids, i.e., it occurs in plants where iridoids are absent but where they would otherwise have been expected. The occurrences of this compound are listed in Table 3 and the distribution shown together with that of the verbascosides in Figure 8. Again we find the center of distribution in Lamianae, but with an occurrence both in Cornales and in Oleales (several species each of *Cornus* and *Forsythia*, respectively).

II. CHEMOTAXONOMY OF THE LOGANIACEAE

INTRODUCTION

I present here the preliminary results of our recent work on the chemotaxonomy of Loganiaceae. The taxonomic conclusions are mainly made with reference to the above distribution patterns for iridoids and verbascosides.

Loganiaceae have recently been revised by Leeuwenberg (1980), and according to him consist



caffeic acid

chlorogenic acid

verbascoside

cornoside

FIGURE 7. Formulas of caffeic acid and its derivatives chlorogenic acid and verbascoside as well as of cornoside.

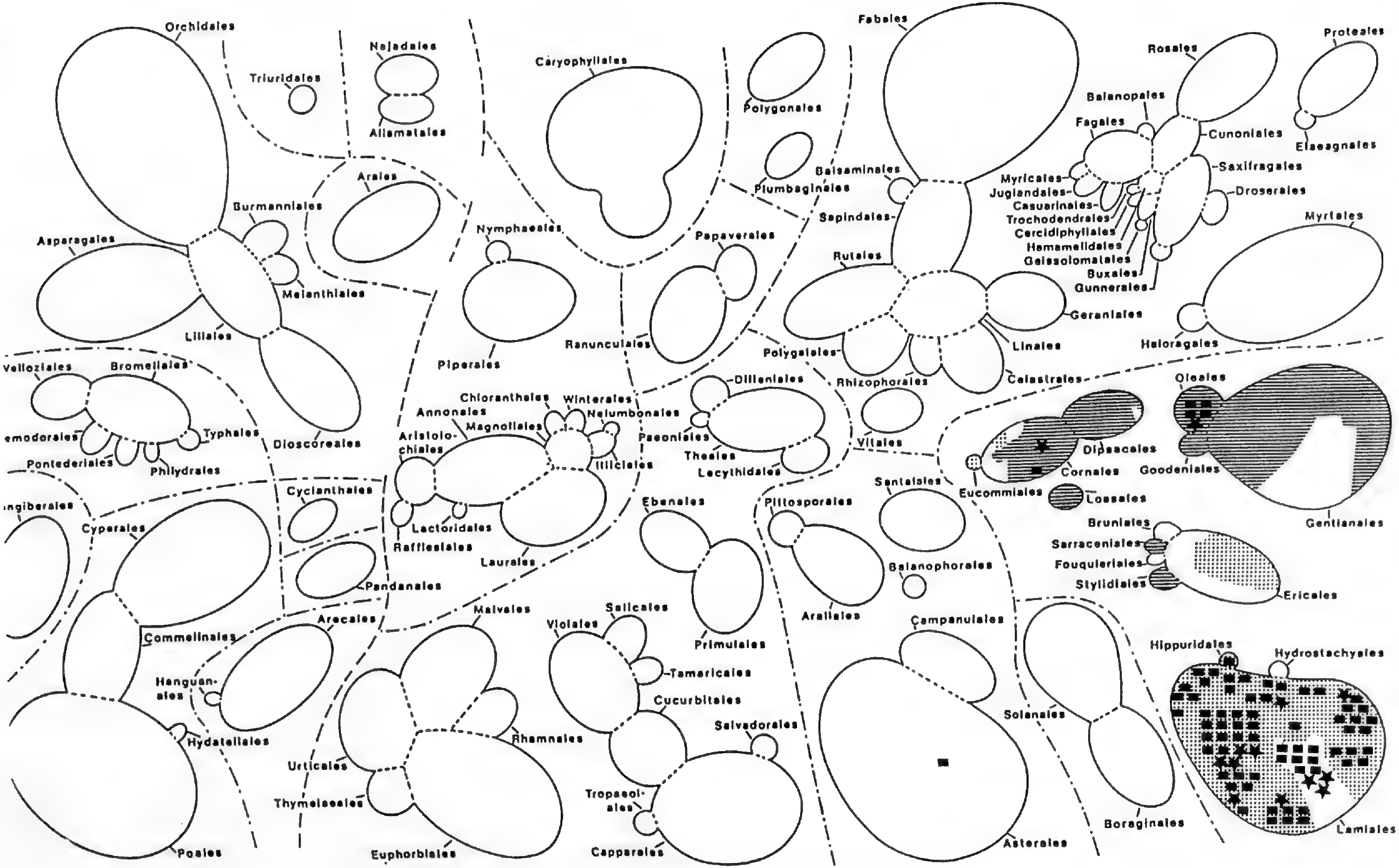


FIGURE 8. Distribution of verbascosides (rectangles) and of cornoside (stars). Hatched and dotted areas same as for Figure 4.

TABLE 3. Occurrence of Cornoside in Angiospermae.

Family	Genus (number)	Reference
Bignoniaceae	*Eccremocarpus* (1)	this work
Cornaceae	*Cornus* (sev)	Jensen et al. (1975a)
Gesneriaceae	several gen.	Jensen & Nielsen (unpublished)
Lamiaceae	*Teucrium* (1)	Bellakhdar et al. (1988)
Loganiaceae (?)	*Polypremum* (1)	this work
Oleaceae	*Forsythia* (sev)	Endo & Hikino (1984) Jensen & Nielsen (unpublished)
Martyniaceae	*Martynia* (1)	Sasaki et al. (1978)
Plocospermaceae	*Plocosperma* (1)	this work
Scrophulariaceae	*Calceolaria* (1)	Nicoletti et al. (1988)
	Digitalis (1)	Jensen et al. (1975b)
	Isoplexis (1)	Navarro et al. (1986)
	Halleria (1)	Messana et al. (1984)
Verbenaceae	*Phyla* (1)	Rimpler & Sauerbier (1986)

of approximately 470 species with 29 genera arranged in 10 tribes (i–x; Table 4). The circumscription of the family has been controversial because each of the ten tribes has been raised to family rank by various systematists. This subject has been treated in depth by Leeuwenberg & Leenhouts (1980).

In our investigation, we have had access to members of all tribes except tribe iii, Strychneae, which is otherwise well investigated chemically, and thus our results would be expected to be rather conclusive. Chemically, the members of the family have mainly been examined for alkaloids (Bisset, 1975), and much interest has been shown in the genera containing the complex indole alkaloids, namely tribes iii and v, Strychneae and Gelsemieae (Kisakürek & Hesse, 1980). Our main interest has been the water-soluble compounds from the plants, and we have investigated for the presence of low-molecular-weight glycosides. Because our own interest in the verbascosides is fairly recent, not all of the plants have been examined with regard to the caffeic acid esters. The results have been compiled in Table 5 with reference to the iridoids depicted in Figures 2, 3, 9, and 10. In the following, I will go through our results as well as earlier published work for each of the tribes and conclude with a discussion of the taxonomic consequences.

RESULTS

The tribes Spigelieae (i) and Loganieae (ii) consist of four and three genera, respectively; we have had access to at least one species of each. Except for reports that most of them were poor in alkaloids (Bisset, 1975), no other relevant chemical work has been published. From Table 5, it can be seen that the iridoids asperuloside, geniposide and geniposidic acid, closely related glucosides of *route I*, are present in most genera of these two tribes. However, *Spigelia* was devoid of systematically

TABLE 4. Tribes and genera in Loganiaceae sensu Leeuwenberg (1980).

Tribe	Genus
i. Spigelieae	*Polypremum* (1)
	Spigelia (50)
	Mitreola (6)
	Mitrasacme (40)
ii. Loganieae	*Geniostoma* (20)
	Labordia (20)
	Logania (15)
iii. Strychneae	*Strychnos* (190)
	Gardneria (5)
	Neuburgia (12)
iv. Plocospermeae	*Plocospermum* (1)
v. Gelsemieae	*Mostuea* (8)
	Gelsemium (3)
vi. Antonieae	*Bonyunia* (4)
	Antonia (1)
	Norrisia (2)
	Usteria (1)
vii. Buddlejeae	*Peltanthera* (1)
	Sanango (1)
	Nuxia (15)
	Androya (1)
	Gomphostigma (2)
	Buddleja (100)
	Emorya (1)
viii. Retzieae	*Retzia* (1)
ix. Potalieae	*Potalia* (1)
	Anthocleista (14)
	Fagraea (35)
x. Desfontainieae	*Desfontainia*

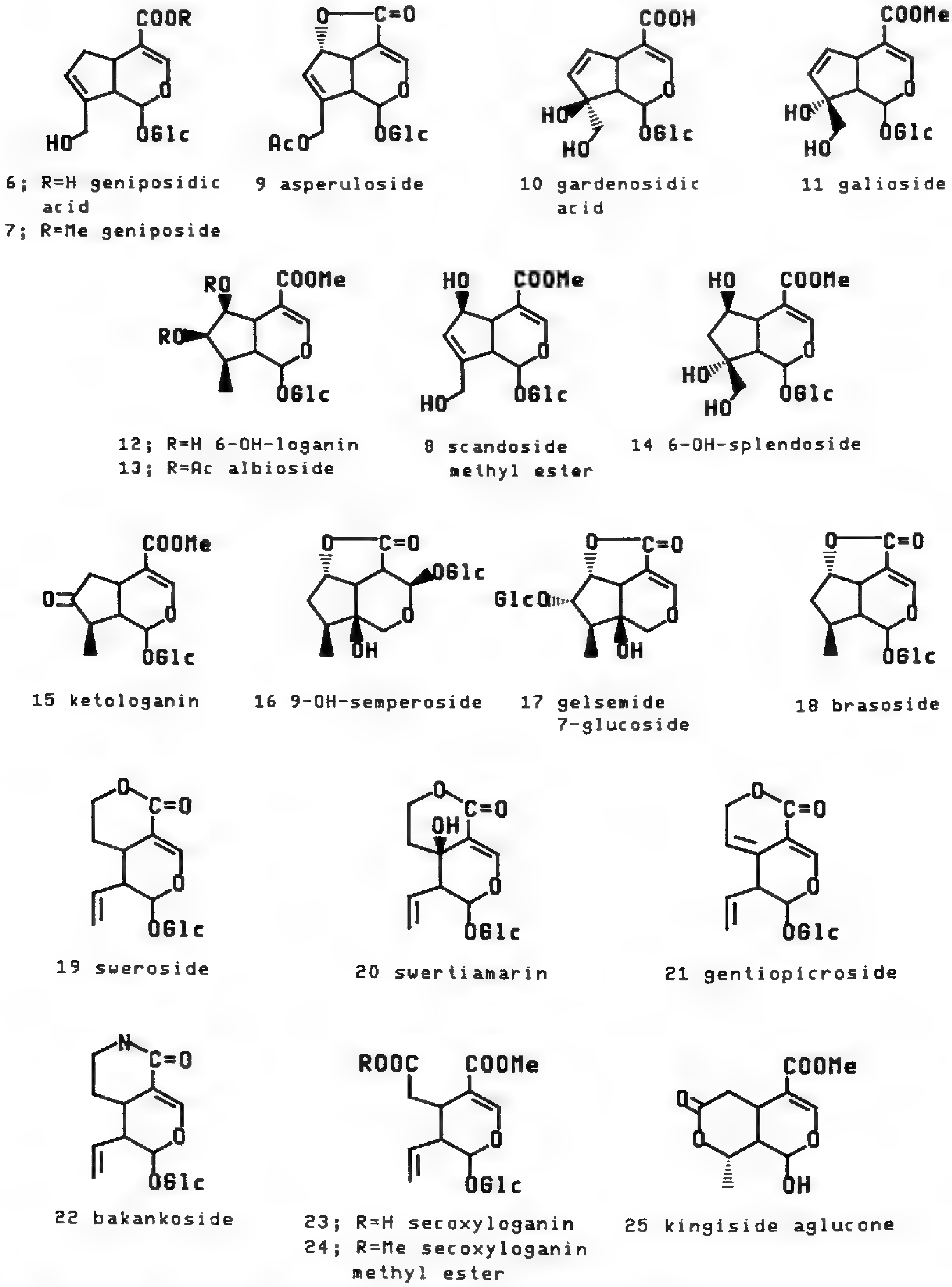


FIGURE 9. Iridoids presumably of *route I* isolated from Loganiaceae.

interesting compounds, while *Polypremum* contained both cornoside and a verbascoside-like compound.

Of the two tribes that are known to be rich in alkaloids, namely Strychneae (iii) and Gelsemieae (v), much chemical work has been done on the former, less on the latter. A number of complex indole alkaloids have been discovered from four of the five genera of the two tribes. From *Strychnos*, loganin and also some seco-iridoids, the precursors of the complex indole alkaloids, have been reported (Bisset, 1975, 1980a, b; Kisakürek & Hesse, 1980). In fact, one of the best known iridoids, loganin, was first isolated from seeds of *Strychnos nux-vomica* and was named after the family. We have investigated *Gelsemium sempervirens* and found it to contain a number of unusual iridoids (Jensen et al., 1987), which by their structure obviously belonged to *route I*, like the seco-iridoids and the complex indole alkaloids.

The chemistry of the monotypic tribe Plocospermeae (iv), with only *Plocospermum buxifolium*, has not been previously investigated. We were able to isolate cornoside as well as two compounds belonging to the verbascoside group. Furthermore, since it was not known whether intraxylary phloem (see below) was present in the plant, we asked Lise Bolt Jørgensen to investigate a sample of our material; she found that it was not present (unpublished).

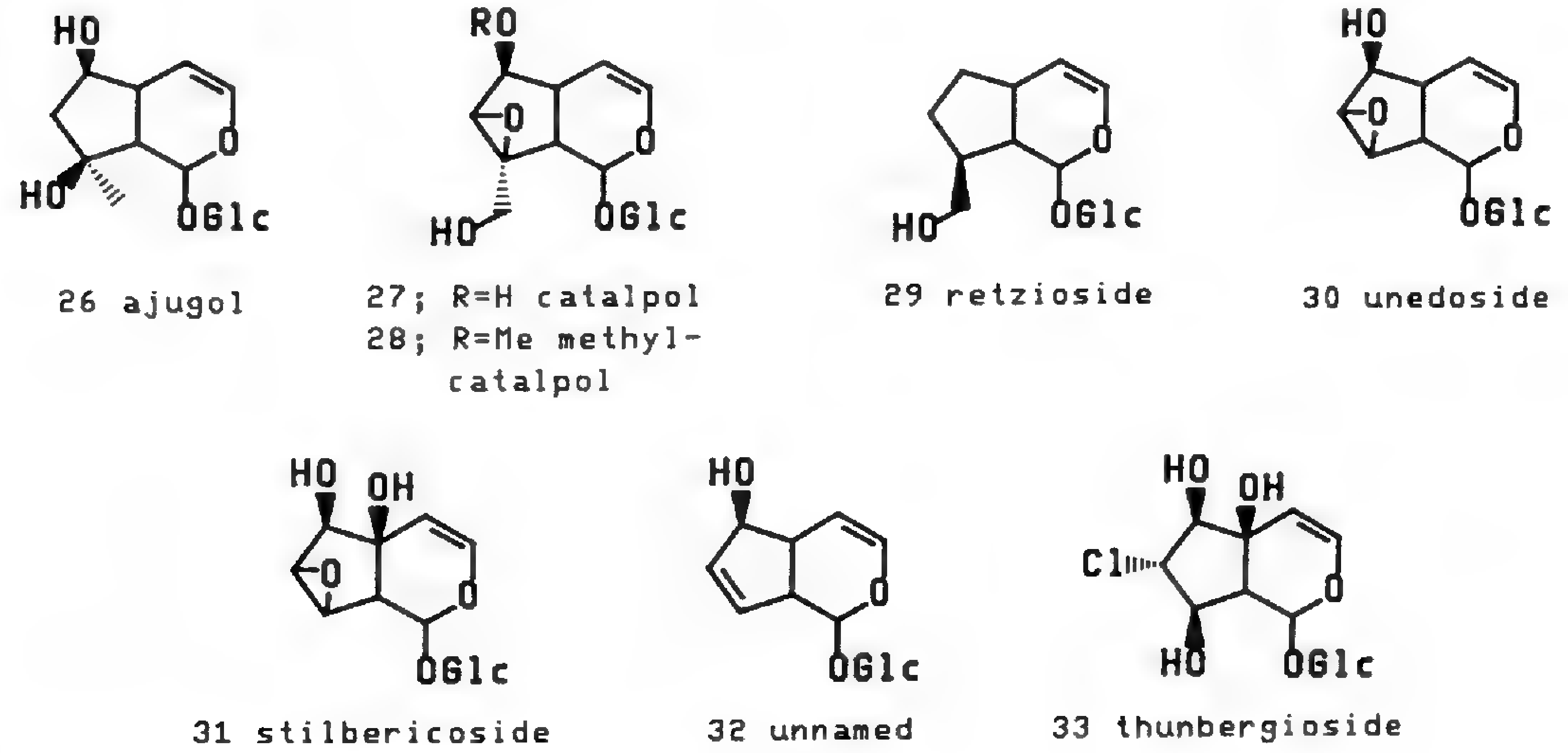


FIGURE 10. Iridoids of *route II* isolated from Loganiaceae.

Tribe Antonieae (vi) consists of four genera, of which we had access to three. Except for reports that alkaloids are absent (Bisset, 1975), no chemical work has been published about this tribe. We were unable to detect either iridoids or caffeic acid esters.

Buddlejeae (vii) is one of the largest tribes in the family. The presence of aucubin and related *route II* iridoids has been known from *Buddleja* for a long time (Duff et al., 1965; Hegnauer & Kooiman, 1978; Houghton & Hikino, 1989), while alkaloids appear to be scarce (Bisset, 1975). In the present study, we investigated representatives of three of the seven genera of Buddlejeae and found aucubin-like compounds, as well as verbascoside, in all species examined.

Retzieae (viii) is the second monotypic tribe in Loganiaceae. Three iridoid glucosides of *route II* have been reported from the sole species *Retzia capensis* (Dahlgren et al., 1979). In the present work, we have found some additional iridoid glucosides belonging to the same group, and we have found verbascoside.

Tribe Potalieae (ix) comprises three genera on which some chemical data have been reported. Complex indole alkaloids appear to be absent, while seco-iridoids and alkaloids derived from these during the isolation procedure are present (cf. Bisset, 1980a, b). The seco-iridoids found in *Anthocleista* (Table 5) are typical of those found in *Gentiana* species, namely sweroside and swertiamarin. We have investigated *Fagraea*, while similar seco-iridoids were present including gentiopicroside. The third genus, *Potalia*, has not been investigated recently, but leaves of *P. amara* have (in agreement with its name) been reported to taste extremely bitter (Bisset, 1980b), an indication of the probable presence of the likewise very bitter *Gentiana* compounds.

Desfontainieae (x) is the third monotypic tribe in Loganiaceae. The only species, *Desfontainia spinosa*, has been thoroughly investigated (Houghton & Ming, 1985; Houghton & Lian, 1986), and a number of seco-iridoids have been found.

DISCUSSION

As stated in the introduction, the delineation of the Loganiaceae has caused much controversy. This is clearly reflected in our results, since iridoids of both *route I* and *route II* are found, although not both in the same tribe. Furthermore, the finding of verbascosides in a Gentiananae family is unexpected if we accept the removal of Oleaceae to a position near Scrophulariaceae (Lamianae) in agreement with the discussion above.

In Table 6, the chemical results have been summed up with regard to tribes. I also have included two of the botanical characters most significant for the delineation of Loganiaceae, namely the presence/absence of intraxylary phloem (Mennega, 1980) and the type of endosperm formation (nuclear/cellular) (Hakki, 1980). For comparison, the corresponding data for Gentianaceae, Oleaceae, and Scrophulariaceae have been included in the table.

If we first consider the tribes i–iii and v–vi, we find (Table 6), with the exception of *Polypremum*, which will be considered in a moment, that all genera with iridoids contain compounds from *route I*. Significantly, except for *Polypremum*, all five tribes also have intraxylary phloem and nuclear endosperm formation. If we combine these facts, we have a fairly homogeneous entity, which may constitute the Loganiaceae proper, with a set of characters fitting well into Gentianales.

Tribe ix, Potalieae, also fits in well at first glance, but if we take into account the iridoid glucosides

TABLE 5. Chemical compounds found in Loganiaceae. (Numbers refer to compounds shown in Figs. 2, 3, 9, and 10. CIA: Complex indole alkaloids.)

Tribe	Species	Iridoids	Verbascoside/ Cornoside	References
i.	*Polypremum procumbens*	—	both	this work
	Spigelia anthelmia	—		this work
	Mitreola petiolata	9	—	this work
	Mitrasacme paludosa	9	—	this work
ii.	*Geniostoma antherotrichum*	6, 10	—	this work
	Labordia fagraeoidea	6, 7, 9	—	this work
	L. hedyosmifolia	9		this work
	L. kaalae	7		this work
	L. waialealae	7		this work
	Logania albiflora	12, 13, 14	—	this work
	L. recurva	—	—	this work
	L. vaginalis	6, 8, 11, 13	—	this work
iii.	*Strychnos* (many spp.)	CIA		Bisset (1980a)
	S. nux-vomica	1, 2, 3, 4, 15		Bisset & Choudhury (1974)
	S. roborans	15		Asai et al. (1987)
	S. spinosa	25		Msonthi et al. (1985)
	S. vacancoua	22		Inouye et al. (1976)
	Gardneria (4 spp.)	CIA		Bisset (1980a)
iv.	*Plocospermum buxifolium*	—	both	this work
v.	*Mostuea* (3 spp.)	CIA		Bisset (1980a)
	Gelsemium (2 spp.)	CIA		Bisset (1980a)
	G. sempervirens	16, 17, 18		this work
vi.	*Bonyunia minor*	—	—	this work
	Antonia ovata	—	—	this work
	Norrisia major	—		this work
vii.	*Gomphostigma species*	5, 26, 27	verbascoside	this work
	Buddleja alternifolia	5, 26	verbascoside	this work
	B. davidii	5, 26, 27, 28	verbascoside	this work
	B. globosa	5, 27	verbascoside	Houghton & Hikino (1989)
	B. saligna	5, 27	verbascoside	this work
	Emorya suaveolens	5, 26	verbascoside	this work
viii.	*Retzia capensis*	29–32		Dahlgren et al. (1979)
		33	verbascoside	this work
ix.	*Anthocleista amplexicaulis*	20		Weber (1974)
	A. grandiflora	19		Chapelle (1973)
	A. liebrechtsiana	20		Cornelis & Chapelle (1976)
	A. procera	20		Koch et al. (1964)
	A. vogelii	4, 19		Chapelle (1974, 1976)
	Fagraea ceylanica	19, 21	—	this work
	F. obovata	19, 21		this work
x.	*Desfontainia spinosa*	2, 3, 19, 24		Houghton & Ming (1985) Houghton & Lian (1986)
		3, 23		this work

present in this tribe, we find that they are of a particularly advanced type almost consistently found in Gentianaceae and elsewhere only in a few species of Dipsacaceae (Jensen et al., 1975b). In addition to this, some xanthones have been reported to occur in *Anthocleista* (Chapelle, 1974; Okorie, 1976). Again, such compounds are rare in higher plants and are only common in Gentianaceae and Hypericaceae (Guttiferae) (Gottlieb, 1982). This chemical information is significant in light of the proposal by Fosberg & Sachet (1980) to include Potalieae in Gentianaceae, a suggestion dismissed by Leeuwenberg (1980) as being "too provisional and too incomplete to form the basis for such an important taxonomic decision." The weight of the additional chemical information may prove decisive

TABLE 6. Chemical and anatomical characters in the tribes of Loganiaceae.

Taxon	Iridoids		Cornoside/ Verbascoside	Intraxylary phloem	Endosperm form.
	Route I	Route II			
Tribe i, ii, iii, v, vi	+	0	0	+	nuclear
ix Potalieae	+	0	0	+	nuclear
x Desfontainieae	+	0	0	0	?
(i) Polypremum	0	0	++	0	cellular
iv Plocospermaeae	0	0	++	0	?
vii Buddlejeae	0	+	+	0	cellular
viii Retzieae	0	+	+	0	cellular
Gentianaceae	+	0	0	+	nuclear (?)
Oleaceae	+	0	++	0	cellular
Scrophulariaceae	0	+	++	0	cellular

in moving Potalieae into Gentianaceae. Even taken alone, the chemical data clearly suggest such a transfer.

Tribe vii, Buddlejeae, has been raised to the family rank Buddlejaceae by most authorities and placed in another order close to Scrophulariaceae (Cronquist, 1981, 1988; G. Dahlgren, 1989; Takhtajan, 1980), although Thorne (1983) retained it in his Gentianales. With regard to chemical characters, the investigated genera are very similar (Table 5), and all the chemical data are in agreement with a position in Lamianae (sensu Dahlgren).

The monotypic genus *Polypremum,* which Leeuwenberg (1980) retained in Spigelieae (tribe i), and the likewise monotypic *Plocosperma* (tribe iv) lack iridoids but contain cornoside and verbascoside or verbascoside-like compounds. Both also lack intraxylary phloem and have cellular endosperm formation. All the characters listed suggest a position in or near Scrophulariaceae or Oleaceae, with Cornales as a less likely alternative. Neither belongs within Loganiaceae as delineated above.

Retzia capensis is the sole member of tribe viii, and its systematic position has recently been controversial (Dahlgren et al., 1979; Cronquist, 1981, 1988; H. F. W. Jensen et al., 1988) mainly because the embryology and chemistry are insufficiently known. The presence of a particularly advanced group of iridoid glucosides belonging to *route II,* and up to then found only in *Arbutus* (Ericaceae) and in *Stilbe* (Stilbaceae, sometimes included in Verbenaceae), suggested a closer relationship between *Retzia* and the Stilbaceae than formerly thought. A detailed study of the available data led Dahlgren et al. (1979) to refute the connection of *Retzia* with Gentianales and to propose that the family Retziaceae had its closest relations in Stilbaceae. Consequently, both families were included in Lamianae with Verbenaceae and Scrophulariaceae despite the lack of embryological evidence. It is curious to notice that Dahlgren, in a parenthetical comment, postulated: "It is expected that the ovules are unitegmic and tenuinucellulate, and that the endosperm is cellular; most likely terminal endosperm haustoria may be present." In fact, recent embryological work by Engell (1987) proved this to be entirely true. Further support for the above view has been obtained by chemical work on Acanthaceae (H. F. W. Jensen et al., 1988; Jensen & Nielsen, 1989) as well as on Stilbaceae (Jensen et al., unpublished). Thus, *Thunbergia* and the four investigated genera of Stilbaceae contain iridoid glucosides similar or identical to those found in *Retzia.* Furthermore, we have found that verbascosides are constituents in Stilbaceae. The chemical information is therefore in complete agreement with a close relationship between Retziaceae and Stilbaceae and a position of both in the vicinity of Buddlejaceae, Scrophulariaceae, and Acanthaceae.

The presence of seco-iridoids in the monotypic Desfontainieae may to some degree let this tribe fit in with Loganiaceae as delineated above. However, the apparently less specialized iridoids, and the absence of intraxylary phloem suggest that a position in this family is doubtful.

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WOOD ANATOMY OF SYMPETALOUS DICOTYLEDON FAMILIES: A SUMMARY, WITH COMMENTS ON SYSTEMATIC RELATIONSHIPS AND EVOLUTION OF THE WOODY HABIT[1]

Sherwin Carlquist[2]

ABSTRACT

Data on wood anatomy are presented in tabular form for 56 sympetalous families of dicotyledons arranged according to the system of Dahlgren, who was influenced by data from presence or absence of iridoids and by embryological information. Each order is reviewed in terms of the degree of correlation of wood data with data from chemistry and embryology. Original data are presented for Buddlejaceae, Globulariaceae, and Selaginaceae. Ericales prove to be a natural and rather primitive group. Cornales as a whole are primitive, but Adoxaceae and Stylidiaceae have distinctively specialized woods. Dipsacales are highly diverse on the basis of woods, creating interpretational questions. Gentianales are a natural group on the basis of wood and of intraxylary phloem in primary stems; Oleales and Rubiales are peripheral to Gentianales. Scrophulariales and Lamiales have specialized wood and are probably natural groupings, but there is no difference between the orders on the basis of wood anatomy. Recognition of particular families within Scrophulariales and Lamiales is aided by wood anatomy: Buddlejaceae, Globulariaceae, and Selaginaceae are distinctive families in Scrophulariales; Avicenniaceae, Chloanthaceae, and Stilbaceae (the last of which should include Retziaceae) should be recognized in Lamiales. Wood anatomy does not aid in differentiating Solanales from Boraginales. Wood of Asterales is rather uniform in characters of major evolutionary significance, despite its diversity in ecological wood anatomy. Lamiales and Scrophulariales have wood similar to that of Asteraceae, but so do Apiaceae, which share chemical features with Asteraceae, Campanulales, and some Dipsacales. Among families *incertae sedis*, Desfontainiaceae (often relegated to Loganiaceae) should be recognized under Cornales near Escalloniaceae, as should Columelliaceae. Fouquieriaceae bear resemblances to Cornales and Ericales, but deserve isolation in a monofamilial order. Familial assignment of the genera *Leucophyllum*, *Oftia*, and *Paulownia* is discussed.

During the past three decades, numerous studies on wood anatomy of sympetalous families have been published; prior to this, these kinds of studies were relatively few. The majority of sympetalous families are predominantly herbaceous, and in the first half of the twentieth century, most wood studies dealt with predominantly woody families. This bias was based upon the origin of wood studies in forestry programs. As wood anatomy entered botany, a broader view developed. Data on wood anatomy suitable for comparison of the sympetalous dicotyledon families are now available, so that a comparison of wood data with other information is timely.

Although I have monographed wood of many sympetalous families, I have not done original research on some, notably Apocynaceae, Bignoniaceae, Rubiaceae, and Verbenaceae. Various workers have contributed data for these families, and the patterns revealed are relatively clear and form a good basis for conclusions about the systematic distribution of wood features.

The predominantly herbaceous nature of several of the sympetalous families is significant, in that wood anatomy in these predominantly herbaceous groups differs from that in typically woody families. Paedomorphosis in secondary xylem (Carlquist, 1962a) is a concept based largely on study of sympetalous families. Paedomorphosis is not encountered in typically woody plants, yet in families such as Plantaginaceae, wood of all species exhibits this phenomenon. Small shrubs of limited duration

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also exhibit a form of this phenomenon (Carlquist, 1989). The occurrence of paedomorphic features in wood is valuable in showing shifts in habit: for example, the raylessness of *Calceolaria* is indicative that the shrubby species of the genus have been derived from herbaceous ancestors. Other paedomorphic features also indicate change in habit, which is discussed in a concluding section of this paper.

Another inherent interest in the wood of sympetalous families is the sensitive way in which wood features reflect ecology. The earliest papers in my survey of wood anatomy of Asteraceae (Carlquist, 1957a, 1958a, 1959) revealed a close relationship between the habitat of a species and its wood anatomy, particularly with respect to vessel features, and a summary paper on Asteraceae (Carlquist, 1966b) profiled the nature of these trends. Subsequent studies on sympetalous dicotyledon families have confirmed and expanded these findings. To be sure, some families of dicotyledons do not cover wide ecological latitude and are characteristic of wet habitats only (e.g., Aquifoliaceae, Cornaceae, Lauraceae). The sympetalous families are unusual within dicotyledons in the degree to which they have entered dry and hot habitats, and thus they show ecological wood anatomy exceptionally well. Ecological wood anatomy is not a focus of the present paper, but is mentioned because features of ecological significance must be separated from those that indicate relationship.

One can point to ecology as the cause for progression not merely in quantitative vessel features, but in major trends as well (e.g., alteration of the perforation plate from scalariform to simple). Because the major trends have developed in a coordinated way (e.g., ray histology has changed concomitantly with vessel specialization), the specialized end products have virtually no possibility of appreciable or wholesale reversion. The features reported as sensitive to local ecology are mostly easily reversible. Asteraceae are virtually uniform with respect to the "major trends of xylem evolution" (storying is absent in the majority of the family and only occurs in a few species). However, vessel features in Asteraceae vary greatly with respect to ecology.

This example shows that if other sympetalous families follow the pattern of Asteraceae, they are excellent for documenting ecological wood anatomy. The Asteraceae, Convolvulaceae, Lamiaceae, and Scrophulariaceae show trends in ecological wood anatomy very well.

Not all wood features of these and other sympetalous families vary with respect to local ecology. There is a residue of wood features distributed according to taxonomic groupings. Wood features have perhaps been thought too often to be decisive in systematic matters—and in a few cases, they are. For the most part, however, wood anatomy is of help to various degrees in various parts of the taxonomic system. Wood anatomy can be used to identify a wood specimen in many cases, so obviously there are wood features that correspond to the taxonomic system. However, wood features tend to be most useful for identification at the generic level, somewhat less at the familial level, and least at the ordinal level. If this generalization is true, it indicates that wood anatomy could aid phylogenetic studies such as this survey of the sympetalous families. Identification of woods has been stressed by such features as inclusion in texts of keys to genera based on wood anatomy; however, it is not as useful as such keys would indicate. Keys and computer programs utilizing wood features of the major genera of economic importance have been presented. If the wood anatomy of large numbers of the world's woody species were added to these presentations, one would find that many species could not be distinguished from one another. I can underline this by saying that if I were handed samples belonging to Scrophulariaceae, Solanaceae, or Lamiaceae, I could not say with certainty, on the basis of wood anatomy, that they were not from species of Asteraceae.

Nevertheless, wood anatomy does show distinctive distribution of features with respect to the taxonomic system. For example, successive cambia occur in Avicenniaceae and Chloanthaceae, but not in Verbenaceae sensu stricto. Thus, occurrence of successive cambia offers reinforcement for segregation of Avicenniaceae and Chloanthaceae (Carlquist, 1981a). Another verbenoid group, Stilbaceae, merits segregation on the basis of wood anatomy (Carlquist, 1986). Two families often assigned to Scrophulariaceae, Globulariaceae and Selaginaceae, are distinctive on the basis of wood anatomy (see below).

Particular distinctive genera may prove to be misplaced according to wood data. In the present study, Buddlejaceae prove not to belong near Loganiaceae, but close to or within Scrophulariales. This agrees with results of other studies presented in this volume. Evidence will be presented for familial reassignment of *Leucophyllum* and *Oftia* (often placed in Myoporaceae) as well. On the basis of wood anatomy, *Retzia*, a monotypic South African genus sometimes placed in its own family, can be assigned to Stilbaceae. The assignment of *Paulownia* (often regarded as intermediate between Bignoniaceae and Scrophulariaceae) is not simplified by data from wood anatomy.

Evolutionary level of wood features is not a reliable indicator of relationships: discrepancies can occur between related families. If families all share essentially the same level of advancement in wood features, the concordance tends to be regarded as a confirmation of relationship. However, gaps in evolutionary level of wood between families claimed to be related on other groups do not negate relationship. They must, presumably, be explained eventually. In the sympetalous families of Dipsacales, Caprifoliaceae have primitive wood, Dipsacaceae somewhat more specialized wood and the Calyceraceae and Valerianaceae highly specialized wood. Various explanations for these divergent levels of wood advancement may be suggested. However, as Bailey (1944) stressed, we cannot envision phylads with primitive wood being derived from those with specialized wood. Thus, Calyceraceae and Valerianaceae cannot be ancestral to Dipsacaceae and Caprifoliaceae. Levels of wood evolution may be regarded as ways of negating relationship even though they cannot decisively confirm relationship. Where wood features of a series of families agree (e.g., banded apotracheal axial parenchyma in Gentianales), similar wood levels (all of these have tracheids or tracheidlike fiber-tracheids) may be regarded as subsidiary evidence of relationship. As stated above, wood rarely gives strong evidence for ordinal groupings. In the present review, Gentianales are the only order in which wood evidence may be an aid to ordinal delimitation.

Because evidence from wood may often be confirmatory though not decisive, comparison with results from other approaches is valuable. In fact, the evidence from wood anatomy does not contradict the evidence and cladograms presented in the other studies presented in this volume. Notable in this regard is the tendency for groups with specialized woods to appear in terminal branches of the clades proposed, whereas those with primitive wood occupy more basal positions. Primitive woods in Ericales can be cited as an example.

The orders and families of sympetalous dicotyledons are discussed here according to the sequence of the Dahlgren (1975) system. A few exceptions to this system have been incorporated, however. Donoghue et al. (1992) show that *Sambucus* (in Sambucaceae of Cornales according to the Dahlgren system) belongs in Dipscales and is closely related to *Adoxa,* which they place in Adoxaceae rather than Caprifoliaceae. They place *Sambucus* in Adoxaceae (older as a familial name than Sambucaceae) and include Adoxaceae in Dipsacales. That treatment is followed here. Although the accompanying papers give evidence for placement of Goodeniaceae in the clade leading to Asteraceae, the noncommittal placement of Goodeniaceae in Goodeniales, following Dipsacales, has been retained here.

Comments on various systems of classification for the sympetalous families are not offered in the present paper. The paper by Wagenitz (1992) summarizes the various schemes of classification as they related to the sympetalous families of dicotyledons.

DATA AVAILABLE

Table 1 summarizes data on iridoid presence, wood features, and selected embryological features. The data in Table 1 on iridoids are based on Jensen et al. (1975) and Dahlgren et al. (1976, 1979). Dahlgren's (1975) classification scheme, which has (with a few exceptions) been followed here, was influenced by patterns of iridoid occurrence. Dahlgren (1975) included choripetalous families within some orders in which sympetalous families occur. All choripetalous families have been omitted from Table 1, with the exception of Apiaceae, which are included in the terminal section of the table among families of uncertain position. Apiaceae have been included as an example of a choripetalous family that might be related to some sympetalous families, such as Asteraceae. Araliaceae, mentioned by Dahlgren (1975) as possibly related to sympetalous dicotyledons, have not been included because the closely related Apiaceae are slightly more specialized with respect to wood features and thus show more similarities to the sympetalous families. Apiaceae have some chemical characters characteristic of Asteraceae: presence of polyacetylenes and sesquiterpene lactones (Hegnauer, 1971). The other families relegated to the end of Table 1 are those in which systematic position either has been controversial (Fouquieriaceae), or in which the systematic position proves to be less clear than previously thought when wood data, along with other kinds of information, are assessed (Desfontainiaceae, Salvadoraceae). The systematic position of some families in the main part of Table 1 is not clear, however (for example, the position of Stylidiaceae). The majority of authors in the present volume who comment on familial interrelationships agree that Buddlejaceae belong in Scrophulariales; that finding, confirmed by wood data, is incorporated in Table 1. Some segregate families are recognized here (Duckeodendraceae, Goetzeaceae, and

TABLE 1. Chemical, xylary, and embryological features of sympetalous dicotyledons.

ORDER	FAMILY	1 IRI	2 PER	3 HEL	4 VES	5 ITE	6 VAS
Ericales	Cyrillaceae	?	C	0	0	T	0
	Ericaceae	1, 4	C, i	(+)	(+)	T	+
	Epacridaceae	?	C	(+)	0	T	0
Cornales	Columelliaceae	?	C	0	0	T	0
	Alseuosmiaceae	?	C	0	0	L	0
	Stylidiaceae	1	I	0	0	F	0
Loasales	Loasaceae	4	c, I	0	0	T	0
Dipsacales	Caprifoliaceae	6, 7, 10	C	0	0	T	0
	Adoxaceae	6, 10	I	0	0	L	0
	Dipsacaceae	6, 7	I	0	0	T	0
	Valerianaceae	6, 10	c, I	0	0	L	0
	Calyceraceae	6	I	0	0	L	0
Goodeniales	Goodeniaceae	6, 7, 10	I	0	0	T	0
Gentianales	Loganiaceae	6, 7, 9, 10	I	(+)	+	F, T	+
	Gentianaceae	6, 7, 10	I	0	0	T	0
	Apocynaceae	1, 6, 7, 9, 10	c, I	(+)	+	F, T	(+)
	Asclepiadaceae	?	I	0	+	F, T	+
	Rubiaceae	1, 2, 9, 10	c, I	(+)	+	F, T	0
Oleales	Oleaceae	4, 6, 10	I	+	(+)	F, T	+
Scrophulariales	Buddlejaceae	1	I	+	0	L	+
	Scrophulariaceae	1, 2, 10	c, I	+	0	F, L	0
	Globulariaceae	1	I	0	0	T	0
	Selaginaceae	10	I	+	0	F, L	+
	Plantaginaceae	1, 10	I	0	0	L	0
	Pedaliaceae	2	I	0	0	L	0
	Marytniaceae	1	I	0	0	L	0
	Gesneriaceae	?	c, I	0	0	F	0
	Bignoniaceae	1, 10	c, I	(+)	0	L	0
	Myoporaceae	1, 10	I	0	0	F	0
	Acanthaceae	10	I	0	0	L	+
Lamiales	Verbenaceae	1, 2, 3, 4, 10	c, I	+	(+)	L	+
	Lamiaceae	1, 2, 10	I	+	0	L	+
	Avicenniaceae	?	I	0	0	L	0
	Chloanthaceae	?	I	0	0	F	0
	Stilbaceae	10	c, I	0	0	F	+
Plumbaginales	Plumbaginaceae	0	I	+	0	L	+
Ebenales	Ebenaceae	0	I	0	0	F	0
Primulales	Primulaceae	0	I	0	0	L	0
	Myrsinaceae	0	I	0	0	L	0
	Theophrastaceae	0	I	0	0	L	0
Asterales	Asteraceae	0	I	+	0	L	+
Campanulales	Pentaphragmataceae	?	C	0	0	F	0
	Campanulaceae	0	c, I	0	0	L	0
	Lobeliaceae	0	I	0	0	L	0
Solanales	Solanaceae	0	I	+	0	F, T	+
	Goetzeaceae	?	I	0	0	F	+
	Duckeodendraceae	?	I	0	0	F	0
	Nolanaceae	?	I	0	0	F	0
	Convolvulaceae	0	I	0	0	F	0
	Polemoniaceae	0	I	0	0	F, L	0
Boraginales	Hydrophyllaceae	0	I	0	0	F	0
	Boraginaceae	0	I	+	+	F	+
Incertae Sedis	Apiaceae	0	I	0	0	L	0
	Desfontainiaceae	?	C	0	0	T	0
	Fouquieriaceae	1, 2, 3, 4	I	0	0	T	0
	Salvadoraceae	?	I	0	0	L	?

Explanation of abbreviations. Column 1 (IRI) = presence of iridoids (types, if present, according to the system of Jensen et al., 1975); Column 2 (PER), perforation plate (I = simple, S = scalariform); Column 3 (HEL) = presence or absence of helical thickenings in vessels; Column 4 (VES) = presence or absence of vesturing in vessels; Column 5 (ITE) = imperforate tracheary elements (F = fiber-tracheids, L = libriform fibers, T = tracheids); Column 6 (VAS) = vasicentric tracheids present or absent; Column 7 (RAY) = ray types (E = heterogeneous, L = rayless, O = homogeneous, P = paedomorphic, numerical types according to the schemes of Kribs, 1935, and Carlquist, 1988a); Column 8 (AXP) = axial parenchyma (Ab = abaxial, Al = aliform, B = apotracheal banded, C = confluent, D = diffuse, DA = diffuse in aggregates, 0 = absent, S = scanty vasicentric, V = abundant vasicentric); Column 9 (STO) = storying present or absent; Column 10 (PAE) = paedomorphic features of wood (L = rayless, R = rays, S = occasional scalariform perforation plates); Column 11 (VAR) = cambial variants (I = interxylary phloem, 0 = normal, S = successive cambia); Column 12 (INT) = integuments (B = bitegmic, U = unitegmic); Column 13 (NUC) = nucellus (Cr = crassinucellate, T = tenuinucellate); Column 14 (END) = endosperm (C = ab initio cellular, H = helobial, N = nuclear). Lower case letters indicate character state is restricted to only one or two genera.

TABLE 1. Continued.

7 RAY	8 AXP	9 STO	10 PAE	11 VAR	12 INT	13 NUC	14 END
E2A, E2B	D	0	0	0	U	T	N
E1, E2A, E3	D, Ab	0	0	0	U	T	N
E2A	D	0	0	0	U	T	N
E3	D, S	0	0	0	?	?	?
E1, L	D	0	L	0	?	?	?
L	0	+	L	I, U	U	T	C
E2A, L, P1	D	+	C, L, R	0	U	T	C
E1, E2A	D, s	0	0	0	U	T	C
E2B	S, T	+	0	0	U	T	C
E2A	D, S	0	0	0	U	T	C
P1, P2	S	+	C, R	0	U	T	C
P1	S	0	R	0	U	T	C
E2B, P1	Ab, D, T	0	R	0	U	T	C
E2A, E3, O1	B, S, T	0	0	I	U	T	N
P1	S	+	R	I	U	T	N
E1, E2A, E3	Ab, DA, S, T	+	0	0	U	T	N
E2B, P1	D, DA, S	0	R	0	U	T	N
E1, E2A, E3, P1	B, D, S	(+)	R	s	U	T	c, N
E1, E2, E2, O1, O2	Al, C, d, S	0	0	0	U	T	C
E2B	Ab, D, S	0	0	0	U	T	C
E1, E2A, E2B, L, P1	S, 0	+	L, R	0	U	T	C
E2B	D, S	0	0	0	U	T	C
L	0	0	L	0	U	T	C
L	0	+	L	0	U	T	C
E2B, P1	S	+	R	0	U	T	C
E2B, P1	S	0	R	0	U	T	C
E2B, P1	S, 0	+	L, R	0	U	T	C
E2	A, Al, C, S	+	0	0	U	T	C
E2B, O1	S	+	0	0	U	T	C
E2B, L, P1	S	0	L, R	I	U	T	C, h
E2A, E2B, O2	Al, C, S, V	+	r	0	U	T	C
E2A, E2B	S, V	0	r	0	U	T	C
O1	D, S, V	0	0	S	U	T	C
E2B, P1	S	0	R	S	U	T	C
E2B, P1	S	0	R	0	U	T	C
E2B, P1	S	0	R	S	B	Cr	N
E2, E3, O1	B, V	+	0	0	B	T	C
L	D	0	L	0	B	T	N
E2B, O2	S	0	0	0	B	T	N
E2B, O2	0, S	0	0	0	U	T	N
E2B, L, P1	S	+	L, R	s	U	T	C, N
L	0	0	L, R, S	0	U	T	C
P1	S	0	R, S, V	0	U	T	C
P1, P2	S	0	R, V	0	U	T	C
E2B, E3, O1, O3, P1	B, D, DA, 0, S	0	R	0	U	T	C
E2B, O1	D, DA	0	0	0	U	?	?
O1	B, V	0	0	0	U	?	?
E2B, P1	B, S	0	0	0	U	T	C, h
E2B, P1, P3	Al, B, D, S	0	R	S	U	Cr, T	N
E2B, L, P1	B, S	0	L, R	0	U	T	N
E2B, L, P1	D, 0	0	L, R	0	U	T	N
E2B, O2, P1	A1, C, D, DA	+	R	0	U	T	C, N
E2, P1	S, T	0	R	0	U	T	N
E3	D	0	0	0	?	?	?
O1	D	0	0	0	B	T	C
E2B	C, S	+	0	I	B	Cr	N

Nolanaceae in Solanales), although other authors may not employ these usages.

Data on wood anatomy in Table 1 are based upon the sources listed below; the atlas of Schweingruber (1990) contains useful data also:

Acanthaceae: Carlquist & Zona (1988). Adoxaceae (Sambucaceae): Greguss (1959). Alseuosmiaceae: Dickison (1986). Apiaceae: Metcalfe & Chalk (1950), Rodriguez (1957), and original data. Apocynaceae: Ingle & Dadswell (1953), Metcalfe & Chalk (1950). Asclepiadaceae: Metcalfe & Chalk (1950) and original data. Asteraceae: Carlquist (1957a, b, 1958a, b, 1959, 1960a, b, 1961, 1962b, 1963, 1965a, b, 1966a, b, 1982a, 1983a, b), Carlquist & Eckhart (1982). Avicenniaceae: Meylan & Butterfield (1978), Metcalfe & Chalk

(1950). Bignoniaceae: Pfeiffer (1926), Metcalfe & Chalk (1950). Boraginaceae (including Ehretiaceae): Barajas Morales (1981), Carlquist (1970b), Gottwald (1983), Nair & Mohan Ram (1989). Buddlejaceae: Mennega (1980) and present paper (see below). Calyceraceae: Carlquist (1983b). Campanulaceae: Shulkina & Zikov (1980). Caprifoliaceae: Ogata (1988), Metcalfe & Chalk (1950). Columelliaceae: Stern et al. (1969). Convolvulaceae: Mennega (1969), Pant & Bhatnagar (1975), Lowell & Lucansky (1986), Carlquist & Hanson (1991). Cyrillaceae: Thomas (1960) and original data. Desfontainiaceae: Mennega (1980). Dipsacaceae: Carlquist (1982b). Duckeodendraceae: Carlquist (1988b). Ebenaceae: Metcalfe & Chalk (1950). Epacridaceae: Meylan & Butterfield (1978), Metcalfe & Chalk (1950). Ericaceae: Metcalfe & Chalk (1950), Carlquist (1985). Fouquieriaceae: Henrickson (1986), Carlquist & Hoekman (1985), and original data. Gentianaceae: Carlquist (1984b). Gesneriaceae: Carlquist & Hoekman (1986a). Globulariaceae: present paper (see below). Goetzeaceae: Carlquist (1988b). Goodeniaceae: Carlquist (1969b). Hydrophyllaceae: Carlquist et al. (1983), Carlquist & Eckhart (1984). Lamiaceae: Rudall (1981), Carlquist (1992). Loasaceae: Carlquist (1984c, 1987c). Lobeliaceae: Carlquist (1969a). Loganiaceae: Mennega (1980), Coulaud (1988). Martyniaceae: Carlquist (1987b). Myoporaceae: Carlquist & Hoekman (1986b). Myrsinaceae: Metcalfe & Chalk (1950), Meylan & Butterfield (1978). Nolanaceae: Carlquist (1987a). Oleaceae: Parameswaran & Vidal Gomes (1981), Baas et al. (1988). Pedaliaceae: Outer & Veenendal (1983), Carlquist (1987b). Pentaphragmataceae: Carlquist (1975) and original data. Plantaginaceae: Carlquist (1970a). Plumbaginaceae: Metcalfe & Chalk (1950) and original data. Polemoniaceae: Carlquist et al. (1984). Primulaceae: original data. Rubiaceae: Koek-Noorman (1969a, b, 1970, 1972, 1976), Koek-Noorman & Puff (1983), Welle et al. (1983). Salvadoraceae: Outer & Veenendal (1981). Scrophulariaceae: Cristiani (1945), Michener (1981, 1983, 1986). Selaginaceae: present paper (see below). Solanaceae: Carlquist (1991). Stilbaceae (including Retziaceae): Carlquist (1986). Stylidiaceae: Carlquist (1981b). Theophrastaceae: Metcalfe & Chalk (1950). Valerianaceae: Carlquist (1983b). Verbenaceae: Metcalfe & Chalk (1950).

References that report only a few features for one or two species in a family (e.g., reports of vesturing in vessels) are not included in the above listing. Data on embryology of the sympetalous families are from Davis (1966) and Kapil & Vijayaraghavan (1965).

MATERIALS AND METHODS

Original data are presented below for one species of Globulariaceae and for two species of Selaginaceae. In addition, original data are presented for several Buddlejaceae as part of a review of that family. Woods of these families were available in dried form. The methods employed in study of these families are the same as those described in my recent papers.

For sympetalous dicotyledons as a whole, wood terminology generally follows that of the IAWA Committee on Nomenclature (1964). Exceptions occur in the cambial variants, for which the terminology follows Carlquist (1988a).

NEW DATA

When contemplating the present paper, I had not intended to report on species belonging to Globulariaceae and Selaginaceae (both families are included in Scrophulariaceae by some authors). However, these segregate families proved to have distinctive wood anatomy, the details of which had not been described before. I collected wood of both families, so that presentation of documented data was possible. There is no information on wood of Globulariaceae or Selaginaceae in Metcalfe & Chalk (1950). This is probably related to the limited size of shrubs in these families, which consist mostly of herbaceous plants. *Globularia salicina* Lam. is exceptional in having stems up to ca. 1 cm diam.; its shrubby habit may be related to occupancy of frost-free localities in the Canary Islands. Selaginaceae form shrubs smaller than that, and stems never attain 1 cm diam., to the best of my knowledge.

GLOBULARIACEAE

Globularia salicina Lam., *Carlquist 2629* (RSA), Tenerife, Canary Islands (Figs. 35–38). Growth rings inconspicuous (Fig. 35). Vessels mostly solitary (Fig. 35), mean number of vessels per group, 1.23. Vessels rounded in transection (Fig. 36). Mean vessel lumen diameter at widest point, 14 µm. Mean number of vessels per mm² transection, 253. Mean vessel element length, 218 µm. Mean vessel wall thickness, 3.0 µm. Perforation plates simple. Lateral wall pitting of vessels consisting of alternate circular pits 3 µm diam. Imperforate tracheary elements are all tracheids (Fig.

38), with pits 3 μm diam. Tracheid diameter at widest point, 18 μm. Mean tracheid length, 312 μm. Mean tracheid wall thickness, 3.0 μm. Axial parenchyma scanty vasicentric, less commonly diffuse (Fig. 36). Axial parenchyma in strands of two cells. Multiseriate and uniseriate rays equally common (Fig. 37). Mean multiseriate ray height, 398 μm. Mean multiseriate ray width at widest point, 2.8 cells. Mean uniseriate ray height, 114 μm. A few series of procumbent cells present in the central portions of the multiseriate rays; the remainder of ray cells upright or square. Ray cell wall thickness, 2.0 μm. All pits among ray cells bordered as seen in sectional view. No crystals observed. Wood nonstoried (Fig. 37).

SELAGINACEAE

Selago thunbergii Choisy, *Carlquist 8061* (RSA), cultivated in Kirstenbosch Botanical Garden, Cape Province, South Africa (Figs. 41, 42). Growth rings absent or only indistinctly demarcated. Vessels mostly solitary; mean number of vessels per group, 1.43. Vessels rounded as seen in transection. Mean vessel lumen diameter at widest point, 20 μm. Mean number of vessels per mm^2 transection, 348. Mean vessel element length, 221 μm. Mean vessel wall thickness, 2.0 μm. Perforation plates simple. Lateral wall pitting alternate, pits about 3 μm diam. Helical thickenings present on vessels (Fig. 42) and vasicentric tracheids (Fig. 41). Imperforate tracheary elements are libriform fibers with simple slitlike pits; some vasicentric tracheids are also present. Mean libriform fiber diameter at widest point, 17 μm. Mean libriform fiber length, 274 μm. Mean libriform fiber wall thickness, 2.5 μm. Axial parenchyma absent. Rays absent (or represented in later formed wood by upright cells virtually indistinguishable from libriform fibers). Crystals absent. Wood nonstoried.

Walafrida nitida E. Mey., *Carlquist 8062* (RSA), cultivated in Kirstenbosch Botanic Garden, Cape Province, South Africa (Figs. 39, 40, 43). Growth rings absent or indistinct (Fig. 39). Vessels solitary or in small groupings (Fig. 39); mean number of vessels per group, 2.7. Mean vessel lumen diameter at widest point, 22 μm. Mean number of vessels per mm^2 transection, 398. Mean vessel element length, 223 μm. Mean vessel wall thickness, 2.3 μm. Perforation plates simple. Lateral wall pits of vessels bearing alternate circular pits about 3 μm diam. vertically, 4 μm horizontally. Helical thickenings present on vessels (Fig. 43) and vasicentric tracheids. Imperforate tracheary elements mostly fiber-tracheids with vestigially bordered pits; a few vasicentric tracheids present. Fiber-tracheids apparently nucleated. Axial parenchyma absent. Rays absent (Fig. 40). Crystals not observed. Wood nonstoried.

DISCUSSIONS OF SYSTEMATIC RELATIONSHIPS

ERICALES

Although data on iridoids are not available for all families of Ericales (Table 1), the presence of iridoids is widespread in this order. Ericales in the sense of Dahlgren (1975) have tenuinucellate ovules with one integument and nuclear endosperm. All of the Ericales have primitive wood features: vessels with scalariform perforation plates; tracheids (rather than fiber-tracheids or libriform fibers); diffuse axial parenchyma; and Heterogeneous Type I or Type IIA rays. Presence of libriform fibers (or fiber-tracheids) together with vasicentric tracheids in the subfamily Arbutoideae of Ericaceae represents a simple step away from the primitive wood configuration as a result of tracheid dimorphism (Carlquist, 1988c). The families of Ericales listed in Table 1 share these primitive wood features with choripetalous ericalean families: Actinidiaceae, Clethraceae, and Empetraceae. The choripetalous family Aquifoliaceae has primitive wood features like those of the Ericales listed, and in addition has the three embryological character states listed for Ericales. Thorne (1976) placed Aquifoliaceae in Ericales.

CORNALES

An interesting feature of Dahlgren's (1975) system is the grouping in Cornales of families that in other systems have been scattered in various portions of "Rosales," "Saxifragales," or other orders. The orders to which the families of Dahlgren's Cornales were previously referred are not close to each other in most systems. Dahlgren's Cornales include iridoid-bearing bicarpellate families; the embryological features agree with those of Ericales except that, in contrast, cornalean families have cellular rather than free nuclear endosperm development. The choripetalous families of Dahlgren's Cornales include Alangiaceae, Cornaceae, Davidiaceae, Escalloniaceae, Garryaceae, Icacinaceae, and Nyssaceae. Notably absent, compared with earlier concepts of Cornales, are Araliaceae and Apiaceae, which lack iridoids. The sympetalous families of Cornales do not form a coherent assemblage—they appear to be isolated instances of sympetaly within a predominantly choripetalous order. Columelliaceae have been most commonly placed in Scrophulariales in the past (see Stern et al., 1969). Columelliaceae have primitive woods like those of Escalloniaceae and Hydrangeaceae, as stressed by Stern et al. (1969). Wood definitely is a key to relationships in this case.

Alseuosmiaceae also have very primitive wood (Dickison, 1986). All but one species are rayless (Dickison, 1986). The raylessness is not indicative of relationship, but rather may indicate derivation from an herbaceous ancestry, as in other rayless groups. Rays do occur in one species of Alseuosmiaceae: *Crispiloba disperma* (S. Moore) van Steenis. Ancestry of the family as a whole may not be herbaceous. Wood anatomy suggests that Alseuosmiaceae are related to Hydrangeaceae (Dickison, 1986), but Columelliaceae may not be the family closest to Alseuosmiaceae.

Stylidiaceae are a curious family once placed in close proximity to other inulin-containing families: Asteraceae, Campanulaceae, Goodeniaceae, and Lobeliaceae. Dahlgren's (1975) decision to place more confidence in iridoids (absent in those families but present in Stylidiaceae) than inulins as a phylogenetic indicator resulted in transfer of Stylidiaceae to an entirely new systematic position. The wood of Stylidiaceae (very few species of which are woody) has several peculiarities. The cambium originates outside the scattered bundles of the stem (which resembles that of a monocotyledon). The cambium acts unilaterally: it produces secondary xylem to the inside but no secondary phloem to the outside. Wood of Stylidiaceae contains tiny strands of interxylary phloem and is rayless. The presence of fiber-tracheids rather than libriform fibers in wood of Stylidiaceae represents retention of a single primitive character state in a wood otherwise highly specialized. Because of this, attempting to use wood anatomy as a basis for relating Stylidiaceae to the other families of Cornales, which have very primitive wood, is difficult. Data from wood anatomy do not negate a relationship between Stylidiaceae and the other families placed in Cornales, however.

LOASALES

The herbaceous habits, peculiar trichomes, and inferior ovary of Loasaceae are distinctive features that have made them difficult to place with woody hypogynous dicotyledonous families. Loasaceae are minimally sympetalous. The various phylogenetic treatments often select a choripetalous order as closest to the family, but most systems also emphasize the distinctiveness of the monofamilial order. Scalariform perforation plates are occasional in secondary xylem, and this probably is indicative of paedomorphosis. The scalariform condition is present in the primary xylem, but is perpetuated irregularly into secondary xylem through paedomorphosis. Primitiveness of loasaceous wood is indicated by possession of tracheids and diffuse axial parenchyma. These various remnants of a primitive wood configuration suggest that Loasales are not far from such orders as Cornales or Dipsacales. The many indicators of paedomorphosis, especially those of rays, suggest that whatever its closest ally, the immediate ancestor of Loasaceae was likely herbaceous.

DIPSACALES

The order Dipsacales as constituted by Dahlgren (1975) contains unusually disparate contents with respect to wood anatomy. The wood anatomy of Caprifoliaceae (including *Viburnum* but excluding *Sambucus*) is quite primitive. In fact, the wood of Caprifoliaceae is essentially like that of such Hydrangeaceae as *Philadelphus*. Vining and lianoid Caprifoliaceae have some acceleration in wood anatomy (simplification of perforation plates), but these changes are minor alternations of the basic plan.

Sambucus, the sole woody genus of Adoxaceae, has very specialized wood that features vessels with simple perforation plates, vascular tracheids (tracheids at the end of a growth ring), libriform fibers, vasicentric axial parenchyma, Heterogeneous Type IIB rays, and storied wood structure. On the basis of wood anatomy, placement of *Sambucus* in Caprifoliaceae, Escalloniaceae, Hydrangeaceae, or any of the Cornales of Dahlgren (1975) would not be indicated. While wood anatomy by itself cannot conclusively indicate relationship, the gap between *Sambucus* and the families named, all of which have notably primitive wood, must be emphasized. The evidence speaks clearly for recognition of *Sambucus* in a family separate from Caprifoliaceae.

Dipsacaceae have woody representatives in dry situations (e.g., Canary Islands, Aegean Islands). As one might expect in such sites, simple perforation plates have evolved in these representatives. Imperforate tracheary elements of Dipsacaceae, however, are tracheids. Axial parenchyma is diffuse. These two features are characteristic of primitive woods and would not be unexpected if Dipsacaceae were a phylad related to Caprifoliaceae that has evolved in drier conditions.

Valerianaceae and Calyceraceae have simple perforation plates, libriform fibers rather than tracheids, and scanty vasicentric axial parenchyma. These families, therefore, represent a higher level of specialization than Dipsacaceae. That does not rule out relationship, but it emphasizes that these families are distinct from those with more primitive woods in Dipsacales (or other orders).

GOODENIALES

In the Dahlgren (1975) system, Goodeniaceae are no longer placed with Campanulaceae and Lobeliaceae, although compelling evidence for placing these three families together on a line leading to Asteraceae has been presented by Olmstead & Palmer (1992). Goodeniaceae have wood features very similar to those of Dipsacaceae in level of specialization: simple perforation plates, tracheids, and diffuse parenchyma. This does not necessarily imply a phylogenetic relationship between Dipsacaceae and Goodeniaceae. It does suggest a similar phylesis: evolution of a group with basically primitive wood in areas with climates strongly seasonal with respect to rainfall. Because Goodeniaceae have relatively primitive wood, they cannot be derived from any phylads that have highly specialized wood (e.g., Valerianaceae). This must be considered in cladistic hypotheses that involve Goodeniaceae.

GENTIANALES

The order Gentianales as defined by Dahlgren (1975) appears to be relatively homogeneous according to the data in Table 1. Wood features common to the families include simple perforation plates and fiber-tracheids (in some species, tracheidlike). Although vasicentric parenchyma occurs in some Gentianales, banded apotracheal axial parenchyma (rarely found in the families that lack iridoids) is common in the order. Vesturing and storying are uncommon in Gentianales, but may be found in most of the families. Because few Gentianaceae are woody, the lack of data on vesturing in that family may be a sampling artifact. Rays are Heterogeneous Type IIA or IIB (or, in certain Gentianaceae, a paedomorphic derivative of one of these types). Unitegmic tenuinucellate ovules are universal in the order. Nuclear endosperm (otherwise nearly restricted to Plumbaginales and Primulales in the sympetalous families) characterizes Gentianales. Perhaps most noteworthy to the concept of Gentianales is the presence of intraxylary phloem—strands of phloem between the primary xylem and the pith in stems. This feature occurs in all of the gentianalean families except Rubiaceae.

Do Rubiaceae fit well into the concept Gentianales? Rubiaceae lack intraxylary phloem, but they do have elongate glandular trichomes ("colleters") on stipules. These stipular glandular trichomes characterize the other gentianalean families (Metcalfe & Chalk, 1950).

Complicating the use of wood features in placing the Rubiaceae is the diversity of wood in the family. This diversity can be shown within a single genus. In *Coprosma montana* Hillebr. (Fig. 1), axial parenchyma is apotracheal banded, diffuse, and scanty vasicentric, all coexisting within the same wood. In another Hawaiian species, *C. foliosa* A. Gray (Fig. 3), axial parenchyma is predominantly scanty vasicentric, with a little diffuse parenchyma. In *C. montana* rays are Paedomorphic Type I, but elsewhere in the genus, less abundant upright ray cells, ranging to predominance of procumbent cells (= Heterogeneous type IIB, verging on Homogeneous Type I), may be found in the eight *Coprosma* species treated with respect to wood anatomy by Meylan & Butterfield (1978). Heterogeneous Type II rays also occur in Rubiaceae (Metcalfe & Chalk, 1950).

Imperforate tracheary elements in *Coprosma* are fiber-tracheids in which pit borders are small but definitely present (Fig. 4). However, in *Galium* (Figs. 5–7), imperforate tracheary elements are tracheids, with relatively large, fully bordered pits (Figs. 6, 7). However, in most Rubiaceae, pits on imperforate tracheary elements range from moderately to vestigially bordered to simple (Koek-Noorman, 1969a, b, 1970, 1972; Koek-Noorman & Puff, 1983), so that a complete range in imperforate tracheary elements is present. In *Galium*, woods are storied (new report for the genus and for the family: Fig. 6). *Galium* is probably a representative of an herbaceous phylad (the tribe Rubieae) that has radiated into more moderate climates where secondary woodiness has occurred. This is probably true for *Rubia fruticosa* L. also (data from Koek-Noorman, 1970). Both *Galium catalinense* A. Gray and *Rubia fruticosa* have upright ray cells only (Fig. 8, right), and both species are thus nearly rayless. *Galium* and *Rubia* show several features that differ from those in other Rubiaceae, demonstrating the diversity of the family.

Raphides are present in ray cells of *Galium* (Fig. 8: new report for the genus) and other Rubiaceae (Koek-Noorman, 1969a), yet rhomboidal crystals occur in ray cells in other species of the family

(Koek-Noorman, 1969a). Raphides in ray cells have not been reported for other families of sympetalous dicotyledons. Presence of tracheids and of rare, scattered (and sometimes malformed) scalariform perforation plates in Rubiaceae are indicators of primitive character states in the wood.

The wood diversity of Rubiaceae presents difficulties when discussing the concept Gentianales, because the other families have wood that is much more uniform. A wider range of character states need not exclude Rubiaceae from Gentianales. The wider range in Rubiaceae may (in part) be related to the large size of the family, although the examples given within the genus *Coprosma* tend to counter the idea that diversity in wood features is proportional to the size of the family. Gentianales might be slightly more coherent if Rubiaceae were excluded, but in that case, Rubiaceae would have to be located in a neighboring monofamilial order, a treatment very close to including the family within Gentianales.

OLEALES

Wood of Oleaceae has been studied thoroughly by Baas et al. (1988), who demonstrated the great diversity of many wood features in the family. As with Rubiaceae, this diversity tends to mask the systematic affinities of the family. For example, imperforate tracheary elements of Oleaceae range from tracheids to fiber-tracheids with vestigial borders on pits to libriform fibers with pits apparently simple. Baas et al. (1988) concluded that Oleaceae belong in or near Gentianales, a conclusion much like that of Mennega (1980); however, citation of wood features to support this placement reveals nothing decisive. The chemical data of Hegnauer (1971) seem more persuasive than wood data. Separation of Oleaceae in their own order seems advisable under the circumstances. The analysis of Coulaud (1988) supports this position.

SCROPHULARIALES

Buddlejaceae traditionally were regarded as a tribe within Loganiaceae. As a family, Buddlejaceae were placed by Dahlgren (1975) among Gentianales because of iridoid content. However, as the data of Table 1 indicate, Buddlejaceae differ from Gentianales in a number of significant respects. The wood anatomy of Buddlejaceae (as tribe Buddlejeae of Loganiaceae) was summarized by Mennega (1980). Illustrations are offered here because wood anatomy of Buddlejaceae has not been figured extensively heretofore, and the features shown indicate the probable affinities of the family. The imperforate tracheary elements of Buddlejaceae are libriform fibers. Because the imperforate tracheary elements are not tracheids, grouping of vessels in response to xeromorphy is marked in *Buddleja*, species of which range from mesic to very dry sites. In *B. globosa* Hope (Fig. 9), vessels are relatively little grouped. The bands of latewood vessels of *B. parviflora* HBK (Fig. 13) form extensive aggregations as tangential bands, as do (much less conspicuously) the latewood vessels of *B. utahensis* Cov. (Fig. 17). Some latewood vessels are as narrow as libriform fibers (Fig. 20, left). Vasicentric tracheids are present in all three species illustrated. Vasicentric tracheids in *Buddleja* are somewhat more common in latewood than in early wood. Helical thickenings are common in vessels of *Buddleja*, although lacking in some species (*B. americana* L., *Hutchinson 3406*, U. C. Berkeley Botanic Garden). In *B. globosa* (Fig. 11) and *B. parviflora* (Fig. 15), all vessels possess helical thickenings. In *B. utahensis*, wide vessels lack helical thickenings (Fig. 19), whereas narrow vessels possess them (Fig. 21). Axial parenchyma in *Buddleja* is scanty vasicentric. No banded parenchyma and no diffuse parenchyma occur. Rays of *Buddleja* are uniformly Heterogeneous Type IIA or IIB (Figs. 10, 14, 18). Procumbent cells predominate in the rays, as shown in tangential section in Figures 10, 14, and 18, and in radial section in Figures 12, 16, and 21 (note horizontal axis of rays oriented vertically in Figs. 12 and 21). Crystals in rays of *Buddleja* are common in most species. In *B. globosa*, crystals are rhomboidal to somewhat elongate (Fig. 12). In *B. parviflora*, crystals are not elongate, and some are paired in mirror-image fashion (Fig. 16). In *B. utahensis*, the crystals are clearly elongate (Fig. 21).

In embryological features, Buddlejaceae differ from Gentianales by having cellular endosperm, a feature characteristic of Scrophulariales and Lamiales. The lack of borders on pits of imperforate tracheary elements allies Buddlejaceae with Scrophulariales or Lamiales: libriform fibers occur in Gentianales only in certain Rubiaceae, and Rubiaceae are, as mentioned above, probably best placed in Gentianales. Axial parenchyma in Buddlejaceae is typical of that found in Scrophulariales or Lamiales (scanty vasicentric), and banded parenchyma, frequent in Gentianales, is absent.

Other features of Buddlejaceae are not decisive: elongate to rhomboidal crystals in rays are frequently found in families of Gentianales, Lamiales, and Scrophulariales. Lack of vesturing in vessel pits of Buddlejaceae is not decisive because in no sympetalous family of dicotyledons does vesturing characterize large portions of a family. In sum, Buddlejaceae clearly should be transferred from Gentianales to Scrophulariales or Lamiales. The fruit type of Buddlejaceae may provide the decisive feature: it is capsular, with many ovules, as in Scrophulariales, rather than composed of nutlets, each with a single ovule, as in Lamiales. Therefore, Buddlejaceae most likely belong in Scrophulariales, and I have included them in that order in Table 1 rather than following Dahlgren's treatment.

Evidence from wood anatomy indicates that Scrophulariaceae sensu lato are more diverse than many current systematic treatments indicate. The diversity need not result in segregation of subfamilies as independent families, although the evidence from wood anatomy does seem to indicate that for two families, Globulariaceae and Selaginaceae.

Raylessness occurs in two subfamilies of Scrophulariaceae, Rhinanthoideae and Antirrhinoideae, of Wettstein's (1891) system. All *Calceolaria* species I have investigated prove to be rayless, as shown for *C. adscendens* Lindl. in Figures 22 and 23; Metcalfe & Chalk (1950) also reported the genus as rayless (no species given). Other distinctive features of the wood of *Calceolaria* include vessels in radial multiples (Fig. 22) and absence of axial parenchyma. The wood is storied, although not conspicuously so (Fig. 23). Axial parenchyma absence is common in rayless woods (Carlquist, 1970a), a condition perhaps related to the relatively thin woody cylinders accumulated by most rayless species. More significantly, raylessness is an excellent indicator of herbaceous ancestry (Carlquist, 1970a), although exceptions may occur. *Calceolaria* is a predominantly herbaceous genus (Wettstein, 1891), so that secondary woodiness is probable on numerical grounds alone; shrubs in the genus are short-lived and herblike.

Raylessness in *Hebe* (Figs. 24–26) has been known for several decades (Metcalfe & Chalk, 1950; Meylan & Butterfield, 1978). In *Hebe*, vessels are in radial multiples, although the groupings are small, and solitary vessels are common (Fig. 24). Axial parenchyma is absent. Wood is nonstoried (Fig. 25). Imperforate tracheary elements have vestigial borders on pits (Fig. 26), as reported for *H. salicifolia* (Forst. f.) Pennell by Meylan & Butterfield (1978). Some pits in imperforate elements in *H. elliptica* Pennell are apparently simple, although others are vestigially bordered (Fig. 26), a fact revealed by the air content of the cell shown in Figure 26. Worthy of investigation in *Hebe* is whether pits are simple as opposed to bordered, both on fibriform cells in "potential ray areas" and on imperforate tracheary elements in fascicular areas. *Hebe* seems to be a woody derivative of *Veronica*, or a *Veronica*-like ancestor. *Hebe* and *Veronica* form a distinctive group within tribe Digitaleae of subfamily Rhinanthoideae (Wettstein, 1891). Raylessness is not evidence for close relationship between *Hebe* and *Calceolaria*, and indeed, the two genera are widely separated in Wettstein's (1891) system for the family. Further comments on the significance of raylessness are offered in a concluding section of this paper devoted to correlations between habit and wood anatomy.

Paulownia has been a genus of uncertain position, referred either to Bignoniaceae or Scrophulariaceae or even an intermediate position (for a history, see Armstrong, 1985). This situation has not received comment with respect to wood anatomy. *Paulownia* wood is illustrated here (Figs. 27–29), along with a genus of Bignoniaceae with some similarities, *Catalpa* (Figs. 31, 32), and, for comparison, a genus (*Tecoma*) with wood typical of Bignoniaceae (Figs. 33, 34). *Paulownia* has been compared to *Catalpa* by some authors.

Paulownia is notable for its well-marked growth rings (Fig. 27). The large earlywood vessels are embedded in a large quantity of initial axial parenchyma. When viewed in longitudinal section, this initial parenchyma is composed of very thin-walled cells in strands of one to two cells (Fig. 28, left; Fig. 29, left). Latewood vessels of *Paulownia* are associated with aliform or aliform-confluent axial parenchyma (likewise in strands of one to two cells when seen in longitudinal section). Rays are narrow, multiseriate, and composed of procumbent cells (Figs. 28, 29) and are Homogeneous Type II in the Kribs (1935) system. This description accords with the Metcalfe & Chalk (1950) reports. None of the axial parenchyma or ray features cited have been reported in Scrophulariaceae (Metcalfe & Chalk, 1950; Michener, 1981, 1986). In Scrophulariaceae, axial parenchyma is scanty vasicentric, and rays are Heterogeneous Type I or Type II. Conceding that the degree of parenchymatization of *Paulownia* wood is unique in arboreal sympetalous dicotyledons, the pattern of parenchymatization is not like that of other genera. For example, in *Faradaya* of the Verbenaceae (Fig. 30), a wood with abundant axial parenchyma, parenchyma takes the form of wider rays and of axial parenchyma that is not adjacent to vessels. Vessels are sheathed with libriform fibers rather than axial parenchyma. To be sure, these features of *Faradaya* may be related to its lianoid habit.

Catalpa (Figs. 31, 32) of the Bignoniaceae has well-demarcated growth rings and, like *Paulownia*, large quantities of initial axial parenchyma. The latewood vessels of *Catalpa* (Fig. 31) form large aggregations that are associated with scanty vasicentric axial parenchyma. Rays of *Catalpa* (Fig. 32) are Heterogeneous Type IIB, transitional to Homogeneous Type II. Thus, *Catalpa* has wood more like that of Scrophulariaceae than does *Paulownia. Paulownia* wood is more similar to that of Bignoniaceae than to that of *Catalpa.* This is underlined by the aliform-confluent axial parenchyma (Fig. 33) of *Tecoma,* which forms strands of four to five cells in longitudinal section (Fig. 34). Rays of Bignoniaceae are not always storied in Bignoniaceae, as shown for *Tecoma* (Fig. 34), but they are storied in many genera. The wood data on Bignoniaceae and Scrophulariaceae of Outer & Veenendal (1981) support the above conclusions.

The South African genus *Oftia* has mostly been placed in Myoporaceae (for a summary, see Dahlgren & Rao, 1971). *Oftia* has the following wood features: perforation plates simple (but often double); libriform fibers septate; axial parenchyma scarce; and upright cells predominant in rays (Carlquist & Hoekman, 1986b). The upright ray cells in *Oftia* are likely indicative of paedomorphosis, whereas the predominance of procumbent cells in rays of Myoporaceae is indicative of a woody ancestry for the family. The septate libriform fibers and the scarce, scanty vasicentric parenchyma of *Oftia* suggest relationship other than to Myoporaceae, in which fiber-tracheids and more abundant vasicentric axial parenchyma are present (Carlquist & Hoekman, 1986b). This supports the opinion of Dahlgren & Rao (1971) that *Oftia* belongs in Scrophulariaceae.

Leucophyllum has often been considered to belong to the Scrophulariaceae. Niezgoda & Tomb (1975) claim a link between *Leucophyllum* and Myoporaceae on the basis of pollen. *Leucophyllum* has vessels with prominent helical thickenings; vascular tracheids abundant in latewood, producing a transition to vasicentric tracheids, as in some Lamiaceae (Carlquist, 1992); scanty vasicentric axial parenchyma; and abundant fibriform vessel elements. These features differ from those of Myoporaceae (see above under *Oftia*). Reexamination of the familial location of *Leucophyllum* is therefore urged.

Globulariaceae are a small group of genera sometimes placed within Scrophulariaceae, and sometimes recognized as a segregate family situated close to Scrophulariaceae. Because material was available (see New Data, above), I have included original data on wood of Globulariaceae here. One significant feature of *Globularia* wood with respect to systematics is the presence of tracheids (Fig. 38) rather than fiber-tracheids or libriform fibers. Presence of tracheids in wood of *Globularia* is related to lack of vessel grouping (Fig. 35), for reasons proposed earlier (Carlquist, 1984a). Another significant feature of *Globularia* wood is the presence of diffuse axial parenchyma (Fig. 36) in addition to scanty vasicentric parenchyma. Rays are Heterogeneous Type IIA (Fig. 37). Tracheids and diffuse axial parenchyma represent maximally primitive character states and are expressions more primitive than found in other families of Scrophulariales. One can conclude that Globulariaceae are a distinct family. The primitiveness of wood in this family means that it cannot be derived from scrophularialean families with more specialized wood, and this should be taken into account in phyletic work. Further studies to assess the precise relationships of this neglected family are needed.

Another small group of genera sometimes included within Scrophulariaceae is represented by the segregate family Selaginaceae. As with Globulariaceae, availability of wood has led to presentation of original information (see New Data, above). The specimens studied differ, although not greatly, with respect to imperforate tracheary elements: *Walafrida nitida* has fiber-tracheids with vestigial pit borders, whereas *Selago thunbergii* has libriform fibers—the pits are apparently simple. Axial parenchyma is absent, a condition that may be related to raylessness, as with *Calceolaria* and *Hebe* mentioned above. The imperforate tracheary elements may be nucleated (the deposits observed suggest either nuclei or residues formed as a result of prolonged duration of protoplasts). There are pronounced helical thickenings in the vessels of *Selago thunbergii* (Figs. 41, 42) and *Walafrida nitida* (Fig. 43); these are similar to those seen in a scattering of Scrophulariaceae from dry localities. Although vascular tracheids (formed at the ends of growth rings) can be seen in some Scrophulariaceae, Selaginaceae are the only family in which typical vasicentric tracheids have thus far been observed. That feature, in addition to the raylessness, reinforces recognition of this group at a familial level. As with Globulariaceae, affinities of Selaginaceae need to be investigated using modern DNA techniques.

Outer & Veenendal (1983) reported on one species of Pedaliaceae. They presented a table with qualitative features for eight species of Acanthaceae, 22 species of Bignoniaceae, but only one atypical species of Scrophulariaceae—*Paulownia tomentosa* (Thunb.) Sond. They concluded that Pedaliaceae are close to Bignoniaceae. When a wider range of Pedaliaceae is looked at (Carlquist, 1987b) and compared with all other families of Scrophulariales, the situation changes. The apotracheal parenchyma bands of *Sesamothamnus* are the result of fiber dimorphism and are not related to the aliform-confluent bands in wood of Bignoniaceae. All of the wood features of Pedaliaceae may be found in Scrophulariales (and, for that matter, in Scrophulariaceae), but Pedaliaceae are not really closer to one family of Scrophulariales than another on the basis of wood anatomy. The similarity in pollen between Martyniaceae and Pedaliaceae is intriguing. However, more studies are needed to resolve interrelationships of the scrophularialean families.

LAMIALES

The Lamiales could once be described as the families Lamiaceae and Verbenaceae. However, segregate families have been recognized, and wood anatomy tends to support these. Studies on phylogeny of Lamiaceae by Cantino (1992) suggest that Lamiaceae may be a collection of independent derivatives from Verbenaceae. If this is true, Lamiaceae must be united with Verbenaceae, or else Lamiaceae may be subdivided into several families representing these independent phylads. Unfortunately, Lu (1990) did not analyze the segregate families of Verbenaceae, so his cladistic analysis of Lamiales is not discussed here.

Avicenniaceae are one of the families frequently segregated from Verbenaceae. Avicenniaceae have successive cambia (Fig. 44) with distinctive bands of sclerenchyma in the conjunctive tissue (Figs. 44, 45). Vessels are in radial multiples (Fig. 44). Imperforate tracheary elements are nonseptate libriform fibers. Crystals are abundant in rays (Fig. 45). In Verbenaceae, cambia are normal; vessels are in clusters; imperforate tracheary elements are mostly septate libriform fibers; crystals are reported in ray cells only in *Vitex* (Carlquist, 1988a), but even in that genus they are rare or absent (Meylan & Butterfield, 1978). These distinctions, added to those from gross morphology, support segregation of Avicenniaceae from Verbenaceae.

Chloanthaceae (= Dicrastylidaceae of some authors) are similar to Avicenniaceae in having successive cambia. The occurrence of successive cambia in Chloanthaceae is not evidence of relationship to Avicenniaceae. In Chloanthaceae, phloem is frequently in continuous tangential bands rather than in isolated strands, and no sclerenchyma bands occur in the conjunctive tissue (Carlquist, 1981a). Imperforate tracheary elements in Chloanthaceae are fiber-tracheids rather than libriform fibers. Verbenaceae have libriform fibers; Metcalfe & Chalk (1950) reported fiber-tracheids in *Petraea arborea* HBK (Verbenaceae), but my material of *Petraea* has only libriform fibers. Upright ray cells predominate in rays of Chloanthaceae (Carlquist, 1981a) but are only on ray margins in Verbenaceae. The differences between wood of Chloanthaceae and Verbenaceae sensu stricto are sufficient to support segregation of Chloanthaceae.

Stilbaceae have frequently been considered a subfamily of Verbenaceae, but several recent authors have recognized them as a segregate family (for a history, see Carlquist, 1986). Wood of Stilbaceae has simple plus scalariform perforation plates; vessels in long radial multiples; an abundance of fibriform vessel elements; either fiber-tracheids or libriform fibers, notably thick-walled; scarce vasicentric axial parenchyma; and Heterogeneous Type IIA rays. Verbenaceae have only simple perforation plates (aberrant scalariform perforation plates exceptionally: Meylan & Butterfield, 1978); vessel elements rarely fibriform; vessels solitary or in clusters; libriform fibers (often septate and thinner-walled than in Stilbaceae); scanty vasicentric axial parenchyma; and rays Heterogeneous Type IIA or IIB transitional to Homogeneous Type II.

The features just cited for Stilbaceae are also characteristic of Retziaceae (Carlquist, 1986). This confirms the opinion of Dahlgren et al. (1979) that the two families are closely related. My conclusion (Carlquist, 1986) is that the two families should be united.

PLUMBAGINALES

Wood of Plumbaginaceae (Table 1) has been little studied to date because few species of the family are woody. Features presently known show that the wood features are similar to those of other sympetalous dicotyledon families. The wood of this family, then, is not helpful in demonstrating affinities of Plumbaginaceae.

EBENALES

Ebenaceae are the only family of Ebenales to be considered here because other families in the order are choripetalous or nearly so. There obviously is a bias introduced by this selection. However, the question at hand is whether Ebenaceae are at all related to other choripetalous families of dicotyledons. Ebenaceae have a distinctive combination of wood features (Figs. 46, 47). Axial parenchyma is diffuse to banded (Fig. 46), and both of these types are infrequent in the other sympetalous families. The imperforate tracheary element type for the family is the fiber-tracheid. Rays are diverse: Heterogeneous Type II, Heterogeneous Type III, and Homogeneous Type I (Fig. 47); only the first of these is common in other sympetalous families. Storied wood structure, common in Ebenaceae (Fig. 47), occurs commonly in only a few of the other sympetalous families. Ebenaceae differ from most other sympetalous families in having bitegmic ovules (Table 1). This underlines the fact that neither wood nor other features indicate close relationship between Ebenaceae and the other sympetalous families.

PRIMULALES

Primulales are united on the basis of embryology (Table 1): the three families have bitegmic tenuinucellate ovules and nuclear endosperm. All three families have libriform fibers. Primulaceae are reported here on the basis of Hawaiian species of *Lysimachia* only. The rayless wood and diffuse axial parenchyma of *Lysimachia* are not representative for the order as a whole. Myrsinaceae and Theophrastaceae are close to each other on the basis of wood anatomy. The concept of Primulales as constituted by Dahlgren (1975) is not countered by wood data if one concedes that *Lysimachia* is not representative. The distinctive wide rays of Myrsinaceae and Theophrastaceae, in which procumbent cells predominate, can be called transitional between Heterogeneous Type IIB and Homogeneous Type II. Rays of this sort are not characteristic of other sympetalous families.

ASTERALES

The affinities of Asteraceae have traditionally been claimed (e.g., in the Engler system) to be with families that contain inulin: Calyceraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, and Stylidiaceae. Inulin characterizes only some Asteraceae. Dahlgren's (1975) decision to disassemble the alliance cited above was based on a different chemical character, iridoid presence or absence. The families placed near Asteraceae in the Engler system all lack iridoids except for Goodeniaceae and Stylidiaceae (Table 1).

Embryologically, Asteraceae agree with virtually all sympetalous families except Plumbaginales, Ebenales, and Primulales. Asteraceae are remarkably uniform (considering the size of the family) with respect to characters of major evolutionary significance. The diversity within woods of Asteraceae is mostly related to ecology; this ecological range is so distinctive that it inspired my earliest ideas about how wood anatomy is related to ecology (Carlquist, 1966b). Although Baas (1986) has reported vestigial borders on pits of imperforate tracheary elements of one species of Asteraceae, the family as a whole is still characterized by having libriform fibers (which have simple pits, according to the definitions of the IAWA Committee on Nomenclature, 1964). With respect to similarities in wood anatomy between Asteraceae and other families, the features characteristic of wood of Asteraceae (Table 1) are all found in woods of Apiaceae, Calyceraceae, Campanulaceae, Lamiaceae, and Scrophulariaceae. A wood sample of one of these families would not yield any diagnostic features different from those of wood of Asteraceae. This is noteworthy in view of the results of Olmstead & Palmer (1992), who find that Goodeniaceae, Campanulaceae, Lobeliaceae, and Calyceraceae are on the clade leading to Asteraceae. Goodeniaceae have wood somewhat more primitive than that of the other families in this clade. If that difference could be explained, there would be no evidence from wood anatomy conflicting with the views of Olmstead and Palmer on the phylogeny of Asteraceae.

CAMPANULALES

The three families of Campanulales (Campanulaceae, Lobeliaceae, and Pentaphragmataceae) recognized by Dahlgren (1975) form a coherent group on embryological grounds (Table 1). The wood anatomy of Campanulales represents variations on the same basic plan, because these variations are due to paedomorphosis. Campanulaceae have scalariform perforation plates in primary xylem (Bierhorst & Zamora, 1965); through paedomorphosis, this perforation plate type has been extended into the secondary xylem. Shulkina & Zikov's (1980) figures for woods of Campanulaceae are clearly indicative of this. Ancestrally in Campanulales there doubtless are scalariform perforation plates in primary xylem. This is more primitive than a condition in which there are simple perforation plates in both primary and secondary xylem, exemplifying the "refugium" theory of Bailey (1944). By means of paedomorphosis, primitive primary xylem characteristics may be extended into secondary xylem. Campanulaceae show more paedomorphosis with respect to perforation plates than do Lobeliaceae, in which scalariform perforation plates are virtually absent from secondary xylem (Carlquist, 1962a, 1969a). Pentaphragmataceae, on the other hand, show the greatest degree of paedomorphosis: scalariform perforation plates are characteristically present throughout the secondary xylem. The secondary xylem is also rayless (a paedomorphic feature), and septate fiber-tracheids are present. One can hardly doubt that *Pentaphragma* is an herb with a moderate amount of secondary xylem, so paedomorphosis, related to wood development in herbs, is definitely represented in this genus. The rays of Campanulaceae and Lobeliaceae are paedomorphic (Carlquist, 1962a, 1969a).

As mentioned above, Campanulales have no wood features that are not found in Asteraceae. Interesting in this regard are the occasional aberrant scalariform perforation plates reported in wood of Asteraceae (Carlquist, 1960a, 1965a, b; Meylan & Butterfield, 1978). These occasional scalariform perforation plates are indicative of paedomorphosis and show that primary xylem of Asteraceae retains, in at least some phylads, scalariform perforation plates. Many Asteraceae have Paedomorphic Type I rays (Carlquist, 1966b). These examples show that the evolutionary level of wood of Asteraceae and the intervention of paedomorphosis shown by the wood of Asteraceae are like what we have seen in Campanulaceae and Lobeliaceae.

SOLANALES

I have recognized segregate families of Solanaceae here using the scheme of Hunziker (1979). Hunziker recognized a constellation of families close to Solanaceae: Duckeodendraceae, Goetzeaceae, Nolanaceae, and Sclerophylacaceae (the last of these is entirely herbaceous, and therefore not considered here). These families differ mainly on the basis of embryo, seed, and fruit types. Wood data support recognition of at least one of these: *Duckeodendron* has abundant vasicentric axial parenchyma, banded apotracheal axial parenchyma, and Heterogeneous Type I rays, none of which typify Solanaceae sensu stricto. Wood anatomy of Goetzeaceae and Nolanaceae falls within the range found in Solanaceae. However, this can be considered evidence that these two families are very close to Solanaceae, if one chooses to recognize them as separate from Solanaceae.

The family closest to Solanaceae and their segregate families is Convolvulaceae. Notable in this regard is the occurrence of intraxylary phloem in primary stems of all species of these families. The occurrence of cellular endosperm in Convolvulaceae is one of the few reasons for excluding this family from Solanales.

BORAGINALES

The Boraginales and Solanales of the Dahlgren (1975) system are problematic because, as shown in Table 1, Dahlgren included Polemoniaceae in Solanales, yet families often considered close to Solanales, such as Boraginaceae and Hydrophyllaceae, fall into his Boraginales. Although other types of evidence may show sharper demarcation among orders containing these families and indicate optimal reassignments, evidence from wood cannot be used to segregate Hydrophyllaceae and Boraginaceae from an order that contains Polemoniaceae. Boraginaceae, Hydrophyllaceae, and Polemoniaceae are families in which certain wood features show considerable diversity. For example, in Boraginaceae, axial parenchyma may be diffuse, diffuse-in-aggregates, aliform, confluent, and even vasicentric (either abundant or, in *Echium*, scanty). In Hydrophyllaceae, imperforate tracheary elements range from tracheids to libriform fibers. With ranges of character states of this sort, one cannot use wood anatomy to assign families decisively to one order or another.

FAMILIES OF UNCERTAIN POSITION

Apiaceae are included in Table 1 for comparison to sympetalous families. Araliaceae, closely related to Apiaceae, might more logically have been used for comparison, because they contain more woody species. Apiaceae were chosen in preference, however, because Araliaceae contain some species with more primitive character states than Apiaceae. Apiaceae are thus on a similar evolutionary level to more of the sympetalous families. In fact, the wood anatomy of Apiaceae may be indistinguishable from that of Asteraceae (Table 1). This similarity may in part be due to habit, for the Araliaceae, more nearly arboreal, modally differ in habit from woody Apiaceae, which are shrubs, much like the majority of woody Asteraceae. The embryological and chemical similarities of Apiaceae and Araliaceae to Asteraceae (polyacetylenes, sesquiterpene lactones), when added to the wood features common to these families, are imposing. Not all of these are likely to be homoplasies. In the Olmstead & Palmer (1992) phylogeny, Apiaceae and Araliaceae fall not far from the line leading to Asteraceae.

Desfontainiaceae are a monogeneric family for which we do not have data in key embryological and chemical categories. Nevertheless, wood anatomy is significant because the wood features of *Desfontainia* are so primitive. Clearly, *Desfontainia* does not belong in Loganiaceae, its most common placement; the data of Mennega (1980) clearly showed how different Loganiaceae are. Considering that Desfontainiaceae have a preponderance of primitive wood features, one might consider families with similar wood as possible relatives. In this regard, Columelliaceae are worthy of consideration, as are a number of Escalloniaceae.

Fouquieriaceae have been difficult to place systematically. Most systems have ranked this family close to Cistaceae, Frankeniaceae, or Tamaricaceae. However, Polemoniaceae have been mentioned by a few authors (e.g., Thorne, 1976) as possibly related to Fouquieriaceae. Because Fouquieriaceae contain iridoids, Dahlgren et al. (1976) placed the family in an order of its own near Cornales and Ericales. A feature of Fouquieriaceae not found in Cornales and Ericales (or, for that matter, Polemoniaceae) is the occurrence of two integuments on ovules. With respect to wood anatomy, two features of Fouquieriaceae are rather primitive: presence of tracheids, and presence of diffuse axial parenchyma. Rays of Fouquieriaceae are wide and of a rather specialized type (Homogeneous Type II) not common in sympetalous families. The wood of Fouquieriaceae lacks features to show the familial relationships decisively, and whatever its relatives, the family may be an ancient divergence. Worth mentioning is that the two primitive features cited show that the family has been derived from a phylad with primitive wood. Although Cornales and Ericales are not the only orders with sympetalous families that have notably primitive wood, potential relatives may be found among families that have at least as many primitive wood features as Fouquieriaceae

The small family Salvadoraceae, in which the petals are free or partly united, is known with respect to major embryological features (Table 1). Wood data are also at hand (Metcalfe & Chalk, 1950; Outer & Veenendal, 1981). The occurrence of strands of interxylary phloem within secondary xylem is noteworthy, but this does not appear at present to be a clue to relationships of Salvadoraceae. Neither wood nor embryological features ally Salvadoraceae to Loganiaceae (in which the subfamily Strychneae has interxylary phloem). Storied structure in the wood of *Azima* of the Salvadoraceae is a distinctive feature. The presence of glucosinolates, not present in any of the sympetalous families, may be a clue that the affinities of Salvadoraceae lie outside of the families considered in the present paper. Salvadoraceae have traditionally been placed in Celastrales because of the supposed presence of a disc. The content of Celastrales has become increasingly uncertain in recent phylogenetic systems of dicotyledons, and Salvadoraceae do not appear to be close to the family Celastraceae. Therefore, Salvadoraceae are currently a good example of a family *incertae sedis*, much in need of further investigation.

CONCLUSIONS CONCERNING EVOLUTION OF HABIT

Raylessness appears to be an indicator of secondary woodiness: evolution of a moderately woody habit from an herbaceous ancestry is what may be chiefly envisioned, judging from the examples that are available to date. The distribution of raylessness as reported thus far in the sympetalous families is as follows: Acanthaceae: *Diapedium, Jacobinia, Thunbergia*; Alseuosmiaceae: all genera except *Crispiloba*; Asteraceae: *Lasthenia, Chrysactinia, Dyssodia, Porophyllum, Santolina, Stoebe*; Gesneriaceae: *Besleria, Cyrtandra*; Hydrophyllaceae: *Phacelia* (one species); Pentaphragmataceae: *Pentaphragma*; Plantaginaceae: *Plantago* (all species); Primulaceae: *Lysimachia* (all species); Polemoniaceae: *Cobaea, Leptodactylon*; Rubiaceae: *Galium*; Scrophulariaceae: *Calceolaria, Hebe* (all species); Selaginaceae: *Selago, Walafrida*; Stylidiaceae: *Stylidium* (all woody species).

Another pertinent listing with regard to shift from herbaceous to woody habit is that for taxa in which woods have predominantly upright ray cells. The similarity to raylessness can be seen if one envisions ray cells so tall that they approximate libriform fibers in height. Families in which predominance of upright cells in rays is common, at least in some species, include: Acanthaceae, Asclepiadaceae, Asteraceae, Boraginaceae (a few, e.g., *Echium*), Calyceraceae, Campanulaceae, Chloanthaceae, Convolvulaceae, Gentianaceae, Gesneriaceae, Goodeniaceae, Hydrophyllaceae, Lamiaceae, Loasaceae, Lobeliaceae, Martyniaceae, Nolanaceae, Pedaliaceae, Plumbaginaceae, Polemoniaceae, Rubiaceae (tribe Rubieae), Scrophulariaceae, Solanaceae (*Cestrum*, some *Solanum* species), Stilbaceae, Valerianaceae, Verbenaceae (a few, such as *Lantana*).

All of the families in both lists or either list are ones in which herbaceous species occur, or are common. Therefore, occurrence of secondary woodiness in at least a few species should not be surprising. Upright ray cells by themselves are not indicative of derivation from an herbaceous ancestry, but only predominance of upright ray cells (preferably combined with other paedomorphic indicators, such as a paedomorphic age-on-length curve in vessel element length: Carlquist, 1962a) indicates secondary woodiness. Thus, some shrubby Asteraceae do not have paedomorphic rays, and this may represent a shrubby ancestry for the family (Carlquist, 1966b). However, most arboreal Asteraceae have a predominance of upright ray cells, thereby indicating that they may be derived from shrubby or even herbaceous ancestors. In a large and complex family such as Asteraceae, progression from more woody to less woody may have occurred many times independently, and secondary woodiness also may have occurred in many phylads independently. Definitely derived from herbaceous ancestors according to all indicators are such families as Campanulaceae, Lobeliaceae, Plantaginaceae, Pentaphragmataceae, and Valerianaceae. There are instances in which only a small proportion of a family is rayless or has upright ray cells, and thus only one segment of a family may represent secondary woodiness. For example, Rubiaceae are undoubtedly derived from woody ancestors, judged from wood anatomy and the systematic distribution of woodiness in the family. However, *Galium* is an herbaceous genus, with annual species. Species of *Galium* in frost-free climates, such as southern California, are perennial and can develop a moderate amount of wood. Given this limited amount of information, one cannot say that all species of *Galium* are secondarily woody; some might represent a transition between woody ancestors and the annual habit. However, in any particular subgenus of *Galium*, distribution of woodiness with relation to character states of other characters might demonstrate the likelihood of secondary woodiness, as demonstrated by cladistic means.

In this regard, the work of Baldwin (1989) on the subtribe Madiinae, tribe Heliantheae of Asteraceae, is noteworthy. Because the DNA evidence with which Baldwin deals is so readily polarizable, the likelihood of a cladistic hypothesis generated from such data is extremely high. Thus, we can say with great assurance, based on the data of Baldwin et al. (1991), that the Hawaiian Madiinae are derived from a clade of Californian Madiinae, and that the Hawaiian Madiinae are derived from ancestors all of which could be put in the genus *Madia*, if a broad generic concept (including *Raillardella* and *Raillardiopsis*) were considered. A hybrid between *Raillardella* and the Hawaiian genus *Dubautia* has been produced (Baldwin & Kyhos, unpublished). The Californian species of *Madia*, even in an extremely broad concept, are annuals or minimally woody perennials. There is every reason to believe that the extant species are very similar in habit to the immediate ancestors of the Hawaiian Madiinae. Thus, the Hawaiian species of *Dubautia* and *Wilkesia*, which are shrubs or trees, are clearly secondarily woody. Increasingly, it will be possible to use DNA evidence to demonstrate, using cladistic means, the likelihood of secondary woodiness in particular groups.

The data from wood anatomy do, however, give excellent circumstantial evidence that phylesis toward herbaceousness is common in the sympetalous families, and that in a number of phylads (very likely the rayless ones plus many of the phylads with predominantly upright ray cells) secondary woodiness has occurred. Compared with dicotyledons at large, trends to or from herbaceousness in the sympetalous families seem relatively common.

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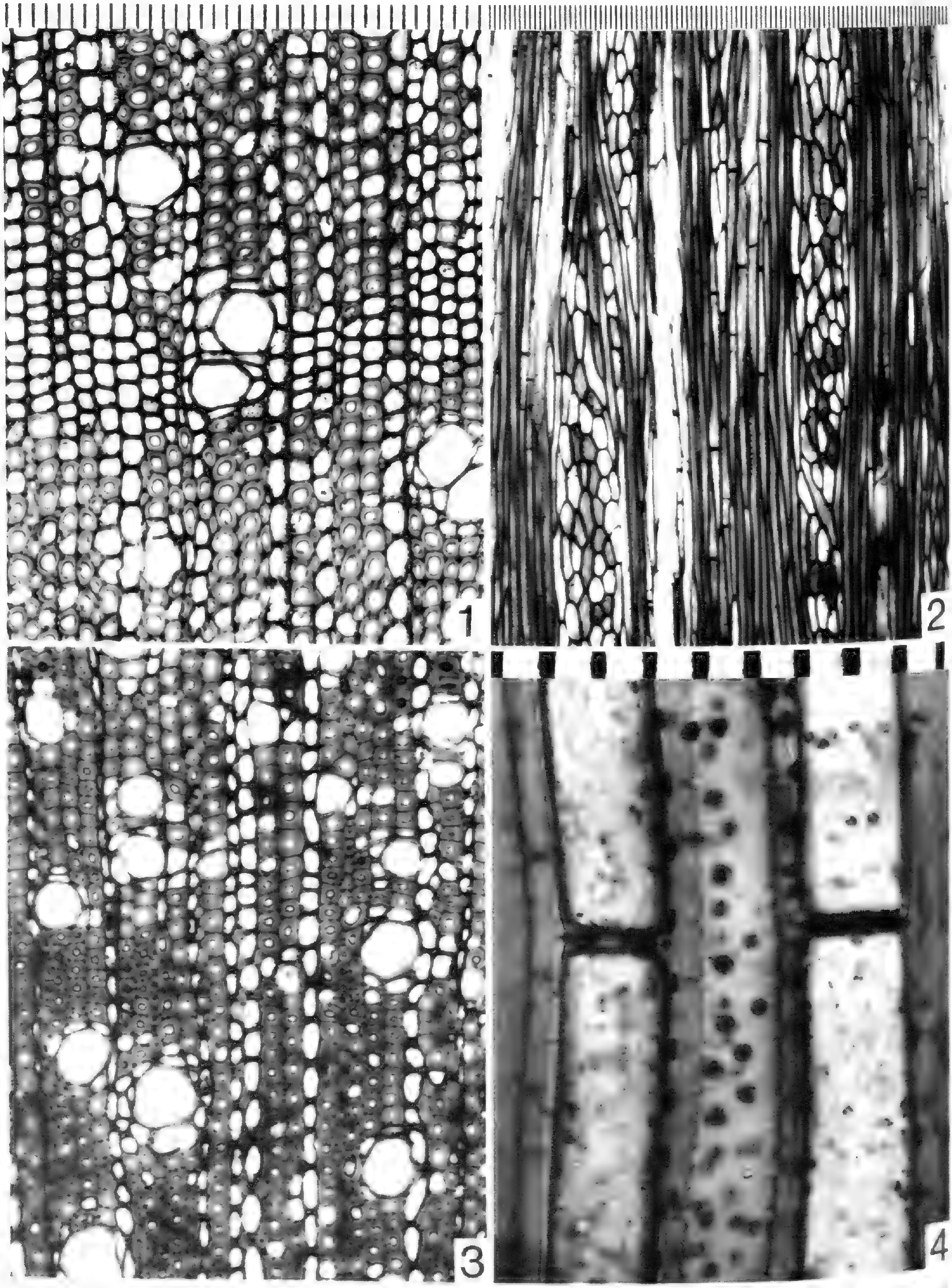
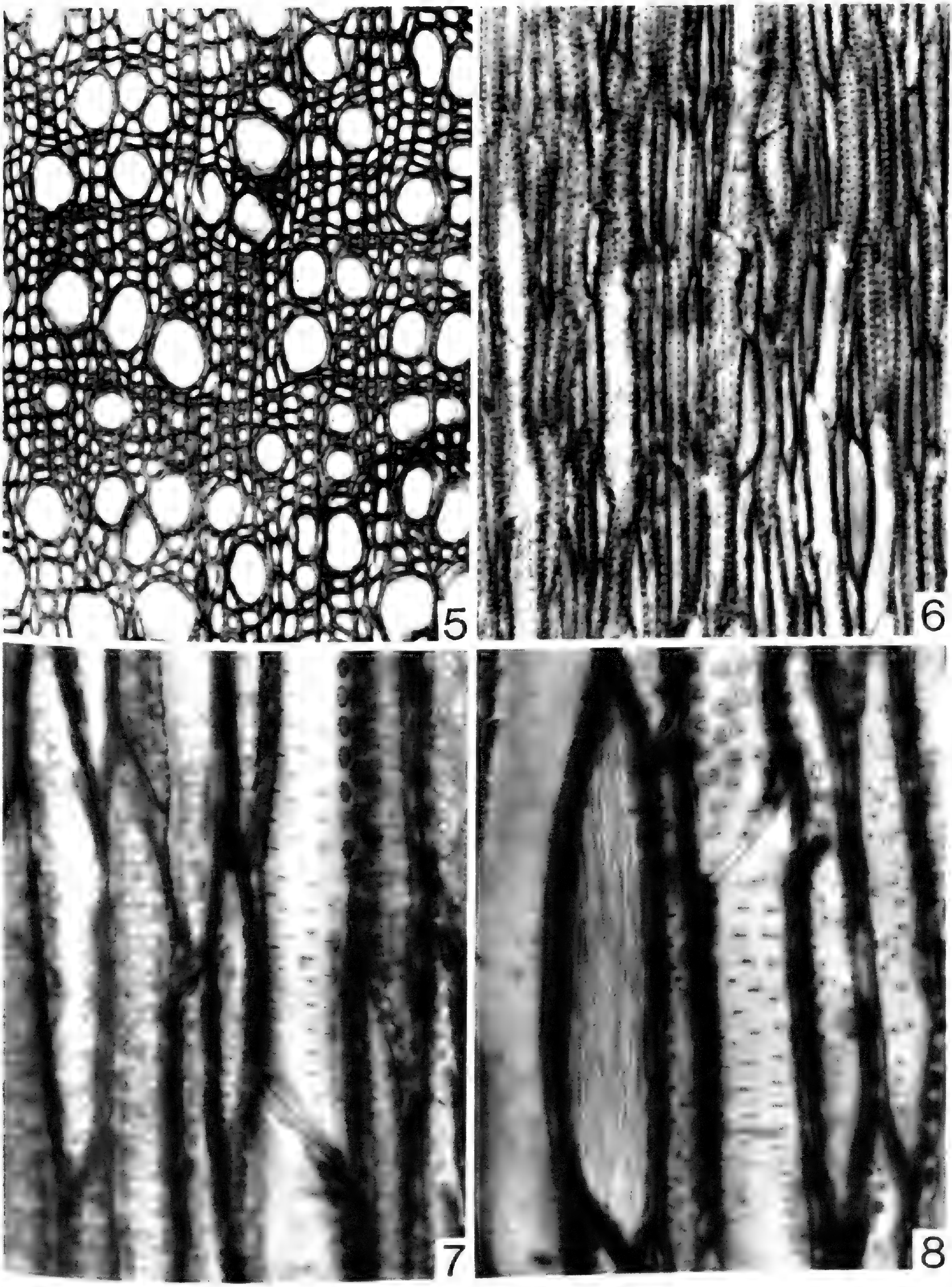
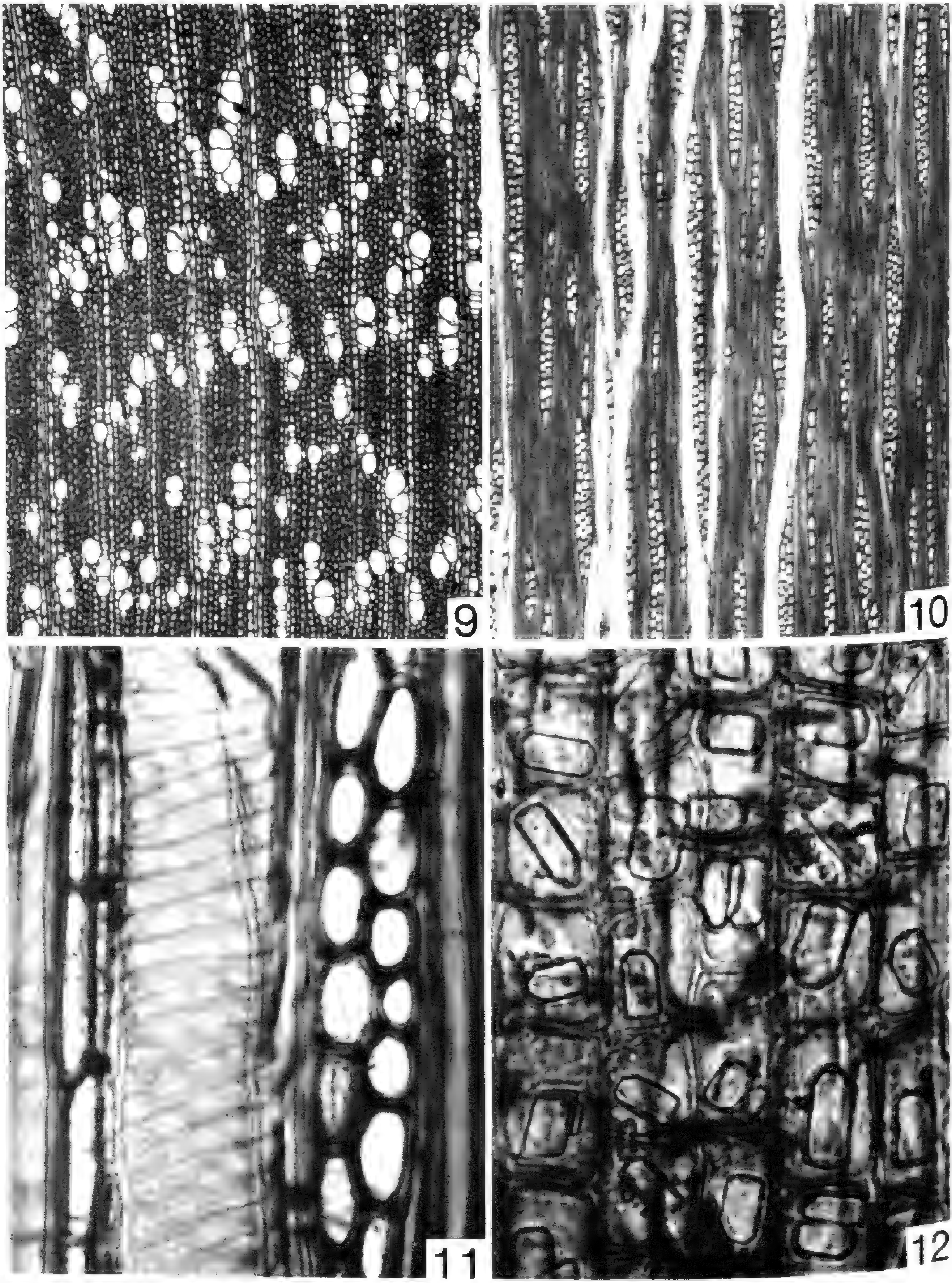


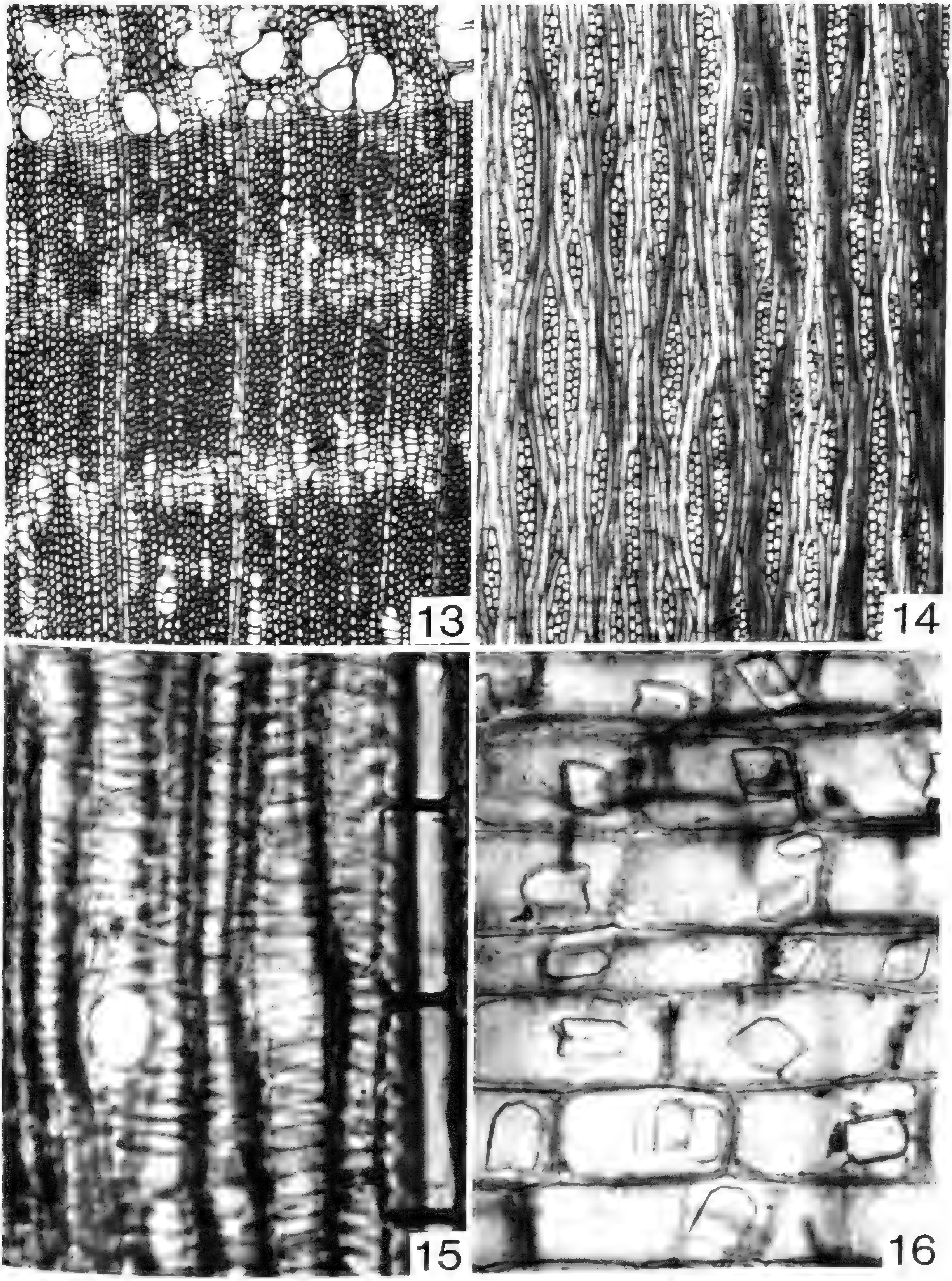
FIGURES 1–4. Wood sections of *Coprosma* (Rubiaceae). 1, 2. *C. montana* (*USw-15336*). 1. Transection; ba of axial parenchyma near middle. 2. Tangential section; rays are multiseriate, composed mostly of upright ce 3, 4. *C. foliosa* (*USw-15307*). 3. Transection; axial parenchyma is scanty vasicentric plus a few diffuse ce 4. Tracheid (center) with axial parenchyma on either side, from radial section; pits on tracheid are small but fu bordered. Figures 1, 3, magnification scale above Figure 1 (divisions = 10 μm). Figure 2, scale above Figure (divisions = 10 μm). Figure 4, scale above Figure 4 (divisions = 10 μm).



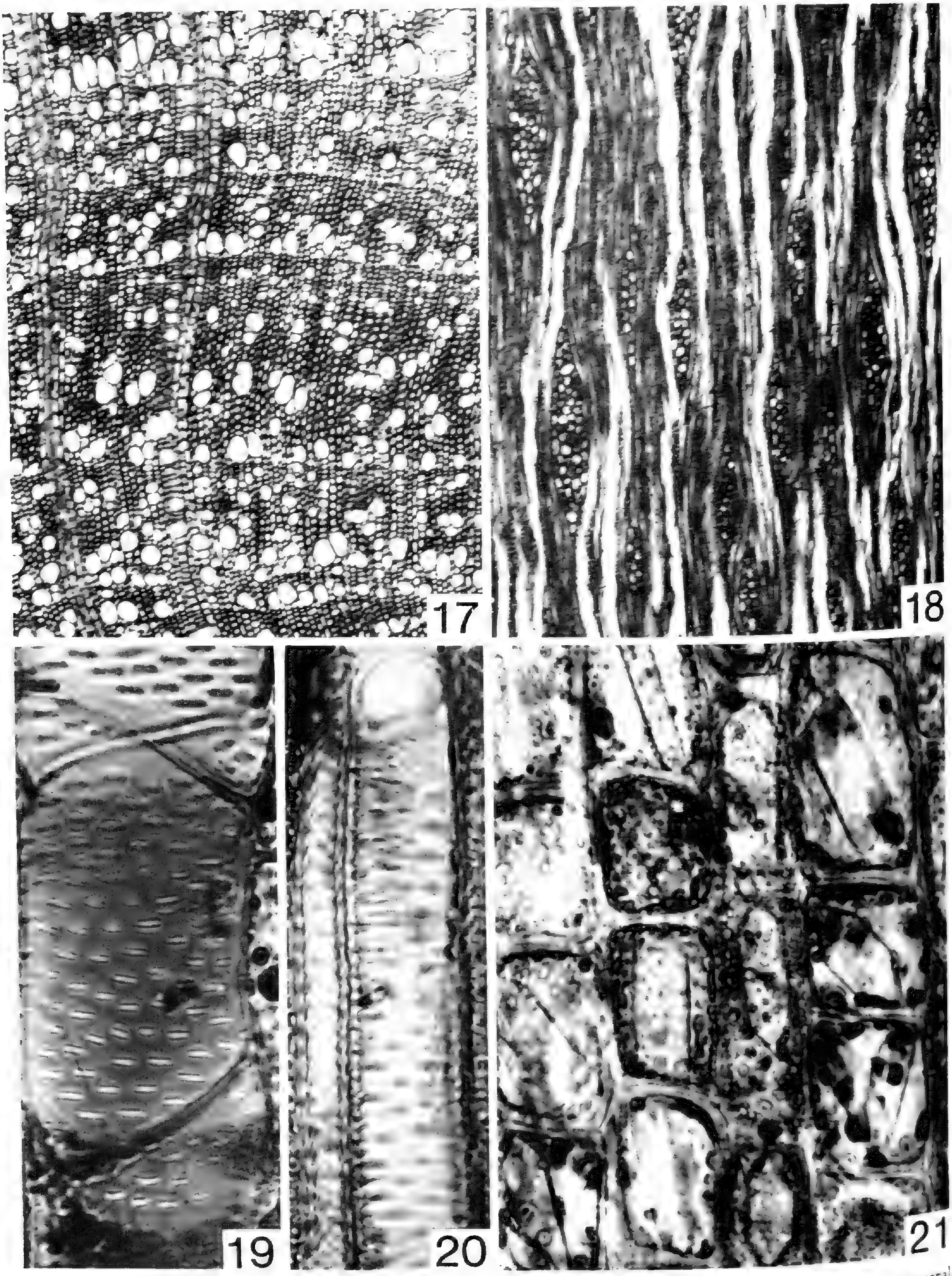
FIGURES 5–8. Wood sections of *Galium catalinense* (*Davidson 1417*, RSA). —5. Transection; vessels are mostly solitary. —6. Tangential section, showing nearly rayless condition; storying is present. —7. Portion of tangential section to show vessel and tracheids with small but fully bordered pits. —8. Portion of tangential section; axial parenchyma cells at right, ray cell containing raphides at left. Figures 5, 6, scale above Figure 1; Figures 7, 8, scale above Figure 3.



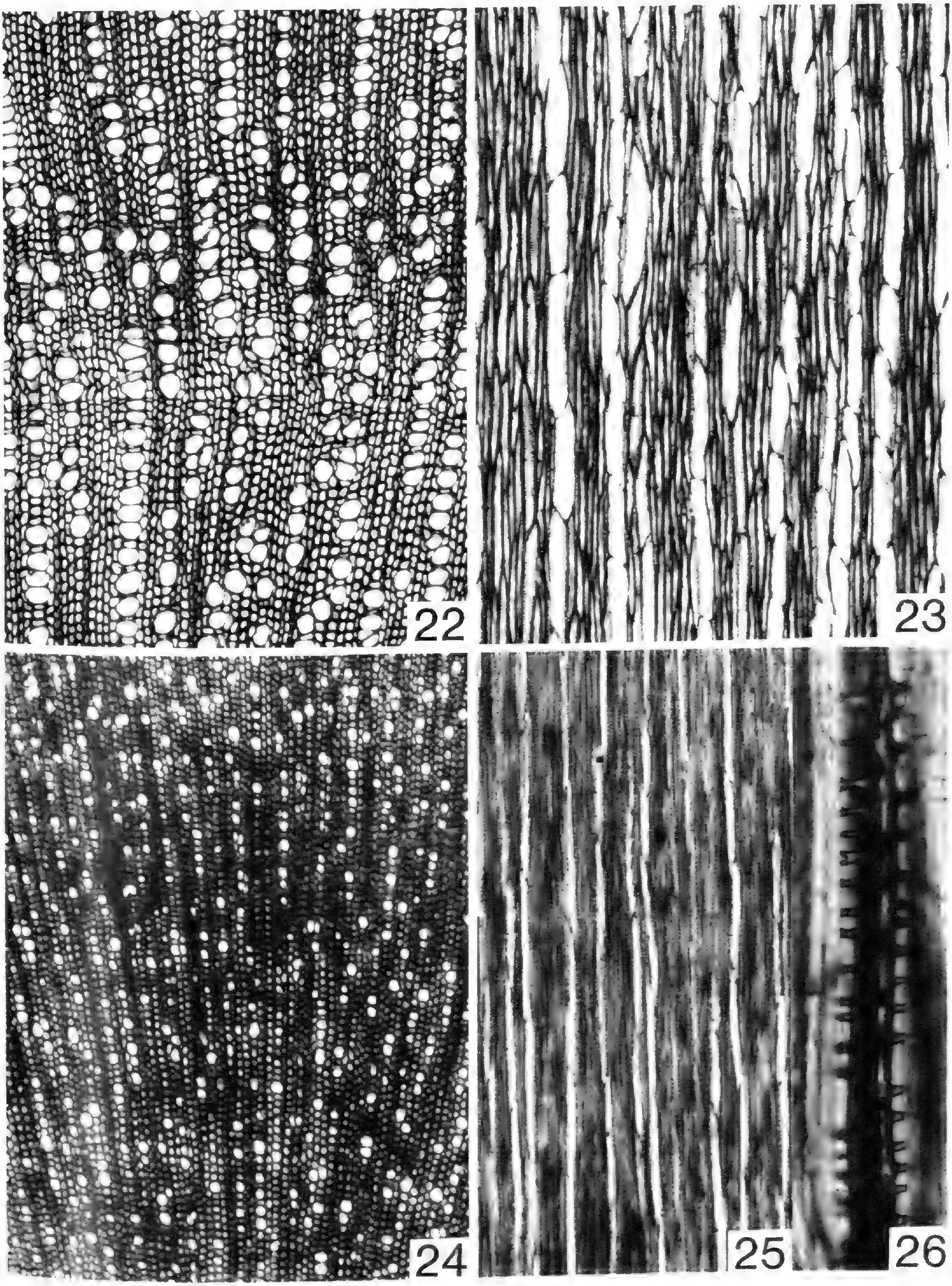
FIGURES 9–12. Wood sections of *Buddleja globosa* (*Carlquist 7278*, RSA). 9. Transection; vessels are not in large groupings.—10. Tangential section; uniseriate rays are about as frequent as multiseriate rays.—11. Vessel and portion of ray from tangential section; helical thickenings present in vessel.—12. Ray from radial section (horizontal axis of ray oriented vertically) to show crystals in ray cells. Figures 9, 10, scale above Figure 2. Figures 11, 12, scale above Figure 4.



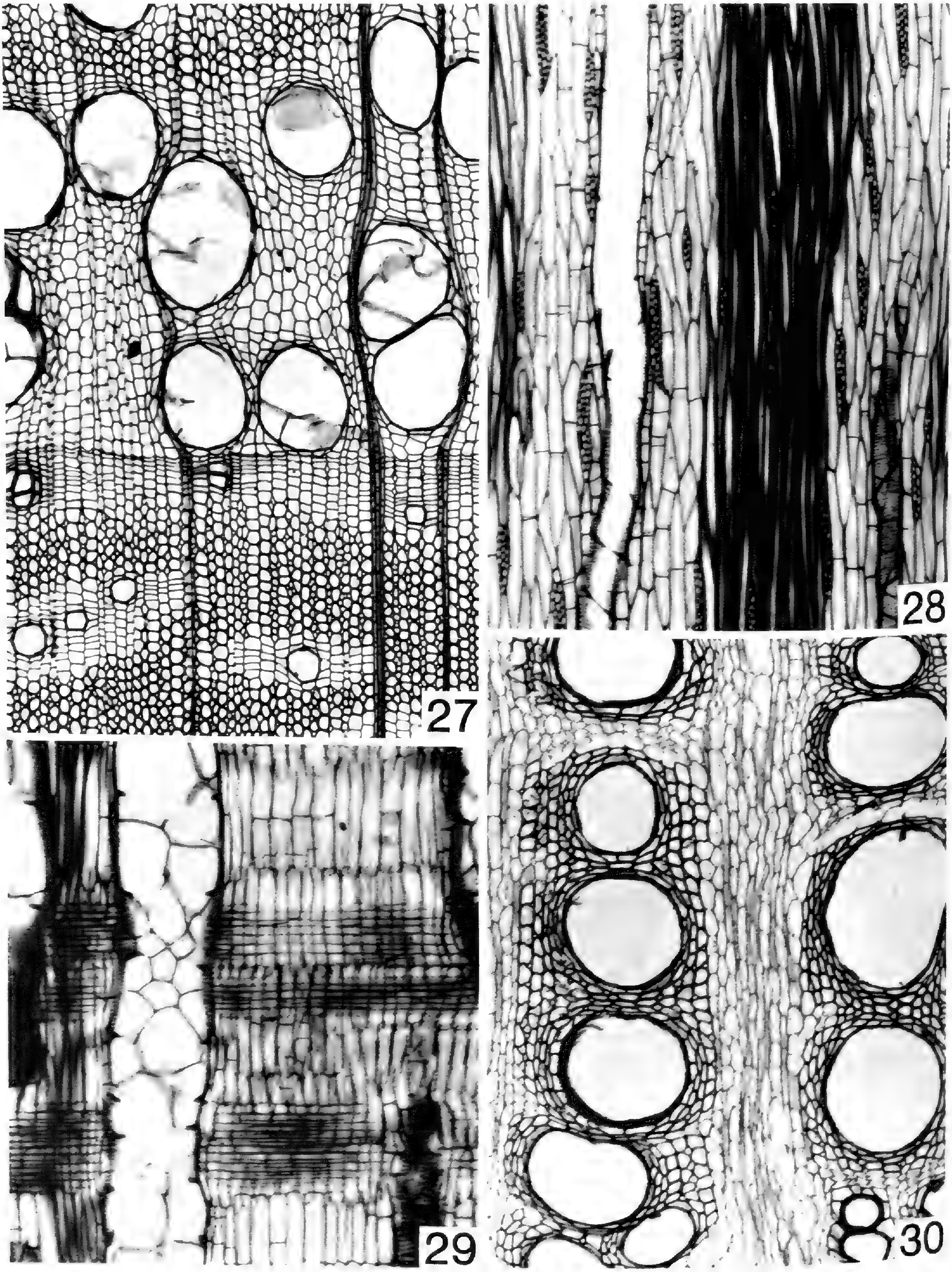
FIGURES 13–16. Wood sections of *Buddleja parviflora* (*Iltis & Koeppen 106*, MAD). 13. Transection, showing earlywood at top; most of photograph is latewood, which contains tangential bands of narrow vessels. 14. Tangential section; uniseriate rays are infrequent. 15. Latewood vessels from radial section, showing helical thickenings. 16. Ray cells from radial section to show types of crystals present. Figures 13, 14, scale above Figure 2. Figures 15, 16, scale above Figure 4.



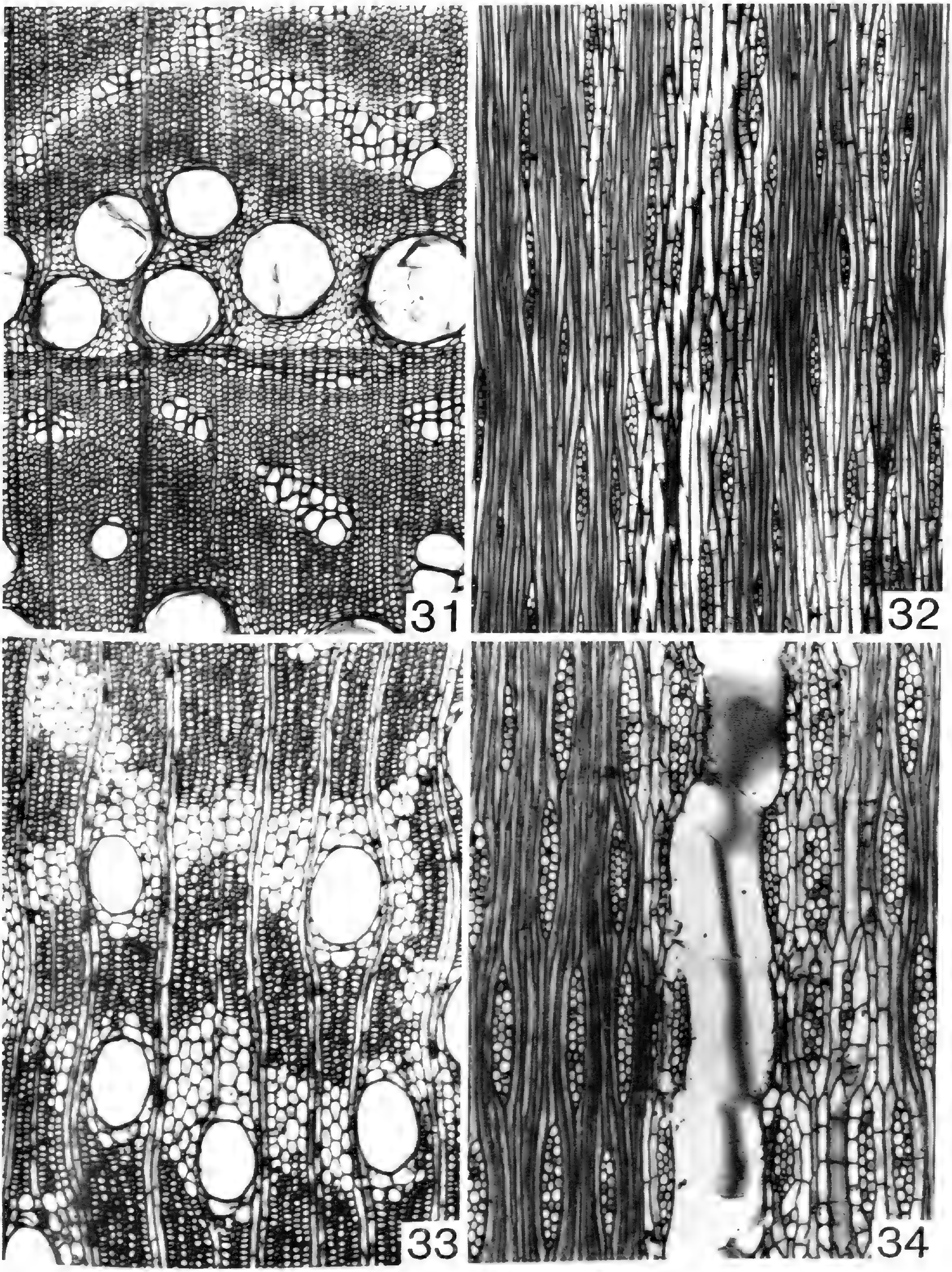
FIGURES 17–21. Wood sections of *Buddleja utahensis* (*Thorne 44537*, RSA).—17. Transection, showing several weakly defined growth rings.—18. Tangential section; rays are few but wide.—19. Vessel from earlywood; helical thickenings are absent.—20. Vessel and (left) vasicentric tracheid from latewood; helical thickenings are present.—21. Ray cells from radial section (horizontal axis of ray oriented vertically) to show elongate crystals. Figures 17, 18, scale above Figure 2. Figures 19–21, scale above Figure 4.



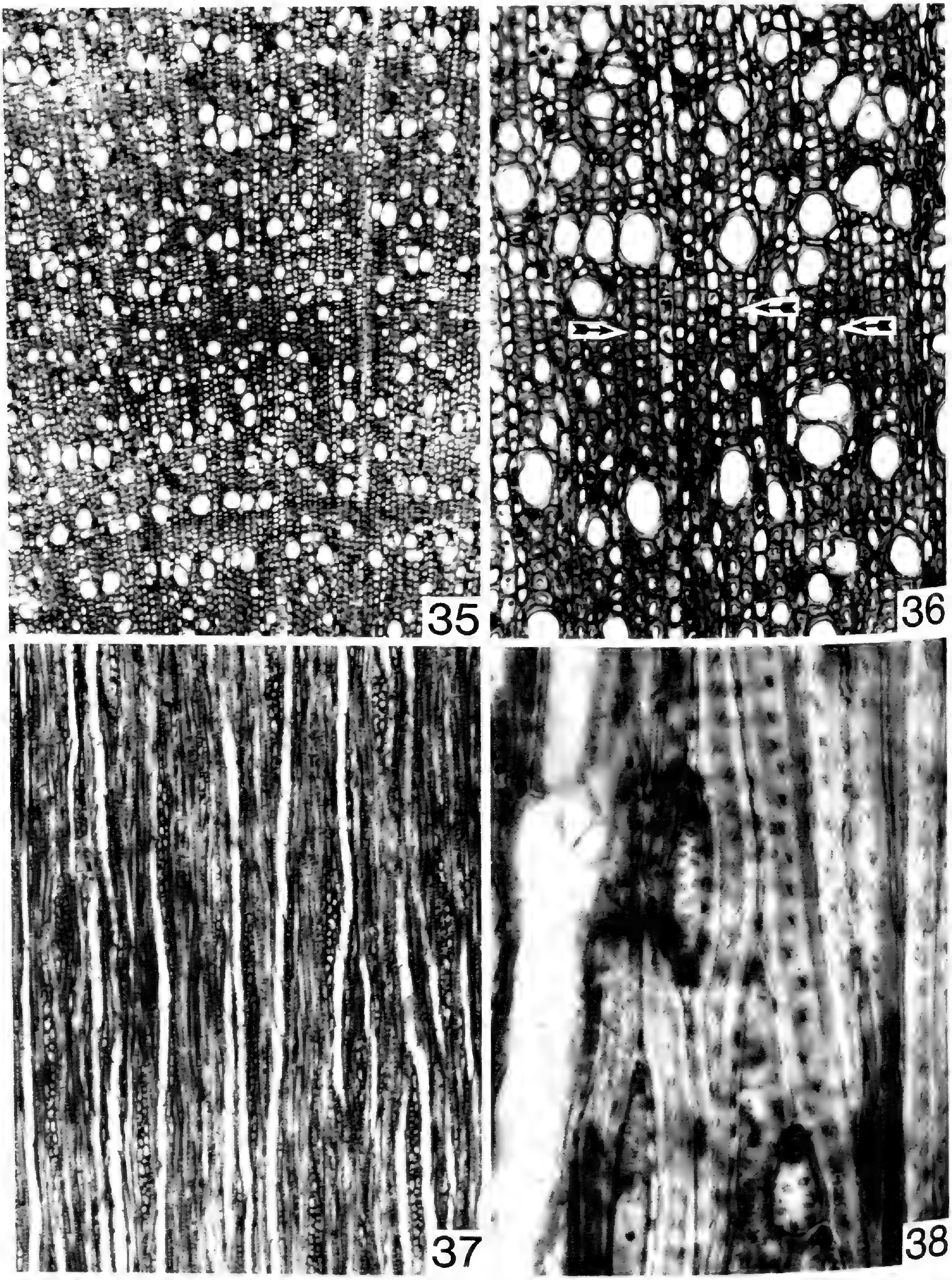
FIGURES 22–26. Wood sections of rayless Scrophulariaceae. 22, 23. *Calceolaria adscendens* (*Carlquist 7224*, RSA). —22. Transection; vessels are in radial chains and radial multiples. —23. Tangential section to show raylessness; some storying is present. 24–26. *Hebe elliptica* (*Carlquist 8151*, RSA). —24. Transection; vessels are very narrow and mostly solitary. —25. Tangential section to show rayless condition. —26. Fiber-tracheid from tangential section; air in the fiber-tracheid outlines the pits, which have vestigial borders. Figures 22–25, scale above Figure 2. Figure 26, scale above Figure 4.



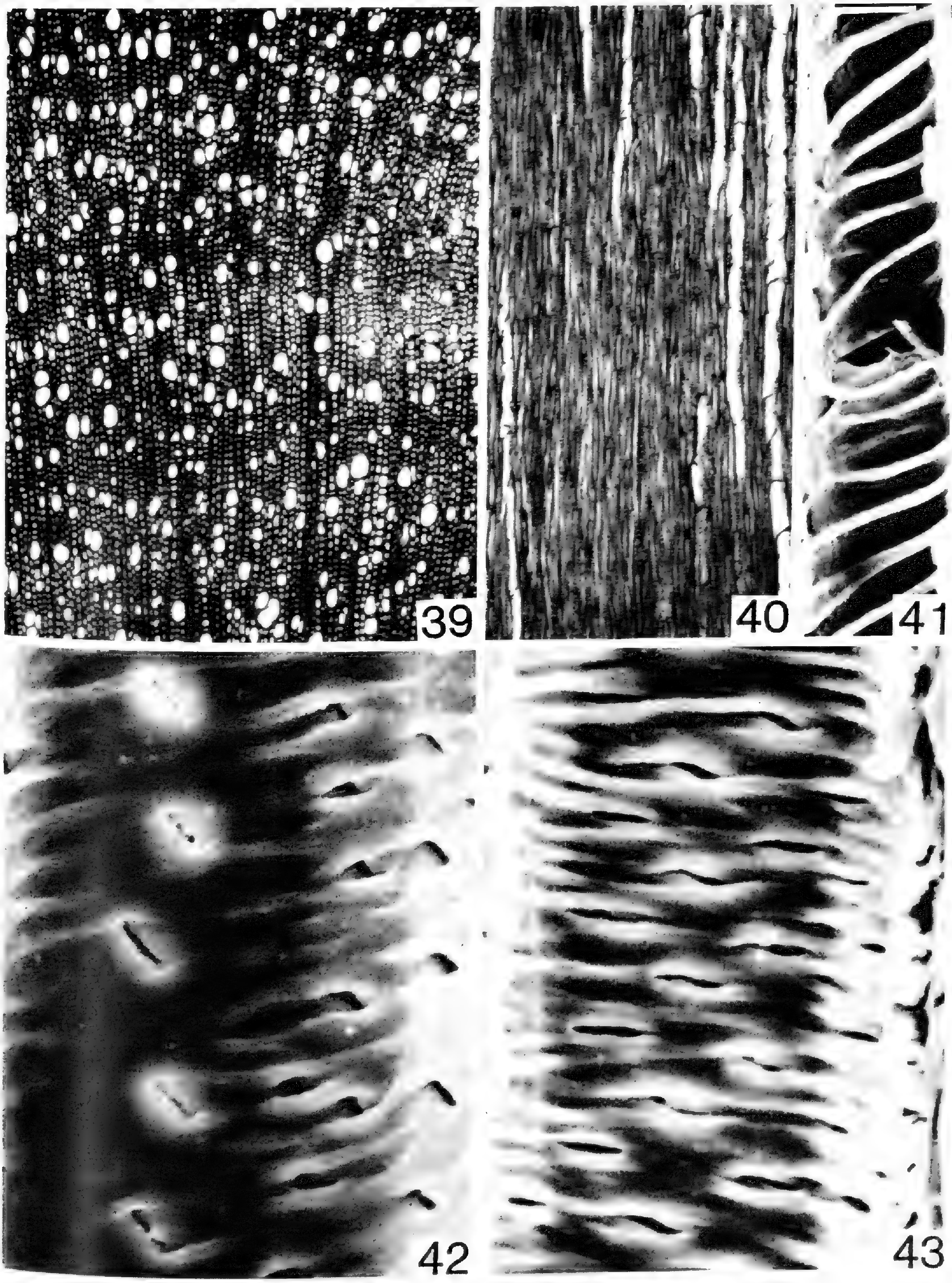
FIGURES 27–30. Wood sections of *Paulownia* and *Faradaya*. 27–29. *Paulownia tomentosa* (no collection data). —27. Transection; extensive axial parenchyma in earlywood (above); aliform axial parenchyma in latewood (below). —28. Tangential section (dark cells, center, are libriform fibers); rays are Homogeneous Type II. —29. Radial section; axial parenchyma cells undivided or in strands of two cells; tyloses in vessels, right. —30. *Faradaya splendens* (SFCw-R1185-110), transection; the vessels are wide, sheathed by libriform fibers. Figures 27–29, scale above Figure 2.



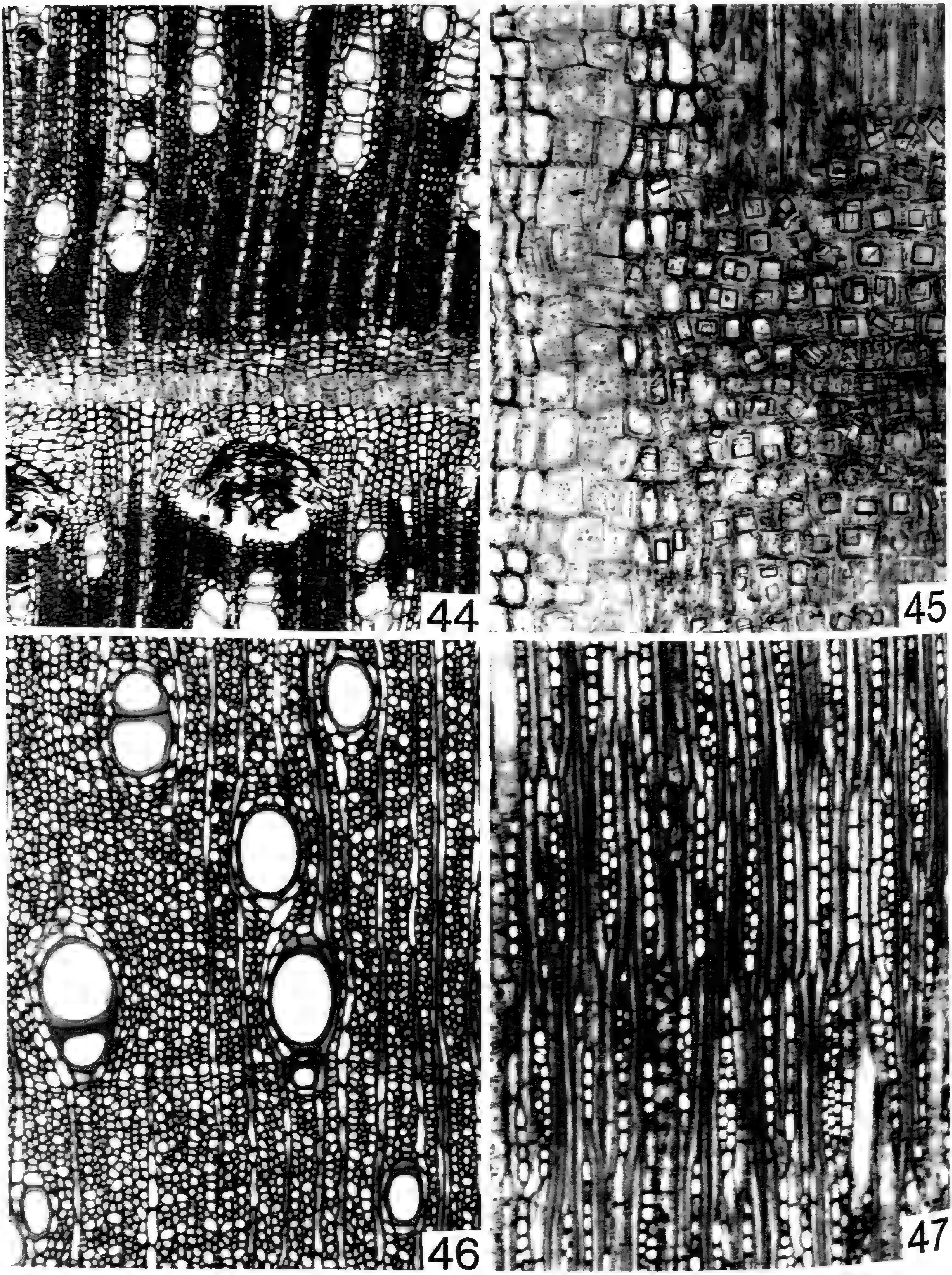
FIGURES 31–34. Wood sections of Bignoniaceae. 31, 32. *Catalpa speciosa* Warder (no collection data). 31. Transection; extensive axial parenchyma in earlywood (just above center); axial parenchyma is scanty vasicentric in latewood (top, latewood vessels are in diagonal aggregations). 32. Tangential section; rays are not storied. 33, 34. *Tecoma pentaphylla* (*USw-5600*). 33. Transection; axial parenchyma is aliform-confluent. 34. Tangential section; rays are storied. Figures 31–34, scale above Figure 2.



FIGURES 35–38. Wood sections of *Globularia salicina* (*Carlquist 2629*, RSA).—35. Transections; vessels are mostly solitary. 36. Portion of transection; axial parenchyma is diffuse (two such cells are indicated with arrows) and scanty vasicentric. —37. Tangential section; rays are Heterogeneous Type IIA.—38. Portion of tangential section to show numerous bordered pits in tracheids. Figures 35, 37, scale above Figure 2. Figure 35, scale above Figure 1. Figure 38, scale above Figure 4.



FIGURES 39–43. Wood sections of Selaginaceae. 39, 40, 43. *Walafrida nitida* (*Carlquist 8062*).—39. Transection; growth rings are absent.—40. Tangential section; rays are absent. 41, 42. *Selago thunbergii* (*Carlquist 8061*). SEM photographs from tangential sections.—41. Vasicentric tracheid; helical thickenings are prominent.—42. Wide vessel wall; helical thickenings are present but not pronounced.—43. SEM photograph of vessel from tangential section to show helical thickenings. Figures 39, 40, scale above Figure 2. Figures 41–43, bar at top of Figure 41 (bar = 1 μm).



FIGURES 44–47. Wood sections of Avicenniaceae and Ebenaceae. 44, 45. *Avicennia marina* Vierh. (*USw-4255*).—44. Transection; conjunctive tissue, just below center, contains a sclerenchyma band.—45. Radial section, showing crystals in conjunctive tissue cells; sclerenchyma band, left. 46, 47. *Diospyros virginiana* L. (*USw-20364*).—46. Transection; axial parenchyma is diffuse, diffuse-in-aggregates, vasicentric.—47. Tangential section; rays are storied. Figures 44–47, scale above Figure 2.

PHYLOGENETIC RELATIONSHIPS OF DIPSACALES BASED ON *rbc*L SEQUENCES[1]

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ABSTRACT

Nucleotide sequences of the chloroplast gene *rbc*L were obtained from *Lonicera, Sambucus, Adoxa,* and *Cornus.* Phylogenetic analyses of these sequences, along with previously sequenced Dipsacales and placeholders for other Asteridae and Rosidae, lead to the following conclusions: (1) the genera of Caprifoliaceae (in any traditional sense) do not form a monophyletic group; (2) *Symphoricarpos* and *Lonicera* (representing Caprifoliaceae sens. str.) are related and are united with Valerianaceae and Dipsacaceae; and (3) *Adoxa* and *Sambucus* are directly linked and are possibly related to *Viburnum.* Our analyses also cast doubt on the monophyly of Dipsacales and Asteridae. These findings are generally congruent with other molecular results and with hypotheses based on morphological data.

Uncertainty has long surrounded the phylogenetic relationships of taxa traditionally assigned to the angiosperm order Dipsacales (Donoghue, 1983). It has been unclear, for example, whether *Adoxa* is related to Dipsacales, whether *Sambucus* and *Viburnum* are closely related to one another or to genera of Caprifoliaceae sens. str., or whether some Caprifoliaceae are more closely related to Valerianaceae and/or Dipsacaceae than they are to each other. The broader phylogenetic relationships of these plants have also been debated. It is still uncertain whether Dipsacales were derived from (i.e., are nested within) Rubiales, as implied by Cronquist (1981, 1988), or whether they (and possibly Asterales) are more closely related to rosid groups such as Cornales, as suggested recently by Takhtajan (1987; also see Dahlgren, 1983; Thorne, 1983).

Donoghue (1983) considered morphological evidence bearing on these questions, especially the relationships of *Viburnum.* However, owing to uncertainty over broader phylogenetic relationships, he was able to reach only tentative conclusions, conditional on particular assumptions. For example, *if* Caprifoliaceae sens. lat. and Dipsacales are both monophyletic, *then* morphological data directly unite *Viburnum* with *Sambucus* plus *Adoxa,* whereas under some other assumptions (e.g., Dipsacales polyphletic) this connection is unclear. Substitution of different outgroup arrangements (sensu Donoghue & Cantino, 1984) yielded few unequivocal conclusions. Happily, however, the position of *Adoxa* was an exception. If *Adoxa* is assumed to be related in some way to other Dipsacales (as opposed, for example, to Saxifragaceae), then it is invariably linked with *Sambucus* on the basis of several morphological features, including *Adoxa*-type embryo sac development.

Here we present a preliminary analysis of the phylogenetic relationships of dipsacalean taxa based on molecular data. In particular, we report the results of parsimony analyses of chloroplast *rbc*L sequences (see Ritland & Clegg, 1987; Palmer et al., 1988; Soltis et al., 1990; Doebley et al., 1990; Olmstead et al., 1992) of various Dipsacales and possibly related groups, including new sequences

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from representatives of four critical genera: *Adoxa*, *Sambucus*, *Lonicera*, and *Cornus*. Although we are able to make some comparisons between the molecular results and those based on morphological characters, a detailed comparison must await the completion of an expanded morphological study (Donoghue, in prep.) and sequencing of additional Dipsacales (in progress). In the meantime, we highlight conclusions that are most strongly supported by *rbc*L data, so that these can be taken into account in formulating a phylogenetic system of Asteridae.

MATERIALS AND METHODS

*rbc*L sequences were newly obtained from four taxa: *Adoxa moschatellina* L. of Adoxaceae, *Cornus mas* L. of Cornaceae, and *Sambucus racemosa* subsp. *sieboldiana* (Miquel) Hara, and *Lonicera prolifera* Rehder of Caprifoliaceae sens. lat. The Wisconsin Department of Natural Resources kindly permitted the collection of *Adoxa* specimens in Vernon County, Wisconsin (*Donoghue, Smith, & Kuetchenreuther 1*, WISC). Material of the other species was obtained by M. Donoghue at the Arnold Arboretum, Jamaica Plain, Massachusetts (where vouchers are deposited). In each case, fresh leaves were collected on ice and then stored at −80°C, and DNA extractions were carried out using a modified CTAB method (Doyle & Doyle, 1987; Smith et al., 1992).

A segment of the chloroplast genome containing the *rbc*L gene was amplified by the polymerase chain reaction (PCR), using the primers described in Olmstead et al. (1992; see their fig. 1). This procedure yielded double-stranded segments of approximately 1550 bp. Each amplification product was then digested with the restriction endonucleases EcoRV and XbaI, known to recognize other Asteridae *rbc*L at nucleotide positions 103–108 and 1269–1274, respectively. As expected, this procedure yielded three fragments in *Adoxa*, *Lonicera*, and *Cornus*: a 5′ segment of 102 bp, an internal segment of 1172 bp including most of the *rbc*L gene, and a 3′ segment of approximately 290 bp (minor variation owing to length difference downstream of *rbc*L). However, in the case of *Sambucus* the double digest yielded four fragments due to an additional EcoRV site present at nucleotide positions 1018–1023 bp. This site is also found in *Vibrunum plicatum*, and more extensive restriction site studies indicate its presence in other (but not all) species of *Viburnum* (Donoghue & Sytsma, unpublished).

The fragments obtained were cloned in the plasmid vector BlueScript Sk+ (Stratagene, Inc.) as described by Olmstead et al. (1992), and single stranded DNAs were prepared (phenol-chloroform extraction) from selected colonies screened for inserts of the larger EcoRV-XbaI fragments (or the equivalent fragments in *Sambucus*). Sequencing was carried out using the dideoxy chain termination technique, with internal primers kindly provided by G. Zurawski (DNAX Research Institute, Palo Alto, California). In some cases the smaller 5′ and 3′ fragments were recovered and sequenced, so that the entire *rbc*L sequence was obtained. However, the analyses reported below are based solely on the internal 1172 bp segment. Using the known tobacco sequence as a reference, differences in our sequences were easily scored; length differences were never encountered in the region of interest. The sequences utilized in the present study will be available in GenBank, and may also be obtained directly from M. Donoghue or R. Olmstead.

A total of twelve taxa were included in the phylogenetic analyses reported here. These were selected so as to represent Dipsacales and other major lines of Asteridae and relevant Rosidae, as well as to include suggested relatives of the dipsacalean taxa, especially *Adoxa*. In addition to the four newly sequenced taxa discussed above, seven sequences were obtained from workers in J. Palmer's laboratory: R. Olmstead provided *Hedera helix* L. (Araliaceae) and *Symphoricarpos albus* Blake (Caprifoliaceae sens. str.) (see Olmstead et al., 1992), as well as *Spigelia marilandica* L. (Loganiaceae) and *Menyanthes trifoliata* L. (Menyanthaceae) (R. Olmstead, unpublished); and H. J. Michaels (pers. comm.; Michaels et al., in prep.) is responsible for *Viburnum acerifolium* L. (Caprifoliaceae sens. lat.), *Dipsacus sativus* Honckeny (= *D. fullonum* L.) (Dipsacaceae), and *Valeriana officinalis* L. (Valerianaceae). The published sequence (Soltis et al., 1990) of *Heuchera micrantha* Dougl. (Saxifragaceae) was also included.

Elimination of invariant nucleotide positions left 194 variable sites, and by omission of autapomorphies this was further reduced to 88 potentially informative characters (Table 1). Of the latter, 74 are binary, 12 are unordered 3-state, and 2 are unordered 4-state characters, so there are a minimum of 104 character state changes (steps) in the absence of homoplasy. Note that the vast majority of potentially informative sites occur at third positions within codons; only eight are at first positions and six at second positions.

Character state changes were equally weighted in most of our analyses, but we did experiment with several differential weighting schemes, includ-

TABLE 1. Twelve taxa scored for 88 potentially informative *rbc*L characters (invariant sites and autapomorphies removed), with characters numbered by base position within the gene. All positions are third positions within codons, unless otherwise indicated above the character number. The complete set of potentially informative nucleotides is given for *Heuchera* (used to root trees); a nucleotide is shown for other taxa only if it differs from *Heuchera* (a dot indicates that the same nucleotide is present). Missing information (due to ambiguity in scoring) is indicated by "?."

	138	147	159	168	177	186	213	225	227(2)	255	267	271(1)	283(1)	284(2)	290(2)	312	345	357	363	393	412(1)	420	426	441	450	459	462	495	501	507	540	555	561	564	579	582	606	612	624	648	672	673(1)	677(2)	682(1)	687	711	732
HEUCHERA	T	A	G	G	T	T	C	C	A	T	C	G	A	G	T	C	C	C	G	C	C	C	T	T	G	T	C	T	T	A	A	C	A	A	C	T	T	A	C	C	A	C	A	G	A	G	A
HEDERA	.	.	A	.	C	.	.	.	G	C	.	.	.	.	.	A	.	.	A	T	.	.	.	.	C	.	.	.	.	G	.	.	.	G	.	.	C	G	.	T	.	.	.	.	G	.	G
CORNUS	.	.	A	.	C	.	.	T	G	C	.	.	.	A	.	.	T	.	.	T	.	T	.	.	C	.	.	.	.	G	.	.	.	.	A	.	.	G	.	.	.	A	T	T	G	.	.
SPIGELIA	C	?	.	A	C	.	.	T	G	C	T	C	G	A	A	.	.	.	A	.	T	.	.	C	.	C	G	.	A	G	.	.	G	G	T	.	.	.	.	T	.	.	T	.	.	A	.
MENYANTHES	.	.	A	A	C	.	.	G	G	.	.	C	.	.	.	A	.	.	A	T	T	.	.	.	C	C	.	.	.	G	.	.	.	T	T	.	.	.	.	T	G	.	.	.	G	.	G
ADOXA	.	.	A	.	C	.	T	.	.	C	.	.	.	C	.	A	.	.	.	.	.	T	.	.	C	.	T	.	.	G	.	.	.	G	.	C	C	G	T	T	C	.	.	.	.	.	G
SAMBUCUS	.	.	A	.	C	.	T	.	G	C	.	.	.	.	.	A	.	.	.	.	.	T	.	?	C	.	T	.	.	G	.	.	.	G	.	C	C	G	T	T	G	.	.	.	.	.	G
VIBURNUM	.	.	A	.	C	.	T	.	G	C	.	.	.	.	.	A	.	.	.	?	.	T	.	.	C	.	.	.	A	G	.	.	.	G	.	C	C	G	.	T	.	A	.	.	.	.	G
LONICERA	C	G	.	.	.	A	.	.	G	C	.	.	.	C	.	A	.	T	.	.	.	.	C	.	C	.	T	C	.	G	.	.	G	G	A	.	.	G	.	T	C	A	T	.	.	.	.
SYMPHORICARPOS	.	G	A	.	.	A	.	.	G	C	.	C	.	C	.	A	.	T	.	.	.	.	C	C	C	.	T	C	C	G	.	.	G	G	A	.	.	G	.	T	C	A	.	.	G	.	.
VALERIANA	G	.	A	.	C	A	.	G	G	C	T	.	G	C	.	A	T	T	.	T	.	.	.	.	C	C	T	C	.	.	G	T	.	G	A	.	.	G	.	T	C	A	.	T	.	.	G
DIPSACUS	C	.	A	A	C	A	.	.	G	C	.	.	.	A	A	A	.	T	.	.	.	T	C	.	C	.	.	.	A	G	G	T	.	.	A	.	.	G	.	T	C	.	.	.	.	A	.

	741	747	753	759	763(1)	771	801	804	808(1)	816	834	836(2)	840	846	885	927	930	950(2)	982(1)	984	990	1020	1032	1047	1050	1059	1095	1116	1128	1131	1137	1149	1164	1185	1194	1197	1209	1224	1242	1245	1266
HEUCHERA	C	A	C	G	G	C	C	T	T	G	T	G	A	T	T	A	C	C	T	T	C	G	C	A	T	C	T	A	C	G	A	T	T	A	T	A	T	A	A	A	T
HEDERA	.	.	G	.	.	.	T	.	.	.	.	C	G	.	C	G	.	G	.	C	.	C	.	G	.	.	C	.	.	.	G	C	.	G	C	.	.	.	.	C	A
CORNUS	.	.	G	.	.	.	T	C	.	.	.	.	G	.	.	G	T	.	G	.	T	.	.	G	.	T	.	.	.	.	G	C	.	G	.	.	.	.	.	G	A
SPIGELIA	.	.	G	A	.	T	T	C	.	T	.	C	.	.	.	G	T	G	G	.	T	C	.	.	C	T	.	.	T	.	.	C	.	G	.	.	.	.	G	.	A
MENYANTHES	.	.	G	.	.	.	T	C	C	T	.	C	G	.	C	.	.	.	.	C	.	.	.	G	.	T	.	.	.	.	.	C	.	G	C	.	.	G	.	C	A
ADOXA	.	.	G	A	A	.	.	C	C	T	.	C	G	.	C	.	.	.	.	C	.	.	T	.	C	T	.	.	G	A	G	C	.	G	C	.	.	.	.	G	A
SAMBUCUS	.	C	G	A	A	.	.	C	.	.	.	C	G	.	C	G	.	.	G	C	.	T	T	G	C	T	.	.	G	.	G	C	.	G	C	.	.	.	.	C	A
VIBURNUM	.	T	G	.	.	.	T	C	.	.	.	C	G	.	C	G	.	.	G	C	.	.	.	G	C	T	.	.	.	.	G	C	C	G	C	.	.	.	.	C	A
LONICERA	T	C	G	.	.	.	.	C	.	.	C	C	G	C	C	G	.	.	G	C	.	A	.	G	.	T	.	G	.	.	G	C	?	.	C	C	C	.	.	T	C
SYMPHORICARPOS	T	C	G	.	.	.	.	C	.	.	C	C	G	C	C	G	.	.	.	C	.	A	.	G	?	T	.	G	.	.	G	.	C	.	C	C	A	.	.	C	C
VALERIANA	T	.	.	.	.	.	.	C	C	.	.	.	G	.	C	.	.	.	.	C	.	.	.	G	C	T	C	G	T	A	G	C	C	G	.	C	C	G	G	T	C
DIPSACUS	T	.	.	.	.	T	T	.	.	.	.	.	G	.	C	.	.	.	?	?	.	.	.	G	C	T	.	G	.	.	G	C	.	G	.	C	C	.	G	C	C

ing omission or down-weighting of various positions within codons and weighting of transversions (Tv) versus transitions (Ts). The Tv : Ts weighting of 1.3 : 1.0 used in the present study is based on calculations by V. A. Albert (pers. comm.; see Albert & Mishler, in press), which in turn rely on substitution rates and Tv : Ts ratios for *rbc*L obtained from a 5-taxon tree of land plants (Albert et al., 1992).

In view of the small number of taxa under consideration, parsimony analyses were conducted using the Branch and Bound option in PAUP for the Macintosh computer (version 3.0L; Swofford, 1990), which guarantees finding all most parsimonious trees. PAUP was also used in computing consensus trees (including "combinable component" trees: Bremer, 1990), optimizing character state changes (Swofford & Maddison, 1987), performing bootstrap analyses (100 replicates: Felsenstein, 1985; Sanderson, 1989), differentially weighting characters (including use of a step matrix in implementing the Tv : Ts weighting), and calculating character and tree statistics, such as consistency index (CI; Kluge & Farris, 1969) and retention index (RI; Farris, 1989; also see Archie, 1989a).

The lengths and implications of alternative tree topologies were explored using the Topological Constraints option in PAUP, and using finalized portions of MacClade test version 2.99.11 (to be published as MacClade 3.0; Maddison & Maddison, 1992). MacClade was also used to calculate character transformations of various types on trees of interest (e.g., transversions versus transitions) and the numbers of changes at different codon positions.

To evaluate further the relative robustness of clades found in the most parsimonious trees, strict consensus trees were constructed of all trees up to one step longer than the shortest trees, then of all trees two steps longer, and so forth, until the consensus tree eventually collapsed to an unresolved bush. This procedure yields a "decay" index, indicating the number of steps that must be added before each clade present in the minimum length trees is no longer unequivocally supported (cf. Bremer, 1988; Hillis & Dixon, 1989).

In order to explore more fully the structure in

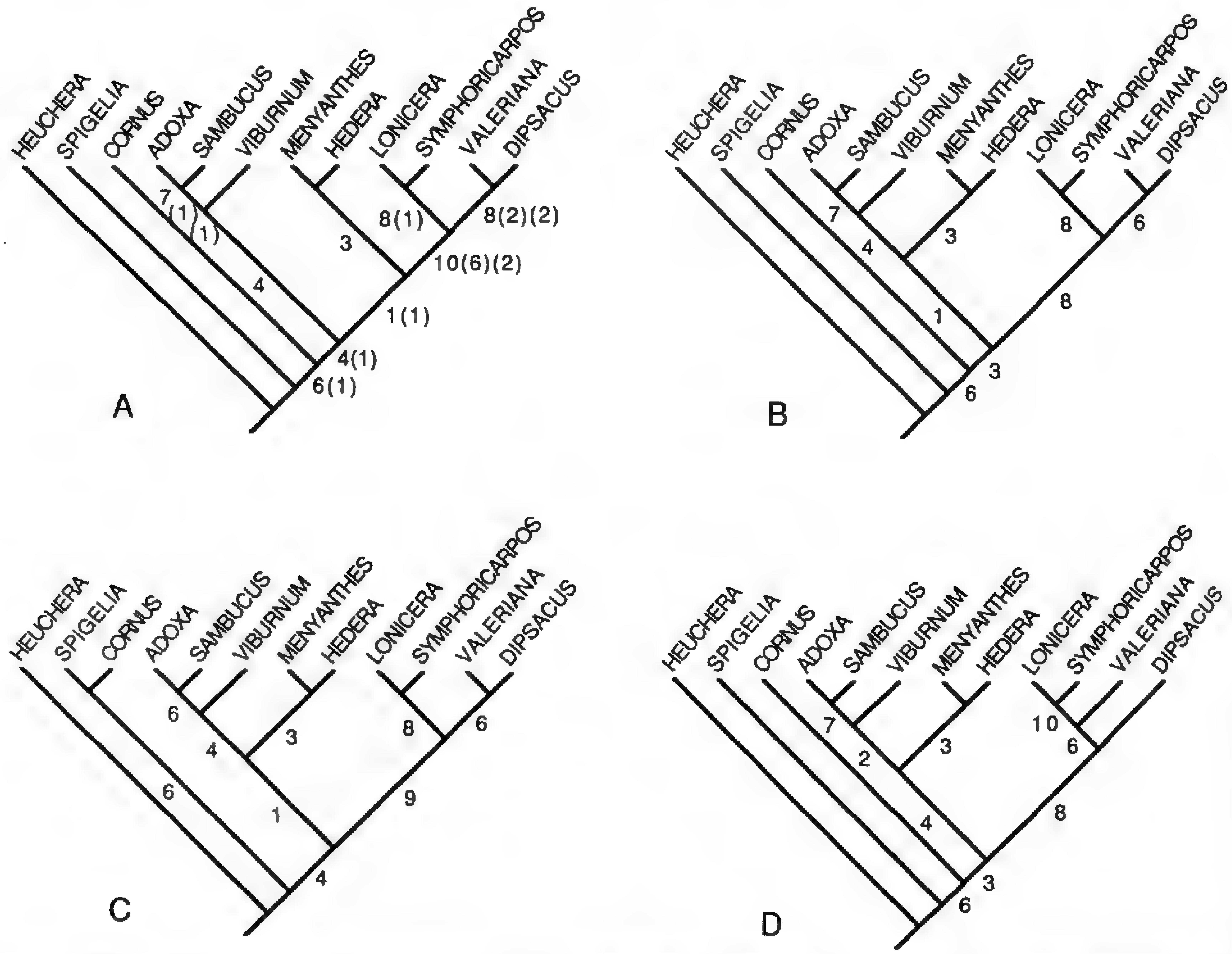

FIGURE 1. Four most parsimonious trees of 202 steps each, rooted by *Heuchera*. The number associated with each internal branch indicates the number of unambiguous nucleotide changes along the branch. In 1A the number of transversions is shown in the first set of parentheses, and changes in first and second positions within codons are indicated in the second set of parentheses: (1) = one first position change; (2) = one second position change.

the data set, two other procedures were utilized. First, the length of the most parsimonious trees for the *rbc*L data was compared to the distribution of most parsimonious trees based on 50 "random" data sets generated under the null model of Archie (1989b). This was accomplished using the "shuffle" option in MacClade, which maintains the same number of states for each character observed in the real data set, but randomly assigns these states to the taxa. To save time, analysis of each of the 50 random data sets was carried out using a heuristic search strategy in PAUP ("closest" add sequence, one tree held with each addition, TBR branch-swapping, and MULPARS). Second, PAUP was used to generate a histogram of tree lengths of 10,000 randomly sampled trees (there being too many taxa in the analysis to examine all trees). This allowed us to determine whether the observed distribution showed significantly greater left-hand skewness than tree-length distributions obtained from randomly generated data matrices (Hillis, 1991; Huelsenbeck, 1991). The comparison is based on the g_1 skewness statistic (i.e., the third central moment divided by the cube of the standard deviation; Sokal & Rohlf, 1981), for which critical values ($P = 0.05$) were provided by David Hillis (pers. comm.).

Rooted trees were obtained by positioning the root along the branch connecting *Heuchera* to the rest of the network (simultaneous resolution; Maddison et al., 1984). Initially, we planned to position the root along the branch connecting the three rosid taxa to the rest of the network, under the assumption that asterid taxa would join the network along a single branch and that the root should not be placed within Asteridae. However, it emerged that the rosids were not attached by a single branch to the asterid taxa in the analysis (see below). Our decision to root the tree along the *Heuchera* branch assumes only that Saxifragaceae is a more basal rosid clade than Cornaceae and/or Araliaceae.

RESULTS

Parsimony analysis of the matrix in Table 1 resulted in the four trees of 202 steps shown in

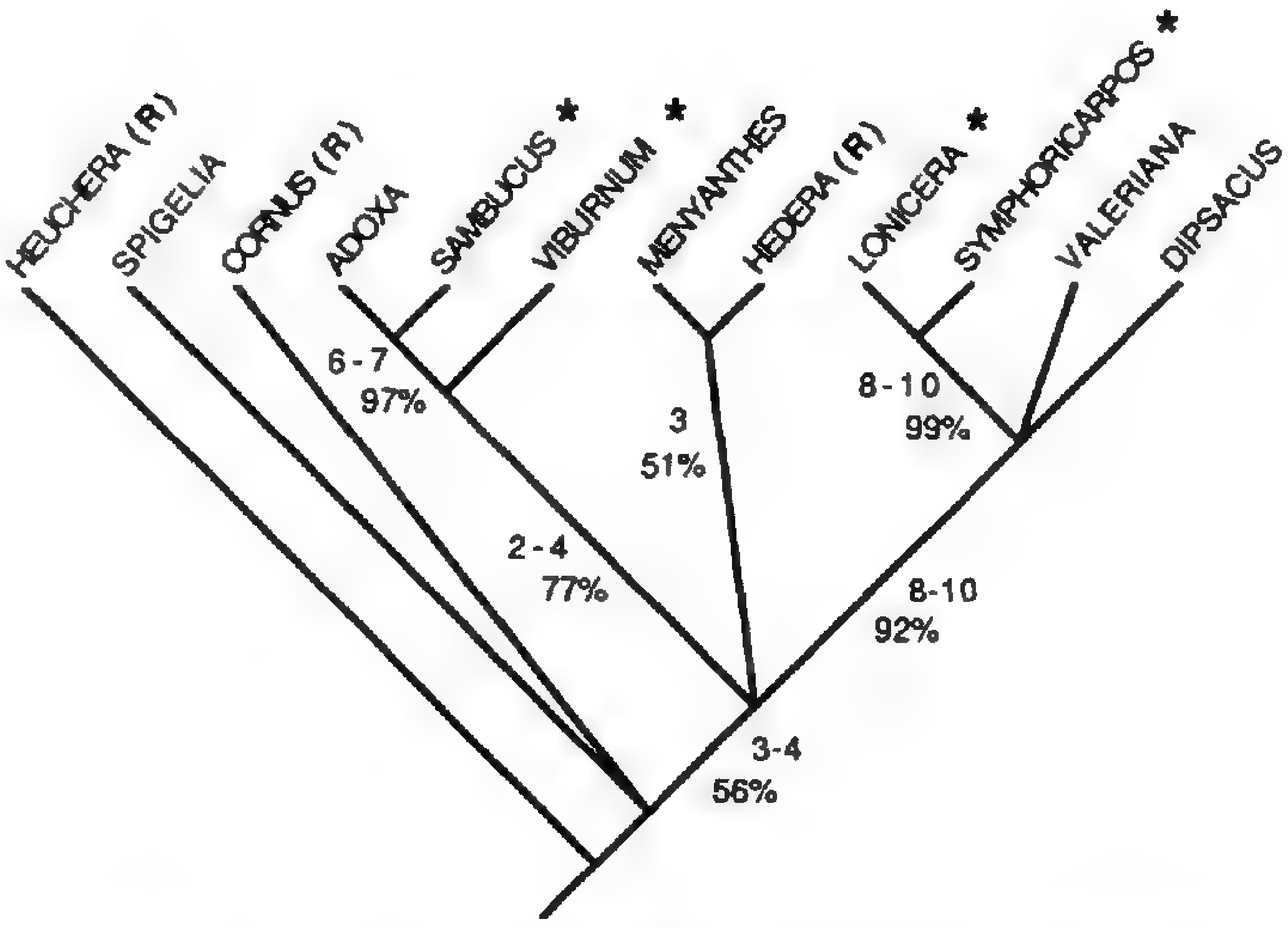

FIGURE 2. Strict consensus of the four most parsimonious trees in Figure 1. Numbers associated with the internal branches indicate the range of unambiguous character changes, and the percentage of times that the branch was recovered in 100 bootstrap samples. Taxa marked by an asterisk are traditionally placed in Caprifoliaceae; taxa marked by (R) are assigned to Rosidae.

Figure 1. The strict consensus of these trees (identical to the combinable component tree) is shown in Figure 2. The CI of 0.515 (RI = 0.470) indicates that there are about twice as many character state changes as there would be in the absence of homoplasy. Although this is a rather low CI for 12 taxa, there is still not a statistically significant departure from the expected value of 0.64 based on an analysis of 60 published data sets (Sanderson & Donoghue, 1989).

Note that in Figure 1 we have indicated the number of character state changes that can be unambiguously assigned to each internal branch, and for one tree (Fig. 1A) we also show the number of unambiguous changes that are anything other than third-position transitions. As expected from the matrix, the vast majority of changes in the most parsimonious trees occur at third positions. Separate analyses of characters at diffeent codon positions confirm that the basic structure seen in the most parsimonious trees is primarily determined by these third position characters. When third positions are analyzed by themselves, one tree of 163 steps (CI = 0.546) is obtained, which is identical to Figure 1B. In contrast, when only the 14 first and second position characters are analyzed the consensus of the 55 trees of 31 steps (CI = 0.484) is completely unresolved. Weighting first and second position changes twice as much as third position changes allows discrimination among the four trees in Figure 1 (A: 240 steps; B: 241; C: 238; D: 239), but we see no justification for such weighting in this case.

Also as expected, the number of transitions far exceeds the number of transversions on the most parsimonious trees, yet the percentages of the two sorts of changes on the trees differ somewhat from the expectation based on the matrix. From the matrix it can be seen that there are a minimum of 76 transitions and 28 transversions, which means that we might expect about ¾ of the changes on the tree to be transitions. However, the tree shown in Figure 1A necessitates 102 unambiguous transitions and 45 unambiguous transversions. Thus, only about ⅔ of the unambiguous changes are transitions, meaning that there are relatively fewer transitions, and relatively more transversions, than one might have expected based on the matrix. Despite the different numbers of changes of the two types, differential weighting of transversions versus transitions had little effect on the outcome. Assigning transversions a weight of 1.3 (see above) yielded 3 trees, corresponding to Figures 1A, 1C, and 1D. The consensus of these trees is identical to the consensus based on equal weighting (Fig. 2). In other words, this weighting scheme has the effect of rendering one of the most parsimonious trees slightly less parsimonious (see Albert et al., 1992, for a similar example in *Clarkia*). Even a weighting of 2 : 1 had no effect on the consensus result.

Along each branch of the consensus tree we indicate the range of unambiguous character changes and the percentage of times the branch was recovered in 100 bootstrap replicates. Only one branch not seen in the strict consensus appeared in over 50% of the bootstrap runs: *Valeriana* and *Dipsacus* were directly united in 52% of the trees. Two clades are seen in over 95% of the samples: *Lonicera* plus *Symphoricarpos* (99%) and *Sambucus* plus *Adoxa* (97%). The connection of *Lonicera* and *Symphoricarpos* with *Valeriana* and *Dipsacus* is not far behind, being found in 92% of the replicates.

The order of "decay" of the six components present in the most parsimonious trees is shown in Figure 3. Two clades are lost when the six trees just one step longer are considered, and the remaining four clades are maintained with the addition of 21 trees of length 204 and 57 trees of 205. When the 182 trees less than or equal to 206 steps are considered, the connection between *Viburnum* and the *Sambucus–Adoxa* clade is lost. With the addition of the 142 trees of 207 steps the consensus tree no longer maintains the connection between *Sambucus* and *Adoxa*, although this link is still found in 99% of the 324 trees. Only the connection between *Lonicera* and *Symphoricarpos* is still present in the consensus of all 594 trees of 208 steps or less, and all structure is lost at 209 steps, only 7 steps from the most parsimonious trees.

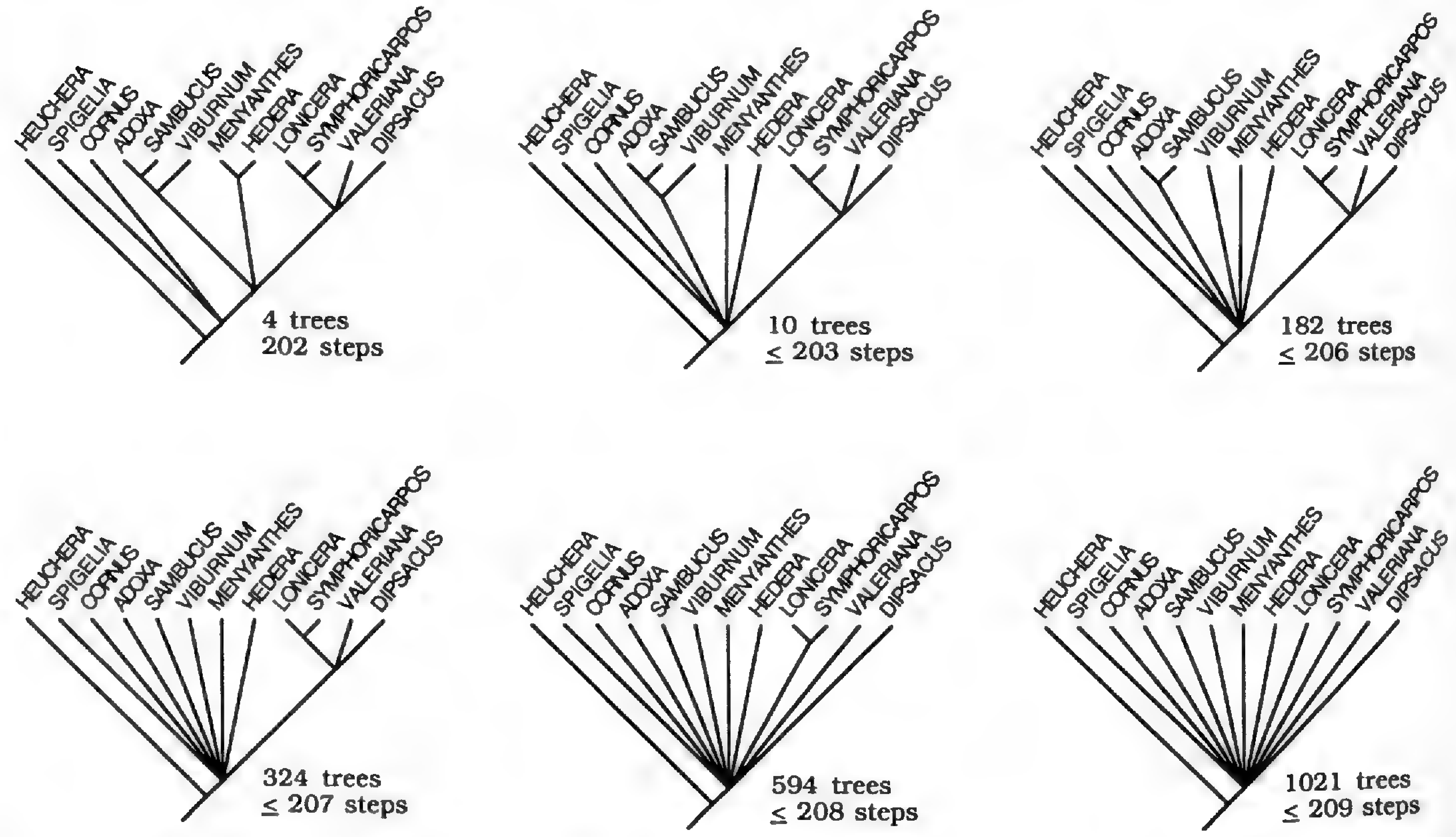

FIGURE 3. Trees showing the order of "decay" of clades. Each tree is the strict consensus of the trees that are less than or equal to the number of steps shown. The basal branch in all trees is an artifact of rooting the network along the branch connecting *Heuchera*.

In Figure 4 the tree lengths of 50 randomized data sets are compared to the length (202) of the most parsimonious trees obtained for the *rbc*L data. Clearly, the real data set falls far (several standard deviations) outside the normal distribution for data sets randomized using the method suggested by Archie (1989b). Whether this result will hold for other null models is uncertain, but it may suggest that there is phylogenetic structure in the *rbc*L data.

The distribution of the lengths of 10,000 randomly generated trees is shown in Figure 5. Note that the shortest random tree recovered was of length 220—18 steps longer than the shortest trees for the *rbc*L data. Although this means that none of the 1,021 trees known (from the decay experiments) to require 209 steps or less were actually found in the sample of random trees, it is presumed that 10,000 trees is sufficient to reveal the shape of the underlying distribution for all trees (D. Hillis, pers. comm.). The skewness of this distribution, measured by g_1, is −0.78, which far

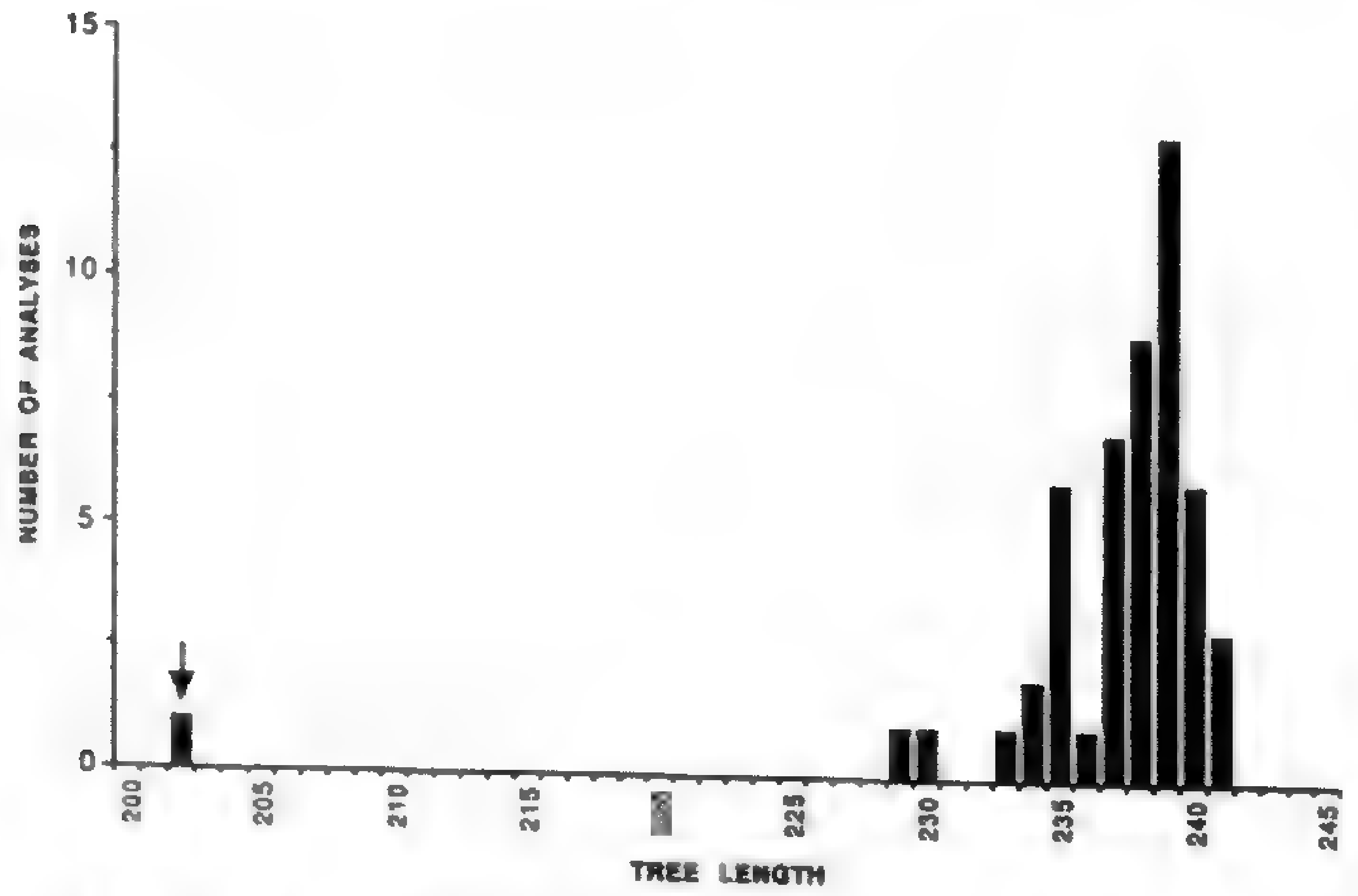

FIGURE 4. Histogram of tree lengths showing the position of the most parsimonious trees (202 steps) for the *rbc*L data in relation to parsimonious trees for 50 randomized data sets (sensu Archie, 1989b); arrow indicates the most parsimonious trees found with the real data set.

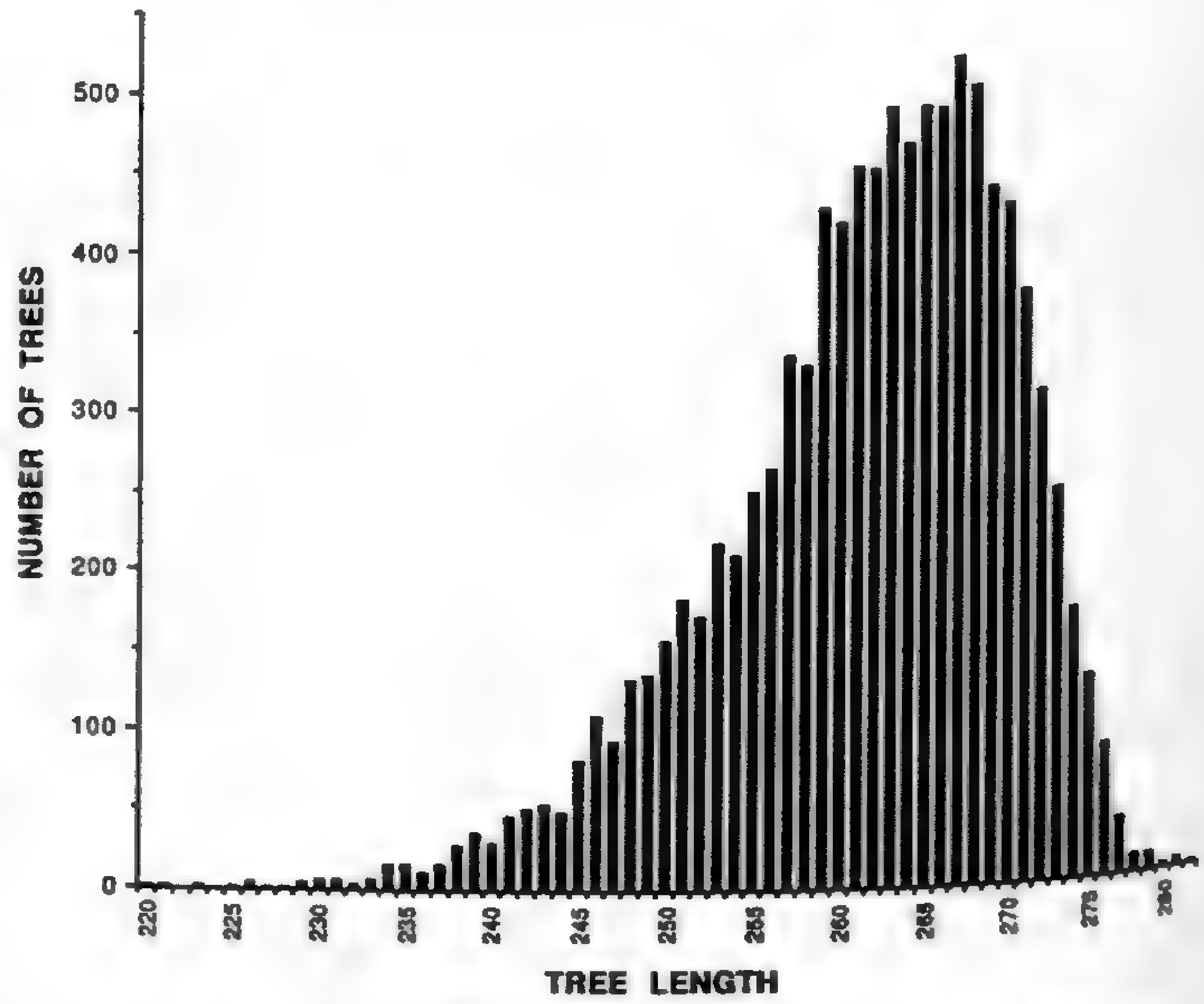

FIGURE 5. Histogram of tree lengths for 10,000 randomly generated trees, showing the degree of left-hand skewness (g_1 = −0.78).

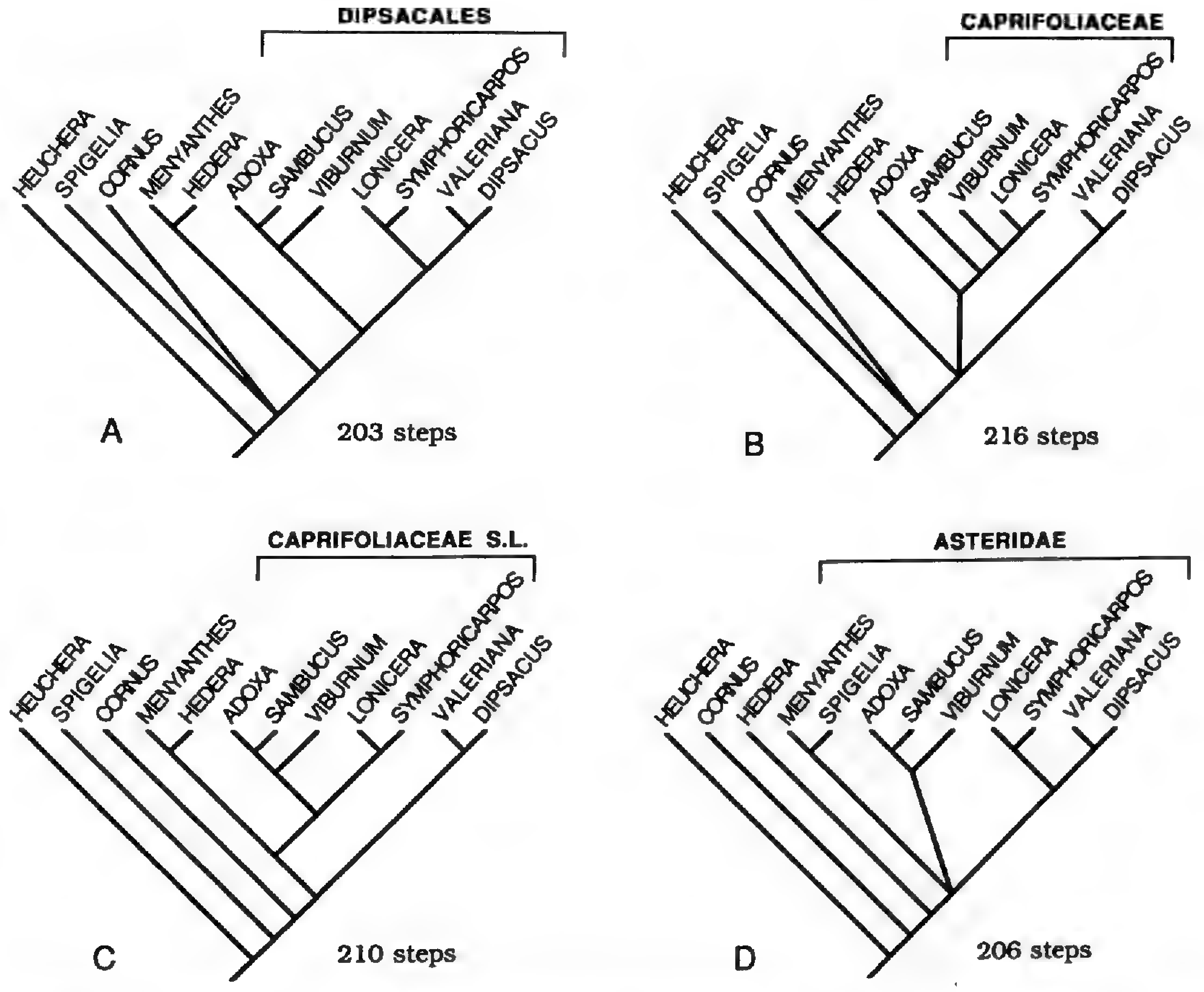

FIGURE 6. Lengths of alternative trees, with the following topological constraints imposed: (A) Dipsacales monophyletic; (B) Caprifoliaceae (*Sambucus, Viburnum, Lonicera, Symphoricarpos*) monophyletic; (C) Caprifoliaceae plus *Adoxa* monophyletic; (D) Asteridae monophyletic. When more than one tree was obtained, the strict consensus is shown.

exceeds the $P = 0.05$ critical value for data sets of 10 to 15 taxa with 50 to 100 characters (D. Hillis, 1991, pers. comm.). Again, this appears to indicate significant phylogenetic signal in the *rbc*L data.

DISCUSSION

DIPSACALES AND CAPRIFOLIACEAE SENS. LAT.

The Dipsacales have generally been considered a "homogeneous," natural element within Asteridae (Wagenitz, 1977, 1992). However, none of our most parsimonious trees support the monophyly of Dipsacales (Fig. 1), even though the consensus of these trees (Fig. 2) seems to allow this possibility. Instead, the clade consisting of *Menyanthes* (representing Asterales sens. lat.; Olmstead et al., 1992) and *Hedera* (representing Apiales, Rosidae) is intercalated between two clades of dipsacalean taxa, namely a *Viburnum–Sambucus–Adoxa* clade and a line comprising *Lonicera, Symphoricarpos, Valeriana,* and *Dipsacus.*

Taken at face value, this result supports the idea, based on immunology (Hillebrand & Fairbrothers, 1970a, b) and morphology, that these two lines of Dipsacales are not closely related (Donoghue, 1983). It is also generally consistent with restriction site studies of the inverted repeat (Downie & Palmer, 1992) and other regions of the chloroplast genome (Sytsma, Smith, & Donoghue, unpublished). However, it is important to recognize that the non-monophyly of Dipsacales is not a strongly supported result of our analysis. In fact, trees in which Dipsacales are monophyletic (Fig. 6A) require only a single additional step. Note that in this case the *Menyanthes–Hedera* clade appears as the sister group of Dipsacales, an arrangement that is more consistent with the broader analysis of *rbc*L sequences of Olmstead et al. (1992).

None of our most parsimonious trees are consistent with the monophyly of Caprifoliaceae in the traditional sense (that is, excluding *Adoxa,* Valerianaceae, and Dipsacaceae), and this conclusion is very strongly supported in the present analysis. In particular, *Viburnum* and *Sambucus* are united with *Adoxa,* and this clade is separated from *Lonicera* and *Symphoricarpos* (of Caprifoliaceae sens. str.), which are united instead with *Valeriana* and *Dipsacus.* Trees in which *Sambucus, Viburnum, Lonicera,* and *Symphoricarpos* are united in a clade require a minimum of 216 steps, 14 more steps than the shortest trees (Fig. 6B). Even if *Adoxa* is considered part of Caprifoliaceae (as it sometimes has been; see Donoghue, 1983), it would still be better to consider the latter to be paraphyletic, because trees with this expanded Caprifoliaceae forming a clade require a minimum of 210 steps (Fig. 6C).

Regarding the status of Caprifoliaceae our results are congruent with morphological characters. Donoghue (1983) summarized earlier evidence, and research available since that time—for example, on pollen (Böhnke-Gütlein & Weberling, 1981; Donoghue, 1985), nectaries (Wagenitz & Laing, 1984), and the tapetum (Weberling & Hildenbrand, 1986)—has strengthened the idea that there are independent and unrelated lines of Caprifoliaceae. This view is also consistent with a phenetic analysis of morphological data (Hsu, 1983), with chromosome structure (Sax & Kribs, 1930), with secondary chemistry (Bohm & Glennie, 1971), and with immunological evidence (Hillebrand & Fairbrothers, 1970a, b). Finally, our results are congruent in this respect with the results of other molecular studies (Olmstead et al., 1992; Downie & Palmer, 1992).

CAPRIFOLIACEAE SENS. STR., VALERIANACEAE, AND DIPSACACEAE

The result that genera of Caprifoliaceae (in the traditional sense) do not form a monophyletic group is partly a function of the solid connection between Caprifoliaceae sens. str., Valerianaceae, and Dipsacaceae. Indeed, the *Lonicera–Symphoricarpos–Valeriana–Dipsacus* clade is one of the best supported in the entire analysis, judging by the number of unambiguous character changes, the bootstrap value of 92%, and the high "decay" index (collapsing in trees 6 steps longer than the shortest trees). This connection is also supported by many morphological features, including reduction of carpellary vascular traces (Wilkinson, 1949), aspects of pollen morphology (Donoghue, 1985), and nectary structure (Wagenitz & Laing, 1984).

Within this clade there is very strong support for a direct connection between *Lonicera* and *Symphoricarpos*. These genera are united by 8–10 unambiguous changes in the most parsimonious trees, and they appeared together in 99% of the bootstrap samples. Furthermore, this link lasted the longest in the decay analyses, appearing in all 594 trees less than or equal to 208 steps. At 209 steps it is possible to find trees in which *Symphoricarpos* and *Lonicera* are dissociated, with either one united with Valerianaceae and Dipsacaceae.

The strong connection between *Lonicera* and *Symphoricarpos* is somewhat surprising. These two genera are not unequivocally connected by morphological characters and they have generally been placed in separate tribes (see Wilkinson, 1949; Donoghue, 1983). *Lonicera* is usually allied with *Leycestaria* in the tribe Lonicereae. More importantly, *Symphoricarpos* has often been placed in the tribe Linnaeeae (e.g., Fukuoka, 1972; Hara, 1983), whose other members appear to be more closely related to Valerianaceae and Dipsacaceae than they are to other genera of Caprifoliaceae sens. str. (Donoghue, 1983, in prep.). If *Symphoricarpos* really belonged with Linnaeeae, and if Linnaeeae are more closely related to Valerianaceae and Dipsacaceae, then it should not have attached directly to *Lonicera* in our analysis, but instead to *Valeriana* and *Dipsacus*. Other molecular data seem to confirm that *Symphoricarpos* is more closely related to *Lonicera* than it is to genera of Linnaeeae. The two genera are united in the trees of Downie & Palmer (1992), and it appears that they may also be united (along with *Triosteum*) by the loss of the chloroplast gene *clp*P (Downie, Donoghue, Sytsma, & Palmer, unpublished).

Our results for *Lonicera* and *Symphoricarpos* might be considered evidence of the monophyly of Caprifoliaceae sens. str., but this conclusion would be premature in view of the limited sample of taxa included in the analysis. As we noted above, one of the strongest results of morphological analyses is that Caprifoliaceae sens. str. are paraphyletic, with the tribe Linnaeeae more closely related to Valerianaceae and Dipsacaceae than to other Caprifoliaceae sens. str. (Donoghue, 1983, in prep.). Some of the strongest evidence is provided by floral anatomy, especially the abortion of carpels during the development of the ovary (Wilkinson, 1949). The link between Linnaeeae and Valerianaceae and Dipsacaceae is also evident in the restriction site studies of Downie & Palmer (1992), although in this case the one representative of Linnaeeae (*Kolkwitzia*) is actually connected directly with *Valeriana*. It seems likely that if representatives of Linnaeeae were included they would be linked with *Valeriana* and *Dipsacus* rather than with *Lonicera* and *Symphoricarpos*. Sequencing of representatives of Linnaeeae (*Dipelta, Kolkwitzia, Linnaea*) is in progress.

In our analysis the position of *Valeriana* is uncertain. In three of the four most parsimonious trees (Fig. 1) it is united directly with *Dipsacus*, but in the fourth it is linked with *Lonicera* plus *Symphoricarpos*. Morphological data support a close connection between Valerianaceae and Dipsacaceae (e.g., Hofmann & Göttmann, 1990; Donoghue, in prep.), as does the more inclusive *rbc*L analysis of Olmstead et al. (1992), which again suggests that there may be a problem of limited sampling of taxa. Inclusion of additional Caprifoliaceae sens. str. might strengthen the connection between Valerianaceae and Dipsacaceae.

VIBURNUM, *SAMBUCUS*, AND *ADOXA*

Viburnum is linked with *Sambucus* plus *Adoxa* in all of our most parsimonious trees, but this connection is not especially srong: 2–4 unambiguous character changes mark this branch, it appeared in 77% of the bootstrap trees, and it decayed at 206 steps. Morphological data also tend to unite *Viburnum* with *Sambucus* and *Adoxa* (under most outgroup arrangements), but by itself the evidence does not inspire great confidence (Donoghue, 1983, in prep.). It is certainly encouraging that the molecular and morphological data point to the same conclusion.

The connection between *Adoxa* and *Sambucus* is quite robust. There are 6–7 unambiguous character changes below this node, and it appeared in 97% of the bootstrap samples. In the decay analyses this connection lasted until trees of 207 steps were added, making it the third most robust result in our analysis. Curiously, this clade decayed before the *Lonicera–Symphoricarpos–Valeriana–Dipsacus* clade, even though the latter had a somewhat lower bootstrap value.

In addition to Caprifoliaceae (e.g., Eichler, 1875; Hooker, 1873), *Adoxa* has been allied with Saxifragaceae (Hutchinson, 1973; Warming & Mobius, 1929), Araliaceae (de Candolle, 1830), and Cornales (Dahlgren, 1975), although it has generally been placed in its own family (reviewed in Wagenitz, 1977; Donoghue, 1983). The *rbc*L data argue against these other connections. Thus, the shortest trees in which *Adoxa* is linked directly with *Hedera* require 213 steps (11 steps longer than the most parsimonious trees), and it takes 214 steps to connect *Adoxa* with *Heuchera*.

Some authors have noted similarities between *Adoxa* and *Sambucus* (e.g., Eichler, 1875; Hallier, 1912; Takhtajan, 1980), and this connection has been supported by preliminary cladistic analyses (Donoghue, 1983, in prep.). One morphological character in particular has seemed compelling, namely the presence of *Adoxa*-type embryo sac development in *Adoxa* and *Sambucus*. This condition is extremely rare in angiosperms and is otherwise very widely scattered in occurrence (Maheshwari, 1946; Donoghue, 1983). Its distribution within *Sambucus* is still somewhat unclear, and it is possible that it will be discovered in some *Viburnum* species, inasmuch as several species are reported to have bisporic development (Sunesson, 1933). Other possible indicators of a close relationship include compound leaves (depending on outgroups) and extrorse anthers (although there is some variation in *Sambucus* and the condition in *Adoxa* is difficult to score). Nevertheless, most authors (e.g., Sprague, 1927) have hesitated to connect the two genera, largely because *Adoxa* is so different (presumably highly derived) in habit and in floral morphology. However, Thorne (1983) adopted Donoghue's (1983) suggestion that *Adoxa* and *Sambucus* (and possibly *Viburnum*) be treated as the family Adoxaceae.

One outstanding problem concerns the relationships of recent additions to Adoxaceae (Wu, 1981; Wu et al., 1981; Hara, 1981, 1983). Although *Tetradoxa omeiensis* (=*Adoxa omeiensis*) is very similar to *Adoxa moschatellina*, and is probably closely related, *Sinadoxa* differs in many respects and may be more closely related to Araliales than to *Adoxa*.

ASTERIDAE AND ROSIDAE

Conclusions regarding the broader relationships of dipsacalean plants are tenuous, because much of the relevant structure seen in the most parsimonious trees disappears when slightly longer trees are taken into consideration. Nevertheless, it is interesting to note that the most parsimonious trees support a clade including the dipsacalean taxa, along with *Hedera* plus *Menyanthes*. The former is a placeholder for Araliales, and the latter represents an Asterales sens. lat. clade (comprising Asteraceae, Menyanthaceae, Goodeniaceae, Calyceraceae, Campanulaceae, and Lobeliaceae), which is consistently supported in the more inclusive *rbc*L analyses of Olmstead et al. (1992). Although the exact arrangement of these groups in relation to dipsacalean taxa is uncertain, the present analysis is consistent with the view that Asterales sens. lat. and Araliales are closely related, and that together they are related either to the *Viburnum–Sambucus–Adoxa* clade or to the Caprifoliaceae sens. str.–Valerianaceae–Dipsacaceae clade.

This result is especially significant in light of the inclusion of *Spigelia* (Loganiaceae) in the analysis, which is intended to represent the remainder of the Asteridae, based on the broader analyses of Olmstead et al. (1992). If Asteridae were monophyletic, *Spigelia* would be linked with *Menyanthes* and the dipsacalean taxa, to the exclusion of the rosids. The shortest trees of this type require

206 steps, four steps more than our most parsimonious trees (Fig. 6D). Instead, *Cornus* and *Hedera* are variously nested among Asteridae in our most parsimonious trees (Fig. 1), which implies that the Asteridae, as they are generally constituted, are not monophyletic. This conclusion is consistent with the larger analyses of *rbc*L (Olmstead et al., 1992).

Although the standard view of morphological systematists has been that Asteridae form a natural group, Takhtajan (1987) proposed that it be subdivided into two major lines: Asteridae sens. str. (Asterales sens. lat. and Dipsacales) and Lamiidae (the remaining Asteridae). These lines, he believes, originated independently from separate lines of Rosidae. Phylogenetic analyses of the morphological evidence are needed before molecular and morphological results can be compared critically.

In the meantime, it is interesting to note that while the results of the present study are consistent with many aspects of other molecular analyses, they also differ in several ways. In trees presented by Olmstead et al. (1992) Araliales are linked directly with Dipsacales, rather than with Asterales sens. lat. Similarly, the trees of Downie & Palmer (1992) show Araliales connected to Caprifoliaceae sens. str., Valerianaceae, and Dipsacaceae. Although these studies include more taxa outside of the groups of immediate concern here, they also contain fewer potentially close relatives. The resolution of this issue requires a more complete sample of relevant taxa as well as additional molecular and morphological evidence.

It is important to recognize that all three of the molecular studies suggest that Asteridae in their traditional sense are not monophyletic, and they imply that some "asterid" features such as sympetaly may have evolved independently in Asterales sens. lat., Dipsacales, and Lamiidae, or may have been lost in Araliales and possibly Cornales. Here, the ontogenetic studies of Erbar (1991) are of special interest. She has demonstrated a difference between "early sympetaly" (corolla tube initiated before petal primordia) and "late sympetaly" (corolla lobes initiated as separate primordia and connected later), which largely corresponds with major clades of Asteridae implied by molecular data. In particular, early sympetaly is found in Asterales sens. lat. (including Campanulales and Menyanthaceae) and Dipsacales, while late sympetaly occurs in virtually all other Asteridae (i.e., in Lamiidae sensu Takhtajan, 1987). Rubiaceae, Oleaceae, and several Acanthaceae are exceptions to this correspondence in having early sympetaly. Unfortunately, the development of sympetaly has not yet been studied in *Viburnum*, *Sambucus*, or *Adoxa*. These observations are consistent with (but do not necessitate) the idea that sympetaly evolved independently at least twice.

Erbar (1991) also noted evidence (see Erbar & Leins, 1988) that in some Araliales the corolla is initiated as a ring primordium. Because this ring does not develop into a conspicuous tube, however, the mature flowers of these plants appear to have separate petals. This similarity to early sympetaly can be interpreted in several ways. It may be that the condition in Araliales is a precursor of early sympetaly in Asterales sens. lat. and Dipsacales. Alternatively, the apparently separate petals of Araliales may have been derived from the early sympetalous condition (i.e., sympetaly was "lost"). The latter hypothesis will be favored if phylogenetic studies continue to nest Araliales among sympetalous groups (see Olmstead et al., 1992).

CONCLUSIONS

The analyses reported here suggest a number of changes in the circumscription of taxa. First, it is clear that the genera of Caprifoliaceae do not form a monophyletic group, and the traditional concept of this family must be abandoned if we hope to achieve a truly phylogenetic system of angiosperms (Donoghue & Cantino, 1988). In particular, the genera of Caprifoliaceae sens. str. are more closely related to Valerianaceae and Dipsacaceae than they are to *Viburnum* and *Sambucus*, and *Sambucus* (very probably) and *Viburnum* (with less certainty) are more closely related to *Adoxa*. The smallest monophyletic group that would include the genera traditionally assigned to Caprifoliaceae would also include the rest of the Dipsacales (Valerianaceae, Dipsacaceae, and Adoxaceae), and possibly also the Asterales sens. lat. and Araliales.

The connection between Caprifoliaceae sens. str., Valerianaceae, and Dipsacaceae should be formally represented, but a decision on the best way to do this must await the publication of the morphological results and additional molecular analyses. The *rbc*L sequence data are still too limited to evaluate properly the morphological hypothesis that Caprifoliaceae sens. str. are paraphyletic, with the tribe Linnaeeae more closely related to Valerianaceae and Dipsacaceae. If this is borne out by further studies, it may be best to merge Caprifoliaceae sens. str., Valerianaceae, and Dipsacaceae into a single family.

Although the status of Caprifoliaceae sens. str. is still uncertain, *Lonicera* and *Symphoricarpos* seem to be more closely related than one might have expected based on previous taxonomic treatments of the family (see discussion above). It should be noted, however, that because ovary development in *Symphoricarpos* does not correspond exactly with Lonicereae or with Linnaeeae (Wilkinson, 1949), its exact relationships based on morphology are still uncertain (Donoghue, in prep.). Our analyses strongly suggest that *rbc*L sequences of representatives of additional genera of Caprifoliaceae sens. str. would be very valuable and might result in tribal realignments.

The close relationship between *Sambucus* and *Adoxa* should be represented in the phylogenetic system, perhaps by expanding Adoxaceae. This has been suggested based on morphological evidence (Donoghue, 1983, in prep.), but these data have not been entirely convincing, owing especially to the extreme modification/reduction of *Adoxa*. The *rbc*L data provide strong support for this connection and argue against alternative hypotheses that *Adoxa* may be related to Araliales or Saxifragaceae. Recently described Adoxaceae, especially *Sinadoxa*, must be evaluated, as should additional representatives of *Sambucus*. This phylogenetic information will be especially critical in understanding the nature of the genetic and developmental changes associated with morphological shifts in the evolution of *Adoxa*-like plants.

The position of *Viburnum* is still somewhat uncertain. It is connected with *Sambucus* and *Adoxa* in our most parsimonious trees, and there is also some morphological support for this arrangement. Although the evidence is not overwhelming in either case, the congruence is satisfying. *Viburnum* might be placed in Adoxaceae along with *Sambucus* and *Adoxa*, but until its relationships are more confidently resolved there may be some merit in placing *Viburnum* in its own family, the Viburnaceae (see Dahlgren, 1980). In the end, the assignment of rank is arbitrary.

Our results are encouraging as regards the quality of *rbc*L data. Although the consistency index is quite low for a data set of this size, randomized data sets and tree-length distributions both suggest that considerable phylogenetic information is present in the data. The bootstrap and decay analyses suggest that this signal may reflect the presence of several very well supported clades: especially the connections between *Lonicera* and *Symphoricarpos*, between these genera and *Valeriana* and *Dipsacus*, and between *Sambucus* and *Adoxa*. Most of the rest of the connections are not strongly supported and decay with the addition of only a single step. Overall, these results are especially encouraging with respect to potential resolution of the relationships of dipsacalean taxa using *rbc*L sequences.

Our analyses also bear on the general issue of differentially weighting characters or character state changes. Our main phylogenetic results are supported by changes at third positions within codons; there are few changes at first and second positions and these show considerable conflict with one another. We see no reason to disregard or even to downweight third sites in this case, and we caution against a priori judgements of this sort. Likewise, we found that much of the phylogenetic structure resided in the much more numerous transition substitutions, and saw no evidence that transitions were less reliable than transversions.

Comparison of this study with the more inclusive *rbc*L analysis of Olmstead et al. (1992) raises important issues concerning the effects of the sampling of taxa in phylogenetic studies. The smaller sample considered here allows a much more detailed examination of the structure in the data set. Exact parsimony solutions can be obtained using branch-and-bound algorithms, which also ensure an accurate picture of the rate of decay of clades, and so on. Studies using randomized data sets and tree-length distributions are also much easier to carry out with smaller data sets. Some of these sorts of analyses can be extended to larger analyses, and we hope that exploration of the robustness of clades (beyond the use of the bootstrap) will soon become routine. In the meantime, it is difficult to ascertain the reliability of the results of the larger analyses, and one must be especially cautious in drawing evolutionary conclusions based on such studies (see Maddison, 1991).

On the other hand, smaller studies are subject to error by virtue of leaving out relevant taxa (Donoghue et al., 1989; Olmstead et al., 1992). In particular, in any analysis of a small portion of Asteridae (for example) one may not discover globally more parsimonious solutions, which might become apparent with the addition of taxa outside the group of interest. Of course, this warning applies to larger studies as well, as does the problem of leaving out taxa within the group of interest that might have an important impact on the outcome. If the sample of taxa within the group is too sparse, errors might arise by virtue of highly divergent branches "attracting" one another due to the chance accumulation of mutations (see Felsenstein, 1978). Increasing the sample of taxa might effectively "shorten" such long branches, thereby decreasing the likelihood of such errors. This sort of consideration could perhaps be translated into a scheme for selecting a set of taxa in the first place.

In our analysis there is a better representation of critical dipsacalean taxa, which probably allows our study to reflect more accurately relationships among Dipsacales than the broader analysis of Olmstead et al. (1992). On the other hand, our representation of other major lines is much poorer than in the analysis of Olmstead et al. (1992). Our failure to achieve any clearer picture of the broader relationships may be largely a function of the limited sample of taxa aside from Dipsacales, rather than any fundamental problem with the use of *rbc*L sequences in addressing the more inclusive phylogenetic questions.

The congruence between molecular and morphological evidence on the phylogeny of Dipsacales is gratifying, if not very surprising (Donoghue & Sanderson, 1992). As is often the case, it is clear that the different data sets provide consistent results, but that the results show different levels of resolution. For example, in our *rbc*L analysis the position of *Valeriana* is unresolved, whereas several morphological characters link Valerianaceae with Dipsacaceae. On the other hand, *rbc*L sequences strongly connect *Symphoricarpos* with *Lonicera*, whereas the relationships of these genera are not clearly resolved in morphological analyses (Donoghue, in prep.). Under these circumstances it will be especialy valuable to combine data sets, so that all of the evidence can be considered at once (Barrett et al., 1991; Donoghue & Sanderson, 1992).

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A CHLOROPLAST DNA PHYLOGENY OF THE SOLANACEAE: SUBFAMILIAL RELATIONSHIPS AND CHARACTER EVOLUTION[1]

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ABSTRACT

Phylogenetic relationships among 42 species of Solanaceae representing 12 of the 14 currently recognized tribes were assessed by chloroplast DNA restriction site mapping. Over 1,000 cleavage sites were identified for 10 restriction enzymes and of these, 447 provided information concerning relationships among the included taxa and the outgroup, *Ipomoea* (Convolvulaceae). The results establish that subfamily Cestroideae is ancestral in the family and is paraphyletic, and that the subfamily Solanoideae is derived from within the Cestroideae and is monophyletic, if it is circumscribed to include *Nolana*. The tribe Salpiglossideae, characterized by floral zygomorphy and reduction in stamen number, is probably polyphyletic and hence artificial. An analysis of character evolution in the family suggests that the tribe Nicotianeae retains the most primitive morphological characters of any tribe in the family and helps to explain the disjoint position of members of the tribe in two distinct lineages in the Cestroideae. The chromosome base number $x = 12$ unites the Solanoideae with the Anthocercideae and *Nicotiana*. The worldwide distribution of the Solanoideae versus the almost exclusively New World distribution of the Cestroideae argues for a predominantly long-distance dispersal, rather than a vicariance explanation of biogeographic distributions in the family. The morphologically distinctive genus *Schizanthus* is the earliest diverging lineage in the family. Tribal relationships within the Solanoideae remain poorly resolved and await more detailed study.

The Solanaceae are one of the most important families of flowering plants economically, floristically (particularly in the New World), ethnobotanically, and scientifically (as a model system for research). The great amount of systematic and biological interest in the family is attested to by three recent symposium volumes dedicated to the Solanaceae (Hawkes et al., 1979, 1991; D'Arcy, 1986). The traditional classification of Wettstein (1895) has recently been revised by Hunziker (1979), who presented a detailed classification of South American members of the family, and by D'Arcy (1979), who incorporated Hunziker's changes into a conspectus for the entire family. However, at the generic level and above, there has been little speculation on phylogenetic relationships, apart from assignment to tribes and subfamilies, and no rigorous phylogenetic analysis encompassing a broad representation of the family.

Current treatments of the family (Hunziker, 1979; D'Arcy, 1979, 1991) recognize two main subfamilies, the Solanoideae, with curved embryos contained in flattened discoid seeds, and the Cestoideae, with straight or slightly bent embryos in prismatic to subglobose seeds. The unusual genus *Nolana*, from the dry coastal region of Chile and Peru, has been included in the Solanaceae in the subfamily Nolanoideae by Thorne (1968) and D'Arcy (1979), whereas others have preferred its segregation at the family level (Hunziker, 1979; Cronquist, 1981; Mesa, 1986; Takhtajan, 1987). Tetenyi (1987), on the basis of secondary chemistry, has proposed two new subfamilies, the Anthocercidoideae (consisting solely of the Anthocercideae) and the Atropoideae (consisting of *Atropa*, *Mandragora*, and the tribe Hyoscyameae). Recent taxonomic revisions and biosystematic studies on many groups have improved generic, tribal, and subfamilial circumscriptions (reviewed in D'Arcy, 1979, 1991).

The Solanoideae have been viewed traditionally as the primitive subfamily (Murray, 1945; D'Arcy,

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1979, 1991; Armstrong, 1986), with the divergence of the Cestroideae occurring early within its diversification. The Nolanoideae are proposed to be derived from the Solanoideae (Johnston, 1936; D'Arcy, 1991), although a similarity in floral anatomy has been noted between *Nolana* and the Cestroideae (Armstrong, 1986). The Cestroideae are more heterogenous in floral morphology, with plants in the tribe Salpiglossideae exhibiting bilateral symmetry and reduction in stamen number. The Salpiglossideae have been elevated to the rank of family (Hutchinson, 1969), or, alternatively, criticized as an artificial group (D'Arcy, 1978).

Several genera of the Solanaceae were the subjects of early attempts to reconstruct phylogeny by assessing chloroplast DNA (cpDNA) restriction site variation (*Lycopersicon*, Palmer & Zamir, 1982; *Nicotiana*, Kung et al., 1982; *Solanum* sect. *Tuberosum*, Hosaka et al., 1984). Species-level studies currently in progress within the family (*Capsicum*, Mitchell et al., 1989; *Jaltomata*, T. Mione et al., pers. comm.; *Nicotiana*, Olmstead et al., 1990; and *Solanum*, D. Spooner et al., pers. comm.) are being coordinated so that the results can be integrated with each other and with higher-level analyses.

The scope of our research in the Solanaceae is a broad survey of cpDNA restriction site variation with the goal of attaining a framework phylogeny of the family. This can then be used as a working hypothesis of sister-group relationships at the generic level for detailed species-level studies within the family, and as the basis for hypotheses of character evolution, thereby enabling research on the evolution of phenotypic traits to focus more profitably on specific problems. The results presented here will address questions concerning relationships among subfamilies and basal lineages within the family and the implications for character evolution at that level.

MATERIALS AND METHODS

Plant material of 42 species of Solanaceae, representing 12 of the 14 currently recognized tribes (D'Arcy, 1991), and the outgroup, *Ipomoea* (Convolvulaceae), were obtained from various sources (Table 1), either as seed (grown in the greenhouse at Matthaei Botanical Gardens, University of Michigan), or as fresh leaf material.

Total cellular DNA was extracted by the modified CTAB technique of Doyle & Doyle (1987) and further purified by cesium chloride/ethidium bromide gradient centrifugation. The DNAs were digested with each of 10 restriction enzymes, electrophoresed in agarose gels, and transferred bidirectionally to nylon filters (Zetabind by Cuno) following the procedure in Palmer et al. (1988), with the following modification. The number of restriction sites for each enzyme was determined from the complete sequence of the *Nicotiana tabacum* chloroplast genome (Shinozaki et al., 1986) and was used as an index to rank the 10 enzymes by the number of expected fragments. Following this index, restriction fragments were separated in agarose gels of different concentration as follows: 1.2% agarose, Eco RV (35 sites in the entire tobacco genome, scoring the inverted repeat only once) and Hind III (32 sites); 1.4%, Bam HI (39 sites) and Xba I (48 sites); 1.6%, Bcl I (53 sites), Bgl II (59 sites), and Cla I (58 sites); 1.8%, Eco O1091 (66 sites); and 2.0%, Ban II (74 sites) and Eco RI (96 sites). This approach enables better resolution of small fragments by using higher concentration agarose gels for those enzymes that cut cpDNA frequently, and of large fragments by using lower concentration gels for those enzymes that cut less frequently. A set of 40 hybridization probes (Table 2, Fig. 1), constructed by subcloning from a set of parent clones of the entire chloroplast genome of tobacco provided by M. Sugiura (Sugiura et al., 1986), was used to construct complete restriction site maps for all 43 species for all 10 enzymes. These probes were radioactively labeled by nick-translation and sequentially hybridized in 20 rounds to the two sets of replica filters. The comparative restriction site mapping was aided by the computer generation of essentially perfect maps for each enzyme for tobacco based on its completely known sequence (Shinozaki et al., 1986) and by including one lane of tobacco cpDNA on each filter for a hybridization standard.

Phylogenetic analyses were performed using PAUP version 3.0 (Swofford, 1989) on a Macintosh II computer. Several analyses were conducted in an effort to examine (1) the statistical support for monophyletic groups identified by the most parsimonious tree; (2) alternative trees suggested by conventional classifications; and (3) the effect of different assumptions concerning the probability of gain versus loss of restriction sites on the outcome of the phylogenetic analysis. Several prospective outgroups were included in the restriction site mapping study, but only the Convolvulaceae were actually used as the outgroup. This is because our concurrent analysis of family relationships in the Asteridae using *rbc*L sequences clearly identified the Convolvulaceae as the sister group to the Solanaceae (Olmstead et al., 1992) and because the extent of sequence divergence between the

TABLE 1. Sources of plants for cpDNA study of Solanaceae.

Species	Source[a]	Voucher information[b]
Solanaceae		
Cestroideae		
Anthocercideae		
1. *Anthocercis viscosa*	Symon	DES 14835
2. *Cyphanthera anthocercidea*	Symon	DES 14836
3. *Duboisia myoporoides*	Symon	DES 14832
4. *Grammosolen dixonii*	Symon	DES 14833
Cestreae		
5. *Cestrum nocturnum*	Matthaei	21314
6. *Vestia lyciodes*	Lester	BIRM/S.0105
Nicotianeae		
7. *Fabiana imbricata*	UCSB	81342
8. *Nicotiana tabacum*	Matthaei	no voucher
9. *Petunia axillaris*	Lester	BIRM/S.0367
Salpiglossideae		
10. *Browallia speciosa*	Lester	BIRM/S.0416
11. *Brunfelsia americana*	Matthaei	840215
12. *Salpiglossis sinuata*	Lester	BIRM/S.0181
13. *Schizanthus pinnatus*	Lester	BIRM/S.0224
14. *Streptosolen jamesii*	JBB	RGO S-106
Solanoideae		
Datureae		
15. *Brugmansia sanguinea*	JBB	RGO S-7
16. *Datura stramonium*	Olmstead	RGO S-16
Hyoscyameae		
17. *Hyoscyamus albus*	Lester	BIRM/S.1218
Juanulloeae		
18. *Dyssochroma viridiflora*	Brown	s.n.
19. *Hawkesiophyton panamensis*	Lester	BIRM/S.1462
20. *Juanulloa aurantiaca*	Lester	BIRM/S.0411
Lycieae		
21. *Grabowskia duplicata*	Lester	BIRM/S.0258
22. *Lycium cestroides*	Lester	BIRM/S.0368
Nicandreae		
23. *Nicandra physaloides*	BealBG	RGO S-38
Solandreae		
24. *Solandra grandiflora*	Matthaei	840415
Solaneae		
25. *Atropa belladona*	Lester	BIRM/S.0078
26. *Capsicum baccatum*	Eshbaugh	WHE 1584
27. *Chamaesaracha coronopus*	Turner	BLT 15854
28. *Cyphomandra betacea*	Bohs	Nee 30359
29. *Exodeconus miersii*	Lester	BIRM/S.1223
30. *Jaltomata edulis*	BealBG	RGO S-24
31. *Lycianthes lycioides*	JBB	RGO S-87
32. *Lycopersicon esculentum*	Palmer	no voucher
33. *Mandragora officinalis*	Lester	BIRM/S.0672
34. *Margaranthus solanaceous*	Lester	BIRM/S.0610
35. *Physalis alkekengi*	D'Arcy	WGD 17707
36. *Saracha spinosa*	UCB	75.0784
37. *Solanum carolinense*	Lester	BIRM/S.1816
38. *Solanum luteoalbum*	Bohs	BIRM/S.0042
39. *Solanum americanum*	Olmstead	RGO S-94
40. *Solanum candidum*	Lester	BIRM/S.0975
41. *Withania coagulans*	Lester	BIRM/S.0678

TABLE 1. Continued.

Species	Source[a]	Voucher information[b]
Nolanoideae		
42. *Nolana spathulata*	Dillon	MOD 3767
Convolvulaceae		
43. *Ipomoea coccinea*	BealBG	RGO s.n.

[a] BealBG = Beal Botanical Garden, Michigan State University, Bohs = Lyn Bohs, Brown = Keith S. Brown, D'Arcy = William G. D'Arcy, Dillon = Michael O. Dillon, Eshbaugh = W. Hardy Eshbaugh, JBB = Jardín Botánico de Bogotá, Lester = Richard N. Lester, Matthaei = Matthaei Botanic Garden, Olmstead = Richard G. Olmstead, Palmer = Jeffrey D. Palmer, Symon = David E. Symon, Turner = B. L. Turner, UCB = University of California, Berkeley, Botanical Garden, UCSB = University of California, Santa Barbara, greenhouse.

[b] Numbers preceded by initials or name indicate collector (BLT = Turner, DES = Symon, Hawkes = J. G. Hawkes, MOD = Dillon, Nee = Michael Nee, RGO = Olmstead, WGD = D'Arcy, WHE = Eshbaugh) and collection number. Material provided by Richard N. Lester bears the accession number of the University of Birmingham Solanaceae Collection. All other numbers are accession numbers for living collections at botanical gardens.

Solanaceae and the more distantly related outgroups precluded effective comparative mapping of large portions of their genomes.

RESULTS

A total of 1,074 different restriction sites was identified among the 43 taxa included. Of these, 194 sites (18.1%) were invariant, 433 (40.3%) were present or absent in all but one species, and therefore did not provide information concerning relationships among taxa, and 447 (41.6%) were phylogenetically informative (a complete data matrix is available upon request from R. Olmstead). The distribution of informative restriction sites was nonrandom. The inverted repeat portion of the genome, which accounts for approximately 20% of the genome complexity, accounts for 44% of the invariant sites and only 6% of the phylogenetically informative sites. This extreme conservation of restriction sites in the inverted repeat is in accord with results from studies of nucleotide sequence evolution (Wolfe et al., 1987) and suggests that comparative restriction-site mapping of the inverted repeat can be applied to problems at greater phylogenetic depth than the genome as a whole (Downie & Palmer, 1992).

Fourteen restriction-fragment length variants, representing probable insertions and deletions ranging in size from 150 to 700 base pairs, were mapped. Five of these length variants are shared by two or more taxa. The length variants were not used directly in the phylogenetic analysis, but extremely accurate mapping, made possible by reference to the completely sequenced tobacco genome, enabled the identification of restriction sites whose presence or absence was the product of the insertion or deletion, and those sites were scored as missing data for those taxa. The five shared length variants are all implied to be deletions by the results of the phylogenetic analysis (Fig. 2). Four of the five variants represent unique events; the fifth deletion is implied to have occurred in parallel on four separate occasions (Fig. 2). Numerous smaller insertions/deletions (<100 bp) were detected, but not mapped.

The phylogenetic analysis conducted using Wagner parsimony (all restriction site changes weighted equally) resulted in 45 equally parsimonious trees with a length of 1,227 and a consistency index of 0.36 excluding autapomorphies, and 0.53 including autapomorphies (Kluge & Farris, 1969), from which a strict consensus tree was constructed (Fig. 2). A bootstrap analysis (Felsenstein, 1985) was conducted with 100 replications to provide a measure of support for the monophyletic groups identified in the consensus tree (Fig. 2). The bootstrap majority rule consensus tree was entirely congruent with the consensus tree from the Wagner parsimony analysis.

Figure 3 shows one of the 45 most parsimonious trees to illustrate the distribution of character support (putative gains or losses of restriction sites) for clades on the tree. Both trees (Figs. 2, 3) show an ancestral, paraphyletic Cestroideae and a derived monophyletic Solanoideae. The earliest branch consists of the morphologically divergent genus *Schizanthus*, while the rest of the Cestroideae comprise three distinct lineages. The Nicotianeae are split among two of the distinct cestroid lineages, with *Nicotiana* forming a clade with the Australian endemic tribe Anthocercideae, whereas *Fabiana* and *Petunia*, along with *Brunfelsia*, constitute another clade. Members of the Salpiglossideae are found on three of the four lineages of Cestroideae

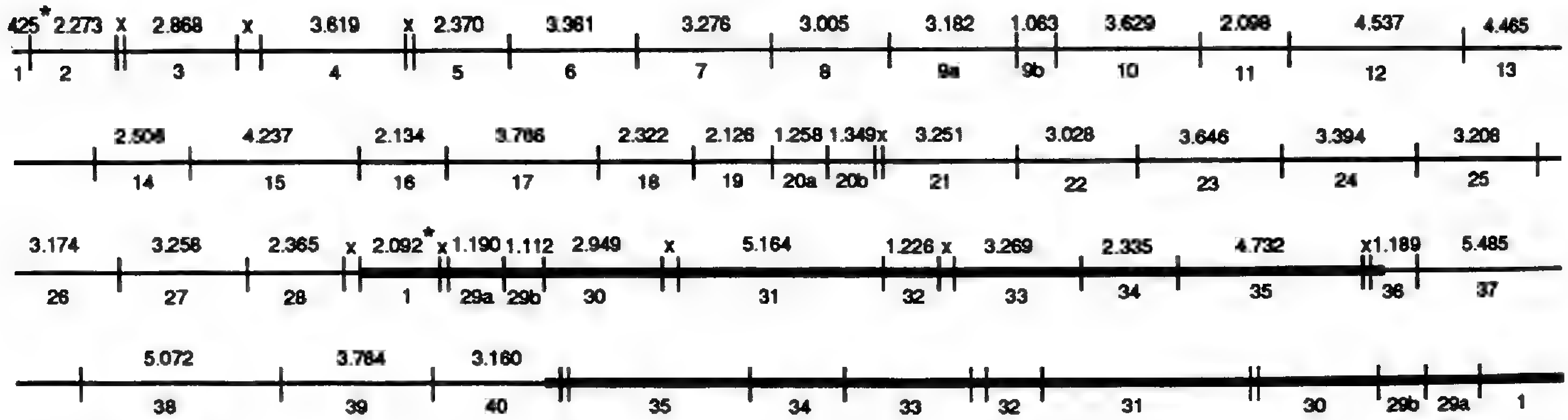

FIGURE 1. Linear map of *Nicotiana tabacum* cpDNA (modified from Shinozaki et al., 1986). The inverted repeat is indicated by the heavy line. SolClone Top40 clone bank fragments are indicated by number (Table 2) below the line and size in kb above the line. Fragments indicated by "x" are not included in the clone bank. SolClone #1 spans the junction between the large single copy region and inverted repeat; the portions belonging to each are indicated by an asterisk.

represented on both trees, supporting D'Arcy's (1978) suggestion that the tribe is artificial.

The major unresolved portion of the consensus tree falls exactly at the point of divergence of the Solanoideae. Several lineages within the Solanoideae correspond to currently recognized tribes, including the Lycieae, Datureae, and Juanulloeae. The large tribe Solaneae appears not to be a monophyletic group. Three genera placed in the Solaneae by D'Arcy (1979, 1991), *Mandragora*, *Atropa*, and *Exodeconus*, fall outside the clade containing most of the representatives of the tribe, whereas the Datureae fall within that clade. *Nolana* (Nolanaceae or Nolanoideae) branches within the Solanoideae, closest to the tribe Lycieae.

A further analysis was performed to test the strength of the result that the Nicotianeae are split between two distinct cestroid lineages by imposing the constraint that the Nicotianeae plus Anthocercideae form a monophyletic group. Including the Anthocercideae in the constraint provided a more liberal test than that of strict monophyly for the Nicotianeae, yet the shortest tree (not shown) was still 16 steps longer than the most parsimonious tree.

Relationships among a larger number of taxa in the Solanoideae are the subject of an analysis currently in progress, but two steps were taken in the current study to try to increase resolution within the Solanoideae. First, to reduce the amount of homoplasy that inevitably arises among distantly related taxa, the cestroid lineage closest to the Solanoideae (Fig. 2) was chosen as a functional outgroup (Watrous & Wheeler, 1981) for an analysis with a reduced number of taxa. The resulting consensus tree of three equal trees (Fig. 4) is congruent with the tree produced by the complete analysis (Fig. 2), but completely resolves the polychotomy at the base of the Solanoideae produced by the global analysis. This tree (Fig. 4) suggests a basal branch of the Solanoideae comprising *Exodeconus* and *Nicandra*. The rest of the taxa form two main clades. One clade consists of the Datureae and most of the Solaneae (as in the global analysis). The other clade consists of two groups, the Solandreae, Juanulloeae, and *Mandragora* in one and the Hyoscyameae, Lycieae, *Atropa*, and *Nolana* in the other.

The second approach to increasing resolution involved varying the assumptions concerning evolution of restriction sites, specifically that there exists a greater probability of loss than of gain of any one restriction site. Asymmetric weighting was implemented using the Stepmatrix option of PAUP with weights for gain : loss of 1.3 : 1.0 as recommended by Albert et al. (1991). The single shortest tree from this analysis (Fig. 5) is congruent with one of the three trees found using the functional outgroup approach, except that the clade comprising the Hyoscyameae, Lycieae, *Atropa*, and *Nolana* groups with the Solaneae in the weighted analysis rather than with the Solandreae, Juanulloeae, and *Mandragora*.

DISCUSSION

CESTROIDEAE

It is clear from the phylogenetic analysis (Fig. 2) that the Cestroideae are the ancestral subfamily of Solanaceae. Traditional views of the family have considered the Solanoideae as ancestral based on a priori assumptions about trends in the evolution of characters from "primitive" to "specialized" that have been postulated to exist throughout the angiosperms (Melchoir, 1964; D'Arcy, 1979). That reversals in these "trends" may characterize particular groups, as is apparent from this analysis in

TABLE 2. SolClone Top40 clone bank[a] constructed from *Nicotiana tabacum* cpDNA.

	Subclone[b]	Size (kb)	Coordinates[c]	Vector[d]
1.	Bam 8—BamHI-SpeI(XbaI)	2.517	153746–419	pTZ19R
2.	Bam 8—SpeI(XbaI)-BamHI	2.273	419–2692	pTZ19R
3.	Bam 15	2.868	2832–5700	pTZ19R
4.	Bam 10a	3.619	6149–9768	pTZ19R
5.	Bam 4—BamHI-SacI	2.370	9935–12305	pTZ19R
6.	Bam 4—SacI-SacI	3.361	12305–15666	BSsk+
7.	Bam 4—SacI-BamHI	3.276	15666–18942	pTZ19R
8.	Bam 13	3.005	18942–21947	pTZ19R
9a.	Bam 12a	3.182	21947–25128	BSsk+
9b.	Bam 25	1.063	25128–26191	BSsk+
10.	Bam 10b	3.629	26191–29820	pTZ19R
11.	Bam 19	2.098	29820–31918	BSsk+
12.	Bam 9a	4.537	31918–36455	pBR322
13.	Bam 9b	4.465	36455–40920	BSsk+
14.	Bam 16	2.506	40920–43426	pTZ19R
15.	Bam 3—BamHI-SacI	4.237	43426–47699	BSsk+
16.	Bam 3—SacI-SalI	2.134	47699–49833	BSsk+
17.	Bam 3—SalI-BamHI	3.766	49833–53599	BSsk+
18.	Bam 17	2.322	53599–55921	pTZ19R
19.	Bam 18	2.126	55921–58047	pTZ19R
20a.	Bam 22c	1.258	58047–59305	pTZ19R
20b.	Bam 20	1.349	59305–60654	pTZ19R
21.	Bam 12b	3.251	60850–64101	pTZ19R
22.	Bam 1—BamHI-SacI	3.028	64101–67129	pTZ19R
23.	Bam 1—SacI-SalI	3.646	67129–70773	pTZ19R
24.	Bam 1—SalI-EcoRV	3.394	70773–74167	BSsk+
25.	Bam 1—EcoRV-SacI	3.208	74167–77375	BSsk+
26.	Bam 1—SacI-BglII	3.174	77375–80549	BSsk+
27.	Bam 1—BglII-BamHI	3.258	80549–83807	BSsk+
28.	Bam 7—BamHI-PstI	2.365	83807–86172	pTZ19R
29a.	Bam 23b	1.190	88991–90181	pTZ19R
29b.	Bam 24b	1.112	90181–91293	pTZ19R
30.	Bam 14b	2.949	91293–94242	pTZ19R
31.	Bam 6b	5.164	94562–99726	pBR322
32.	Bam 22b	1.226	99726–100952	pTZ19R
33.	Bam 11b	3.269	101532–104801	pTZ19R
34.	Bam 5b—BamHI-NheI(XbaI)	2.335	104801–107136	BSsk+
35.	Bam 5b—NheI(XbaI)-BamHI	4.732	107136–111868	BSsk+
36.	Bam 21	1.189	111924–113113	pTZ19R
37.	Bam 2—BamHI-XhoI	5.485	113119–118604	BSsk+
38.	Bam 2—XhoI-PstI	5.072	118604–123676	BSsk+
39.	Bam 2—PstI-SacI	3.764	123676–127440	BSsk+
40.	Bam 2—SacI-BamHI	3.160	127440–130600	BSsk+

[a] These clones may be obtained by writing to J. Palmer.

[b] Subclones are derived from parent clones provided by M. Sugiura (Sugiura et al., 1986) and are either BamHI clones or subclones derived from BamHI clones as noted. CpDNA restriction sites not found in the multiple-cloning region of vectors pTZ19R and BSsk+ are cloned into sites noted in parentheses. Each set of paired subclones (9a+b, 20a+b, and 29a+b) is intended to be used as a single hybridization probe. The one large gap in coordinate coverage (between clones 28 and 29a) represents one end of the large inverted repeat and is covered by clone 1. Ten smaller gaps, nine of which are shown in Figure 1, totaling 2641 bp in size, are not covered by this clone bank.

[c] Coordinates for the *Nicotiana tabacum* cpDNA sequence are those of Shinozaki et al. (1986).

[d] All plasmids are ampicillin-resistant.

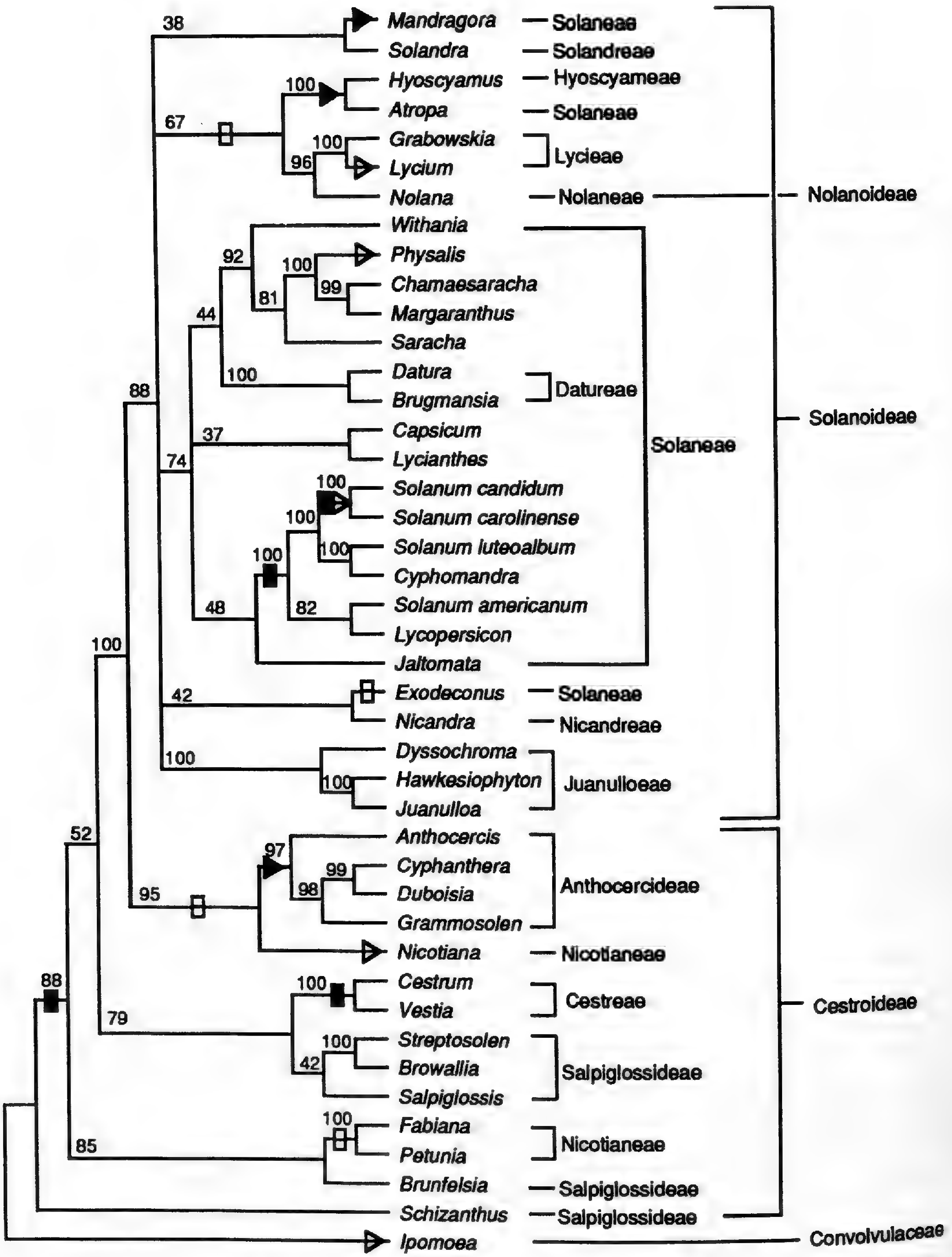

FIGURE 2. Strict consensus of 45 equally parsimonious trees derived from the Wagner parsimony analysis of 447 informative restriction sites in the Solanaceae. The percentage of bootstrap replicates supporting each clade is indicated along the internode for that clade. Tribal and subfamilial designations follow D'Arcy (1991). Solid triangles indicate groups with strictly Old World or Australian native distributions. Open triangles indicate groups with New World and Old World native distributions. All others are New World only. Note that not all Solanoideae taxa with New/Old World distributions are included in this analysis. Rectangles indicate mapped deletions, which were not used to infer phylogeny; solid rectangles indicate unique deletions, and open rectangles indicate homoplastic occurrences of one deletion (see text).

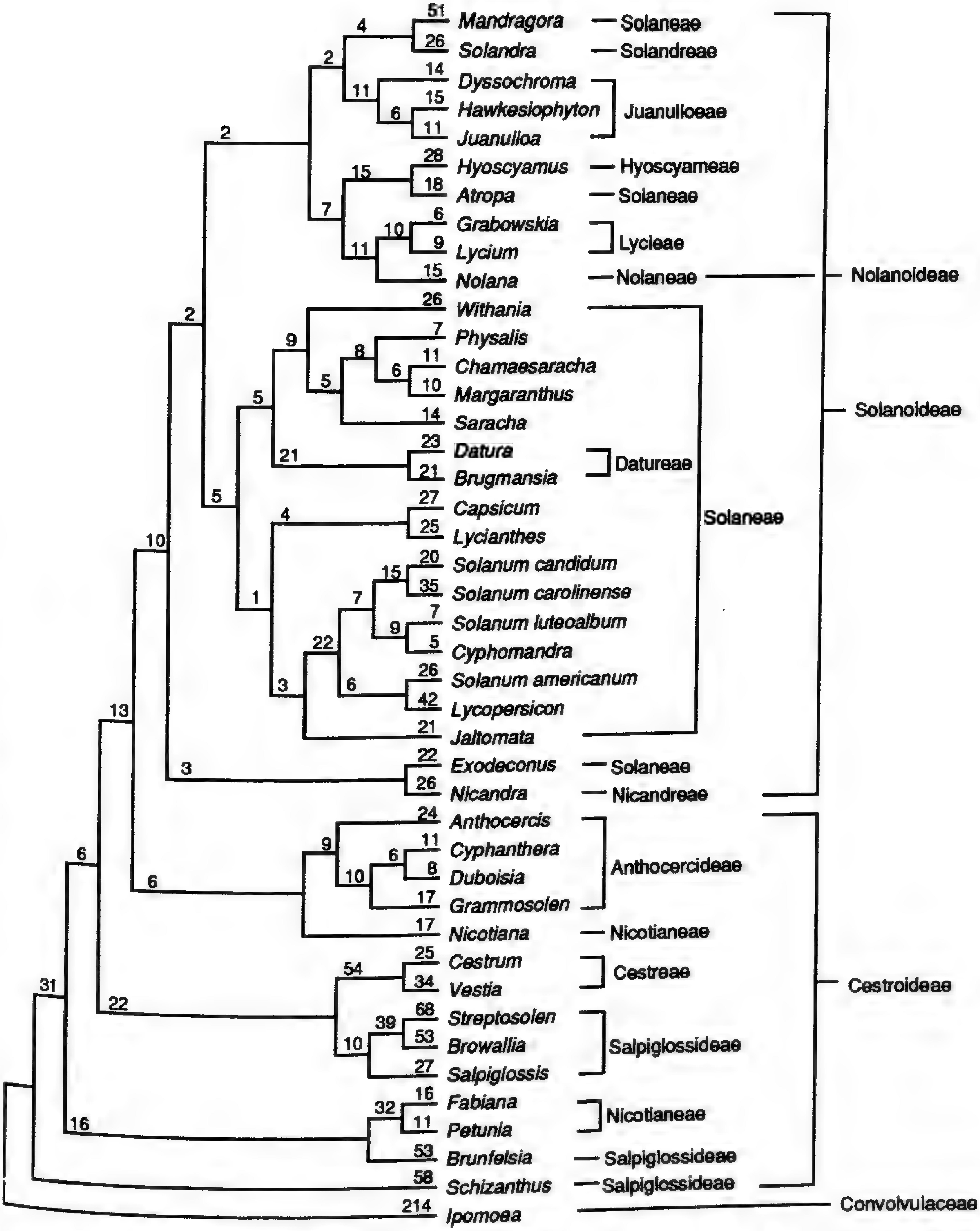

FIGURE 3. One of the 45 equally parsimonious Wagner trees of the Solanaceae (length = 1227, CI = 0.36, both calculated excluding autapomorphies). Total tree length, including 433 autapomorphies, is 1660. Number of restriction site changes supporting each clade is indicated. Terminal branch lengths include autapomorphies and implied homoplasies.

the Solanaceae, could not be tested without a rigorous phylogenetic analysis. Four of the five recognized tribes of Cestroideae are represented in the analysis. Material of the fifth tribe, Schwenckieae, was not available at the time of this study. The representatives of two of the tribes, Cestreae and Anthocercideae, correspond to clades on the tree, whereas the two other tribes, Salpiglossideae and Nicotianeae, do not. The Salpiglossideae, characterized by their zygomorphic floral symmetry, are

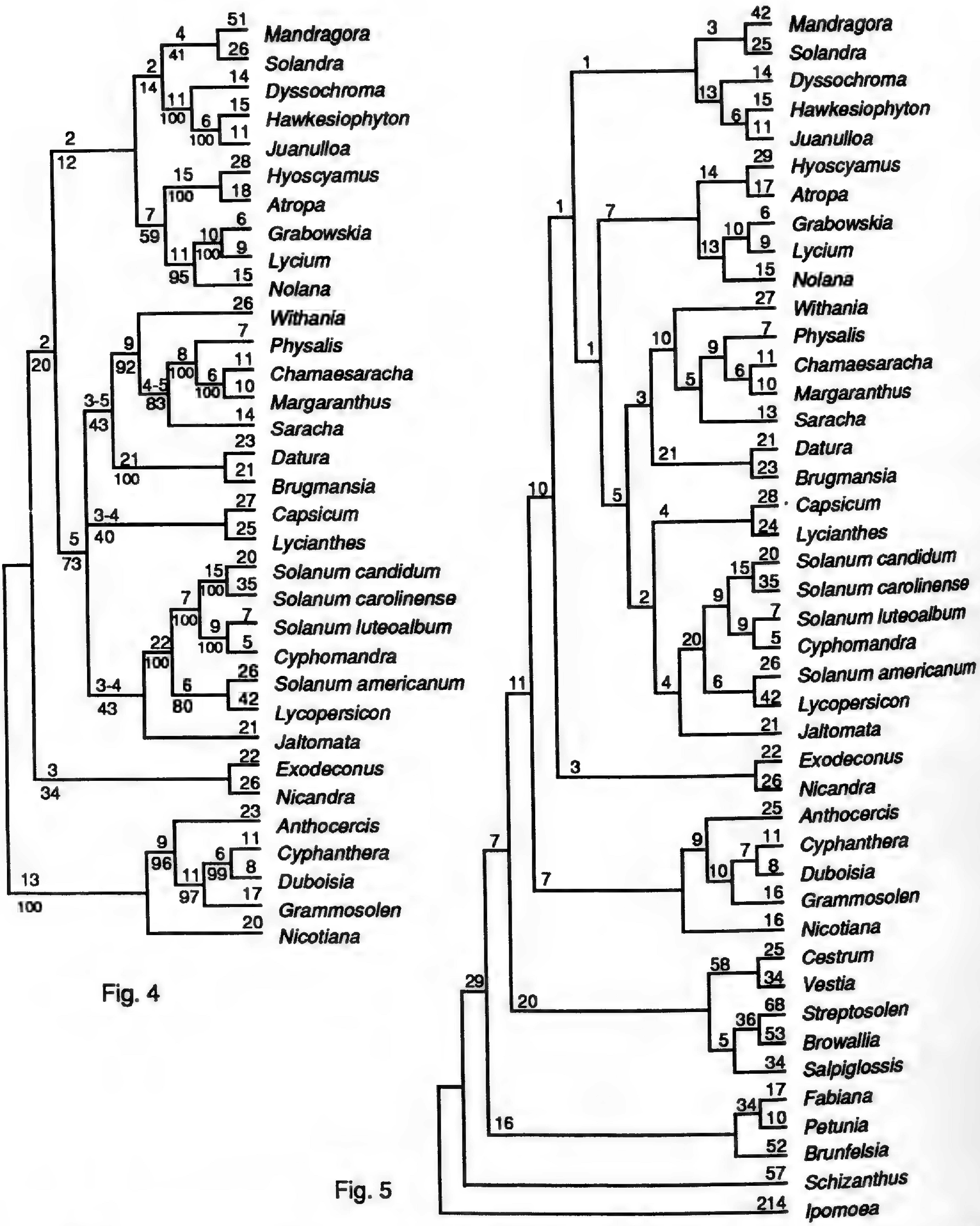

Fig. 4

Fig. 5

FIGURES 4, 5.—4. Strict consensus of three equally parsimonious Wagner trees of the subfamily Solanoideae using its sister clade comprised of *Nicotiana* and the Anthocercideae as a functional outgroup (length = 629, CI = 0.441, excluding autapomorphies). Total tree length, including 249 autapomorphies, is 878. Number of restriction site changes supporting each clade is indicated. Terminal branch lengths include autapomorphies and implied homoplasies. The branch lengths for the three alternate topologies are indicated by a range of values. The percentage of bootstrap replicates supporting each clade is indicated beneath the internode for that clade.—5. The single most parsimonious tree resulting from asymmetric weighting of gains vs. losses of 1.3 : 1.0. This tree is one of the 45 equally parsimonious Wagner trees. Number of restriction site changes supporting each clade is indicated.

represented in this study by: *Schizanthus*, which forms the earliest diverging lineage of Solanaceae; *Brunfelsia*, which appears as the sister group to a part of the Nicotianeae; and a clade composed of *Browallia*, *Salpiglossis*, and *Streptosolen*, which forms the sister group to the Cestreae. We concur with D'Arcy's argument (1978, 1979) that taxonomic recognition of the Salpiglossideae in its current broad sense is unwarranted, but suggest that a narrowly defined Salpiglossideae, consisting of *Salpiglossis*, *Browallia*, *Streptosolen*, and other genera closely related to them might be retained. *Schizanthus* stands apart both morphologically and phylogenetically and appears to warrant recognition as a monogeneric tribe. *Brunfelsia* might best be combined with the excluded elements of the Nicotianeae, *Petunia* and *Fabiana*, in a new tribe.

The Nicotianeae appear to present a situation similar to the Salpiglossideae, with *Fabiana* and *Petunia* in one lineage and *Nicotiana* in another. However, the characters uniting the Nicotianeae, such as herbaceous habit, actinomorphic floral morphology, nonarticulated pedicels, capsular fruits, and small seeds, all appear to be ancestral for the Cestroideae and the entire Solanaceae and are retained in separate lineages, rather than being independently derived in different lineages as was the case with the Salpiglossideae (Fig. 6). The results presented here indicate that a clade composed of *Nicotiana* and the Anthocercideae forms the sister group to the Solanoideae, a conclusion supported by 100% of the bootstrap replicates. This relationship is congruent with DNA sequence data from the chloroplast *rbc*L gene (Palmer et al., 1988; Olmstead et al., unpublished) and the nuclear *rbc*S gene (Pichersky et al., 1986; Meagher et al., 1989), from both of which a closer relationship was inferred for *Nicotiana* and *Lycopersicon* than for either with *Petunia*. The Nicotianeae also can be divided into two groups on the basis of chromosome base number, with *Fabiana*, *Petunia*, *Latua*, and *Nierembergia* having $x = 7$, 8, or 9 and *Nicotiana*, *Combera*, *Pantacantha*, and *Benthamiella* having $x = 11$ or 12 (Hunziker, 1979; Moscone, 1989). The transition series for chromosome base number in the family is not clear as to the disposition of $x = 11$ (see discussion below). However, the evolution of base number $x = 12$ appears to provide a synapomorphy for the clade comprised of *Nicotiana*, the Anthocercideae, and the Solanoideae (Fig. 6).

The Anthocercideae and *Nicotiana* are sister groups on the cpDNA tree. A substantial amount of molecular data, including a large (ca. 650 bp) deletion in the cpDNA unique to *Nicotiana* (Olmstead et al., 1990), indicates that both *Nicotiana* and the Anthocercideae are monophyletic. The Australian species of *Nicotiana* form a derived clade within *Nicotiana* and are very homogeneous with respect to their cpDNA (Olmstead et al., 1990). *Nicotiana* is well represented in Australia, where the Anthocercideae are endemic, but there is much greater morphological and cpDNA divergence among the members of the Anthocercideae than among the Australian species of *Nicotiana* (Olmstead et al., 1990). This combination of phylogenetic inference, biogeographic distribution, and cpDNA divergence leads to the following conclusions: (1) the most recent common ancestor of the two groups was South American and (2) two separate colonizations of Australia occurred, one in the proto-Anthocercideae, prior to diversification of that lineage, and one late in the diversification of *Nicotiana*. The amino acid sequence data of Martin & Dowd (1984) also suggest a recent arrival of *Nicotiana* in Australia. These two introductions of Solanaceae into Australia resulted in the only cestroid elements native outside of the New World (the single species of *Nicotiana* in Africa is believed to be a secondary immigrant from Australia; Martin & Dowd, 1984).

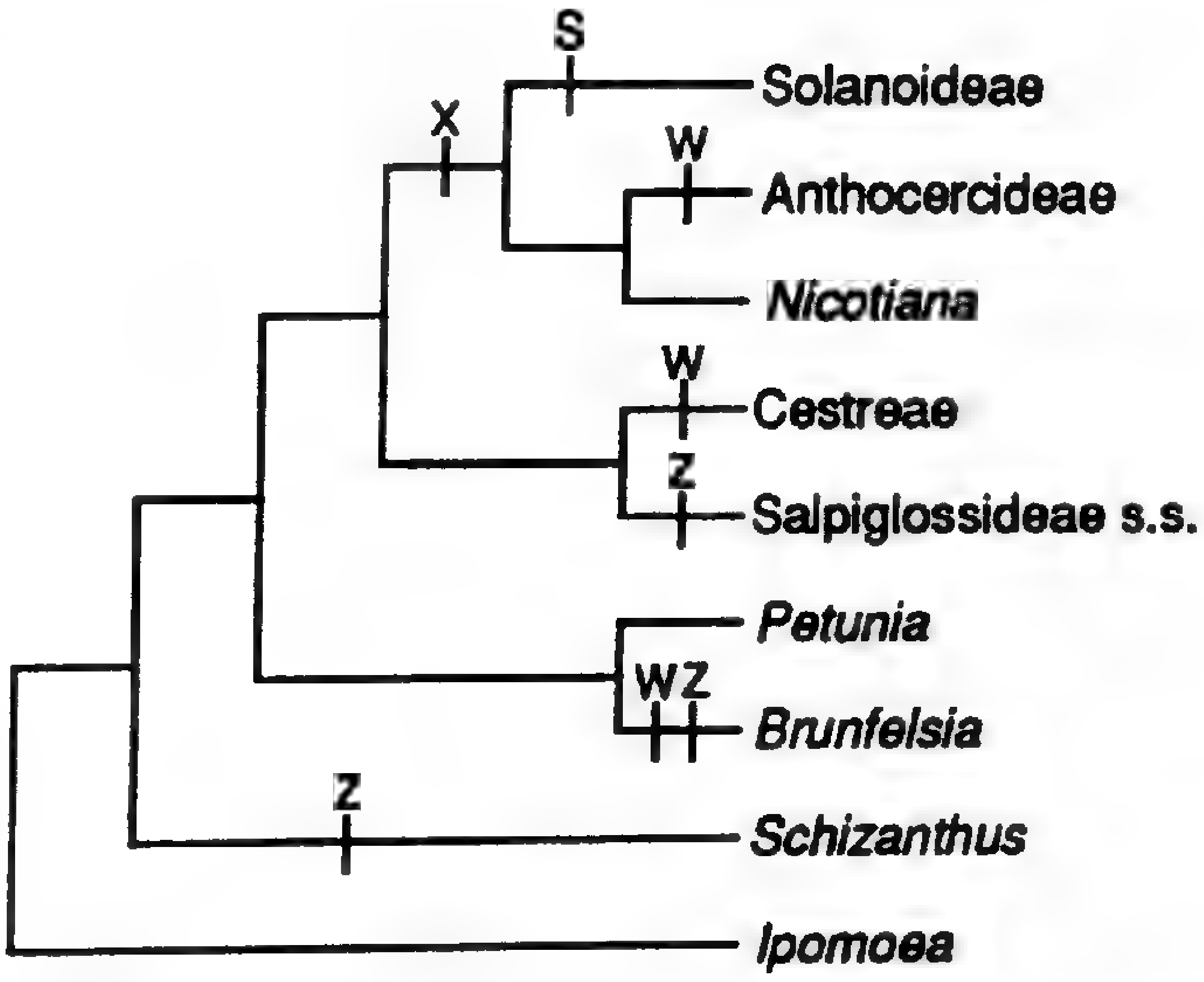

FIGURE 6. Reduced cladogram of the Solanaceae with character state transformations for some prominent morphological (S = seed discoidal with curved embryo, W = woody habit, Z = zygomorphic floral symmetry) and chromosomal (X = base chromosome number $x = 12$) characters indicated. Note the absence of morphological apomorphies on the lineages leading to members of the tribe Nicotianeae, *Nicotiana* and *Petunia*.

SOLANOIDEAE

The cpDNA tree indicates that the subfamily Solanoideae is monophyletic and derived from the Cestroideae, contrary to previously held views (D'Arcy, 1979, 1991). The results of Martin and coworkers (Martin & Dowd, 1984; Martin et al., 1984), using partial amino acid sequences from the small subunit of rubisco, are ambiguous with respect to the direction of evolution in the family; the Solanoideae are depicted as ancestral in one study (Martin & Dowd, 1984), whereas the cestroid representatives form a basal branch in the other (Martin et al., 1984). Several clades, corresponding to currently recognized tribes, emerge from the unresolved portion of the consensus cpDNA tree (Fig. 2) at the base of the Solanoideae. In addition to the substantial agreement with traditional classification, the cpDNA tree offers solutions for some genera that have been difficult to place in the current classification. D'Arcy places *Atropa* and *Mandragora* in the Solaneae "more for convenience than conviction" (D'Arcy, 1991). The present study unambiguously places *Atropa* with *Hyoscyamus* of the Hyoscyameae, in agreement with Tetenyi (1987). *Mandragora* is isolated in the cpDNA analysis, at best only loosely related to *Solandra*, and is remote from either the Solaneae or the *Atropa*/Hyoscyameae clade, where it is placed by Tetenyi (1987). The monotypic *Nicandra* (and tribe Nicandreae) likewise is isolated within the Solanoideae and may represent an early diverging lineage (Figs. 4, 5). *Nicandra* is possibly related to *Exodeconus* (Figs. 4, 5), previously classified in the Solaneae, with which it shares a native distribution in coastal Peru. D'Arcy (1991) suggested that the tribe Solaneae is "inconveniently large," but that appropriate divisions are not readily apparent. The tribe Datureae forms one of several lineages within the Solaneae in the cpDNA tree, suggesting that the Solaneae should be split and that tribes or subtribes may be circumscribed along phylogenetic lines. A more extensive survey of the Solanoideae, currently in progress, should help clarify tribal boundaries and relationships in the subfamily.

Attempts were made using two approaches, each with different underlying assumptions, to gain greater resolution within the Solanoideae. In the functional outgroup approach (Watrous & Wheeler, 1981), the more distantly related taxa in the study are removed and only the closest sister group to the Solanoideae is retained and used as the outgroup. This approach risks sacrificing global parsimony (Maddison et al., 1984) in order to gain resolution by eliminating a large amount of spurious restriction site similarity. The weighted parsimony analysis assumes that equal weighting of all restriction site changes, both gains and losses, does not accurately reflect the probability of gains versus losses of restriction sites (Albert et al., 1991). The fact that both the functional outgroup (Fig. 4) and weighted parsimony (Fig. 5) analyses yielded largely congruent estimates of relationships within the Solanoideae suggests that the weakly supported patterns of relationship implied by each individual analysis may reflect actual phylogenetic history. A comparison of the two approaches used here shows that the weighted parsimony method provided greater resolution than the functional outgroup method (i.e., one shortest tree vs. three), but that the functional outgroup method identified greater character support for the critical, closely spaced branch points that were unresolved in the original analysis. The scant character support for branchings at the base of the Solanoideae is reflected in the very low bootstrap values associated with them (Fig. 4) and suggests a relatively rapid diversification within the subfamily.

Asymmetrically weighted parsimony has been proposed (Albert et al., 1991) as a method for analyzing restriction site data that is preferable to Wagner parsimony (for the above-stated reason) and Dollo parsimony. Dollo parsimony, which allows only a single gain of a character state and prefers the tree with the fewest losses, has been suggested by Debry & Slade (1985) to be more appropriate than Wagner parsimony for use with restriction site data. However, the absolute restriction against parallel gain of a restriction site imposed by Dollo parsimony is viewed as too restrictive (Albert et al., 1991). Two justifications might be advanced for the weighted parsimony approach: (1) that the assumptions concerning restriction site change are more realistic and (2) that greater resolution can be achieved than is often possible using Wagner parsimony. Any phylogenetic analysis is an approximation of the true phylogeny and can be only as reliable as the assumptions underlying the method; therefore, the first point seems to be sufficient justification for asymmetric weighting. The second point is not valid justification in our view, because the resolution (i.e., number of shortest trees) achieved is a function of the asymmetry in weight assigned. A justification based simply on achieving greater resolution should be viewed with caution, bearing in mind that, as an approximation, a cladogram may carry implications concerning relationships that vary in strength as the distribution in character support varies. For example, with this data set, an asymmetric weighting of 1.9 : 1.0 yields three shortest trees, whereas a weighting of 2.0 : 1.0 yields 13 trees (results not shown). The consensus trees from both analyses are congruent and it is doubtful that the greater resolution of the former offers a significantly better approximation of the phylogeny. Instead of relying only on a weighted parsimony analysis to discriminate among many nearly equal trees, alternate methods for assessing the strength of relationships should be used, including testing alternative topologies, bootstrap analysis, successive analyses using functional outgroups, and decay analysis (to determine how many steps longer the best tree is in which a given clade of interest fails to hold up). With very large data sets the computer time required for some analyses (e.g., weighted parsimony, bootstrap, decay analysis) may be excessive, and more approximate methods may be required. Nevertheless, adequate taxonomic sampling should be a primary consideration for parsimony analyses of large and divergent groups, because a more approximate analysis with a well-represented taxonomic sampling may yield more accurate results than an exact analysis of an inadequately sampled study group (Swofford & Olsen, 1990; Olmstead et al., 1992).

NOLANOIDEAE

The cpDNA tree clearly places *Nolana* within the Solanoideae in a clade with the Lycieae. The association of *Nolana* with *Lycium* has been made by Carlquist (1987) on the basis of wood anatomy, and by Armstrong (1986) on the basis of calyx vasculature. If the subfamily Nolanoideae is recognized, then the Solanoideae would not be strictly monophyletic. Carpel morphology—the primary basis for the maintenance of the distinct family Nolanaceae—has long been a heavily weighted character in traditional angiosperm classifications. Even recent treatments (Thorne, 1968; D'Arcy, 1979), which include *Nolana* and *Alona* in the Solanaceae, maintain a sharp taxonomic distinction through the creation of a new subfamily, Nolanoideae, while admitting that "most of its morphology corresponds to that of the Solanoideae" (D'Arcy, 1991). We suggest that it is time to deemphasize gynoecial morphology for defining higher taxonomic classes and, instead, define taxonomic classes on hypotheses of phylogenetic relationship whenever such schemes are available. In the case of *Nolana*, it seems entirely justified to place it in the tribe Nolaneae in the Solanoideae or, perhaps even more appropriately, in the tribe Lycieae, to which it is closely related molecularly (Figs. 2–5) and anatomically (see above).

CHARACTER EVOLUTION

Characters that distinguish subfamilies in the Solanaceae can be polarized by reference to the hypothesis of phylogeny derived from cpDNA. Defining characters of the Solanoideae, including discoidal seeds containing curved embryos, small pollen grains, and berrylike fruits, should all be viewed as derived traits within the family, whereas the respective states of these characters in the Cestroideae are primitive. D'Arcy (1979, 1991), following the criteria of Melchior (1964), pointed out that the Cestroideae exhibit more advanced characteristics than the Solanaoideae. Likewise, Armstrong (1986) considered cestroid floral anatomy to be advanced and solanoid floral anatomy to be primitive on the basis of a priori assumptions of trends in angiosperm evolution. In the Solanaceae, criteria of advancement not derived from a phylogenetic analysis of the family prove to be in error. It has been recognized that the Solanoideae are more homogeneous in chromosome number and many other attributes than the Cestroideae and that the latter is "somewhat discordant as a taxonomic unit" (D'Arcy, 1991). In light of the cpDNA tree, both observations may be taken as evidence that members of the Solanoideae share a more recent common ancestry than do members of the Cestroideae.

Chromosome base number has been cited commonly (D'Arcy, 1979), along with the morphological characters discussed above, as a trait distinguishing subfamilies. The Solanoideae are almost uniformly $x = 12$, whereas in the Cestroideae base number is more variable, with most genera having base numbers lower than 12. Raven (1975) postulated $x = 7$ for the subclass Asteridae and $x = 7$ for the Convolvulaceae, but $x = 12$ for the Solanaceae, with aneuploid reduction to $x = 7$, as in *Petunia*. The prominent exceptions in the Cestroideae are *Nicotiana*, with $x = 12$ (Goodspeed, 1954), and the Anthocercideae, with $n = 30$ or 36 (Haegi, 1986), which is probably based on $x = 12$. In light of the phylogenetic relationships suggested by the cpDNA analysis, the presence of $x = 12$ should not be considered as ancestral in the Cestroideae, nor be interpreted as a parallelism with the Solanoideae. Rather, $x = 12$ represents a synapomorphy (Fig. 6) uniting the Solanoideae with the Anthocercideae, and part of the Nicotianeae (*Nicotiana* and, perhaps, *Combera*, *Pantacantha*, and *Benthamiella*, but excluding *Petunia*, *Latua*, *Fabiana*, and *Nierembergia*).

Floral zygomorphy, exhibited to a varying extent in the asymmetry of the corolla, but more discretely in the reduction in anther number, has long been used as the defining characteristic of the tribe Salpiglossideae (Wettstein, 1895; Hunziker, 1979). Other treatments have placed the Salpiglossideae in the Scrophulariaceae (Bentham, 1876) or in a family of its own (Hutchinson, 1969). However, D'Arcy (1978) concluded that the Salpiglossideae are an artificial assemblage of independent lineages in which stamen reduction and corolla asymmetry have arisen. His reasoning, which was not clearly stated in his original paper (D'Arcy, 1978), follows from the floral morphological evidence, which indicates that different pathways are responsible for the development of floral asymmetry in various genera of Salpiglossidae, hence that the plants were probably not closely related (D'Arcy, pers. comm.). The phylogenetic hypothesis presented here supports D'Arcy's conclusion and suggests that floral zygomorphy has evolved independently in at least three lineages within the Cestroideae (Fig. 6).

BIOGEOGRAPHY

Two alternative processes have been postulated to account for the extant distribution of the Solanaceae (D'Arcy, 1991): Present distributions represent (1) vicariant remnants of a former Gondwana distribution (Hawkes & Smith, 1965), or (2) numerous long-distance dispersal events. These two alternatives carry different implications. For the vicariance argument to be correct, the ancestral Solanaceae must have been in the right place (i.e., Southern Hemisphere) at the right time (i.e., prior to the break-up of Gondwana), but dispersal ability is relatively unimportant due to the continuous land connection. For the long-distance dispersal hypothesis to be correct, time of origin is less important, but high dispersability is essential.

The cpDNA tree (Fig. 2) does not indicate absolute dates of origin or diversification, but it does imply relative timing of divergence among lineages by the order of branching on the tree. The predominantly South American Cestroideae were clearly in the right place and were well diversified prior to the appearance of the Solanoideae. If the vicariance hypothesis is viable for the family as a whole, an appropriate distribution should be exhibited by the Cestroideae. However, only two cestroid groups, the Anthocercideae and *Nicotiana*, exhibit disjunctions consistent with a vicariance explanation. Both occur entirely or in part within Australia and have their closest extant relatives in South America. One of these, *Nicotiana*, can be ruled out as a recent event (Martin & Dowd, 1984; Olmstead et al., 1990), leaving a single possibility of a vicariant distribution in the Cestroideae, the Anthocercidae. The Solanoideae are of much more recent origin, but contain many more lineages with worldwide distributions (D'Arcy, 1991). If the global distribution of the Solanoideae is the product of the break-up of Gondwana, then one might expect the more ancient Cestroideae to exhibit a similar pattern.

Seed dispersibility, on the other hand, exhibits an association that is consistent with a long-distance dispersal hypothesis to account for much of the global distribution of the Solanaceae. Animal dispersal of fleshy fruits is commonly associated with long-distance dispersal and the colonization of oceanic islands (Carlquist, 1974), whereas dry capsular fruits and small, unornamented seeds tend to be local in their dispersal. The animal-dispersed, fleshy-fruited Solanoideae have many lineages that exhibit intercontinental distribution. Most notably, *Solanum* subg. *Leptostemonum*, which is one of the most widely distributed groups in the family, is implied by the cpDNA tree to be of recent origin (*S. candidum* and *S. carolinense* in Fig. 2) relative to most of the Solanaceae.

D'Arcy (1991) concluded that the pattern of geographic distribution in the family is likely to be the product of both long-distance dispersal and vicariance resulting from continental drift, their relative importance depending upon the age of the family. Our cpDNA analysis argues against vicariance and in favor of long-distance dispersal to account for the distribution of most solanaceous taxa with intercontinental distributions. The best case for a vicariant distribution may be the Anthocercideae, but even here only a single lineage in an already substantially diversified Cestroideae is found outside the New World (except for the recent colonization of Australia and Africa by *Nicotiana*). This suggests that the origin, or at least much of the early diversification of the Solanaceae (i.e., Cestroideae), appears to have followed the split-up of Gondwana and the disappearance of land connections among the continents of the Southern Hemisphere approximately 50 million years ago (Parrish, 1987).

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EVIDENCE FOR A POLYPHYLETIC ORIGIN OF THE LABIATAE[1]

Philip D. Cantino[2]

ABSTRACT

A preliminary cladistic analysis suggests that the Labiatae are polyphyletic as presently circumscribed. The gynobasic-styled Labiatae emerge as a clade, nested within a larger group characterized by suprareticulate pollen and a fruit composed of nutlets. The latter includes the bulk of the Labiatae plus the verbenaceous genera *Garrettia* and *Holmskioldia*; its closest relatives are in tribe Viticeae (Verbenaceae). In contrast, *Teucrium* and five other genera of Ajugeae (Labiatae) belong to a large clade characterized by pollen with branched to granular columellae, most members of which are currently assigned to tribes Clerodendreae and Caryopterideae (Verbenaceae). Another group traditionally placed in the Labiatae, tribe Prostanthereae, appears to be most closely related to subfamily Chloanthoideae (Verbenaceae). The hypothesis that the gynobasic-styled Labiatae evolved in southern China or Indomalaysia (Wu & Li, 1982) is supported by this analysis. An Australian origin is hypothesized here for the cosmopolitan genus *Teucrium* based on the distributions of its closest relatives.

The Labiatae, one of the largest and most distinctive angiosperm families, have long been considered a "natural" group (in the pre-Darwinian sense of the word; see Stevens, 1984). It is often tacitly assumed that such a group is monophyletic. However, palynological evidence (Abu-Asab, 1990; Abu-Asab & Cantino, 1992) suggests that the Labiatae are polyphyletic as traditionally circumscribed. This hypothesis is tested here by means of a cladistic analysis of mainly morphological and anatomical data.

THE POLYPHYLY HYPOTHESIS

CURRENT CLASSIFICATION OF THE LABIATAE

The classification of the Labiatae that is most widely used today (Briquet, 1895–1897) is based heavily on the work of Bentham (1832–1836, 1848, 1876). Briquet subdivided Bentham's taxa more finely, increased the rank of some of them, and reclassified a few genera, but his treatment differs from Bentham's in only one fundamental way: Briquet recognized a large subfamily Lamioideae ("Stachyoideae"), which is at best paraphyletic and probably polyphyletic (Cantino & Sanders, 1986). Neither Bentham nor Briquet attempted to reconstruct the phylogeny of the family, and no phylogeny of the Labiatae has yet been published.

An alternative classification of the Labiatae was proposed by Erdtman (1945) on the basis of palynological features. He divided the family into two subfamilies: Lamioideae, with tricolpate pollen shed in a two-celled stage, and Nepetoideae, with hexacolpate pollen shed in a three-celled stage. This division correlates well with a variety of embryological and phytochemical characters (Wunderlich, 1967; Zoz & Litvinenko, 1979; Cantino & Sanders, 1986). Erdtman's subfamilial classification is highly congruent with Bentham's (1876) tribal classification, four of Bentham's tribes composing subfamily Lamioideae, and the other four composing subfamily Nepetoideae (Cantino & Sanders, 1986).

A numerical phenetic study conducted by El-Gazzar & Watson (1970) provided further support for Erdtman's subfamilies. Their results cast doubt on the phenetic cohesiveness of some of Bentham's and Briquet's groupings, but the two principal branches of their phenogram correspond to Erdtman's subfamilies. Although Erdtman's subfamilies appear to be primary phenetic units of the Labiatae,

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TABLE 1. Taxa included in study group. Numbers in parentheses: number of genera included in this analysis/number of genera in the taxon. Parenthetical acronyms are used in Table 2 and Figures 1–4.

- Verbenaceae sensu lato
  - Caryopteridoideae (6/6)
    - Caryopterideae (5/5) (CAR)
    - Teijsmanniodendreae (1/1) (TEI)
  - Chloanthoideae (10/10)
    - Chloantheae (5/5) (CH)
    - Physopsideae (5/5) (PH)
  - Verbenoideae (2/ca. 38)
    - Monochileae (2/2) (MO)
  - Viticoideae (26/28)
    - Callicarpeae (3/4) (CAL)
    - Clerodendreae (10/10) (CL)
    - Tectoneae (3/3) (TEC)
    - Viticeae (10/11) (VI)
- Labiatae
  - Lamioideae (32/ca. 83)
    - Ajugeae (12/12) (AJ)
    - Prostanthereae (7/7) (PR)
    - Scutellarieae (4/4) (SC)
    - Gynobasic-styled Lamioideae (8/ca. 60) (GL)
  - Nepetoideae (4/ca. 160) (NE)

the question remains whether they are monophyletic. Synapomorphies can be demonstrated for subfamily Nepetoideae but not for subfamily Lamioideae (Cantino & Sanders, 1986). The latter group is of interest because it includes the two tribes (Ajugeae and Prostanthereae) that are intermediate in gynoecial morphology between the other Labiatae and the Verbenaceae.

POLYPHYLY OF LABIATAE: INITIAL EVIDENCE

It is widely accepted that the Labiatae evolved from the Verbenaceae, the latter thus being paraphyletic. The two families form the core of the order Lamiales of Cronquist (1981), Dahlgren (1983), Takhtajan (1987), and Thorne (1983). They have traditionally been distinguished on the basis of stylar position—terminal in the Verbenaceae and gynobasic in the Labiatae. However, in two tribes of Labiatae the gynoecium is intermediate in structure; the ovary is only shallowly four-lobed and the style is sunken but not fully gynobasic. Within tribes Ajugeae and Prostanthereae, the ovary may be essentially unlobed (e.g., *Amethystea*, *Schnabelia*), lobed a third to halfway to the base (many members of both tribes), or, rarely, lobed as much as three-quarters of the way to the base with the style thus almost gynobasic (e.g., *Microcorys longifolia* Benth.). Indeed, this full range of gynoecial structure occurs within *Microcorys* (Prostanthereae). In the Verbenaceae, the ovary is usually unlobed but may be lobed as much as halfway to the base (e.g., some species of *Oxera*). In summary, there is a continuum in the degree of ovary lobing, with some intermediates assigned to the Labiatae and some to the Verbenaceae. Since this is the only character distinguishing the two families as currently circumscribed, the taxonomic limits of the Labiatae are unclear, and there is no synapomorphy supporting their monophyly.

On the contrary, a palynological survey of subfamily Lamioideae has provided evidence that tribe Ajugeae (and hence the Labiatae as well) is polyphyletic, its component genera having arisen independently from several different lineages of Verbenaceae (Abu-Asab, 1990; Abu-Asab & Cantino, 1992). Derived pollen features appear to delimit three clades that transcend the family boundary, comprising the following taxa (hypothesized synapomorphies in parentheses): (1) the gynobasic-styled Labiatae, tribe Scutellarieae, six genera of Ajugeae and at least two genera of Verbenaceae (suprareticulate sculpturing); (2) *Teucrium* (Ajugeae) and three genera of Verbenaceae (verrucate sculpturing, operculate colpi); (3) five genera of Ajugeae and ten genera of Verbenaceae (spinulose sculpturing). The latter two clades are linked to each other and to a few other genera of Verbenaceae with different forms of sculpturing by their shared possession of branched columellae (varying to granular in a few taxa), a hypothesized synapomorphy.

Materials and Methods

THE STUDY GROUP

Because the question of primary interest concerns the origin of the Labiatae, the study group (Table 1) centers on the primitive Labiatae (viz., tribes Ajugeae and Prostanthereae) and those groups of Verbenaceae sensu lato that appear to be most closely related to the Labiatae (viz., subfamilies Caryopteridoideae, Chloanthoideae, and Viticoideae). Of the genera that compose these groups, only *Adelosa* Blume and *Archboldia* E. Beer & H. J. Lam (Viticoideae) have been omitted from the analysis because of unavailability of material for study.

These three groups of Verbenaceae share with the Labiatae a distinctive and possibly synapomorphic ovary structure, in which the carpel walls recurve into the interior of the carpel, with the ovules borne short of the carpel margins (Junell, 1934). The group thus delimited may also include the segregate families Avicenniaceae and Symphoremataceae, but excludes Verbenoideae and the segregate families Stilbaceae, Nesogenaceae, and Cyclocheilaceae; in the latter four groups, the ovules are borne directly on the carpel margins (Junell, 1934). Sequence data for the *rbc*L gene (Olmstead et al., in press) also suggest that subfamily Viticoideae is more closely related to the Labiatae than is subfamily Verbenoideae (no members of Chloanthoideae, Caryopteridoideae, or the segregate families have yet been included in Olmstead's study).

Subfamily Verbenoideae and the other outlying groups of Verbenaceae sensu lato, for which data collection is still very incomplete, will be included in a subsequent analysis. However, they have been used here in a limited way as outgroups (discussed below). *Amasonia* and *Monochilus*, usually assigned to subfamily Verbenoideae as tribe Monochileae (e.g., Briquet, 1895; Moldenke, 1971), have been included here because their gynoecial morphology (Junell, 1934), pollen morphology (Raj, 1983, 1987), and leaf epidermal anatomy (Cantino, 1990a) strongly suggest that their true affinities lie with the Viticoideae.

In the Labiatae, all genera of Ajugeae and Prostanthereae, as well as 16 other genera, are included in the analysis. The two large clades of gynobasic-styled Labiatae, subfamily Nepetoideae sensu Erdtman (1945) and subfamily Lamioideae sensu Wunderlich (1967) (= tribe Lamieae sensu Abu-Asab & Cantino (1987)), are represented by only a few exemplar genera each. The monophyly of both groups is well supported (Cantino & Sanders, 1986; Abu-Asab & Cantino, 1987). An unfortunate omission from the study group is *Wenchengia* C. Y. Wu & S. Chow. Its shallowly lobed ovary (Wu & Chow, 1965) is reminiscent of tribes Ajugeae and Prostanthereae, but its alternate leaves and unique fruit structure (a schizocarp with four mericarps attached to carpophores) led Wu & Chow (1965) to segregate it as a monotypic subfamily Wenchengioideae. An effort will be made to borrow herbarium material of this rare and possibly primitive Chinese taxon so that it may be included in a future analysis.

Although most of the 106 unit taxa (OTUs) are genera (Table 2), a few genera whose monophyly is seriously in question have been divided into less inclusive units. In the case of *Pityrodia*, for example, a paraphyletic genus of 41 species, 10 exemplar species were used as separate OTUs.

SOURCES OF DATA

Seventy-one of the 85 characters employed in the analysis (Table 3) concern floral, fruit, or vegetative morphology. The remaining characters are embryological (3), palynological (5), phytochemical (1), or concern leaf epidermal anatomy (5). The data for embryological characters 68 and 79 were obtained from Junell (1934), Misra (1939), Martin (1946), Pal (1951), Wunderlich (1967), and my own observations on character 79. Information on pollen morphology was obtained from Cantino (1982a), Raj (1983, 1987), Raj & Grafström (1984), Abu-Asab & Cantino (1989), Abu-Asab (1990 and unpublished SEM photos), and S. Wagstaff (unpublished SEM photos of Nepetoideae). The data for the single phytochemical character were obtained from Hagemann et al. (1967), and unpublished information was supplied by Robert Kleiman. The data for characters 2–6 derive from an ongoing survey of leaf epidermal anatomy in the Lamiales (Abu-Asab & Cantino, 1987; Cantino, 1990a, and unpublished data).

The scoring of the 71 morphological characters was based largely on my firsthand observations. Herbarium specimens provided the bulk of the morphological data, but living plants and liquid-preserved flowers and fruits were examined whenever possible. The extensive living collections of Labiatae and Verbenaceae at the Royal Botanic Gardens, Kew, and those maintained by me at Ohio University were helpful in understanding the variation in floral and fruit morphology. Descriptions in monographs and floras were consulted in order to reduce the likelihood of errors and to develop a better understanding of intra-OTU variation, but this study has not relied heavily on the literature for the morphological data.

Characters 50 and 78 have been included with a bit of trepidation because their states are frequently difficult to distinguish in herbarium material. Their low consistency indices may be due in part to incorrect observations rather than true homoplasy. Clades supported principally or entirely by these characters cannot be accepted with much confidence. Other characters (particularly 68 and 85) are problematical because of small sample size (i.e., only a few species have been examined per OTU). They do not suffer from excessive homoplasy, but further study may reveal more intra-OTU variation than is recognized at present.

An effort has been made to code the characters so as to maximize their independence, but it has not been possible to eliminate character correlation entirely. Non-independence of characters can result in unintentional weighting (see Affinities of *Physopsis* and *Faradaya* for an example). Most multistate characters were treated as unordered (i.e., a change from any state to any other adds a single step to the tree), but nine characters (spec-

TABLE 2. Unit taxa (OTUs) employed in the cladistic analysis. Names at left are OTU labels in Figures 1–4. Parenthetical acronyms indicate infrafamilial taxa to which the OTU is generally assigned (see Table 1).

ACRYMIA = *Acrymia* Prain (AJ)
AEGIPHIL = *Aegiphila* Jacq. (CAL)
AJUGA = *Ajuga* L. (AJ)
AMASONIA = *Amasonia* L.f. (MO)
AMETHYST = *Amethystea* L. (AJ)
ANISOMEL = *Anisomeles* R. Br. (GL)
CALLICAR = *Callicarpa* L. (including *Geunsia* Blume) (CAL)
CARYBICO = *Caryopteris bicolor* (Hardw.) Mabb. (CAR)
CARYCARY = *Caryopteris* Bunge sect. *Caryopteris* (CAR)
CARYDIVA = *Caryopteris divaricata* (Siebold & Zucc.) Maxim. (CAR)
CARYGRAT = *Caryopteris grata* Benth. & Hook. f. (CAR)
CARYNEPA = *Caryopteris nepalensis* Mold. (CAR)
CARYNEPE = *Caryopteris nepetifolia* (Benth.) Maxim. (CAR)
CARYPANI = *Caryopteris paniculata* Clarke (CAR)
CARYSICC = *Caryopteris siccanea* W. W. Smith (CAR) (including *Cardioteucris* C. Y. Wu; see Cantino [1991])
CARYTERN = *Caryopteris terniflora* Maxim. (CAR)
CHLOANTH = *Chloanthes* R. Br. (CH)
CLERCYCL = *Clerodendrum* L. subg. *Cyclonema* (Hochst.) Gurke (except sect. *Pleurocymosa*) (CL)
CLERKONO = *Clerodendrum* L. subg. *Clerodendrum* sect. *Konocalyx* B. Thomas (CL)
CLERMINA = *Clerodendrum minahassae* Teijsm. & Binnend. (CL)
CLERNUDI = *Clerodendrum nudiflorum* Mold. (CL)
CLERODEN = *Clerodendrum* L. (all species not included in other OTUs) (CL)
CLERPLEU = *Clerodendrum* L. subg. *Cyclonema* (Hochst.) Gurke sect. *Pleurocymosa* B. Thomas (CL)
CLERVOLK = *Clerodendrum* L. subg. *Volkameria* (L.) Briq. (CL)
COLEBROO = *Colebrookea* Smith (GL)
CORNUTIA = *Cornutia* L. (VI)
CYANOSTE = *Cyanostegia* Turcz. (CH)
CYMARIA = *Cymaria* Benth. (AJ)
DICRASTY = *Dicrastylis* J. L. Drumm. ex Harvey (PH)
EICHLERA = *Eichlerago* Carrick (PR)
FARADAYA = *Faradaya* F. Muell. (CL)
GALEOPSI = *Galeopsis* L. (GL)
GARRETTI = *Garrettia* Fletcher (VI)
GLECHOMA = *Glechoma* L. (NE)
GLOSSOCA = *Glossocarya* Wallich ex Griffith (CAR)
GMELINA = *Gmelina* L. (VI)
HARLANLE = *Harlanlewisia* Epling (SC)
HEMIANDR = *Hemiandra* R. Br. (PR)
HEMIGENI = *Hemigenia* R. Br. (PR)
HEMIPHOR = *Hemiphora* (F. Muell.) F. Muell. (CH)
HOLMSKIO = *Holmskioldia* Retz. sensu Fernandes (1985) (CL)
HOLOCHEI = *Holocheila* (Kudo) S. Chow (AJ)
HOSEA = *Hosea* Ridley (CL)
HUXLEYA = *Huxleya* Ewart (CL)
HYMENOPY = *Hymenopyramus* Wallich ex Griffith (CAR)
KALAHARI = *Kalaharia* Baillon (CL)
KAROMIA = *Karomia* Dop sensu Fernandes (1985) (CL)
LACHNOST = *Lachnostachys* Hook. (PH)
LAMIUM = *Lamium* L. (GL)
MALLOPHO = *Mallophora* Endl. (PH)
MELISSA = *Melissa* L. (NE)
MICROCOR = *Microcorys* R. Br. (PR)
MOLUCCEL = *Moluccella* L. (GL)
MONARDA = *Monarda* L. (NE)
MONOCHIL = *Monochilus* Fischer & C. Meyer (MO)

TABLE 2. Continued.

NEORAPIN = *Neorapinia* Mold. (TEC)
NEWCASTE = *Newcastelia* F. Muell. (PH)
ONCINOCA = *Oncinocalyx* F. Muell. (CL)
OXERA = *Oxera* Labill. (CL)
PARAVITE = *Paravitex* Fletcher (VI)
PERILOMI = *Perilomia* Kunth (*Scutellaria* L. sects. *Perilomia* (Kunth) Epling and *Perilomioideae* (Benth.) Epling) (SC)
PERONEMA = *Peronema* Jack (CAR)
PETITIA = *Petitia* Jacq. (TEC)
PETRAEOV = *Petraeovitex* Oliver (CAR)
PHYSOPSI = *Physopsis* Turcz. (PH)
PHYSOSTE = *Physostegia* Benth. (GL)
PITYANGU = *Pityrodia angustisepala* Munir (CH)
PITYBART = *Pityrodia bartlingii* (Lehm.) Benth. (CH)
PITYBYRN = *Pityrodia byrnesii* Munir (CH)
PITYDILA = *Pityrodia dilatata* (F. Muell.) Benth. (CH)
PITYHALG = *Pityrodia halganiacea* (F. Muell.) E. Pritzel (CH)
PITYLOXO = *Pityrodia loxocarpa* (F. Muell.) Druce (CH)
PITYOLDF = *Pityrodia oldfieldii* (F. Muell.) Benth. (CH)
PITYPANI = *Pityrodia paniculata* (F. Muell.) Benth. (CH)
PITYSALV = *Pityrodia salvifolia* R. Br. (CH)
PITYUNCI = *Pityrodia uncinata* (Turcz.) Benth. (CH)
POGOSTEM = *Pogostemon* Desf. (including *Eusteralis* Raf.) (GL)
PRASIUM = *Prasium* L. (GL)
PREMNA = *Premna* L. (VI)
PROSKLAN = *Prostanthera* Labill. sect. *Klanderia* (F. Muell.) Benth. (PR)
PROSPROS = *Prostanthera* Labill. sect. *Prostanthera* (PR)
PRUNELLA = *Prunella* L. (NE)
PSEUDOCA = *Pseudocarpidium* Millsp. (VI)
PYGMAEOP = *Pygmaeopremna* Merr. (VI)
RENSCHIA = *Renschia* Vatke (AJ)
RUBITEUC = *Rubiteucris* Kudo (AJ)
SALAZARI = *Salazaria* Torrey (SC)
SCHNABEL = *Schnabelia* Hand.-Mazz. (AJ)
SCUTELLA = *Scutellaria* L. (excluding *Perilomia*, *Salazaria*, and *Harlanlewisia*) (SC)
SPARTOTH = *Spartothamnella* Briq. (CH)
TECTONA = *Tectona* L. f. (TEC)
TEIJSMAN = *Teijsmanniodendron* Koord. (TEI)
TETRACLE = *Tetraclea* A. Gray (AJ, CL)
TEUCRIDI = *Teucridium* Hook. f. (CL)
TEUCRIUM = *Teucrium* L. (including *Kinostemon* Kudo) (AJ)
TINNEA = *Tinnea* Kotschy ex Hook. f. (AJ)
TRICARIZ = *Trichostema arizonicum* A. Gray (AJ)
TRICCHRO = *Trichostema* L. sect. *Chromocephalum* F. Lewis (AJ)
TRICORTH = *Trichostema* L. sect. *Orthopodium* Benth. (including *Isanthus* Michaux) (AJ)
TRICPURP = *Trichostema purpusii* Brandegee (AJ)
TRICTRIC = *Trichostema* L. sect. *Trichostema* (AJ)
TSOONGIA = *Tsoongia* Merr. (VI)
VITEX = *Vitex* L. (VI)
VITICIPR = *Viticipremna* H. J. Lam (VI)
WESTRING = *Westringia* Smith (PR)
WRIXONIA = *Wrixonia* F. Muell. (PR)

ified in Table 3) were treated as ordered because there was a reasonable basis to hypothesize a transformation series. For example (character 1), it is unlikely that an annual plant (state 2) would evolve directly from a tree or shrub (state 0), or vice versa, without passing through an herbaceous or subligneous perennial stage (state 1).

In an intergeneric study of this magnitude, it is

TABLE 3. Characters used in cladistic analysis. Character type (multistate characters only): ORD, ordered; UNO, unordered. *, hypothesized ancestral state (none designated when polarity assessment through outgroup comparison was not possible; see text).

1. (ORD) Habit: 0, woody plant; 1, herbaceous perennial or subshrub (i.e., woody only at very base); 2, annual or biennial.
2. If leaves not glabrous, multicellular trichomes present: 0, yes; 1, no (i.e., all trichomes unicellular). If leaves glabrous, character scored as missing.
3. Branched, multicellular trichomes present anywhere on plant: 0*, no; 1, yes. If plant entirely glabrous, character scored as missing.
4. Leaves bear subsessile glandular trichomes with a unicellular cap: 0, no; 1, yes.
5. Anisocytic stomata on leaves: 0, absent; 1, present.
6. (ORD) Diacytic types of stomata on leaves: 0, absent; 1, simple diacytic, but not diallelocytic, present; 2, both diacytic and diallelocytic present.
7. (UNO) Phyllotaxy: 0, opposite; 1, helical (alternate); 2, whorled.
8. (UNO) Leaf Structure: 0*, simple, unlobed; 1, three-lobed; 2, palmately lobed (more than 3 lobes); 3, pinnately lobed (more than 3 lobes); 4, once ternately compound; 5, once palmately compound (more than 3 leaflets); 6, once pinnately compound (more than 3 leaflets); 7, twice ternately compound. If there is developmental variation on a specimen, the higher state is assigned. Exception (not known to occur): if palmate and pinnate construction were to co-occur on the same specimen the character would be scored as variable.
9. Inflorescence a head: 0, no; 1, yes.
10. Inflorescence structure, if not a head: 0, axillary cymes or panicles or a thyrse (including "verticillate"); 1, flowers solitary in axils of foliage leaves or forming a raceme or spike. If inflorescence a head, character scored as missing.
11. Peduncles or pedicels within the cymules bear bractlets (excluding the bract or leaf subtending the cymule): 0, yes; 1, no.
12. Floral symmetry: 0, actinomorphic (i.e., corolla radially symmetrical and stamens isomerous and equal in length); 1*, zygomorphic (corolla or androecium not as above).
13. Calyx opening freely at anthesis: 0*, yes; 1, no, the elongating corolla forces its way through the fleshy or leathery, unlobed, hoodlike calyx, tearing it into lobes of irregular number and shape.
14. (UNO) Calyx symmetry: 0–2, radially symmetrical or nearly so: 0, four-lobed; 1, five-lobed; 2, with six or more lobes. 3–7, bilaterally symmetrical: 3, three-lobed upper lip and two-lobed lower lip; 4, two-lobed upper lip and two-lobed lower lip; 5, one-lobed upper lip and two-lobed lower lip; 6, one-lobed upper lip and four-lobed lower lip; 7, one-lobed upper lip and one-lobed lower lip. If calyx unlobed (truncate) or absent, character scored as missing.
15. Calyx with scutellum: 0*, no; 1, yes.

TABLE 3. Continued.

16. Flowering calyx gibbous: 0*, no; 1, yes.
17. Calyx with a ring of long trichomes in tube: 0*, no; 1, yes.
18. (ORD) Lobes of flowering calyx: 0, rounded to obtuse (including rounded and mucronate); 1, acute to attenuate; 2, spine-tipped or aristate; 3, uncinate. If calyx absent or unlobed, character scored as missing.
19. Fruiting calyx is closed apically by reflexing of one or both lips, enclosing fruit inside: 0*, no; 1, yes.
20. Fruiting calyx is closed apically by some other method, enclosing fruit inside: 0, no; 1, yes.
21. Fruiting calyx greatly inflated, bladderlike: 0*, no; 1, yes.
22. Fruiting calyx enlarged, patelliform: 0*, no; 1, yes.
23. Fruiting calyx enlarged, with elongate, winglike lobes: 0*, no; 1, yes.
24. Fruiting calyx enlarged, with elongate, plumose lobes: 0*, no; 1, yes.
25. Corolla in bud stalked, expanding abruptly on anterior (abaxial) side only; 0*, no; 1, yes.
26. (UNO) Corolla shape: States 0–3 are actinomorphic. 0, limb with four similar lobes; 1, limb with five similar lobes; 2, limb with six or more similar lobes; 3, corolla lacking lobes (tube truncate). States 4–8 are zygomorphic but not lipped (i.e., some lobes differ from others in size or shape, but all arise at the same level on the tube). 4, limb with four similar lobes, the other (anteriormost) different in shape and usually larger; 5, limb with three similar lobes, and the other (anteriormost) larger; 6, limb with three similar lobes, the other (posteriormost) larger; 7, limb with two posterior lobes of one sort and three anterior lobes of a different shape or size; 8, lobes of three shapes and/or sizes, the two posterior ones of one sort, the two lateral ones of another sort, and the anterior lobe of a third sort. States 9, A, B are bilabiate (i.e., the sinus separating the two lips is deeper than the sinuses separating the lobes on one or both lips). 9, posterior lip two-lobed, anterior lip three-lobed; A, posterior lip three- to four-lobed, anterior lip one-lobed; B, both lips one-lobed. States C–E are unilabiate. C, all lobes fall on posterior lip; D, all lobes fall on anterior lip and are similar in size and shape; E, all lobes fall on anterior lip, the middle lobe larger than the other four.
27. Corolla tube gibbous: 0, no; 1, yes.
28. Corolla tube curved: 0, no; 1, yes.
29. (UNO) Interior of corolla: 0, glabrous or nearly so; 1, with an incomplete annulus; 2, with a complete annulus; 3, densely pubescent on most or all of surface.
30. Anteriormost corolla lobe fimbriate: 0*, no; 1, yes.
31. (ORD) Shape of upper (posterior) lip of corolla: 0*, flat; 1, slightly galeate; 2, strongly galeate.
32. Corolla persistent, its expanded base forming a sheath covering the fruit: 0, no; 1, yes.
33. (ORD) Number of stamens: 0, two or four; 1, five; 2, more than five.
34. If less than five stamens, posterior pair reduced to

TABLE 3. Continued.

staminodes or absent: 0*, no (i.e., posterior pair fertile or five or more stamens present); 1, yes.

35. If less than five stamens, anterior pair reduced to staminodes or absent: 0*, no (i.e., anterior pair fertile or five or more stamens present); 1, yes.
36. Stamen insertion: 0, in corolla tube; 1, at or very near the rim of the tube, where the lobes diverge.
37. (ORD) Relative length of stamens if at least four fertile stamens present: 0, anterior pair longest; 1, all stamens approximately the same length; 2, posterior pair longest. If only two fertile stamens present, character scored as missing.
38. Anterior stamens, if fertile, dimidiate (i.e., one theca of each stamen consistently aborted): 0*, no; 1, yes. If anterior pair sterile or absent, character scored as missing.
39. Posterior stamens, if fertile, dimidiate: 0*, no; 1, yes. If posterior pair sterile or absent, character scored as missing.
40. (ORD) Anther locule confluence at dehiscence: 0*, locules fully distinct or stamens dimidiate; 1, locules confluent but recognizable as two; 2, locules totally merged, appearing as one locule.
41. Thecae of the same anther (if not dimidiate or fully fused) similar in size and shape: 0, yes; 1, no. If stamens dimidiate or anther thecae fully fused, character scored as missing.
42. Anther theca orientation: 0, parallel; 1, divergent. If connective elongate, stamens dimidiate, or locules fully merged, character scored as missing.
43. Anthers appendaged at base: 0, no; 1, yes.
44. Anther dehiscence aperture shape: 0*, a longitudinal slit; 1, a subterminal pore.
45. Anther dehiscence aperture ciliate: 0*, no; 1, yes.
46. Anther dehiscence aperture bordered by one or more small teeth: 0*, no; 1, yes.
47. Anther connective appendaged: 0*, no; 1, yes.
48. Anther connective elongate, the thecae widely separated or (if one theca missing) the sterile branch of the connective prolonged down or out from the filament: 0*, no; 1, yes.
49. Connective or its appendage cristate (i.e., bearded with a cluster of broad-based trichomelike projections): 0*, no; 1, yes.
50. (UNO) Orientation of stamen filaments: 0, straight or only slightly curved or irregularly twisted; 1, strongly curved toward anterior of flower; 2, strongly curved toward posterior of flower; 3, strongly curved laterally. If there is variation among the stages of anthesis between state 0 and one of the other states, only the latter is assigned.
51. Stamen filaments bearded: 0, at base only or not at all; 1, in the middle and/or upper portions of the filament.
52. Filaments markedly dilated apically: 0*, no; 1, yes.
53. Filament extends beyond anther: 0*, no; 1, yes.
54. Ovary elevated on elongate gynophore above level of rest of disk: 0*, no; 1, yes.
55. Gynoecial structure: 0*, ovary unlobed or, if lobed, then the lobes not as in state 1; 1, ovary lobes wholly free from each other but laterally attached to a more or less elongate upward extension of the disk that terminates between them.

TABLE 3. Continued.

56. Elongation of ovary lobes during fruit development: 0*, the free (lobed) portion of the ovary does not elongate greatly relative to the fused portion (or ovary not lobed); 1, the free (lobed) portion of the ovary elongates greatly during fruit maturation.
57. (ORD) Depth of ovary lobing (if character 55 = 0): 0*, unlobed; 1, divided up to ¾ of the way to the base to form four lobes; 2, divided more than ¾ of the way to the base, the style thus gynobasic. If character 55 = 1, character 57 is scored as missing due to uncertainties about homology.
58. Nectary disk below ovary: 0, absent or poorly developed; 1, well developed.
59. (UNO) Number of vertically elongate lobes on nectary disk: 0*, none (or no disk); 1, one; 2, two; 3, three; 4, four.
60. Style persists after abscission of corolla: 0, no; 1*, yes.
61. (UNO) Style pubescence: 0*, glabrous; 1, pubescent only in the lower half of the unlobed portion; 2, pubescent only in the upper half of the unlobed portion; 3, pubescent in most or all of unlobed portion.
62. (ORD) Relative length of lobed versus unlobed portion of style-stigma complex: 0, unlobed portion more than 3 times the length of the lobes; 1, unlobed portion 1–3 times the length of the lobes; 2, unlobed portion shorter than the lobes.
63. (UNO) Relative length of lobes of style-stigma complex: 0, lobes equal or nearly so; 1, lobes distinctly unequal in length; 2, unlobed.
64. Shape of lobes of style-stigma complex: 0, linear or lingulate; 1, at least one lobe enlarged due to elaboration of stigmatoid tissue.
65. Number of ovules in ovary: 0, more than four; 1*, four or fewer.
66. (UNO) Ovary structure as seen in cross section: 0, carpel walls do not recurve into the interior of the carpel; 1, carpel walls recurve into interior of carpel, the ovules borne on their margins; 2, as in state 1, but the ovules borne short of the carpel margins.
67. Placentation: 0*, axile (including subbasal) or intermediate between axile and parietal; 1, free-central.
68. Shape of embryo sac: 0*, micropylar lobe shorter than or equal to and/or narrower than the chalazal lobe; 1, micropylar lobe much longer and broader than the chalazal lobe.
69. (UNO) Fruit type: 0, dehiscent capsule; 1, indehiscent capsule, developing from 4-ovulate ovary, containing four seeds (or fewer due to ovule abortion); 2, indehiscent capsule, developing from 2-ovulate ovary, containing two seeds (or only one due to ovule abortion); 3, a single achene developing from a 1-ovulate ovary; 4, drupe with more than four 1-seeded pyrenes; 5, drupe, developing from 4-ovulate

TABLE 3. Continued.

ovary, with one pyrene containing four seeds (or fewer seeds by ovule abortion); 6, drupe, developing from 4-ovulate ovary, with two pyrenes, each normally containing two seeds; 7, drupe, developing from 4-ovulate ovary, with four 1-seeded pyrenes (or fewer pyrenes by ovule abortion); 8, drupe, developing from 2-ovulate ovary, with two 1-seeded pyrenes (or one pyrene by ovule abortion); 9, drupe, developing from 2-ovulate ovary, with one 2-seeded pyrene (or only one seed by ovule abortion); A, fruit separates into four fleshy 1-seeded mericarps (or fewer by ovule abortion); B, fruit separates into four dry 1-seeded mericarps ("nutlets") (or fewer by ovule abortion); C, fruit (from 4-ovulate ovary) separates into two dry 2-seeded nutlets (or fewer seeds by abortion); D, fruit (from 4-ovulate ovary) separates into two fleshy 2-seeded mericarps (or fewer seeds by ovule abortion). The few genera that have fruits that split into mericarps only with pressure were scored as intermediate between 1 and B or between 7 and A.

70. Surface of pericarp (if dry) or pyrene (if drupaceous) ridged, the ridges often forming a reticulum: 0, no; 1, yes.
71. (UNO) Surface of pericarp (if dry) or pyrene (if drupaceous) with tuberculate or elongate outgrowths: 0*, no; 1, outgrowths tuberculate, papilliform or verrucate; 2, outgrowths greatly elongate, usually plumose, developing during fruit maturation from papilliform outgrowths on ovary (probably homologous to outgrowths in state 1).
72. Pericarp (if dry fruit) highly lustrous, appearing polished: 0, no; 1, yes. If fruit fleshy, character scored as missing.
73. (UNO) Mericarp shape: 0, obovoid to obloid; 1, quarter-sphere; 2, boat-shaped; 3, nearly flat; 4, subspherical to spherical; 5, clavate; 6, trigonal; 7, boomerang-shaped (abruptly bent); 8, fusiform; 9, ovoid; A, lenticular; B, elongate and straight-sided; C, half-sphere.
74. Mericarps with lateral wings: 0*, no (or fruit not a schizocarp); 1, yes.
75. Mericarps with basal wing: 0*, no (or fruit not a schizocarp); 1, yes.
76. Mericarp attachment scar with reflexed spinelike projections: 0*, no; 1, yes.
77. Mericarp attachment scar with vertical membranaceous outgrowth: 0*, no; 1, yes.
78. Seed albuminous: 0, no; 1, yes.
79. (UNO) Embryo shape: 0, spatulate, straight or slightly curved; 1, abruptly bent but not doubled over; 2, doubled over on itself; 3, investing.
80. (UNO) Pollen sculpturing types: 0, psilate, microreticulate to tectate-perforate (tectum relatively even (vs. 1)); 1, tectate-perforate to microreticulate with muri exhibiting an alternation of distinctly raised and nonraised segments; 2, striato-reticulate; 3, rugulose; 4, suprareticulate to suprarugulose; 5, supraverrucate; 6, supraspinulose to spinose; 7, minutely supraspinulose or supragranulate (the projections no more than 0.1 μm long); 8, suprareticulate-spinose; 9, bearing irregular, blunt supratectal protuberances.
81. (UNO) Pollen aperture type: 0, colpate; 1, colporate; 2, porate.
82. Pollen colpi operculate: 0*, no; 1, yes.
83. (UNO) Number of pollen apertures: 0*, three; 1, four; 2, five; 3, six to eight, zonocolpate; 4, six-pantocolpate.
84. (UNO) Structure of columellate stratum of exine: 0*, with simple columellae; 1, with branched to granular columellae; 2, massive, undifferentiated.
85. Allenic component (probably laballenic acid) present in the seed oils: 0*, no; 1, yes.

not feasible to examine every species. For small genera, the morphology of most or all species has been studied, but larger genera have been sampled using an exemplar method. Before initiating data collection for a large genus, available monographs and revisions were consulted, as well as basic works such as Briquet's treatments of the Verbenaceae (1895) and Labiatae (1895–1897). Based on accepted infrageneric classifications, a sample was selected to encompass most or all of the morphological variation in the genus. For example, in the case of *Teucrium*, with ca. 200 species, the 37 species chosen for examination included representatives of every previously recognized infrageneric grouping and every major portion of its geographic range.

When variation was encountered within an OTU, the character was scored as uncertain except in those few cases in which it was possible to assess with confidence the ancestral state within the taxon. For example, it is clear that the ostensibly primitive drupaceous fruit in *Ajuga postii* Briq. is secondarily derived, because the distribution of other characters shows that this species is far from basal within the genus. As a result, only state B (dry nutlets) was scored for character 69 in *Ajuga*.

Scorings of "uncertain" and "missing" are treated differently in the parsimony package used in this analysis (PAUP version 3.0L; Swofford, 1990). If a character state is scored as missing ("?" in the data matrix) for a taxon, it will be assigned whichever state is most parsimonious given the placement of the taxon on the tree by the other characters. If a character is scored as uncertain (i.e., two or more states are assigned to the taxon in the data matrix), the algorithm will choose from among the assigned states the one that minimizes the overall tree length. Thus, an uncertain state plays a role in determining the tree topology, while a missing state does not. This is an important distinction for multistate characters. For example, if only two of the ten possible states of character 80 occur within a taxon, scoring it as uncertain rather than missing prevents the algorithm from assigning a state that is known *not* to occur in the OTU.

There are two situations other than intra-OTU variation that resulted in scoring a character as "uncertain": character state intermediacy and true uncertainty. An example of the first situation can be found in *Caryopteris grata*, in which the slightly fleshy fruit contains four pyrenes. The fruit usually does not split spontaneously (at least in herbarium material) but can be broken apart with slight thumb pressure to form four mericarps. Because the fruit is intermediate between a drupe and a fleshy schizocarp, character 69 was scored as intermediate ("uncertain") between states 7 and A.

An example of the second situation can be found in *Hosea*, in which the corolla has three similar lobes and one larger one, but it has not been possible to determine from the available herbarium material and published descriptions whether it is the anterior or posterior lobe that is enlarged. If character 26 (corolla shape) were binary, the state would simply have been scored as missing for *Hosea*. However, since the true corolla shape could be narrowed down to two of the 15 possible states, it was preferable to score the character as "uncertain," with states 5 and 6 listed as the only possibilities.

A character was scored as missing for a taxon under two circumstances: (1) the information was indeed missing (i.e., *any* of the possible states could occur in the taxon); (2) the character is inapplicable to the taxon. For example, if the calyx is unlobed, character 18 (calyx lobe shape) is inapplicable and was scored as missing.

Because of its length, the data matrix has been excluded from this report. It is on file in the libraries of the Harvard University Herbaria and the Royal Botanic Gardens at Kew, and copies are available from the author on request.

OUTGROUPS

The closest outgroups are those Verbenaceae sensu lato that lie outside the study group—viz., subfamily Verbenoideae and the segregate families Cyclocheilaceae, Nesogenaceae, Phrymaceae, and Stilbaceae. The Scrophulariales, the closest relatives of the Verbenaceae sensu lato and Labiatae (discussed below), constitute a second, more distant set of outgroups. The forenamed segregate families are treated here as close outgroups under the assumption that the Verbenaceae sensu lato plus the Labiatae form a clade. Upon further study, however, it may turn out that some of these segregate families originated from different scrophularialean lineages than the rest of the Verbenaceae. Their inclusion among the primary outgroups, if incorrect, may have prevented polarity assessment for some characters due to variation among the outgroups, but it should not have resulted in incorrect polarities, as agreement among all five primary outgroups was required for polarity assessment.

Because data collection for both sets of outgroups is still incomplete, they were not included in the data set. Rather, the results of this analysis have been left as an undirected tree, but the most plausible rooting positions have been determined a posteriori based on those characters for which data are available for the outgroups (i.e., Lundberg Rooting; Lundberg, 1972). The hypothesized ancestral states used in the rooting procedure are indicated with an asterisk in Table 3.

A close relationship to the Verbenaceae and Labiatae has been claimed for the Boraginaceae (Cronquist, 1981) and the Scrophulariales (Dahlgren, 1977; Wagenitz, 1977; Cantino, 1982b). The former hypothesis is based primarily on a suite of related gynoecial features, while the latter is supported by a variety of chemical, embryological, and morphological characters. Recent molecular studies corroborate the Scrophulariales hypothesis. Both sequence data for the *rbc*L gene (Olmstead et al., 1992, in press) and restriction site data for the inverted repeat of the chloroplast genome (Downie & Palmer, 1992) delimit a major clade comprising the Scrophulariales sensu Cronquist (1981) plus the Verbenaceae, Labiatae, and Callitrichaceae. The two molecular studies disagree, however, on the precise position of the Verbenaceae and Labiatae within this clade. Acanthaceae, Bignoniaceae, Buddlejaceae, Callitrichaceae, Gesneriaceae, Myoporaceae, Pedaliaceae, and Scrophulariaceae are placed relatively close to the Verbenaceae and Labiatae by one or both studies, with Oleaceae more distantly related.

A recent cladistic analysis based mainly on morphological data (Lu, 1990) concluded that the sister group of the Verbenaceae–Labiatae clade is a group composed of Phrymaceae (included in Verbenaceae by Cronquist, 1981), Trapellaceae (included in Pedaliaceae by Cronquist, 1981), Hippuridaceae, Callitrichaceae, and Hydrostachyaceae, with Mendonciaceae and Thunbergiaceae (both frequently included in the Acanthaceae) the next closest groups.

Unfortunately, flaws in character scoring and polarity assessment in this paper render these conclusions questionable. For example, the single synapomorphy cited by Lu (1990) as linking the Verbenaceae–Labiatae clade to its sister group is loss of diacytic stomata. However, diacytic stomata are widespread in the Verbenaceae and occur in nearly all genera of Labiatae (Cantino, 1990a).

Other problems in Lu's analysis include the scoring of Labiatae as having an actinomorphic corolla and Verbenaceae as having alternate leaves. What may appear to be simple errors in the data matrix actually result from Lu's handling of variation within the unit taxa. If more than one state occurs in a family, only the plesiomorphic state was assigned. Although this procedure is correct, it requires that proximal outgroups be used. In Lu's analysis, polarity assessments were based on the outgroups to the Lamiiflorae as a whole (viz., Oleaceae, Clethraceae, and Solanaceae) rather than on the immediate relatives of the OTU in which the variation occurred. Thus an actinomorphic corolla, which is clearly a reversal from a primitively zygomorphic condition within the Labiatae, was treated as plesiomorphic and assigned to the family as a whole. Similarly, spiral phyllotaxy ("alternate leaves") is a rare and probably derived condition within the Verbenaceae. A better approach when dealing with variation within OTUs is to attempt to determine the basal state within the taxon or, if this is not possible, score the taxon as uncertain for that character and allow the parsimony algorithm to assign the character state that minimizes the overall tree length.

Based on the above considerations, the best candidates for sister group of the Verbenaceae–Labiatae clade are Acanthaceae sensu lato, Bignoniaceae, Buddlejaceae, Callitrichaceae, Gesneriaceae, Myoporaceae, Pedaliaceae, and Scrophulariaceae. All of these except the Callitrichaceae were used as secondary outgroups when assessing the most likely positions for the root of the undirected tree, but greater emphasis was placed on the primary outgroups (i.e., Verbenoideae and the segregate families of Verbenaceae sensu lato).

CLADISTIC ANALYSIS

The analysis was carried out using PAUP version 3.0L (Swofford, 1990) on a MacIntosh IIfx computer. All three branch-swapping algorithms used by PAUP were employed in an attempt to find the most parsimonious trees. In order to test the relative parsimony of the hypothesis that the Labiatae are monophyletic, a second analysis was carried out with the data set constrained such that only trees in which the Labiatae form a clade were saved.

When optimizing characters on the trees, the delayed transformation option, which favors parallelisms over reversals when they are equally parsimonious, was used in most cases. The accelerated transformation option was used in a few instances (see Results and Discussion) when the character state distribution within an OTU suggested that the internal variation was more likely due to reversal than parallelism. The tree topology and overall parsimony are not affected by the choice of optimization routine, but the positions of certain character transformations are altered.

RESULTS AND DISCUSSION

The shortest trees found by PAUP are 399 steps long, with a consistency index (CI) of 0.298 (autapomorphies were excluded from these calculations, although they have been mapped onto the consensus tree). The low CI value is due in part to the large number of OTUs in the analysis. Sanderson & Donoghue (1989) found consistency index to be highly correlated with number of taxa. The largest data sets in their study included 65–68 taxa and had CI values of 0.32–0.37. Thus, a CI of 0.298 in an analysis that includes 106 taxa is not unreasonably low. Indeed, when the data matrix in the present study was cut in half by deleting alternate entries in the alphabetical list of taxa and the analysis was rerun with the remaining 53 taxa, the CI was 0.46. When the matrix was reduced to 27 taxa by the same procedure, the CI rose to 0.55. These figures are all close to the regression line in Sanderson and Donoghue's study.

Although the exact number cannot be determined, it is clear that there are a great many equally parsimonious trees. PAUP found 4,100 399-step trees before the analysis was aborted due to overflow of the tree buffer, and it is possible that many more exist. In spite of the existence of many equally parsimonious trees, there is a high degree of resolution in some parts of the strict consensus tree based on them (Fig. 1).

Space limitations preclude mapping of the character state changes onto the full consensus tree. Rather, they have been separately mapped (Figs. 2–4) onto the three large groups labeled A, B, and C in Figure 1. Because no outgroups were included in the data set, the consensus tree was initially undirected and is shown as such in Figure 1. How-

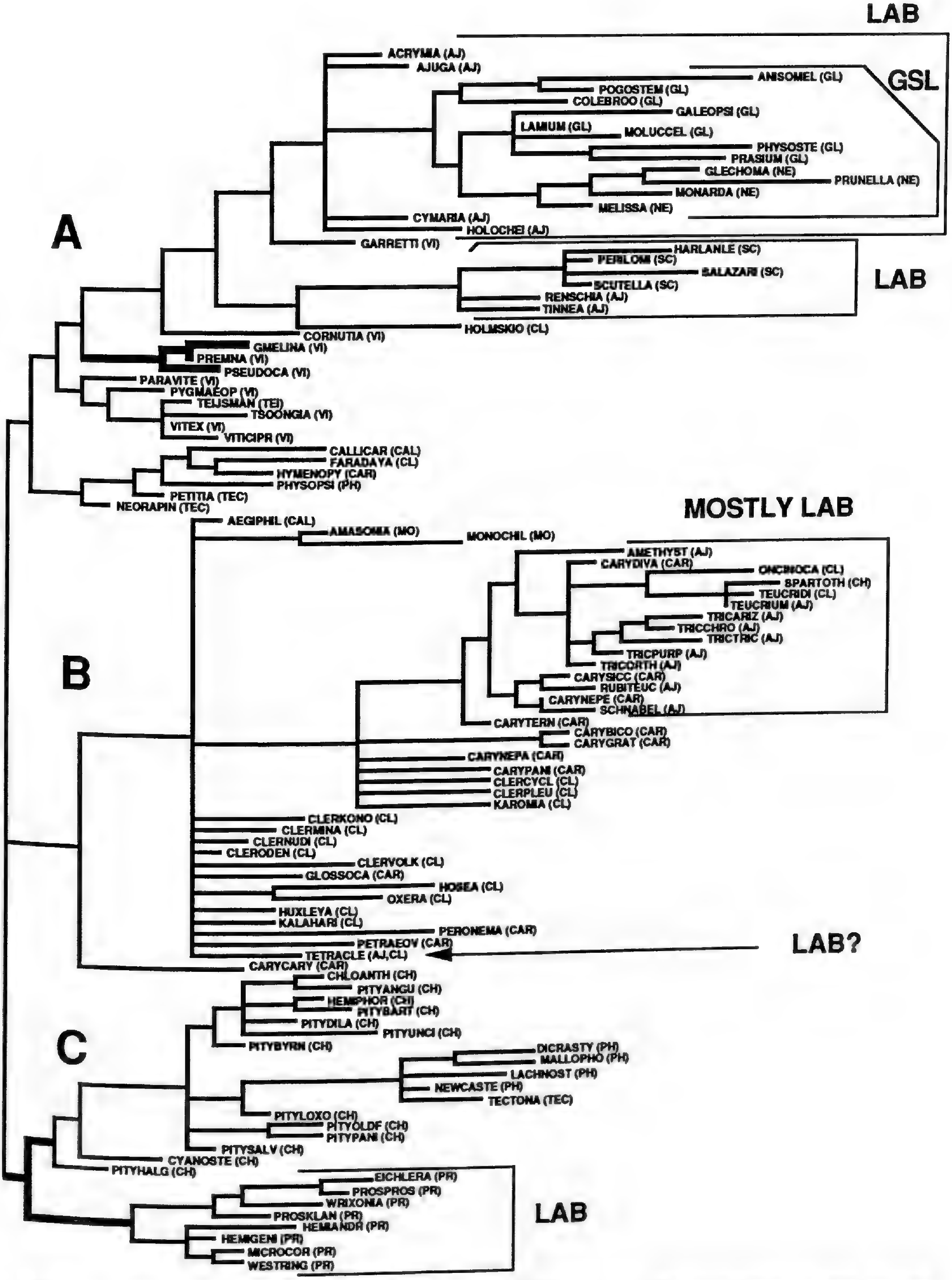

FIGURE 1. Strict consensus tree (undirected) based on 4,100 399-step trees. Thickened stems indicate positions where the tree most likely roots (see text). Branch lengths are proportional to the number of character changes. See Table 2 for full names of OTUs. Parenthetical abbreviations (infrafamilial taxa) are defined in Table 1. A, B, C: groups discussed in text. LAB, taxa usually assigned to Labiatae; GSL, gynobasic-styled Labiatae.

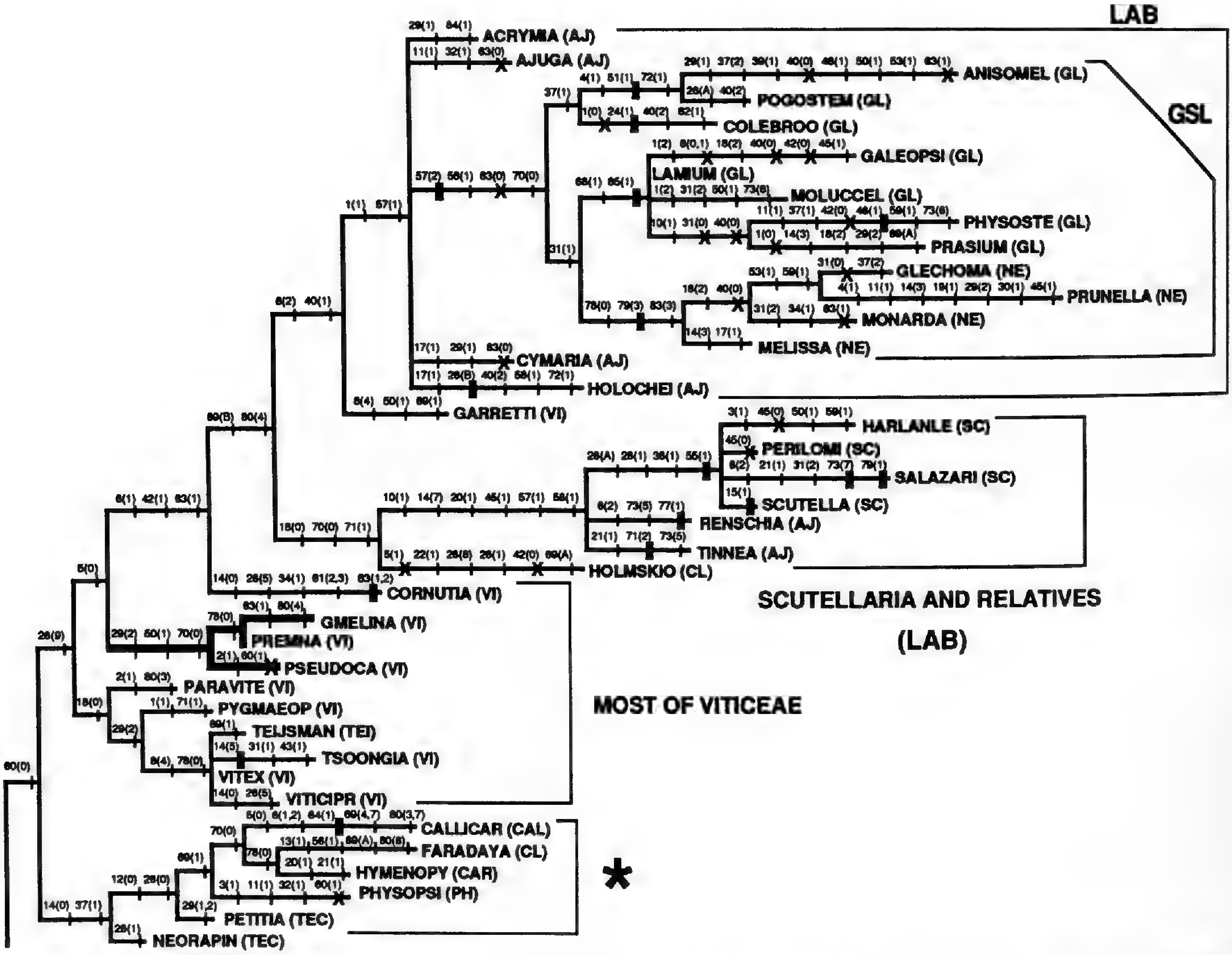

FIGURE 2. Character changes in Group A (see Fig. 1). Character states are designated by digits and (if more than 10 states) letters. Because the tree as a whole may root in the region designated by thickened stems (see text), the polarity of character changes within this zone and on the three stems basal to it may be incorrect. Parenthetical abbreviations (infrafamilial taxa) are defined in Table 1. LAB, taxa usually assigned to Labiatae; GSL, gynobasic-styled Labiatae; *, group discussed in text. Heavy bars = unique synapomorphies; light bars = parallelisms; X = reversals.

ever, some rooting positions are more plausible than others, based on the limited data presently available for the outgroups. Using the Lundberg Rooting approach (Lundberg, 1972), with the outlying Verbenaceae sensu lato as the primary outgroups and some families of Scrophulariales as more distant outgroups (see Outgroups above), eight equally parsimonious positions for the root have been hypothesized (designated by thick lines in Figs. 1, 2, and 4), which lie in two separate parts of the tree. The polarities of the character changes mapped onto these two hypothesized rooting regions and the three internodes that lie between them may be incorrect, but changes elsewhere on the strict consensus tree represent hypothesized synapomorphies.

For the most part, the delayed transformation option was used when mapping characters onto Figures 2–4, but accelerated transformation was used in the following instances: (1) State 1 of character 45 (ciliate anthers) is hypothesized to be a synapomorphy of the *Tinnea–Renschia*–Scutellarieae clade (Fig. 2), with reversals in *Harlanlewisia*, *Perilomia*, and a few species of *Tinnea*, rather than arising separately in *Salazaria*, *Scutellaria*, *Renschia*, and *Tinnea*. (2) In both characters 47 and 49, state 1 (anther connective appendaged and cristate, respectively) is hypothesized to be a synapomorphy of a clade comprising *Eichlerago* and *Prostanthera* sect. *Prostanthera*, with subsequent reversal in a few species of the latter (Fig. 4), rather than arising separately in the two taxa. (3) State 7 of character 80 (minutely spinulose pollen) is hypothesized to be a synapomorphy of a clade comprising *Eichlerago*, *Wrixonia*, and both sections of *Prostanthera*, with subsequent reversal in some species of *Prostanthera* sect. *Klanderia* (Fig. 4). The delayed transformation option would place the origin of state 7 on the stem leading to *Wrixonia*, *Eichlerago*, and *Prostanthe-*

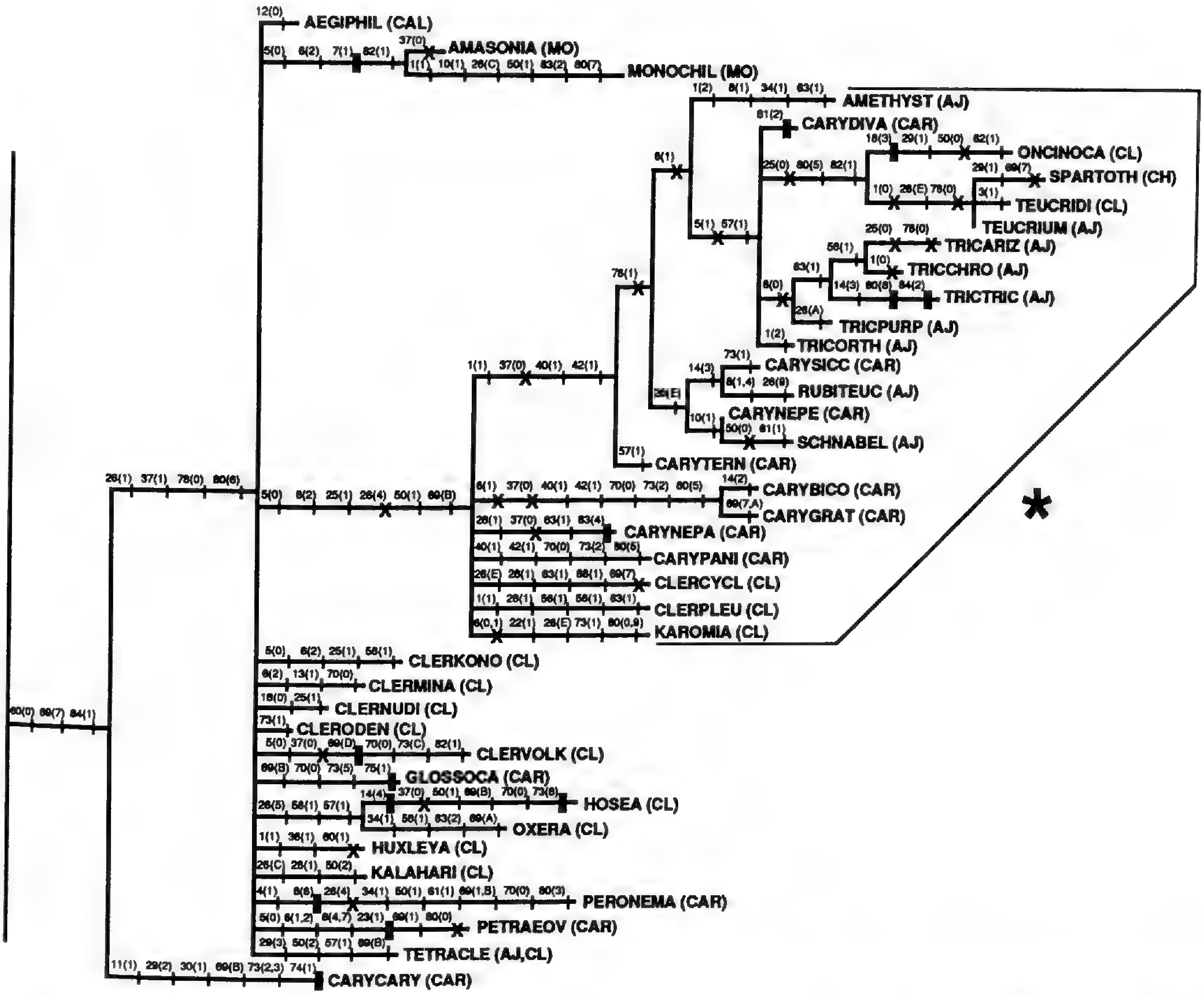

FIGURE 3. Character changes in Group B (see Fig. 1). Parenthetical abbreviations (infrafamilial taxa) are defined in Table 1. *, group discussed in text. Heavy bars = unique synapomorphies; light bars = parallelisms; X = reversals.

ra sect. *Prostanthera.* (4) State 1 of character 82 (operculate pollen) is hypothesized to be a synapomorphy of the clade comprising *Dicrastylis, Mallophora, Lachnostachys, Newcastelia,* and *Tectona,* with subsequent reversal in *Tectona* and a few species of *Dicrastylis* and *Newcastelia,* rather than arising independently in the first four genera listed (Fig. 4).

POLYPHYLY OF LABIATAE

The hypothesis that the Labiatae are polyphyletic is strongly supported by this analysis. The strict consensus tree (Fig. 1) requires at least four separate origins of the Labiatae from the Verbenaceae, in three widely separate parts of the tree. When the Labiatae were constrained to form a monophyletic group, the shortest trees required 412 character changes—13 steps longer than the most parsimonious trees without this constraint.

The four groups of Labiatae that emerge as distinct in the strict consensus tree ("LAB" in Fig. 1) are composed of: (1) the gynobasic-styled Labiatae plus four genera of Ajugeae (*Ajuga, Acrymia, Cymaria,* and *Holocheila*); (2) tribe Scutellarieae plus *Renschia,* and *Tinnea*; (3) *Amethystea, Rubiteucris, Schnabelia, Teucrium,* and *Trichostema* (because three species of *Caryopteris* and three other genera of Verbenaceae are included in this clade as well, more than one origin of the labiate genera within the group is likely); and (4) tribe Prostanthereae. In addition, *Tetraclea* (placed in the Labiatae by some authors and the Verbenaceae by others) is unconnected to the other groups of Labiatae.

GYNOBASIC-STYLED LABIATAE AND THEIR RELATIVES

With the exception of a few species in tribe Scutellarieae (discussed below), the gynobasic-styled Labiatae ("GSL" in Figs. 1 and 2) form a monophyletic group. Although this major clade is represented by only 12 genera here, it comprises about 90% of the Labiatae. It is nested within a larger clade characterized by suprareticulate pollen and

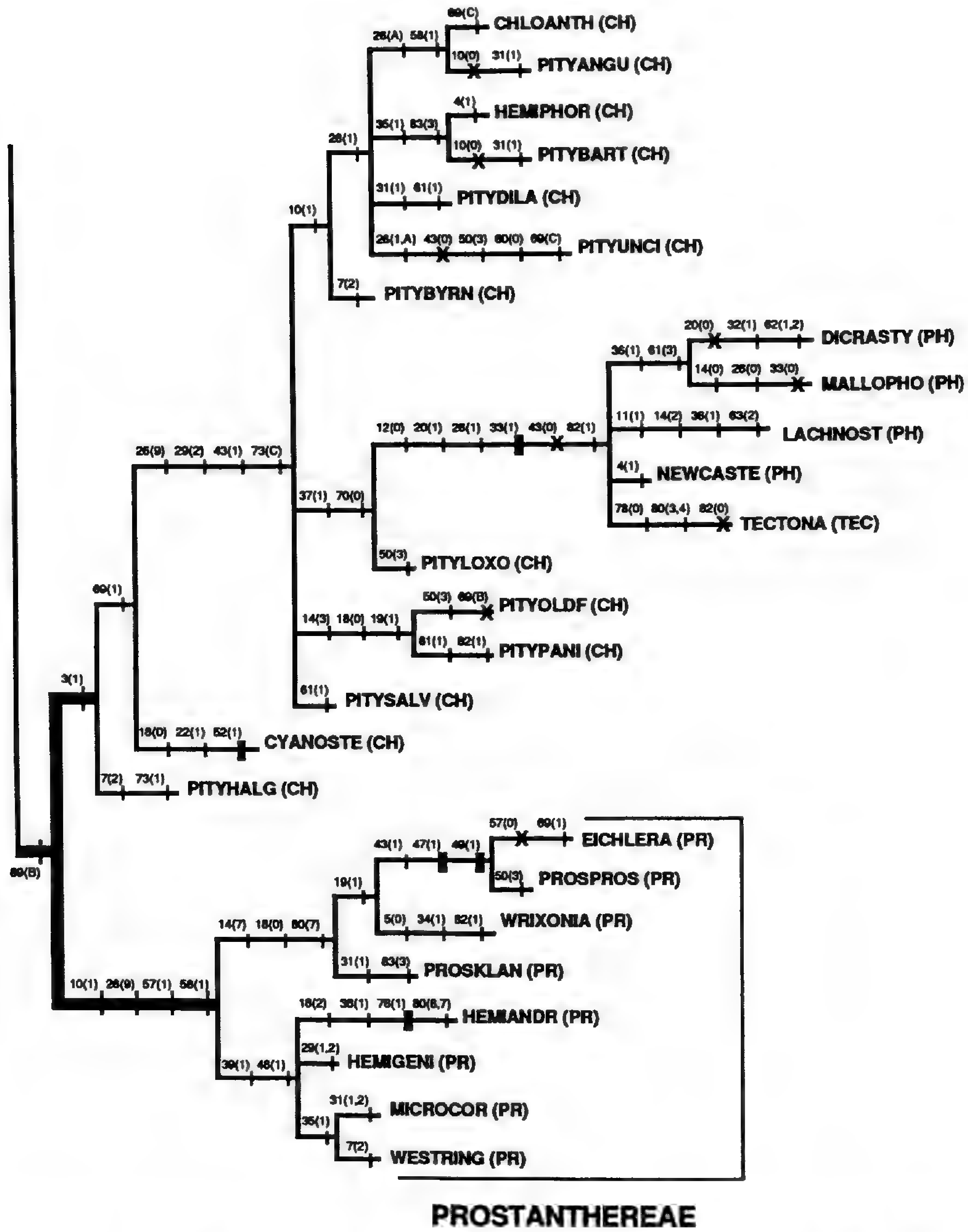

FIGURE 4. Character changes in Group C (see Fig. 1). Because the tree as a whole may root in the region designated by thickened stems (see text), the polarity of character changes within this zone may be incorrect. Parenthetical abbreviations (infrafamilial taxa) are defined in Table 1. Heavy bars = unique synapomorphies; light bars = parallelisms; X = reversals.

a fruit composed of nutlets, which includes (in addition to the gynobasic-styled Labiatae) tribe Scutellarieae, six genera of Ajugeae, and the verbenaceous genera *Garrettia* and *Holmskioldia*. This larger clade arises out of a verbenaceous assemblage comprising most of tribe Viticeae plus *Teijsmanniodendron* (Caryopteridoideae).

Although the Scutellarieae are traditionally grouped with the gynobasic-styled Labiatae, the style is truly gynobasic only in some species of *Perilomia* and a few (perhaps only one) species of *Scutellaria* sensu stricto (viz., *S. nummulariifolia* Hook. f.). In the rest of *Scutellaria* and *Perilomia*, as well as in *Salazaria* and *Harlanlewisia*, the ovary lobes are wholly free from each other but are laterally attached to a more or less elongate upward extension of the disk. The style is attached to the ovary lobes above the apex of the disk extension and is thus not truly gynobasic. Because this gynoecial morphology could have evolved from either a shallowly lobed ovary (character 57 = 1; e.g., tribe Ajugeae) or the sort of gynoecium found in the gynobasic-styled Labiatae (character 57 = 2), character 57 was coded as missing for the Scutellarieae. As it turned out, the most parsimonious hypothesis groups the Scutellarieae with two genera (viz., *Renschia* and *Tinnea*) that have a shallowly lobed ovary (Fig. 2), implying that the gynobasic style that occurs in a few species of *Perilomia* and *Scutellaria* arose independently from that in the other gynobasic-styled Labiatae.

A close relationship among the four genera of Scutellarieae (viz., *Scutellaria*, *Salazaria*, *Perilomia*, and *Harlanlewisia*) is well accepted (Epling, 1942, 1955), and Paton (1990) treats them as congeneric. Similarly, *Renschia* and *Tinnea* have long been regarded as close relatives (Vollesen, 1975 and references therein). In contrast, the relationship suggested here between *Scutellaria* sensu lato and *Renschia* and *Tinnea* runs counter to the prevailing classifications of the Labiatae, in which *Renschia* and *Tinnea* are assigned to tribe Ajugeae and *Scutellaria* to either tribe Lamieae (Bentham, 1876) or its own subfamily (Briquet, 1895–1897; Wunderlich, 1967). Nonetheless, the hypothesized *Renschia–Tinnea*–Scutellarieae clade is supported by six synapomorphies (Fig. 2). Two of these concern its distinctive calyx, which is bilabiate with entire, rounded lips that become tightly appressed after anthesis, enclosing the developing nutlets inside. Vollesen (1975) suggested that this calyx morphology evolved separately in *Scutellaria* versus *Renschia* and *Tinnea,* but it is more parsimonious to hypothesize a single origin in a common ancestor of these taxa. When the analysis was redone without these calyx characters, the *Renschia–Tinnea*–Scutellarieae clade remained intact, thus there is no circularity in this argument.

The strict consensus tree shows *Holmskioldia* (Verbenaceae) as the sister group of the *Renschia–Tinnea*–Scutellarieae clade (Figs. 1, 2), implying a separate verbenaceous origin for this group of Labiatae. *Holmskioldia* is monotypic as delimited here, comprising only the Asian species, *H. sanguinea* Retz. The African species formerly assigned to *Holmskioldia* are included here within *Karomia,* as by Fernandes (1985). The two genera do not appear to be closely related, *Karomia* falling in the central part of group B (Figs. 1, 3) and *Holmskioldia* in group A. Although a close relationship between *Scutellaria* and *Holmskioldia* has not previously been suggested, the fruit of *Holmskioldia* bears a distinctive tuberculate sculpturing very similar to that found in *Renschia* and most species of Scutellarieae. In *Tinnea,* the fruit bears long, usually plumose, trichomelike projections that elongate greatly during fruit maturation from tiny papillae on the ovary. Further investigations of the pericarp ornamentation in these genera using scanning electron microscopy (in progress) will help determine whether the structures are truly homologous.

OTHER "LABIATAE"

Another intriguing group that cuts across traditional taxonomic boundaries (marked with an asterisk in Fig. 3) comprises five genera of Ajugeae (Labiatae), parts of the genera *Caryopteris* (Verbenaceae, Caryopterideae) and *Clerodendrum* (Verbenaceae, Clerodendreae), three other genera of Clerodendreae, and *Spartothamnella* (Verbenaceae, Chloanthoideae). While it is tempting to dismiss such a taxonomically diverse assemblage as an artifact, the strong character support for this clade is noteworthy (Fig. 3). The most distinctive of its six synapomorphies is the shape of the flower bud, in which the corolla expands abruptly on the lower (anterior) side only, so that it looks something like a golf club. This feature is absent (presumably due to reversal) in *Trichostema arizonicum* and most members of the "teucrioid" subgroup.

The closest relatives of *Teucrium,* one of the largest and most widespread genera of Labiatae, are the verbenaceous genera *Teucridium, Spartothamnella,* and *Oncinocalyx.* My earlier suggestion (Cantino, 1990b) that *Monochilus* also belongs to this group is apparently incorrect, its affinities lying rather with *Amasonia* (near top of Fig. 3). This teucrioid clade, which is characterized by its distinctive operculate, verrucate pollen, deserves special comment because of the widely divergent taxonomic positions of its four genera. *Teucridium* and *Oncinocalyx* are members of tribe Clerodendreae (subfamily Viticoideae) (Briquet, 1895; Moldenke, 1971), while *Spartothamnella* is generally assigned to the Chloanthoideae (Briquet, 1895). Since the Chloanthoideae have been elevated to familial rank by some authors (Moldenke, 1971; Munir, 1976, 1979), the teucrioid clade draws its membership from what are currently treated as three different families.

Tribe Prostanthereae (Labiatae) is monophyletic in the strict consensus tree (Figs. 1, 4) and comprises two subgroups: (1) the prostantheroid clade, delimited by calyx morphology and pollen sculpturing, and (2) the hemigenioid clade with its peculiar androecial morphology (dimidiate stamens with an elongate connective). Within the former subgroup, *Prostanthera* is paraphyletic if *Eichlerago* and *Wrixonia* are segregated from it. The derived position of *Eichlerago* indicates that the ostensibly primitive unlobed ovary in *Eichlerago* represents a character reversal rather than a plesiomorphic condition.

Within the hemigenioid subgroup, *Hemigenia* is delimited by a single autapomorphy—an annulate corolla. However, a partial to complete annulus also occurs in some species of *Microcorys* and *Westringia.* In view of the weak character support for the monophyly of *Hemigenia,* a plausible alternative hypothesis is that it is a paraphyletic group that has given rise to both *Hemiandra* and the *Microcorys–Westringia* clade.

BROADER VIEW OF THE CONSENSUS TREE

The unrooted consensus tree can be divided into three large groups (A, B, and C in Fig. 1), at least two of which appear to be clades. The monophyly of Group B is supported by character 84, branched columellae (discussed below). It is unclear which of the other two groups represents a clade, because the consensus tree may be equally parsimoniously rooted near the base of groups A and C (Fig. 1). The three groups comprise: (A) the gynobasic-styled Labiatae, the Ajugeae (Labiatae) that have suprareticulate pollen, tribe Scutellarieae (Labiatae), tribe Viticeae (Verbenaceae), and eight other genera of Verbenaceae representing three subfamilies and six tribes (viz., Callicarpeae (1), Clerodendreae (2), Tectoneae (2), Caryopterideae (1), Teijsmanniodendreae (1), and Physopsideae (1)); (B) the Ajugeae that have spinulose or verrucate supratectal sculpturing, tribe Monochileae (Verbenaceae), *Aegiphila* (Callicarpeae), *Spartothamnella* (Chloantheae), and most genera of tribes Clerodendreae and Caryopterideae; (C) tribe Prostanthereae (Labiatae), most of subfamily Chloanthoideae (Verbenaceae), and *Tectona* (Verbenaceae, Tectoneae).

Group A is the most incongruent with the current classification of the two families and may be paraphyletic. An argument will be presented below that suggests that the true affinities of *Faradaya* and *Physopsis* are with Groups B and C, respectively, in spite of their assignment to Group A in the consensus tree.

Group B, although taxonomically diverse, is probably monophyletic. All but one of the genera of Labiatae and Verbenaceae that have spinulose or verrucate supratectal sculpturing fall within this group in the most parsimonious trees. (The affinities of the one exception, *Faradaya*, probably lie with this group as well; discussed below.) Only a few members of Group B have other sorts of exine ornamentation. Moreover, all but one of the taxa in Group B for which data are available have pollen with branched columellae (occasionally varying to granular), a feature that is very rare elsewhere in the Lamiales. The one exception, *Trichostema* sect. *Trichostema*, has a massive, undifferentiated columellate stratum, an autapomorphy. Branched columellae are not known to occur in the outgroups, thus their presence is hypothesized to be a synapomorphy of Group B.

With the exception of *Tectona*, Group C is an entirely Australian assemblage. A close relationship between *Tectona* and tribe Physopsideae (Chloanthoideae) may at first seem unlikely, inasmuch as *Tectona* species are large Indomalaysian trees, while the Physopsideae are Australian shrubs. However, there are many derived similarities between these taxa (Fig. 4), including actinomorphic flowers with isomerous stamens, an indument of branched trichomes, and a fruiting calyx that is constricted apically, enclosing the fruit. Moreover, Carlquist (1981) noted that *Tectona* is one of only two non-chloanthoid Verbenaceae with bordered pits on the imperforate tracheary elements of the secondary xylem, a feature found in all Chloanthoideae. One can speculate that *Tectona* arose following the dispersal of an Australian physopsid ancestor to an environment in the Malay Archipelago that was conducive to the evolution of an arborescent habit. The range of *Tectona* currently comes within about 500 miles of that of the Physopsideae.

Since ten of the OTUs in Group C are exemplar species of the paraphyletic genus *Pityrodia*, the relationships hypothesized within the group might have been quite different if the other 31 species of *Pityrodia* had been included as well. Furthermore, there are additional characters (e.g., leaf morphology) that were excluded because of excessive intra-OTU variation in other parts of the study group but that would be useful in an analysis restricted to Group C. Consequently, the relationships shown within the Chloanthoideae (the upper two-thirds of Group C) are presented with relatively little confidence. For example, *Chloanthes* would probably have grouped with *Pityrodia uncinata* rather than *P. angustisepala* if more leaf characters had been included in the data set. On the other hand, the relationship hypothesized here between *Hemiphora* and *Pityrodia bartlingii* is well supported by shared foliar features that were not used in this analysis. The similar and unusual pollen morphology exhibited by these two taxa has already been noted by Raj & Grafström (1984).

AFFINITIES OF PHYSOPSIS AND FARADAYA

Although the groupings in Figure 1 are markedly incongruent with the accepted taxonomy of the Verbenaceae, they make intuitive sense if one is willing to look beyond the single-character taxonomy that underlies our current classification and consider the range of characters used here. However, the validity of one grouping (marked with an asterisk in Fig. 2) must be questioned. Its five genera belong to five different tribes in three subfamilies. The synapomorphies of this ostensible clade and the slightly larger one that includes *Neorapinia* are actinomorphic flowers, a corolla with four similar petals, a calyx with four similar sepals, and stamens of equal length. Although these characters are not obligately correlated with each other in the data set as a whole (and therefore all of them have been retained in the analysis), neither can they be viewed as fully independent. Not only does the definition of actinomorphy overlap the other three characters, but the tetramerous construction of the corolla and calyx is very likely genetically linked. Thus the four characters that delimit this group would perhaps better be viewed as constituting only a single derived floral syndrome. While the true affinities of *Callicarpa, Hymenopyramus,* and *Petitia* remain obscure, *Physopsis* and *Faradaya* are probably not related to them.

In my opinion, a more plausible position for *Physopsis* is its traditional placement within tribe Physopsideae (perhaps close to *Mallophora* and *Dicrastylis* in Fig. 4), although it lengthens the tree by one step. Derived states that support this hypothesis include an indumentum of branched trichomes and the persistence of the corolla as a sheath around the fruit. Similarities in habit and foliar features that were not included in the analysis provide further support for a close relationship between *Physopsis* and the other Physopsideae.

The true affinities of *Faradaya* most likely lie within group B, where it may be closely related to *Oxera* (lower part of Fig. 3). This hypothesis is only one step longer than the most parsimonious trees. Like most members of group B, *Faradaya* has spinulose pollen; indeed, it is the only genus outside of group B that exhibits this derived state. Another unusual feature (character 56), found only in *Faradaya, Oxera, Hosea,* and a few species of *Clerodendrum* (all except *Faradaya* in group B), is the marked elongation of the ovary lobes relative to the unlobed portion of the ovary during fruit maturation. The exine of *Faradaya* has not yet been examined with transmission electron microscopy; if it proves to have branched columellae, a position in group B will be further supported, whereas simple columellae would argue against this hypothesis.

TAXONOMIC IMPLICATIONS

If future work supports the preliminary results presented here, some realignments in the classification of the Labiatae and Verbenaceae will be in order. The relationships shown in Figure 1 present two basic problems: polyphyly of the Labiatae and paraphyly of the Verbenaceae. The former could be remedied by restricting the family to the clade that includes the gynobasic-styled Labiatae, tribe Scutellarieae, the six genera of tribe Ajugeae that have suprareticulate pollen, and two genera currently placed in the Verbenaceae: *Garrettia* and *Holmskioldia.* The remaining 13 genera currently assigned to the Labiatae by some or all authors (viz., tribe Prostanthereae, *Amethystea, Rubiteucris, Schnabelia, Tetraclea, Teucrium,* and *Trichostema*) would be transferred to the Verbenaceae, which would, however, remain paraphyletic. An alternative approach that would remedy this problem as well would be the adoption of Junell's (1934) proposal that the Verbenaceae be restricted to subfamily Verbenoideae and that most other groups of Verbenaceae sensu lato (including all ingroup genera in this analysis) be transferred to the Labiatae. Synapomorphies can be hypothesized for both families if delimited in this way. These two approaches to the classification of the Lamiales are considered in more detail elsewhere (Cantino, 1992).

Regardless whether one recircumscribes the Verbenaceae and Labiatae as suggested above or retains the conventional family boundary, it is clear that the current taxonomy of the Verbenaceae provides a very poor reflection of phylogenetic relationships. If the relationships shown in Figure 1 are essentially correct, subfamily Caryopteridoideae and tribes Callicarpeae, Chloantheae, Clerodendreae, Physopsideae, and Tectoneae are all polyphyletic while the Viticeae are paraphyletic. Only Monochileae emerge as a clade. At the generic level, *Pityrodia* and *Clerodendrum* are at best paraphyletic, and *Caryopteris* appears to be polyphyletic. If the slightly less parsimonious placements of *Physopsis* and *Faradaya* (discussed above) are correct, Physopsideae would no longer be polyphyletic, but the other problems would remain unchanged.

Infrafamilial groupings in the Labiatae hold up far better, in spite of the polyphyly of the family as a whole. Tribe Prostanthereae, Subfamily Nepetoideae sensu Erdtman (1945), and subfamilies Scutellarioideae and Lamioideae sensu Wunderlich (1967) emerge as monophyletic, the lattermost represented here by *Galeopsis, Lamium, Moluccella, Physostegia,* and *Prasium* (Fig. 2). Tribe Ajugeae, however, is polyphyletic. The implications of this analysis with regard to infrafamilial classification of the Labiatae are discussed in more detail elsewhere (Cantino, 1992).

BIOGEOGRAPHIC IMPLICATIONS

The gynobasic-styled Labiatae, which emerge as a clade in the strict consensus tree (Fig. 1), make up about 90% of the family. The distributions of their closest relatives suggest that this large and successful clade originated in southern China or Indomalaysia, as suggested by Wu & Li (1982). *Holocheila* is known only from southern China (Yunnan Province), while *Acrymia*, *Cymaria*, and *Garrettia* are endemic to southeast Asia and/or Indomalaysia. *Ajuga* is widespread in the Old World but particularly diverse in China.

Two groups of Labiatae appear to have originated in Australia—tribe Prostanthereae and *Teucrium*. The former observation is trivial since the Prostanthereae are endemic to Australia, but an Australian origin for *Teucrium* runs counter to expectations, inasmuch as its center of diversity is in the Mediterranean region. The closest relatives of *Teucrium* (Figs. 1, 3) are *Teucridium*, *Spartothamnella*, and *Oncinocalyx*, the former endemic to New Zealand and the latter two to Australia.

While *Teucrium* clearly experienced a major radiation in the Mediterranean region, there is no reason to assume it was the primary radiation rather than a secondary burst of evolution some time after the genus came into existence in another part of the world. In this regard, an argument can be made that the most primitive portion of the genus is section *Teucrium*. The rest of the genus is united by a derived calyx morphology: a bilaterally symmetrical and more or less gibbous calyx with an oblique attachment of the pedicel (Kästner, 1978; Cantino, unpublished data). In contrast, the calyx in section *Teucrium* is radially symmetrical with a central pedicel attachment, very similar to the calyx morphology in *Teucridium*, *Spartothamnella*, and most members of the *Trichostema–Caryopteris* alliance. If one accepts the basal position of section *Teucrium*, an Australian origin for the genus is no longer improbable. Section *Teucrium* is widespread in the Southern Hemisphere, including Australia and southern Africa, but also occurs in the Mediterranean region. It is suggested here that the current diversity of the genus resulted from a secondary radiation following the arrival of section *Teucrium* in the Mediterranean region, perhaps via Africa. A cladistic analysis of relationships within *Teucrium*, utilizing a wider range of characters, would provide a test of this hypothesis.

FURTHER RESEARCH

This analysis is preliminary in several important ways. First, the existence of a large number of equally parsimonious trees, with the resulting poor resolution of the strict consensus tree, may in part be due to the extent of missing data for certain characters and taxa. An effort is in progress to fill many gaps in the data matrix. Second, a future analysis will benefit from the inclusion of the segregate families Avicenniaceae and Symphoremataceae, as well as a more extensive sample of the gynobasic-styled Labiatae. Most important, the primary outgroups (Verbenoideae, Cyclocheilaceae, Nesogenaceae, Phrymaceae, and Stilbaceae) will be included in the data set of a subsequent analysis once data collection is complete, thereby eliminating the need for Lundberg Rooting. If relationships within the Scrophulariales–Lamiales clade can be better resolved, the most closely related groups of Scrophulariales should also be included as secondary outgroups.

This study provides a set of explicit hypotheses about relationships in the Lamiales. These will be tested by means of the improved analysis discussed above and through molecular–phylogenetic studies that have recently been initiated by R. G. Olmstead (pers. comm.). It is hoped that this paper will stimulate phylogenetically oriented investigations using other sorts of characters as well (e.g., terpenoids). The consensus of all such studies should provide a greatly improved understanding of the phylogeny of the Lamiales and a more natural and predictive classification of the Verbenaceae and Labiatae.

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PHYLOGENY OF THE RUBIACEAE (CHIOCOCCEAE) BASED ON MOLECULAR AND MORPHOLOGICAL DATA—USEFUL APPROACHES FOR CLASSIFICATION AND COMPARATIVE ECOLOGY[1]

Birgitta Bremer[2]

ABSTRACT

Phylogenies reconstructed with molecular data may provide new hypotheses of relationships. These may serve as a basis for improved morphological analyses and comparative analyses of ecological features. In this study a new phylogenetic hypothesis based on a chloroplast DNA restriction site analysis of the Rubiaceae prompted a critical analysis of morphological characters. Several unique morphological characters were identified that support a large, previously unrecognized monophyletic group, including the tribe Chiococceae. Hence, the tribe Chiococceae is amended to include members of the former Condamineeae (subtribe Portlandiinae) and the genera *Exostema* and *Coutarea* (formerly in the Cinchoneae). The new phylogeny of the Rubiaceae, based on molecular data and the great variety of fruits in the family, makes this family suitable for comparative studies of evolution of dispersal systems and for testing hypotheses of species diversity in connection with the different dispersal systems. In the Rubiaceae, fleshy fruits, adapted to animal dispersal, have originated a limited number of times and have remained unchanged since the time of origin. The hypothesis that animal dispersal should promote species diversity is not supported for the Rubiaceae.

The position of the Rubiaceae in the order Gentianales close to the Loganiaceae was first suggested by Utzschneider (1947) and later established by Wagenitz (1959, 1964). This systematic position is accepted by most systematists dealing with higher-level classification (Dahlgren, 1980; Thorne, 1983; Takhtajan, 1987) and also is supported by phytochemistry (cf. Bisset, 1980) and sequence data of the *rbc*L gene (R. Olmstead & J. Palmer, pers. comm.). Relationships within the order are unresolved and have been proposed to be reticulate (Leeuwenberg & Leenhouts, 1980), with the Loganiaceae as a central or "ancestral" paraphyletic taxon. A morphological study, aimed at identifying the sister group to the Rubiaceae, analyzed representatives of all tribes of the Loganiaceae as well as a few taxa of the other families of the Gentianales (Bremer & Struwe, unpublished data). The results confirmed that the Loganiaceae were paraphyletic. The closest relatives to the Rubiaceae were found to be a part of the Loganiaceae, *viz* the tribe Gelsemieae or at least a part of it.

The Rubiaceae are, with the exception of a few aberrant taxa, an easily circumscribed family, characterized by inferior ovary, opposite leaves with stipules, and absence of internal phloem. Intrafamilial delimitations have always been complicated and uncertain, however. There are two main reasons for this uncertainty. First, "traditional" classification is based on phenetic similarities, and hence several groups are defined by symplesiomorphies or mere absences of characters. Second, much emphasis has been put on fruit structures for sorting genera into subfamilies and tribes. Single structures have been used as cardinal characters. However, in this family comprising about 10,000 species and 600 genera (Mabberley, 1987), many different fruit traits occur. If evolutionary shifts in these traits are common, i.e., highly homoplastic, they may be a source of error in classification. During the past 35 years three important treatments of the family with new classification schemes have been presented (Verdcourt, 1958; Bremekamp, 1966; Robbrecht, 1988). A comparison of these

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different schemes (Bremer & Jansen, 1991, table 2) displays many dissimilarities and conflicts, even though there is also much congruency. The merits of the different systems are difficult to evaluate because, in several cases, they are based on a few cardinal characters only, and no strict character analyses are presented. So far, studies of relationships between the subfamilial entities have been rare. Affinities between high-level Rubiaceae taxa have been addressed by serological similarities (Lee & Fairbrothers, 1978). The first phylogenetic analysis of representatives of different tribes of the family is the one by Bremer & Jansen (1991) based on chloroplast DNA (cpDNA) variation.

In order to evaluate different classification schemes, and to use the classification as a framework for evolutionary studies, phylogenetic analyses are necessary. In this context, neither molecular nor morphological data are superior. Both types of data are useful for phylogenetic reconstruction. When a phylogeny based on molecular data is compared with an "accepted" classification, the latter is often rejected because most classifications today are based on phenetic similarity and do not reflect the phylogeny (cf. Sytsma, 1990). However, this does not mean that morphological data should be dismissed as inferior for phylogenetic reconstruction. With cladistic analysis, both molecular and morphological data may be useful and complementary in phylogenetic reconstruction. It is also important to get rid of preconceived notions concerning which characters are "good" or "useless." Character homoplasy and hence usefulness can only be determined a posteriori, following an analysis involving comparison with other characters.

Due to the correlation between large data sets (many taxa) and a high level of homoplasy (Sanderson & Donoghue, 1989; Archie, 1989), it is probably not realistic to expect to resolve all relationships in one analysis of all genera of a large family such as the Rubiaceae. However, if not all taxa are analyzed, character optimization and tree topology may be affected (Donoghue et al., 1989). In Rubiaceae it is not sufficient to sample only a few examples of each tribe in order to resolve tribal relationships, since the tribes in many cases are badly circumscribed (cf. Hallé, 1961; Steyermark & Kirkbride, 1975; Kirkbride, 1979; Ridsdale, 1982; Tirvengadum, 1984; Robbrecht & Puff, 1986; Bremer, 1987; Robbrecht, 1988). One strategy for tackling the sampling problem is to use "common knowledge" of relationships and select a limited number of taxa for a pilot study with molecular data. Results of a pilot study may suggest new hypotheses of relationships, as in the study by Bremer & Jansen (1991). In that study, a cladistic analysis of cpDNA restriction data was performed for 33 genera representing 18 tribes and four subfamilies. Several monophyletic groups postulated in this analysis were congruent with "traditional" classification, e.g., the subfamilies Rubioideae and the Ixoroideae. However, the large subfamily Cinchonoideae was shown to be paraphyletic. In addition, totally new relationships were indicated.

Following such a molecular pilot study, the postulated new relationships may then be tested by morphological data. If the new groupings are supported, it should be possible to identify larger monophyletic groups defined by particular morphological characters. This morphological study may subsequently suggest suitable taxa for new molecular and morphological analyses that may provide further support for particular intrafamilial taxa. Using a sample of representatives from these larger corroborated monophyletic taxa, it should be possible to analyze and reconstruct the phylogeny and resolve the relationships for the whole family. This is an enormous task for the Rubiaceae, but important for a stable and informative classification.

The first steps in the strategy outlined above are here illustrated by an example in which a new relationship indicated by a cpDNA analysis (Bremer & Jansen, 1991) provides the basis for a morphological analysis, resulting in the identification of a large monophyletic group including the tribe Chiococceae, the subtribe Portlandiinae (of the Condamineeae) and some genera from other tribes.

Another kind of analysis that can be performed is comparative study of ecologically important characters. Such an analysis is founded on the assumption that phylogenetic reconstruction provides information on evolutionary sequences. The usefulness of a phylogenetic reconstruction based on molecular data for testing ecological characters or hypotheses will be illustrated and discussed.

A CASE STUDY—CHIOCOCCEAE

The cpDNA cladogram of the Rubiaceae (Bremer & Jansen, 1991, fig. 2) revealed several hitherto unknown relationships. One of the branches in the cladogram (Bremer & Jansen, 1991, fig. 2) included four genera, *Exostema* and *Coutarea* of the tribe Cinchoneae and *Erithalis* and *Chiococca* of the Chiococceae. The members of the tribe Chiococceae (*Chiococca*, Fig. 1) have many small flowers in axillary inflorescences, mostly fleshy fruits (drupes), and one seed per carpel, whereas *Exo-*

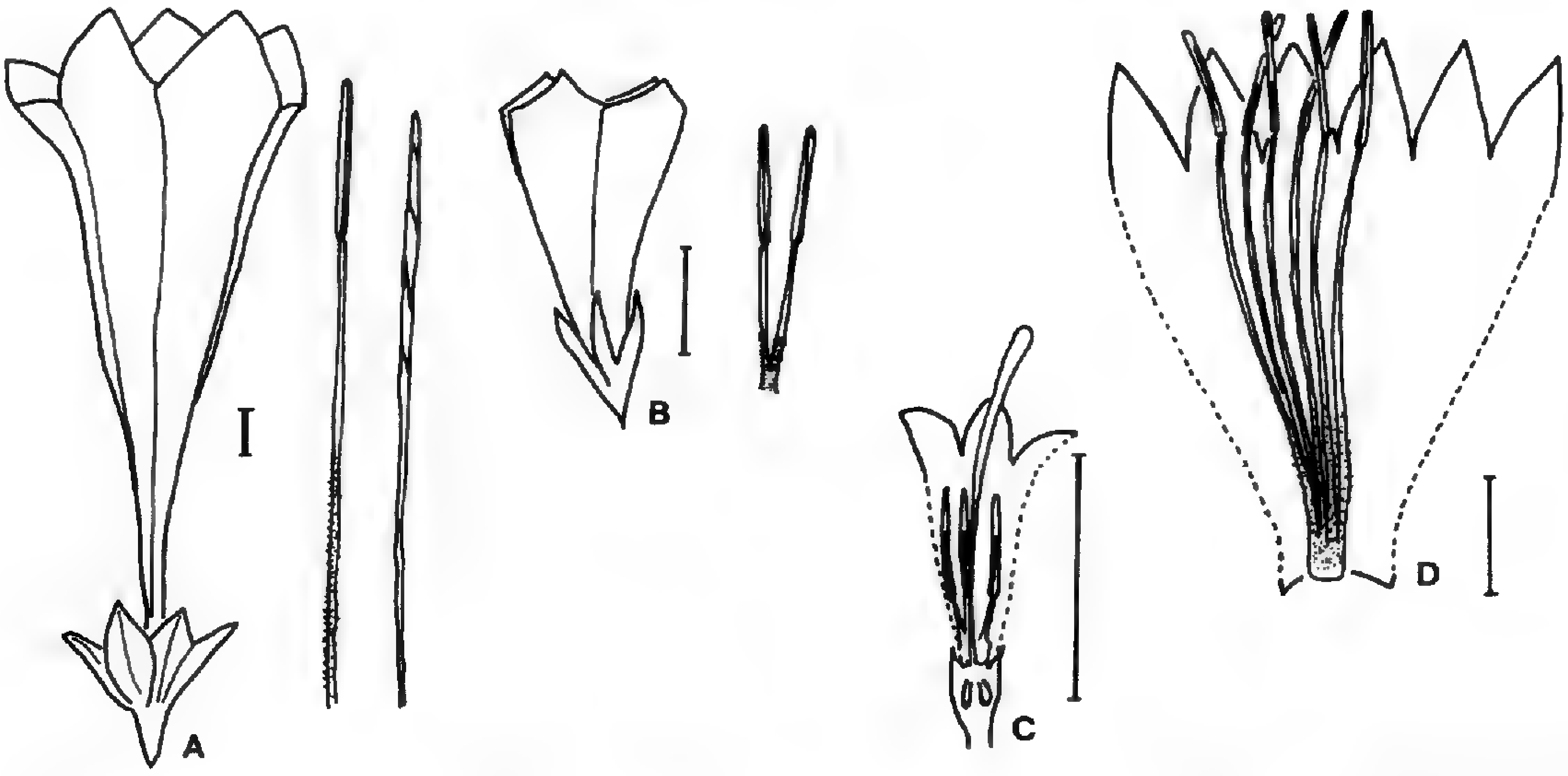

FIGURE 1. Flower parts.—A. *Portlandia* (redrawn after Aiello, 1979).—B. *Bikkia* (redrawn after Jérémie & Hallé, 1976).—C. *Chiococca* (redrawn after Correll & Correll, 1982).—D. *Coutarea* (redrawn after Steyermark, 1974). Bar scales = 1 cm.

stema and *Coutarea* (Fig. 1) usually have few large flowers and dry, many-seeded capsules. An affinity between these taxa has never been proposed, and in the latest classification (Robbrecht, 1988) they are placed in different subfamilies, with the Chiococceae in the Antirheoideae and the others in the Cinchonoideae.

The molecular analysis prompted a more detailed morphological analysis of these taxa. I found that they share several specific characters (Table 1, characters 1–7): corolla funnelform or rotate; corolla aestivation imbricate; stamens inserted at the corolla base; filaments fused into a basal ring; anthers linear, basifixed; and stigmas entire or indistinctly lobed. The combination of these characters, particularly the staminal arrangement, is rare in the family, but not unique to these four genera, because they also characterize the subtribe Portlandiinae (*Portlandia*, Fig. 1) of the tribe Condamineeae. In addition, members of the Portlandiinae usually have very large flowers; in the genera *Cubanola*, *Osa*, *Portlandia*, and *Thogsennia*, it is not unusual to have 20-cm-long corollas.

The neotropical genus *Portlandia* and associated taxa (≈ Portlandiinae) have recently been revised by Aiello (1979), who identified the same characters (Table 1, characters 1–7) and indicated that *Exostema*, *Coutarea*, and other genera also have identical character states. Aiello did not reconsider the established tribal classification and did not associate *Exostema* and *Coutarea* with *Portlandia*, because the first two genera have vertically arranged winged seeds, characteristic of the Cinchonoideae, while *Portlandia*, of the tribe Condamineeae, has horizontally arranged wingless seeds. However, the orientation of the ovules to the placentas and the occurrence of a seed wing are characters that can vary even within the same genus (e.g., in *Steenisia* and *Cinchona*). Because these homoplastic characters have been the main criteria for tribal delimitation in the subfamily Cinchonoideae, it is not surprising that the classification seems arbitrary (see Robbrecht, 1988). The paraphyly of the tribe Cinchoneae was also indicated by the cpDNA analysis (Bremer & Jansen, 1991).

Because the tribal classification is uncertain, it seemed possible that other genera could be closely related to *Portlandia*, *Exostema*, and *Coutarea*. Hence I gathered additional morphological information from most genera of the Chiococceae and the Condamineeae (listed in Robbrecht, 1988), as well as from other genera reported to have the same staminal arrangements (Hooker, 1873; Schumann, 1891). A majority of the genera were studied from herbarium material (in S and UPS), and complementary data were taken from the literature (Mueller, 1861; Hooker, 1873; Schumann, 1891; Verdcourt, 1958; Bremekamp, 1966; Steyermark, 1974; Jérémie & Hallé, 1976; Darwin, 1977; Aiello, 1979; Jansen, 1979; Correll & Correll, 1982; Ridsdale, 1982). The following genera of the tribe Condamineeae (Robbrecht, 1988) were studied but rejected as unrelated to *Portlandia*, *Exostema*, and *Coutarea*, because they lack characters 1–7 listed in Table 1, particularly the staminal characters: *Chimarris*, *Condaminea*, *Flexanthera*, *Kerianthera*, *Parachimarris*, *Picardaea*, *Pinckneya*, *Pogonopus*, *Rustia*, and *Tresanthera*. The following genera of the Chiococceae were also rejected: *Allenanthus*, *Chiona*, *and Hodgkinsonia*. *Allenanthus* and *Chiona* have neither the staminal characters nor the same corolla shape, but they have imbricate aestivation. The flowers of

TABLE 1. Character list. Plesiomorphic state = 0. Apomorphic state = 1 or 2. Character 10 is treated as non-additive and character 12 as additive.

1. Corolla: neither funnel-shaped nor rotate, 0; funnel-shaped or rotate, 1.
2. Aestivation: not imbricate, 0; aestivation imbricate, 1.
3. Stamens; not inserted at the corolla base, 0; inserted at the corolla base, 1.
4. Stamens: not fused, 0; stamens fused into a basal ring, 1.
5. Anthers: not linear, 0; linear, 1.
6. Anthers: dorsifixed, 0; basifixed, 1.
7. Stigma: distinctly lobed, 0; indistinctly bilobed or not, 1.
8. Inflorescence: terminal, 0; axillary, 1.
9. Flowers: not yellowish, 0; often yellowish, 1.
10. Corolla: between 1 and 2 cm, 0; < 1 cm, 1; > 10 cm, 2.
11. Corolla lobes: neither recurved nor reflexed, 0; recurved or reflexed, 1.
12. Corolla lobes: ovate, 0; triangular, 1; linear, 2.
13. Cross section of corolla: circular, 0; distinctly angled, 1.
14. Filaments: glabrous, 0; hairy, 1.
15. Anthers: not exserted, 0; exserted, 1.
16. Stigmatic area: not of two twisted lines, 0; of two twisted lines, 1.
17. Mesocarp: dry, 0; fleshy, 1.
18. Endocarp: not compressed, 0; compressed, 1.
19. Number of seeds per carpel: more than one, 0; one, 1.
20. Seed: not winged, 0; winged. 1.

Hodgkinsonia are very different, with pitcher-shaped corollas, valvate aestivation, short filaments inserted at the midlength of the corollas, dorsifixed anthers, and three to four branched stigmas. The fruit of *Hodgkinsonia* is a drupe with a very hard bilocular endocarp and elongated seeds almost devoid of endosperm. These fruit characters clearly demonstrate that the genus belongs to the tribe Guettardeae, which also was indicated in the original description of the genus (Mueller, 1861). The genus *Phialanthus* has also been excluded since the anthers are ovate and the filaments are free, inserted at the corolla base. I have not been able to study material of the genus *Placocarpa*, but the description (Schumann, 1891) does not indicate any close connection to the *Chiococca* group.

Three genera of uncertain position in the Rubiaceae have been mentioned in connection with the Chiococceae or the Condamineeae (Robbrecht, 1988): *Mastixiodendron* (revised by Darwin, 1977); *Kajewskiella* (revised by Jansen, 1979); and *Pseudomussaenda* (treated and illustrated in Bridson & Verdcourt, 1988). None of these genera have the characteristic staminal arrangements or stigma shape. In addition, the pollen of *Mastixiodendron* (Darwin, 1977) is tectate, while the pollen of the *Portlandia* group is diffusely foveolate with echinate processes (Aiello, 1979).

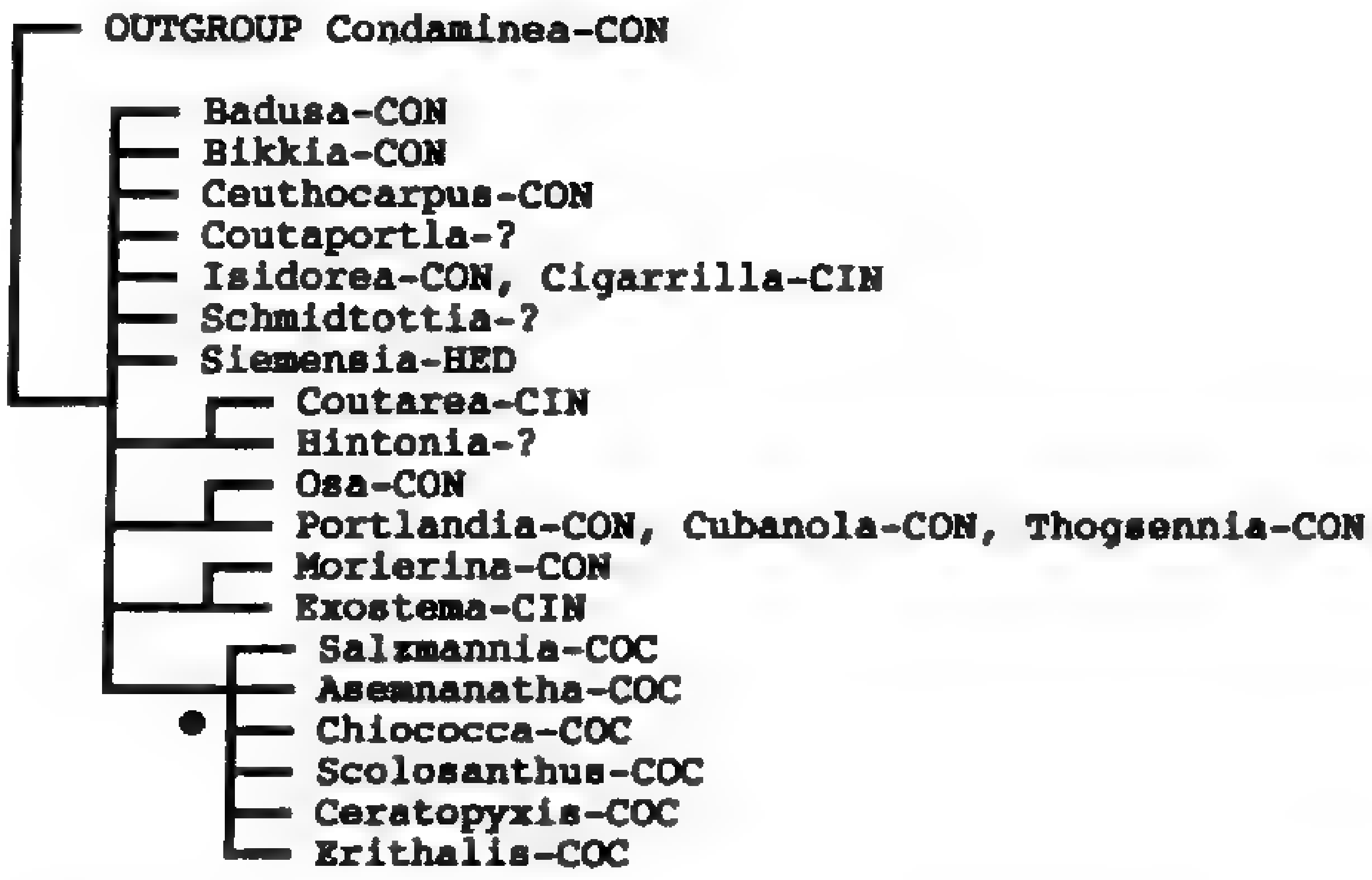

FIGURE 2. A strict consensus tree for 92 equally parsimonious Wagner trees with *Condaminea* as outgroup. The tribal position of each taxon is indicated by a three-letter suffix (CIN = Cinchonoideae, CON = Condamineeae, COC = Chiococceae, and HED = Hedyotideae, according to Robbrecht, 1988). A question mark indicates uncertain tribal position. The dot indicates the tribe Chiococceae sensu Hooker f.

All taxa with fused filaments and the combination of characters 1–7 (Table 1) were hypothesized to form a new monophyletic group. A character matrix (Table 2) for these taxa was constructed and analyzed with Wagner parsimony (Hennig86; Farris, 1988). As the sister-group relationships within the family are mostly unknown, four functional Rubiaceae outgroups, representing three tribes, were used: *Condaminea* (Condamineeae), *Luculia* (Cinchoneae), *Rondeletia* (Rondeletieae), and these three together. With *Condaminea* as the outgroup the result was 92 equally parsimonious trees, 34 steps long, with a consistency index of 0.41, and a retention index of 0.71 (Fig. 2). With *Luculia* as the outgroup there were 16 equal-

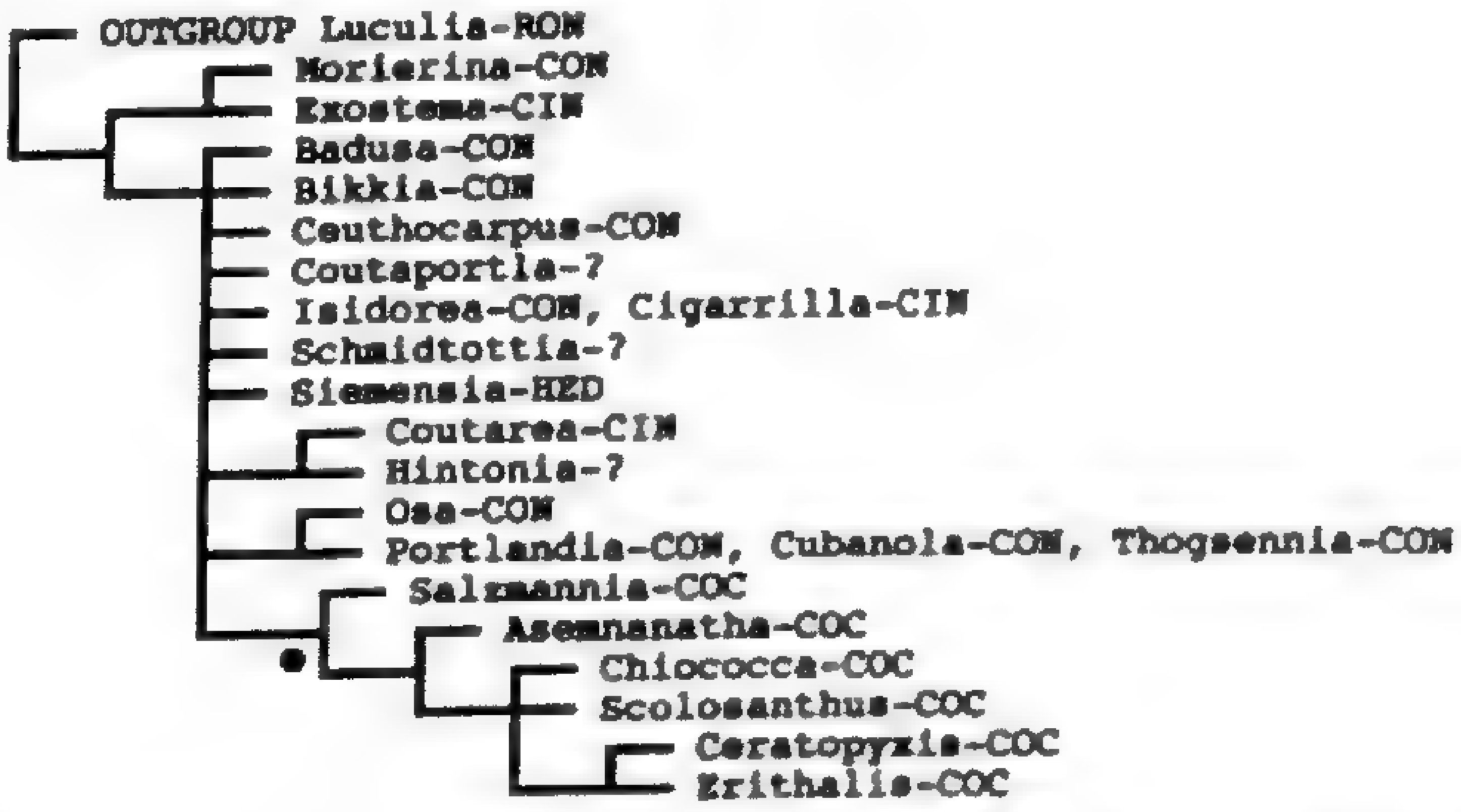

FIGURE 3. A strict consensus tree for 16 equally parsimonious Wagner trees with *Luculia* as outgroup. The tribal position of each taxon is indicated by a three-letter suffix (Robbrecht, 1988). A question mark indicates uncertain tribal position. The dot indicates the tribe Chiococceae sensu Hooker f.

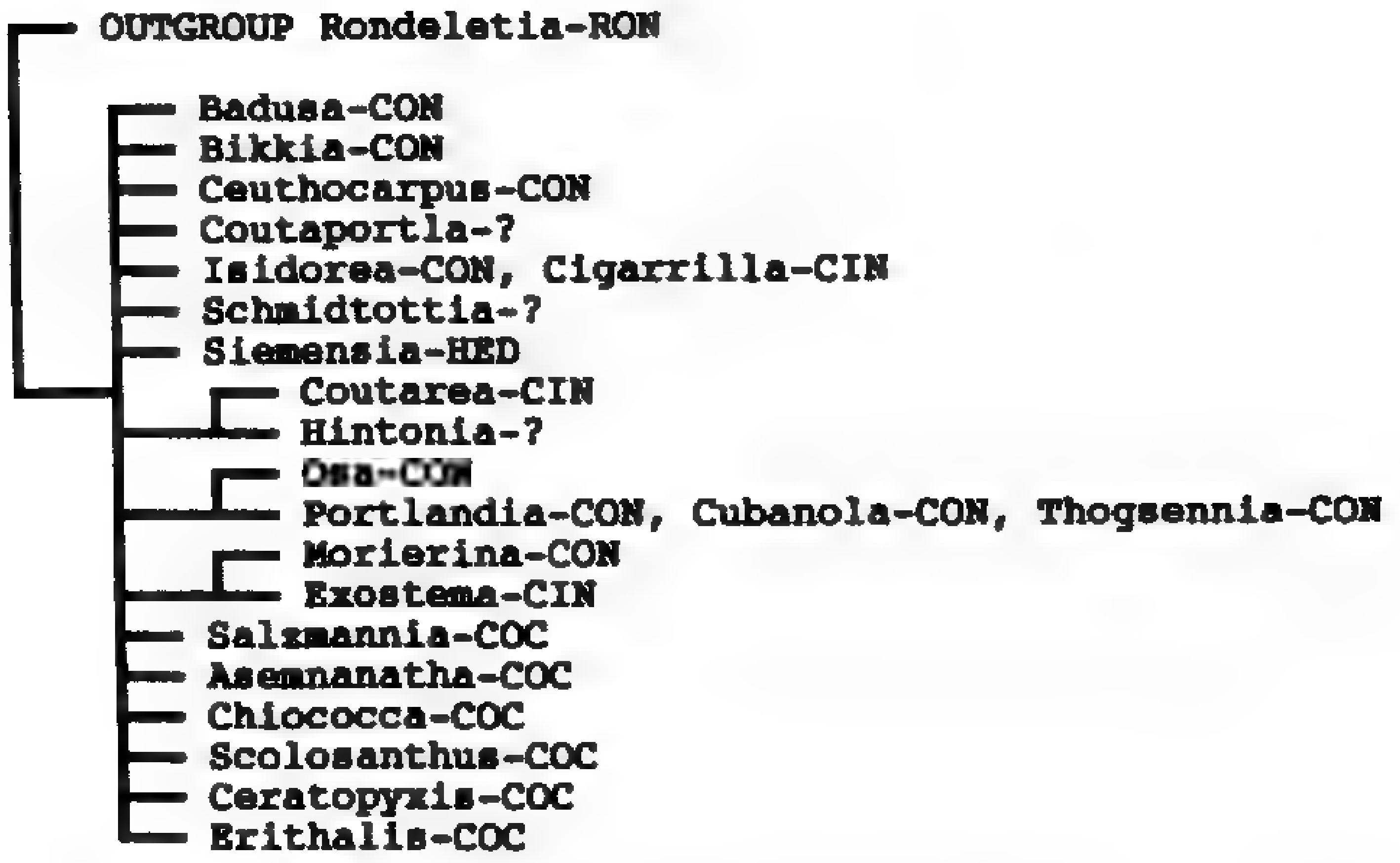

FIGURE 4. A strict consensus tree for 17 equally parsimonious Wagner trees with *Rondeletia* as outgroup. The tribal position of each taxon is indicated by a three-letter suffix (Robbrecht, 1988). A question mark indicates uncertain tribal position.

ly parsimonious trees, 35 steps long, with a consistency index of 0.42, and a retention index of 0.71 (Fig. 3). With *Rondeletia* there were 17 equally parsimonious trees, 34 steps long, with a consistency index of 0.44 and a retention index of 0.72 (Fig. 4). When all three genera were used as the outgroup, the result was 58 equally parsimonious trees, 37 steps long, with a consistency index of 0.40, and a retention index of 0.71 (Fig. 5). Most relationships within the ingroup remain unresolved or uncertain, because of the lack of available characters. There were only 13 phylogenetically informative characters and 22 ingroup taxa. However, all genera with small flowers and one-seeded carpels (≈ Chiococceae sensu Hooker f.) were shown to form a monophyletic group (indicated by a dot in Figs. 2, 3, 5) in all analyses except that with *Rondeletia* as the outgroup. This small-flowered group is supported by several flower and fruit characters (Tables 1, 2). If we retain Chiococceae in the narrow sense, all the remaining taxa considered in this analysis (≈ Portlandiinae) become a paraphyletic cluster; so far, no single character has been found to unite the remaining taxa. The best solution to this taxonomic problem is to redefine and widen the tribe Chiococceae, as follows.

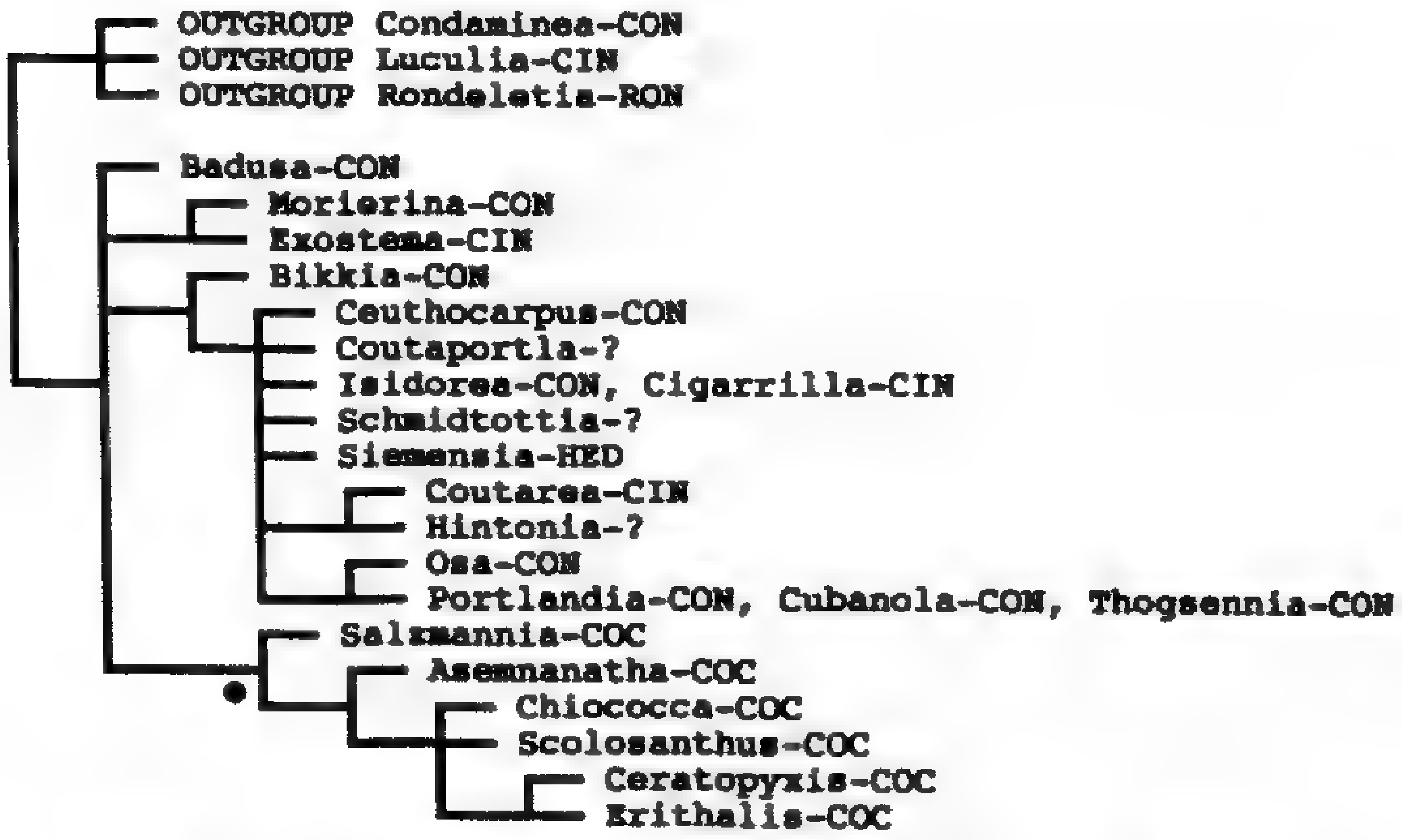

FIGURE 5. A strict consensus tree for 48 equally parsimonious Wagner trees with *Condaminea, Luculia* and *Rondeletia* as outgroup. The tribal position of each taxon is indicated by a three-letter suffix (Robbrecht, 1988). A question mark indicates uncertain tribal position. The dot indicates the tribe Chiococceae sensu Hooker f.

TABLE 2. Data matrix of 20 morphological characters. Characters 1–7 are synapomorphies defining the study group and not included in the Wagner parsimony analyses. Character numbers are the same as in Table 1. *Condaminea*—CON, *Luculia*—CIN, *Rondeletia*—RON, as well as all three together were used as outgroups. A question mark indicates an unknown or variable state.

		Character number	
			1 2
		1234567	8901234567890
1	*Condaminea*	0000000	0000100100000
2	*Luculia*	0100000	0000000000001
3	*Rondeletia*	0100000	1000000000000
4	*Asemnanatha*	1111111	1111101001010
5	*Ceratopyxis*	1111101	0111101100110
6	*Chiococca*	1111111	1111111001110
7	*Erithalis*	1111111	0011101101110
8	*Salzmannia*	1111111	1?10100001?10
9	*Scolosanthus*	1111111	1111101001110
10	*Badusa*	1111111	1?0010100000?
11	*Bikkia*	1111111	1000111000000
12	*Ceuthocarpus*	1111111	00001?1110000
13	*Cigarrilla*	1111111	1000111010000
14	*Cubanola*	1111111	1020111010000
15	*Coutaportla*	1111111	0000111010100
16	*Coutarea*	1111111	1000111110101
17	*Hintonia*	1111111	1000111110001
18	*Isidorea*	1111111	1000111010000
19	*Morierina*	1?11111	00212?1100001
20	*Osa*	1111111	1020110010000
21	*Portlandia*	1111111	1020111010000
22	*Schmidtottia*	1111111	0100111010000
23	*Siemensia*	1111111	0000111010000
24	*Thogsennia*	1111111	1020111010000
25	*Exostema*	1111111	?101200100001

Chiococceae J. D. Hooker, Gen. Pl.: 9, 21. 1873. Portlandiinae J. D. Hooker, Gen. Pl: 12. 1873, as "Portlandieae." Type genus: *Chiococca* P. Browne.

The tribe Chiococceae is characterized by funnelform or rotate corollas, imbricate aestivation, stamens inserted at the corolla base, filaments mostly villous and fused into a basal ring, anthers linear and mostly basifixed, stigma entire, carpels one- or many-seeded, and fruits drupes or capsules.

The included genera are *Asemnanatha, Badu-*

sa, Bikkia (Fig. 1), *Ceratopyxis, Ceuthocarpus, Chiococca* (Fig. 1), *Cigarrilla, Coutaportla, Coutarea* (Fig. 1), *Cubanola, Erithalis, Exostema, Hintonia, Isidorea, Morierina, Osa, Portlandia* (Fig. 1), *Salzmannia, Schmidtottia, Scolosanthus, Siemensia,* and *Thogsennia.*

PHYLOGENETIC ASPECTS OF SEED DISPERSAL

The Rubiaceae display a wide array of seed-dispersal mechanisms (Bremer & Eriksson, 1992). By making outgroup comparisons with different parts of the Loganiaceae, it can be inferred that the ancestral, plesiomorphic fruit condition in the family is likely to be a many-seeded capsule (Bremer & Struwe, unpublished data). This condition has been altered several times in relation to various dispersal agents, both biotic and abiotic. Adaptations for wind dispersal, in the form of winged seeds or pterophyll, occur in many genera. Bird- and mammal-dispersed fleshy fruits are also common in the family. These are basically of three kinds: drupes, berries, and "*Gardenia*-fruits." The "*Gardenia*-fruits" are characterized by a fleshy to leathery or fibrous to woody mesocarp, covering a juicy or fleshy pulp of placental origin (Robbrecht & Puff, 1986). Berries are the predominant fruit type in the tribe Iserteae. Drupes dominate in the Psychotrieae and Guettardeae. The subfamily Ixoroideae has the most variable array of fleshy fruits; in addition to "*Gardenia*-fruits," which occur solely in this subfamily, drupes and berries are common. The great variety of fruits in the Rubiaceae makes this family particularly suitable for comparative studies of the evolution of dispersal systems. Ecological considerations of seed-dispersal evolution have to a large extent focused on coevolutionary relationships between fruit characters and dispersal agents. The "traditional view" of a close adaptative association between plants and animals has recently been challenged (e.g., Howe, 1984, 1986; Herrera, 1986; Wheelwright, 1988). A persistent problem for evaluation of "coevolutionary" hypotheses is the scarcity of phylogenetic studies of fruit evolution incorporating taxa above the genus level. Until recently only a few such studies had been performed (e.g., Tiffney, 1986; Raven, 1988; Stone, 1989). In order to provide some insight into this research field, Bremer and Eriksson (1992) analyzed fruit evolution in the Rubiaceae. The study was based on the phylogenetic relationships of the family derived from cladistic analysis of cpDNA variation (Bremer & Jansen, 1991). The principal results indicated that fleshy fruits, adapted to animal dispersal, have originated only a limited number of times (approximately 12), and that they evolved mostly during a period from Eocene to Miocene. The inferences on when fleshy fruits appeared were made indirectly from information on pollen fossils (Bremer & Eriksson, 1992). Moreover, optimization of the fleshy fruit character on the cladogram implied that fruit structure in general has remained unchanged since that period. The analysis rested on two assumptions: that capsules with many seeds do not evolve from other fruit types and that seed number reduction is a "fixed" condition. Given these assumptions, the origin events were positioned in the phylogenetic tree on the lowest (oldest) possible branch that was allowed. Since the time of origin of the different fruit types, thousands of species have evolved; there are now ca. 7,000 extant species with fleshy fruits. These results indicate that specific adaptive interpretations of animal-dispersal modes based on contemporary ecological conditions are unwarranted. In contrast to the fleshy fruits, optimization of the wind dispersal by winged seed character on the cladogram suggested a much less conservative evolutionary pattern. Wind-dispersal adaptations may have been changed repeatedly during the course of evolution in several lineages.

Another issue, much debated in recent years, is how ecological features influence taxonomic diversification patterns (e.g., Stanley, 1979, 1989; Kitchell, 1985). For angiosperms, the prevalent view is that aspects of reproduction and dispersal have been responsible for the tremendous diversification of this group since Late Cretaceous (Raven, 1977; Burger, 1981; Stebbins, 1981; Crepet, 1984). One of several hypotheses of angiosperm diversification states that animal dispersal promotes species richness (Regal, 1977; Tiffney, 1984, 1986). Herrera (1989) tested this hypothesis and concluded that it was inconsistent with data on species number in relation to dispersal modes in both angiosperms and "gymnosperms." This conclusion was, however, not based on explicit phylogenetic inferences; since extant species number is directly correlated to diversification rate only if compared taxa are of equal age (cf. Mitter et al., 1988), the conclusion is difficult to evaluate. Eriksson & Bremer (1991) investigated the "animal dispersal hypothesis" in closer detail for the Rubiaceae. We found no consistent support for the hypothesis, but we did find evidence suggesting a positive association between dispersal ability and species diversification. In shrubs, fleshy fruits are likely to enhance seed dispersal, whereas abiotic dispersal modes are more efficient seed dispersers among herbaceous life forms (Eriksson & Bremer, 1991). These two life form/dispersal mode categories were both comparatively species-rich. This conclusion was robust since it was founded on generic and sister-group comparisons. Hence, this study indicated that diversification patterns are influenced by a combination of features. Future hypotheses should be based preferably on several life cycle characteristics, instead of single features.

The use of phylogenetic approaches in ecology has been considered by several authors (e.g., Ridley, 1983; Felsenstein, 1985; Donoghue, 1989; Funk & Brooks, 1990; Wanntorp et al., 1990; Brooks & McLennan, 1991), but empirical studies in botany are still scarce. A synthesis of ecology and phylogenetic inferences based on molecular and morphological data is a promising field for research. As the research on Rubiaceae has shown, data, hypotheses, and conclusions from molecular and morphological phylogeny and ecology, when considered together, have provided new insights that scarcely had been revealed by studies of ecological, morphological, or molecular data in isolation.

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CIRCUMSCRIPTION AND PHYLOGENY OF THE CAMPANULALES[1]

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ABSTRACT

Systematic relationships of the Campanulales were reexamined through the integration of data accumulated from morphological, anatomical, embryological, palynological, cytological, ultrastructural, chemical, molecular, and paleontological studies. Interpretation of these data suggests that the most natural circumscription of the order may be achieved by retaining Asteraceae and Calyceraceae, adding Menyanthaceae, removing Donatiaceae and Stylidiaceae to Ericales, and including *Brunonia* in Goodeniaceae rather than its own family. Phylogenies based on chloroplast DNA restriction fragment analysis and *rbc*L sequencing, supported by embryological and chemical data, suggest a basal dichotomy into two clades. The first (Menyanthaceae, Goodeniaceae, Calyceraceae, and Asteraceae) has multinucleate tapetal cells, lacks endosperm haustoria, and produces deterrent chemicals (either seco-iridoids or sesquiterpene lactones, but not both) via the mevalonate pathway. The second (Campanulaceae, Cyphiaceae, Lobeliaceae, Sphenocleaceae, and Pentaphragmataceae) has binucleate tapetal cells and terminal endosperm haustoria, but cannot synthesize deterrent chemicals via the mevalonate pathway. Numerous characteristic morphological features (e.g., epigyny, zygomorphy, secondary pollen presentation, uniovulate ovaries) appear to have had multiple origins within the order, vitiating their use as synapomorphies. The order originated no later than the Oligocene, very near the base of the Asteridae, probably in the Cornales–Saxifragales complex.

The Campanulales are an angiosperm order of vacillating circumscription (Wagenitz, 1977). Comparison of current classifications reveals major disagreements on its constituency, the relationships among its constituents, and its relationships to other orders. Possible relationships to the Asteraceae have been of special interest for many years (Greene, 1904; Small, 1919; Leonhardt, 1949; Turner, 1977; Bremer, 1987). In this review, three questions are posed: (1) What is the most natural circumscription of Campanulales? (2) What are the relationships among its component families? (3) To what other orders are the Campanulales related?

OVERVIEW OF CURRENT CLASSIFICATIONS

A complete taxonomic history of the order, which dates at least to Lindley (1833), is not presented here. The discussion is limited to the five major systems in current use: the most recent version of the traditional Englerian classification (Wagenitz, 1964) and the Besseyan classifications referred to as the "Big Four" (i.e., the systems of Cronquist, Dahlgren, Takhtajan, and Thorne). The sequence in which these classifications are discussed reflects a progressively narrower circumscription of Campanulales.

WAGENITZ

The broadest circumscription of Campanulales is that of Wagenitz (1964), who included the following families: Campanulaceae (subfamilies Campanuloideae, Cyphioideae, and Lobelioideae), Sphenocleaceae, Pentaphragmataceae, Goodeniaceae, Brunoniaceae, Stylidiaceae (subfamilies Donatioideae and Stylidioideae), Calyceraceae, and Asteraceae (subfamilies Asteroideae and Cichorioideae). The order was assigned to the dicotyledonous subclass Sympetalae and characterized largely as follows: herbaceous plants (rarely woody), storing carbohydrate as inulin; leaves exstipulate; flowers tetracyclic; corolla sympetalous, pentamerous; androecium isomerous (rarely oligomerous),

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with introrse (rarely extrorse) dithecal anthers, and often with specialized adaptations for secondary pollen presentation; gynoecium oligomerous, inferior (rarely superior), with 1–3(–5) locules, 1(–3) styles, and 1–many anatropous, unitegmic, tenuinucellate ovules.

TAKHTAJAN

The classification proposed by Takhtajan (1980, 1983) differs primarily in the removal of Asteraceae and Calyceraceae to monofamilial orders. Nonetheless, a close relationship was maintained by grouping these three orders as the Asteranae. This superorder is one of several in Asteridae, a subclass essentially identical to the Sympetalae of Wagenitz. The only other differences from the system of Wagenitz involved rank: Brunoniaceae, Pentaphragmataceae, and Sphenocleaceae were demoted to subfamilies (the first under Goodeniaceae, the last two under Campanulaceae), while the Donatioideae were promoted to familial rank. Additional taxonomic structure was provided by grouping the families into two suborders, Campanulineae (Campanulaceae, Donatiaceae, Stylidiaceae) and Goodeniineae (Goodeniaceae).

Takhtajan excluded Asteraceae and Calyceraceae primarily on morphological grounds, although anatomical, embryological, and palynological differences were also cited. Their removal tightened up the morphological characterization of Campanulales by removing families with involucrate capitulate inflorescences, 1-loculed ovaries, and solitary ovules.

In Takhtajan's (1987) recent revision of his system, the treatment of Campanulales at first appears very different. The subfamilies of Campanulaceae have been elevated to familial rank as Pentaphragmataceae, Sphenocleaceae, Campanulaceae, Cyphiaceae, Nemacladaceae, Lobeliaceae, and Cyphocarpaceae (Nemacladaceae and Cyphocarpaceae were segregated from Cyphioideae). The remainder of the Campanulineae formed the new order Stylidiales, while the Goodeniineae were raised to ordinal rank as Goodeniales (with Brunonioideae elevated to familial rank). These three orders, together with Calycerales and Asterales, constitute a smaller subclass Asteridae; the remainder of the sympetalous orders are assigned to a new subclass Lamiidae. The only real difference, however, is an across-the-board inflation in rank; the taxa that constituted a family in the earlier version now make up an order, and what was formerly an order or superorder is now a subclass. The relationships expressed are essentially unaltered from the earlier system, or from that of Wagenitz.

CRONQUIST

The system of Cronquist (1981, 1987a) resembles Takhtajan's original classification in its removal of Calyceraceae and Asteraceae to monofamilial orders, but differs in its complete dissociation of these orders from any relationship with the Campanulales. Instead, Calycerales were allied to Dipsacales, and Asterales to Rubiales. Brunonioideae, Pentaphragmatoideae, and Sphenocleoideae were restored to familial status, while the Cyphioideae, a small group of "transitional" genera connecting Campanuloideae and Lobelioideae, were not recognized formally.

THORNE

A conspicuous difference in the system of Thorne (1968, 1976, 1977, 1981, 1983) is the division of the angiosperms into numerous superorders rather than a few subclasses. Like Cronquist, he completely dissociated Asteraceae and Calyceraceae from Campanulales; the latter family, however, was assigned to Dipsacales rather than to its own order. The Campanulales were reduced further by the removal of Donatiaceae and Stylidiaceae. This action left only Pentaphragmataceae, Campanulaceae (subfamilies Campanuloideae, Cyphioideae, Lobelioideae, and Sphenocleoideae), and Goodeniaceae (subfamilies Brunonioideae and Goodenioideae) in the order.

In justifying the exclusion of Donatiaceae and Stylidiaceae, Thorne (1976: 81) stated that they "have no basic relationships" to the remainder of the order. Rather, they "seem closely related to the Saxifragaceae but are more specialized in various ways" (Thorne, 1976: 89), a conclusion that resulted in their assignment to Rosales suborder Saxifragineae. Their exclusion narrowed the morphological characterization of the order by removing families with less than five stamens, filaments adnate to the style, and distinct styles.

Originally (Thorne, 1968, 1976), the Campanulales were assigned to the superorder Malviflorae, together with Euphorbiales, Malvales, Rhamnales, Solanales, and Urticales. Subsequently (Thorne, 1981, 1983), Campanulales and Solanales were segregated as the Solaniflorae. In both versions, the Asterales were placed in the monofamilial superorder Asteriflorae, Dipsacales in Corniflorae, and Rosales in Rosiflorae.

DAHLGREN

Like Thorne, Dahlgren (1975a, 1977, 1980, 1983; Dahlgren et al., 1981) fragmented Takhtajan's and Cronquist's Asteridae into numerous superorders; removed Calyceraceae and Asteraceae to Dipsacales and Asterales, respectively; and excluded Donatiaceae and Stylidiaceae from the order. Originally, he assigned these last two families to Cornales, between Columelliaceae and Hydrangeaceae. In a revision published posthumously by his wife (G. Dahlgren, 1989a, b), however, he removed them from that order, where he considered their terminal endosperm haustoria out of place, and segregated them as Stylidiales.

Dahlgren reduced Campanulales further by removing Brunoniaceae and Goodeniaceae to their own order Goodeniales. This action left Campanulales with only Campanulaceae, Pentaphragmataceae, Lobeliaceae, and Sphenocleaceae (included in Campanulaceae in the later versions). The disposition of the Cyphioideae was not explicitly stated.

Dahlgren's circumscription of Campanulales resembles that of Takhtajan (1987) in that it has become so narrow, its contents are identical to the family Campanulaceae of earlier workers (e.g., Schönland, 1889). It differs in the complete dissociation of Brunoniaceae, Calyceraceae, Donatiaceae, Goodeniaceae, and Stylidiaceae from any relationship with Campanulales and Asterales. This action was largely justified on chemical grounds; these five families produce iridoids, which were considered foreign to Campanulales and Asterales (Jensen et al., 1975; Dahlgren, 1977, 1983; Dahlgren et al., 1981). Their removal also narrowed the morphological description of the order by excluding families with involucrate capitulate inflorescences, hypogynous flowers, uniovulate ovaries, and stylar indusia.

Originally (Dahlgren, 1975a, 1977), the Campanulales were treated as the sole member of Campanulanae and were positioned near the likewise monofamilial Asteranae. In the subsequent versions, Campanulanae and Asteranae were merged as a single superorder under the latter name. The Cornales were assigned to Cornanae, Stylidiales to Ericanae, and Dipsacales and Goodeniales to the Gentiananae.

INCLUSION OF MENYANTHACEAE

No taxonomist working with morphological data has ever suggested that the Menyanthaceae were related to Campanulales. Most taxonomists, including Takhtajan and Thorne, put the family in Gentianales. Cronquist (1981), however, transferred it to Solanales, a move supported on chemical grounds by Gershenzon & Mabry (1983). Dahlgren (1983) commented that neither placement was satisfactory and subsequently (G. Dahlgren, 1989a) removed Menyanthaceae to the already heterogeneous Cornales, between Viburnaceae and Adoxaceae.

Recently, however, molecular data (discussed below) have consistently placed Menyanthaceae among Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, and Lobeliaceae, and at some distance from members of Gentianales and Solanales. Because molecular data are less prone to homoplasy than many other types of data (Jansen & Palmer, 1988; Palmer et al., 1988), and because they are supported by various chemical data (discussed below), it is prudent to include Menyanthaceae provisionally in this review of Campanulales.

SUMMARY

Twelve taxa are candidates for inclusion in the Campanulales (for uniformity, their names at familial rank are used pro tempore): Asteraceae, Brunoniaceae, Calyceraceae, Campanulaceae, Cyphiaceae, Donatiaceae, Goodeniaceae, Lobeliaceae, Menyanthaceae, Pentaphragmataceae, Sphenocleaceae, and Stylidiaceae. The common denominator of all classifications is the group comprising Campanulaceae, Cyphiaceae, Lobeliaceae, Pentaphragmataceae, and Sphenocleaceae. Surrounding this core are five satellites whose inclusion in the order is controversial: (1) Asteraceae, (2) Brunoniaceae and Goodeniaceae, (3) Calyceraceae, (4) Donatiaceae and Stylidiaceae, and (5) Menyanthaceae. The central problem of circumscription involves determining which, if any, of these satellites belong with the core group. The integrity of the core group and each of the bifamilial satellites cannot be assumed, however, and must also be examined.

DATA SETS

Traditionally, the circumscription of angiosperm orders has been based primarily upon a limited set of morphological data. An improved classification may be obtained by better reflecting the totality of similarities and differences among the taxa (Heywood, 1977; Kubitzki, 1977; Cronquist, 1987b; Stuessy, 1990). Among Campanulales, a significant body of data has accumulated from studies of their embryology, palynology, cytology, ultrastructure, chemistry, molecular biology, and paleontology. In the present review, I attempt to integrate these data, as a means of answering the questions posed at the beginning of this article. This synthetic approach should produce a revised classification of the order that is maximally predictive (Stuessy, 1990).

However, it soon will be clear to the reader that the data base for Campanulales is not yet as complete as could be desired. The coverage is uneven, with a great deal known about certain families and certain types of data, but very little known about others (Hegnauer in Moeliono & Tuyn, 1960). Gibbs's (1974: 1190) lament regarding chemical data ("We obviously need much more information before we can help the taxonomists!") is equally true for other types of data, and Heywood's (1977) call for the accumulation of a better organized data base on angiosperm families is still appropriate today. For this reason, a formal revision of the classification of the order is delayed pending the conclusion of certain studies, described later, that are currently under way.

In this section, the data sets that pertain to the classification of the Campanulales are discussed. Most of this information was gleaned from the literature. The genera and species cited parenthetically are intended as examples of taxa with a given feature and not as an exhaustive list, unless otherwise indicated.

MORPHOLOGY

Morphology is the foundation upon which all taxonomy rests. In the following discussion, features considered important in previous classifications of Campanulales are described.

Habit and stems. Most species are iteroparous herbs with diverse perennating mechanisms, but nearly the entire range of habits among dicotyledons is represented, including annuals, biennials, shrubs and subshrubs, trees, pachycaul rosettes, twining vines (*Cyphia* Berg, Cyphiaceae; *Mikania* Willd., Asteraceae), leaf succulents (*Othonna* L., Asteraceae), stem succulents (*Brighamia* A. Gray, Lobeliaceae), and various types of hydrophytes, such as cabomboids (*Megalodonta* Greene, Asteraceae), isoetids (*Lobelia dortmanna* L., Lobeliaceae), and nymphaeoids (*Nymphoides* Seguier, Menyanthaceae). In most cases, the woody species are believed to be derived from fundamentally herbaceous ancestors (Carlquist, 1962, 1969a, b), with the exception of Asteraceae, in which woodiness appears to be plesiomorphic (Carlquist, 1966; Stebbins, 1977; Jansen & Palmer, 1988). The small amount of secondary growth in some species of *Stylidium* Sw. ex Willd. (Stylidiaceae) is anomalous, as no cambial activity has been detected within the vascular bundles (Carlquist, 1981).

Campanulaceae, Cyphiaceae, Lobeliaceae, and certain Asteraceae (most notably Lactuceae) accumulate latex, a viscous white or colored fluid that is produced in a network of articulated lactifers. Brunoniaceae, Calyceraceae, Donatiaceae, Goodeniaceae, Menyanthaceae, Pentaphragmataceae, Sphenocleaceae, and Stylidiaceae do not produce latex.

Leaves. Leaves typically are simple and correspond to the dillenid type of Hickey & Wolfe (1975). Deeply parted or compound leaves do occur, however (*Menyanthes trifoliata* L., Menyanthaceae; *Cyanea shipmanii* Rock, Lobeliaceae; *Bidens bipinnata* L., Asteraceae). An alternate arrangement of the leaves is most common, although opposite (*Eupatorium perfoliatum* L., Asteraceae) or whorled (*Ostrowskia* Regel, Campanulaceae) patterns also occur. The markedly asymmetric leaf base of Pentaphragmataceae is noteworthy. True stipules are lacking, although stipulelike processes occur in some Asteraceae (*Simsia* Pers.), and the winged petioles of Menyanthaceae have been called stipulelike. Stomates are anomocytic, except in Sphenocleaceae, where they are tetracytic, and in Brunoniaceae and Donatiaceae, where they are paracytic.

Inflorescences. In Donatiaceae and *Phyllachne* Forster & G. Forster (Stylidiaceae), there is a single sessile flower at the apex of the stem. Although solitary axillary flowers occur in some taxa (*Burmeistera* Triana, Lobeliaceae; *Cyphocarpus* Miers, Cyphiaceae), most have flowers aggregated into some sort of inflorescence, which may be terminal or less often axillary. Campanulaceae, Cyphiaceae, Goodeniaceae, Lobeliaceae, and Stylidiaceae have a diverse array of monotelic and polytelic inflorescences (Carolin, 1967). Pentaphragmataceae are characterized by a sympodial helicoid cyme, and Sphenocleaceae, by a dense terminal spike. In Asteraceae, Brunoniaceae, Calyceraceae, and some Campanulaceae (*Jasione* L.), the flowers are condensed into a tight capitulum subtended by an involucre, which often resembles an individual flower. These capitula may be aggregated into secondary groupings (synflorescences or capitulescences).

Flowers. Although the flowers are characteristically complete (tetracyclic) and perfect, various types of structural and functional dicliny characterize certain taxa. Dioecious (*Lobelia dioica* R. Br.; *Pentaphragma tenuiflorum* Airy Shaw, Pentaphragmataceae) or gynodioecious (*Lobelia siphilitica* L.) species occur sporadically, while monosporangiate flowers are common components of the capitula of Asteraceae. Many Menyanthaceae are heterostylous (*Villarsia capitata* Nees). Proterandry characterizes Brunoniaceae, Calyceraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, and Stylidiaceae. This is correlated with their specialized mechanisms for the secondary presentation of pollen, discussed below.

The flowers of Lobeliaceae, with rare exceptions (*Downingia laeta* (Greene) Greene), and of some Stylidiaceae (*Stylidium petiolare* Sonder) are resupinate at anthesis, i.e., rotated 180° via torsion of the pedicel. As a result, the visually dorsal lobes of the perianth actually arise from the ventral portion of the floral primordium.

Calyx. The calyx is fundamentally pentamerous, although taxa and individuals with as few as two and as many as ten sepals are found in Calyceraceae, Campanulaceae, Donatiaceae, Goodeniaceae, and Stylidiaceae. The sepals are connate, with the exception of a few Menyanthaceae. In Brunoniaceae, some Goodeniaceae, and Menyanthaceae, this synsepalous calyx is free from the other floral organs. Otherwise, it is adnate to the corolla and androecium for some portion of their lengths, forming a hypanthium that is crowned by the distal portions of the sepals. With rare exceptions (*Cyananthus* Wallich ex Benth., Campanulaceae), this hypanthium is adnate to the ovary. In Pentaphragmataceae, however, it is connected only by five narrow longitudinal septa, which leave intervening lacunae or pits in which nectar is produced.

In many Asteraceae (*Chrysanthemum* L., *Xanthium* L.), nothing resembling a calyx lobe is evident, while in other genera of the family, various barbs, hairs, or scales are found where calyx lobes are expected. These structures, known collectively as the pappus, are presumed to be modified calyx lobes. The rigid persistent calyx lobes of Brunoniaceae and many Calyceraceae may represent an approach to this condition.

In Cyphiaceae and Lobeliaceae, the odd (unpaired) lobe originates in a ventral (anterior) position, a situation otherwise found only in *Logania* R. Br. (Loganiaceae) and some papilionoid legumes (Kaplan, 1967). However, in Lobeliaceae, this lobe is brought into a dorsal (posterior) position by the resupination of the flower (see above).

Corolla. The corolla is essentially pentamerous but with sporadic variation in taxa and individuals of some families. In *Stylidium* and *Levenhookia* R. Br. (Stylidiaceae), the odd (unpaired) petal is often so reduced as to give the impression of a tetramerous corolla. Petals are connate in all but Donatiaceae and a few species of Pentaphragmataceae (*Pentaphragma decurrens* Airy Shaw).

Radial symmetry (actinomorphy) characterizes Brunoniaceae, Calyceraceae, Campanulaceae, Donatiaceae, Menyanthaceae, Pentaphragmataceae, and Sphenocleaceae. Actual shape of the corolla may be rotate, campanulate, urceolate, infundibular, tubular, or salverform. Bilateral symmetry (zygomorphy) characterizes Cyphiaceae, Goodeniaceae, and Lobeliaceae. The irregularity may be slight (*Cyphia brevifolia* Thulin, *Lobelia donanensis* van Royen), but is nonetheless perceptible. In Stylidiaceae, *Levenhookia* and *Stylidium* are zygomorphic, while *Forstera* L. f., *Phyllachne*, and *Oreostylidium* Berggren are actinomorphic. In Asteraceae, inflorescences may be composed of zygomorphic flowers only (ligulate capitula), actinomorphic flowers only (discoid capitula), or both (radiate capitula).

Zygomorphy among Campanulales involves several distinct patterns. In Goodeniaceae, the corolla typically is bilabiate with two dorsal and three ventral lobes, though unilabiate corollas with five ventral lobes are not uncommon (*Scaevola sericea* Vahl). In both types, the odd (unpaired) lobe is in a ventral position.

Three basic patterns are seen in Cyphiaceae and Lobeliaceae: (1) bilabiate with three dorsal and two ventral lobes (*Nemacladus* Nutt., Cyphiaceae; *Lobelia erinus* L.); (2) bilabiate with one dorsal and four ventral lobes (restricted to *Cyphocarpus*, Cyphiaceae); (3) unilabiate with five dorsal lobes (*Lobelia tupa* L.). At anthesis, the flowers of Lobeliaceae appear more similar to those of Goodeniaceae than to those of Cyphiaceae, because of their resupination. However, in both Cyphiaceae and Lobeliaceae, the odd (unpaired) lobe originates in a dorsal position, and their flower is thus fundamentally different from that of Goodeniaceae.

In Stylidiaceae (Erickson, 1958), the odd petal originates in a ventral position. In the zygomorphic genera, this takes the form of a highly reduced and modified labellum, which is irritable (pressure-sensitive) in *Levenhookia*. The remaining four lobes may be similar in size and shape or they may be heteromorphic. Most commonly, they are gathered into two pairs. Each pair may consist of a ventral and a dorsal lobe (*Stylidium diuroides* Lindley), or of like lobes (*S. emarginatum* Sonder). In others, the four major lobes may be cruciform (*S. xanthopis* Erickson & Willis) or unilabiate (*S. divaricatum* Sonder). The throat is often marked by a series of glandular appendages of diverse shape and size.

Among Asteraceae (Bremer, 1987), the zygomorphic flowers of most tribes are essentially unilabiate; those in ligulate capitula have five ventral lobes, while those in radiate capitula have but three. In Mutisieae, however, the zygomorphic flowers are bilabiate. Most genera have corollas with two dorsal and three ventral lobes, though in some Barnadesiinae, there are one dorsal and four ventral lobes.

Androecium. Anthers are tetrasporangiate (rarely bisporangiate in Asteraceae), basifixed, and dehiscent via longitudinal slits. The thecae are parallel, with the exception of Stylidiaceae, where they are divergent and sometimes (*Forstera*, *Phyllachne*) apically confluent. A single cycle of five is characteristic. Asteraceae with tetramerous disc corollas (*Oparanthus* Sherff, *Petrobium* R. Br., *Remya* Hillebrand) have four stamens, as do Campanulaceae with tetramerous corollas (*Phyteuma tetramerum* Schur). One species of Donatiaceae, *Donatia fascicularis*, has three stamens while the other, *D. novae-zelandiae* J. D. Hook., has two. Stylidiaceae likewise have two stamens.

The stamens are antisepalous (i.e., alternate with the corolla lobes) in all families. In Asteraceae, Calyceraceae, *Cyphocarpus*, Sphenocleaceae, and sympetalous Pentaphragmataceae, the stamens are epipetalous, i.e., inserted on the corolla tube at or above the middle. In Brunoniaceae, most Campanulaceae, most Cyphiaceae, Donatiaceae, Goodeniaceae, Lobeliaceae, Menyanthaceae, and polypetalous Pentaphragmataceae, the stamens are inserted at the base of the corolla tube, on the floral receptacle, or on the top of the inferior ovary. In *Cyananthus*, the stamens arise from the rim of the free hypanthium. In a few Lobeliaceae, the basally inserted filaments are adnate to the corolla tube, either dorsally (*Rollandia* Gaudich.) or completely (*Siphocampylus* Pohl sect. *Hemisiphocampylus* A. DC.). In Stylidiaceae, the two stamens are wholly adnate to the style, forming a gynandrium or gynostegium in which the divergent anther thecae flank the large stigma.

A distinctive feature of Asteraceae, Brunoniaceae, Calyceraceae, Campanulaceae, Goodeniaceae, and Lobeliaceae is their specialized pollination mechanisms. These involve the presentation of pollen to potential pollinators in or on certain structures associated with the style (Carolin, 1960a; Erbar & Leins, 1989; Leins & Erbar, 1990). Such flowers are proterandrous, with an introrse discharge of pollen onto stylar structures preceding the elongation of the style and maturation of the stigma.

A major structural aspect of these mechanisms is the gathering of the stamens around the style. Asteraceae, Brunoniaceae, Lobeliaceae, and some Goodeniaceae (*Dampiera* R. Br., *Leschenaultia* R. Br.) are syngenesious, i.e., the anthers are connate, forming a definite tube into which the pollen is shed. Lobeliaceae differ from the remaining syngenesious taxa in having the two ventral anthers shorter than the other three. In Lobeliaceae, the syngenesious Goodeniaceae, and some Asteraceae, the filaments are connate for part of their length. However, in Calyceraceae and certain Cyphiaceae (*Nemacladus*, *Parishiella* A. Gray, *Pseudonemacladus* McVaugh, and some species of *Cyphia*), the filaments are connate for part of their length, though the anthers are distinct. In *Nemacladus*, the two dorsal filaments bear small stipelike structures with one or more terminal transparent rod-shaped cells. These structures are unique and of unknown function.

In Campanulaceae and the remaining Goodeniaceae (*Scaevola* L., *Selliera* Cav.), the stamens are connivent around the style, separating once the pollen is shed onto the style. In many species of *Phyteuma* L. (Campanulaceae), the distal portions of the corolla lobes are connate, forming a tube that functions much like the anther tube of syngenesious taxa.

A second aspect of these mechanisms is the presence of various stylar structures that collect pollen from the anthers and present it to pollinators. In Asteraceae, Brunoniaceae, Campanulaceae, and Lobeliaceae, various sorts of hairs on the style and stigma perform this function. The stylar hairs of Campanulaceae are unique in their ability to invaginate as a means of dislodging pollen grains (Carolin, 1960a; Shetler, 1979; Erbar & Leins, 1989). Brunoniaceae and Goodeniaceae are unique among angiosperms in possessing an indusium, a cuplike structure subtending the stigma, into which pollen is shed.

The gynandrium or gynostegium of Stylidiaceae is structurally and functionally different from the mechanisms described above. The column is irritable (pressure-sensitive) in *Stylidium* and to a lesser degree in *Levenhookia* (Erickson, 1958). The movements of an insect on the flower cause the gynandrium to spring suddenly. Either the extrorse anther locules deposit pollen directly on the insect (if the proterandrous flower is in staminate phase), or the stigma picks up a load of pollen from the insect (if the flower is in carpellate phase). This structure cannot be derived evolutionarily from the typical campanulalean mechanisms, but must have had an independent origin from the apostemonous condition (Carolin, 1960a; Erbar & Leins, 1989; Leins & Erbar, 1990).

Gynoecium. In Brunoniaceae and Menyanthaceae, the ovary is superior. The remaining families are characterized by an inferior ovary, though sporadic taxa have ovaries half-inferior (*Diastatea* Scheidw., Lobeliaceae) or superior (*Cyananthus*, Campanulales; *Velleia* Smith, Goodeniaceae). Epigyny in Campanulaceae is exclusively appendicular in origin, i.e., via the adnation of outer floral whorls to the ovary (Carolin, 1959, 1960b; Kaplan, 1967). Nonetheless, the hypanthia of Campanulaceae sens. lat. and Goodeniaceae are not strictly homologous in their formation (Carolin, 1978). In the former, coalescence of the outer whorls preceded their adnation to the ovary, while in the latter, the outer whorls became adnate to the ovary centrifugally.

The ovary is syncarpous. In most families, two or more fertile locules are evident. Bilocular ovaries characterize Cyphiaceae, Goodeniaceae, Lobeliaceae, Pentaphragmataceae, Sphenocleaceae, Stylidiaceae, and *Donatia novae-zelandiae*, while *D. fascicularis* is trilocular. Campanulaceae characteristically have three locules, though some have two (*Wahlenbergia linarioides* (Lam.) A. DC.) or five (*Campanula* L. subsect. *Quinqueloculares* Boiss., *Cyananthus*), and others appear to have more, due to intrusive partitions from the carpellary midribs (*Michauxia* L'Her., *Ostrowskia*). A few Goodeniaceae (*Scaevola porocarya* F. Muell.) have four locules.

Each locule typically contains several to many ovules attached to axile placentae, although this sometimes is reduced to one or two, in which case, placentation may be apical (*Catosperma* Benth., Goodeniaceae; *Siphocodon* Turcz., Campanulaceae).

In Asteraceae, Brunoniaceae, Calyceraceae, and Menyanthaceae, the ovary has one locule. In Menyanthaceae, this locule contains a pair of parietal placentae bearing numerous ovules; this condition is also found in some taxa of otherwise bilocular families (*Downingia yina* Applegate, Lobeliaceae). In the other three families, the single locule contains a solitary ovule, which is apical in Calyceraceae and basal in Asteraceae and Brunoniaceae. Unilocular ovaries with a single basal ovule also characterize certain genera in otherwise multilocular families (*Merciera* A. DC., Campanulaceae; *Unigenes* F. Wimmer, Lobeliaceae; *Verreauxia* Benth., Goodeniaceae).

Only the Donatiaceae are characterized by multiple styles: *Donatia fascicularis* has three and *D. novae-zelandiae*, two. However, in *Calogyne* R. Br. (Goodeniaceae), the style divides into two, three, or four branches, each with its own indusium. In Brunoniaceae, Calyceraceae, a few Campanulaceae (*Cephalostigma* A. DC.), some Goodeniaceae, Pentaphragmataceae, Sphenocleaceae, and Stylidiaceae, the style terminates in a simple unlobed stigma. In most Campanulaceae, the number of stigmas or stigmatic branches equals the number of locules. Asteraceae, most Goodeniaceae, Lobeliaceae, Menyanthaceae, and most Cyphiaceae have a bifid stigma. *Cyphia* features a unique stigmatic cavity that is filled with fluid and communicates with the outer air via a lateral aperture (Thulin, 1978).

At maturity, multiovulate ovaries commonly form a capsule, which may be loculicidal or less often poricidal; that of Sphenocleaceae is circumscissile. In most, the seeds have no obvious adaptations for dispersal, though anemochorous (winged) seeds occur in some taxa (*Cyphia reducta* F. Wimmer; *Calogyne*, Goodeniaceae; *Trematolobelia* A. Zahlbr., Lobeliaceae). Baccate fruits, better adapted to zoochory, characterize Pentaphragmataceae and occur sporadically elsewhere (*Clermontia* Gaudich., Lobeliaceae; *Canarina* L., Campanulaceae; *Scaevola* sect. *Scaevola*, Goodeniaceae). The families with uniovulate ovaries form one-seeded indehiscent fruits: achenes in Brunoniaceae, cypselas in Asteraceae and Calyceraceae. Here, the calyx is often persistent and modified in ways that facilitate anemochory (plumose) or zoochory (barbate).

EMBRYOLOGY

Embryology is here defined broadly, so as to include all aspects of growth and development of the anther and ovule; only features of the mature pollen grain (palynology) are discussed separately. Data for angiosperms have been summarized by Davis (1966) and Palser (1975), and the following data are taken from these reviews, unless otherwise noted.

Anthers. The dicotyledonous type of anther wall development, producing a single middle layer, characterizes Asteraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, Sphenocleaceae (Kausik & Subramanyam, 1946), and Stylidiaceae. The basic type, producing two middle layers, characterizes Pentaphragmataceae. Both patterns have been reported from Menyanthaceae. The endothecium contains fibrous thickenings in all these families as well as in Calyceraceae.

The tapetum functions in the nutrition of developing microsporocytes (Pacini et al., 1985). The glandular or secretory type, in which the tapetal cells remain in their original position but discharge their contents, characterizes Calyceraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, Menyanthaceae, Pentaphragmataceae (Kapil & Vijayaraghavan, 1965), Sphenocleaceae (Kausik & Subramanyam, 1946), Stylidiaceae, and some Asteraceae. The amoeboid or periplasmodial type, in which the protoplasts fuse to form a multinucleated periplasmodium, characterizes most Asteraceae. Tapetal cells are binucleate in Campanulaceae, Lobeliaceae, Pentaphragmataceae (Kapil & Vijayaraghavan, 1965), Sphenocleaceae (Kausik & Subramanyam, 1946), and Stylidiaceae, but multinucleate in Asteraceae, Goodeniaceae, and Menyanthaceae.

Ovules. The anatropous ovules are unitegmic and tenuinucellar, conditions that characterize virtually all Asteridae (Philipson, 1977). Embryo sac formation is monosporic (*Polygonum*-type), though bisporic (*Allium*-type) and various tetrasporic types occur in some Asteraceae. The inner layer of the integument develops as an endothelium (integumentary tapetum) upon coming in contact with the embryo sac. Embryogeny follows the Asterad pattern in Asteraceae and Menyanthaceae, and the Solanad pattern in the others. Endosperm formation characteristically is cellular ab initio, though nuclear endosperm development is found in some Asteraceae. Typically, copious endosperm forms, though it is absent or nearly so from mature seeds of Asteraceae, Brunoniaceae, and Sphenocleaceae. It is oily in most families, but starchy in Pentaphragmataceae and some Campanulaceae.

Terminal endosperm haustoria (i.e., with haustoria at both the chalazal and micropylar ends) characterize Campanulaceae, Lobeliaceae, Sphenocleaceae, and Stylidiaceae. In the first three families, the two ends are equally aggressive; in the last, the micropylar haustorium is more aggressive. In Pentaphragmataceae, a haustorium develops only at the micropylar end, while Asteraceae, Calyceraceae, Goodeniaceae, and Menyanthaceae lack them altogether.

PALYNOLOGY

Data on pollen morphology in angiosperms was summarized by Erdtman (1952). This review is supplemented by data presented in more recent papers (Chapman, 1966; Brewbaker, 1967; Dunbar, 1975a, b, 1978, 1981, 1984; Dunbar & Wallentinus, 1976; Skvarla et al., 1977). Typically, the grains are spheroidal or variously compressed (oblate or prolate); those of Pentaphragmataceae are trilobate.

Apertures. Tricolporate pollen characterizes Asteraceae, Brunoniaceae, Calyceraceae, Cyphiaceae (6-colpate in *Parishella*), Donatiaceae, Goodeniaceae, Lobeliaceae, Menyanthaceae, Pentaphragmataceae, and Sphenocleaceae, though the pores are lacking from some Lobeliaceae, Menyanthaceae, and Pentaphragmataceae (i.e., the grain is tricolpate). Pollen grains of Stylidiaceae are 3–8-colpate. In most Campanulaceae, the grains are 3–4(–5)-porate (6-porate in *Githopsis* Nutt.). A few species of *Campanula* have 8–, 12–, or 14–20-pantoporate pollen, while other genera are characterized by pollen that is 3–6-colporate (*Platycodon* A. DC., *Canarina*) or 6–10-colpate (*Cyananthus, Ostrowskia*).

Surface. There is great variation in the sculpturing and ornamentation of the surface, with various types of ridges, reticulations, granulations, striae, pits, and protrusions noted. One such character is the presence or absence of spinules. These are all but ubiquitous among Campanulaceae with porate grains, but are largely reduced to verrucae in the colpate and colporate genera. Among Cyphiaceae, spinules characterize *Nemacladus* and *Parishella*, but are lacking in *Cyphia* and *Cyphocarpus*. Spinuliferous pollen is widespread in Asteraceae; notable exceptions are the relatively smooth grains of many Mutisieae. Grains of Brunoniaceae, Goodeniaceae, and Stylidiaceae are also spinuliferous, while spinules are lacking in Calyceraceae, Donatiaceae, Lobeliaceae, Menyanthaceae, Pentaphragmataceae, and Sphenocleaceae.

Nuclei. Pollen grains when shed may contain either two or three nuclei. The latter condition is clearly derived from the former, and in no instance is a reversal apparent (Brewbaker, 1967). Binucleate pollen characterizes Brunoniaceae, Calyceraceae, Goodeniaceae, and Pentaphragmataceae, while the pollen of Asteraceae, Sphenocleaceae, and Menyanthaceae is exclusively trinucleate. Taxa of Campanulaceae, Lobeliaceae, and Stylidiaceae may be binucleate or trinucleate. *Lobelia* is one of only ten angiosperm genera with both binucleate and trinucleate species, and in no case does a single species produce both types of pollen (Brewbaker, 1967).

Pollinators. Pollen grains are typically shed singly, though permanent tetrads occur in a few genera (*Leschenaultia*, Goodeniaceae; *Namacodon* Thulin, Campanulaceae). Dispersal typically is zoophilous (Wagenitz, 1977). Generally speaking, taxa with actinomorphic flowers and pseudanthia are visited by a broad suite of generalized insects, including various bees, flies, wasps, butterflies, and settling moths. Taxa with zygomorphic flowers have a narrower range of more specialized, often vertebrate visitors. In Lobeliaceae, for example, ornithophily is well developed (Lammers & Freeman, 1986), involving hummingbirds and passerines, while chiropterophily reportedly occurs in *Burmeistera* (Vogel, 1969); a few genera with salverform corollas (*Brighamia*, *Hippobroma* G. Don) are sphingophilous (Lammers & Freeman, 1986).

CYTOLOGY

The chromosome numbers discussed below, unless otherwise indicated, were taken from the standard indices (Darlington & Wylie, 1955; Cave, 1958a, b, 1959a, b, 1960, 1961, 1962, 1963, 1964, 1965; Ornduff, 1967, 1968; Moore, 1973, 1974, 1977; Goldblatt, 1981, 1984, 1985, 1988; Goldblatt & Johnson, 1990). For convenience, all reports are presented as gametic (haploid or n) numbers. The ancestral base number (x), from which other numbers in the family have been derived via euploidy or aneuploidy, is of primary interest. In some cases, this is relatively easy to determine, while in others it remains controversial despite numerous counts. No chromosome numbers are known for any species of Pentaphragmataceae.

Asteraceae are well known cytologically; Solbrig (1977) summarized data on chromosome numbers from nearly 8,000 species. Numbers range from $n = 2$ to $n = 120$, though most lie in the range of $n = 4$ to $n = 18$, and high polyploids are very rare. The most common number is $n = 9$, found in more than 20% of the species. Solbrig cautiously suggested that this could be the ancestral base number for the family, a view accepted by Raven (1975). Although the Barnadesiinae are believed to be the most primitive extant Compositae (Jansen & Palmer, 1988; Palmer et al., 1988), this information is not particularly helpful in suggesting a base number for the family. Chromosome numbers known from these genera are $n = 8$, 12, 24, 25, 27, and 54, from which one could argue for $x = 8$ or 9 (or even 4, 5, or 6).

Campanulaceae also are well known, with more than 1,150 counts published. Numbers reported are $n = 6$–21, 23–30, 32, 34–36, 40, 45, 48, 51, and 52. By far, the commonest number is $n = 17$, with more than 480 (42%) of the published counts. Another 150 (13%) are presumably tetraploid ($n = 34$) and hexaploid ($n = 51$) derivatives of this number. However, a gametic chromosome number as large as 17 probably is derived from some smaller number via aneuploidy following polyploidization or via allopolyploidy.

Bocher (1964) and Contandriopoulos (1984) considered $x = 8$ to be the most likely base number for Campanulaceae. Raven (1975), however, suggested that Campanulaceae, like their apparent sister group the Lobeliaceae, have $x = 7$. Although species with $n = 7$ are rare among Campanulaceae (only 12 such counts have been reported), that number is found in both species of *Cyananthus* that have been examined (Kumar & Chauhan, 1975; Hong & Ma, 1991). *Cyananthus* is widely regarded as the most primitive extant genus in the family on morphological grounds (Hutchinson, 1969; Carolin, 1978; Takhtajan, 1980; Dunbar, 1984; Hong & Ma, 1991), and its possession of $n = 7$ supports the hypothesis of $x = 7$ for the Campanulaceae. Hong & Ma (1991) hypothesized that taxa with $n = 8$ and $n = 9$ are the result of ascending aneuploidy from $x = 7$, and that the numerous taxa with $n = 17$ are allopolyploids, derived from hybridization between taxa with these two numbers.

The Lobeliaceae clearly have $x = 7$ (Foster, 1972; Raven, 1975; Thulin, 1983; Lammers, 1987, 1988). More than 135 species have been counted; almost 75% have $n = 7$, 14, 21, or 35. The exceptions are largely members of genera that are morphologically quite specialized: *Downingia* Torrey and its allies *Porterella* Torrey and *Howellia* A. Gray, with an aneuploid series derived from $x = 11$ or 12; and *Lysipomia* Kunth, with $n = 10$ (Casas, 1981).

For Stylidiaceae, counts of $n = 5$–16, 18, 26, 28, and 30 have been published. Unfortunately, nearly all are from the derived genus *Stylidium*; no counts are available for the less specialized genera *Phyllachne* and *Forstera*. Despite the presence of lower numbers, James (1979) believed 15 to be the base number of the family. As with Campanulaceae, one suspects that so high a base number may be derived via aneuploidy from some polyploid or via allopolyploidy. *Donatia fascicularis*, widely regarded as an even less specialized relative or member of Stylidiaceae, has $n = 24$ (Moore, 1983). From this, one might speculate $x = 6$ or 8 for both families.

The Goodeniaceae have $n = 7$, 8, 9, and multiples thereof ($n = 16$, 24, 32; 18, 27, 36, 45). Peacock (1963) considered $n = 7$ to be derived via descending aneuploidy, because it occurred only in three species of *Goodenia* Smith, a genus otherwise based on eight. He was unable to decide whether $x = 8$ or $x = 9$ was the ancestral base number. On the basis of correlations with morphology, the former, which also occurs in twice as many genera, would appear to be more likely (Carolin, 1978). Brunoniaceae clearly have $x = 9$, with counts of $n = 9$, 18, and 36 reported.

Menyanthaceae clearly have $x = 9$. Over 90% of the reported counts are $n = 9$, 18, 27, or 54. The few reports of $n = 8$, 20, and 28 are interpreted as aneuploid derivatives of these numbers.

Although few species of Cyphiaceae have been examined, they appear to have $x = 9$. This is based on counts of $n = 9$ from two species each of *Cyphia* and *Nemacladus.*

Few Calyceraceae have been examined, and the base number is uncertain. Counts reported are $n = 8$, 15, 18, and 21. From this, one could argue for $x = 7$, 8, or 9 (Stebbins, 1977).

The base number of Sphenocleaceae is uncertain, because the five published counts for *Sphenoclea zeylanica* Gaertner each report a different number: $n = 12$ (Lewis et al., 1962), 16 (Bir & Sidhu, 1974), 20 (Larsen, 1966), 21 (Bhattacharyya, 1972), and 24 (Sidhu & Lata, 1984). While it is not unlikely that an invasive pantropical weed would exhibit intraspecific variation in ploidy level, alternative hypotheses must be considered. Misidentification of the material is scarcely credible for so distinctive a species. Miscounts also seem unlikely, at least in the reports by Lewis and Bhattacharyya, because of the details and figures presented. However, the number reported by Larsen could be erroneous, as he reported difficulties in counting discrete chromosomes due to their "sticky" nature. Even discounting this report, the ancestral base number could be $x = 6$, 7, or 8, none of which would be inconsistent with base numbers in related families.

ULTRASTRUCTURE

Protein intranuclear inclusions with a fibrillar structure are unique to Campanulaceae (Taler & Gailhoffer-Dengg, 1972; Bigazzi, 1986), where they are found in all 27 species of *Campanula, Edraianthus* A. DC., *Jasione, Phyteuma,* and *Trachelium* L. that have been examined. However, they are absent from the 11 species of *Asyneuma* Griseb. & Schenck., *Canarina, Legousia* Durand, *Petromarula* Vent., *Platycodon,* and *Wahlenbergia* Schrader ex Roth that have been examined, as well as from the seven species of Lobeliaceae examined in the genera *Downingia, Isotoma* (R. Br.) Lindley, *Lobelia, Pratia* Gaudich., and *Solenopsis* C. Presl.

Sieve-element plastids have been examined in the phloem of over 300 species of Asteridae, representing 42 families and 280 genera (Behnke, 1981; Behnke & Barthlott, 1983). All, including representatives of Asteraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, and Stylidiaceae, lack proteinaceous inclusions (i.e., they have S-type plastids).

CHEMISTRY

Various types of primary and secondary metabolites have played a significant role in the classification of Campanulales (Gershenzon & Mabry, 1983; Harborne & Turner, 1984). Unfortunately, virtually nothing is known of the chemistry of Brunoniaceae, Cyphiaceae, Donatiaceae, Pentaphragmataceae, and Sphenocleaceae (Gibbs, 1974; Wagenitz, 1977).

Oligosaccharides. Inulin, straight chain polymers of one to 40 fructose residues linked *alpha*(1–2) to a terminal sucrose molecule, replaces starch as a storage carbohydrate in some dicotyledons. Pollard & Amuti (1981) detected inulin in all examined samples (representing 96 species in 48 genera) of Asteraceae, Brunoniaceae, Calyceraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, Menyanthaceae, and Stylidiaceae; it has been reported also from Cyphiaceae (Thulin, 1978) and Donatiaceae (Gibbs, 1974).

Iridoids. Iridoids are monoterpenoid cyclopentanoid lactones produced by the mevalonate pathway. They are found only in dicotyledons and apparently serve to deter herbivores and pathogens (Harborne & Turner, 1984). Analyses of numerous species of Asteraceae, Campanulaceae, and Lobeliaceae have yielded negative results (Jensen et al., 1975; Hegnauer, 1977; Kaplan & Gottlieb, 1982).

All species of Stylidiaceae examined produce carbocyclic iridoids, specifically 10-hydroxylated compounds similar to monotropein (Jensen et al., 1975; Kaplan & Gottlieb, 1982). All species of Calyceraceae, Goodeniaceae, and Menyanthaceae examined produce seco-loganin, a simple seco-iridoid (Jensen et al., 1975; Kaplan & Gottlieb, 1982). Some Menyanthaceae also produce sweroside, a gentiopicroside seco-iridoid. Furthermore, loganin, an iridoid precursor of both carbocyclic and seco-iridoids, occurs in some Menyanthaceae, as well as in many other families.

Sesquiterpene lactones. These bitter substances are 15-carbon terpenoids derived from the mevalonate pathway, which may function as feeding deterrents (Hegnauer, 1977; Harborne & Turner, 1984). Though diverse, their distribution among angiosperms is extremely restricted (Herz, 1977; Gershenzon & Mabry, 1983). Of the 1,400 compounds known, approximately 90% have been isolated from Asteraceae, where they are either deposited in latex (Lactuceae) or associated with various glands (nonlactiferous tribes).

Polyacetylenes. These highly unsaturated hydrocarbons, containing 8–21 carbon atoms, are synthesized from oleic acid. Their function is uncertain, but they may serve to deter pathogens and herbivores (Harborne & Turner, 1984). They are best known as Asteraceae, where almost 700 compounds with 8–18 carbon atoms have been isolated; over 95% of the known polyacetylene-producing species are members of this family (Bohlmann et al., 1973; Sørenson, 1977; Ferreira & Gottlieb, 1982; Gershenzon & Mabry, 1983). Diverse species of Campanulaceae have yielded various 14-carbon polyacetylenes. Similar compounds have been reported from two species of Lobeliaceae, and a 13-carbon polyacetylene has been detected in a species of Goodeniaceae.

Alkaloids. Alkaloids are diverse compounds containing a basic group and one or more nitrogen-containing heterocyclic rings, synthesized primarily from protein amino acids (Hegnauer, 1966a; Harborne & Turner, 1984). Many alkaloids have significant physiological effects on higher vertebrates, and presumably function in deterrence of herbivores and pathogens. Among angiosperms, alkaloids are found in 15–20% of the species examined.

Pyridine alkaloids appear to be ubiquitous among Lobeliaceae, where they commonly accumulate in the latex (Willaman & Schubert, 1961; Raffauf, 1970; Vagujfalvi, 1971; Gibbs, 1974; Gomes & Gottlieb, 1980); many compounds (e.g., lobeline, lobinaline, siphocampiline) have been isolated from a diverse array of taxa. Various Asteraceae, primarily species of *Senecio* L., produce not only pyridine alkaloids, but pyrrolizidine, quinoline, and diterpenoid types as well (Willaman & Schubert, 1961; Gibbs, 1974). Alkaloids of an unspecified nature have also been detected in eight species of Goodeniaceae (Willaman & Schubert, 1961). Despite numerous assays, alkaloids are all but absent from Campanulaceae and Stylidiaceae, having been found in just a few species (Willaman & Schubert, 1961; Hegnauer, 1973), nor have any been detected in Cyphiaceae, Donatiaceae, or Pentaphragmataceae (Gibbs, 1974).

Phenolics. Various phenolic constituents appear to be of some taxonomic utility among Campanulales (Bate-Smith, 1962; Gornall et al., 1979). Most notably, caffeic acid occurs in Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, Menyanthaceae, and Stylidiaceae, primarily as esters with quinic acid, notably chlorogenic acid. However, it is wholly lacking from Lobeliaceae, where it seems to be replaced by chelidonic acid (Hegnauer, 1966b; Mølgaard, 1985).

MOLECULAR BIOLOGY

Recently, analyses of chloroplast DNA restriction sites and *rbc*L sequences have contributed an entirely new set of data to studies of relationships among Campanulales. These studies have not yet incorporated representatives of all 12 candidate taxa, and as a result, the picture that emerges is only partially resolved.

The most important result is the discovery that all but a few Asteraceae share a unique inversion that is 22 kb in length (Jansen & Palmer, 1988; Palmer et al., 1988). The exceptions are members of the Barnadesiinae, in which the configuration of that region is colinear with that found in other vascular plants. This fact offers persuasive evidence that the Barnadesiinae are the most primitive Asteraceae extant.

Several attempts are underway to understand better phylogenetic relationships among Asteridae, using these techniques (Downie & Palmer, 1992; Olmstead & Palmer, 1992). Of the candidate taxa, only representatives of Asteraceae, Calyceraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, and Menyanthaceae have been examined thus far. Extensive rearrangements of the chloroplast genome distinguish Campanulaceae and, to a lesser extent, Lobeliaceae; such rearrangements have not been noted in the other taxa (S. R. Downey, pers. comm.).

Cladistic analyses of these molecular data indicate the following phylogenetic relationships. Calyceraceae and Goodeniaceae form a clade that is the sister group of Asteraceae. Menyanthaceae form the sister group of these three families. The several representatives of Gentianales, to which Menyanthaceae supposedly belong, are quite distant, and the representatives of Solanales are even more so. This clade, comprising Asteraceae, Calyceraceae, Goodeniaceae, and Menyanthaceae, will be referred to as the "asterad" clade in the subsequent discussion. Campanulaceae and Lobeliaceae (the "campanulads") form the sister clade of the asterads. This asterad–campanulad major clade incorporates all candidate taxa that have been examined to date. Adoxaceae, Caprifoliaceae, Dipsacaceae, Valerianaceae, and Viburnaceae form a clade (the "dipsacads") that is the sister group to Apiaceae and Araliaceae (the "apiads"). This apiad–dipsacad major clade is then the sister group to the asterad–campanulad major clade.

PALEONTOLOGY

Asteraceae are represented in the macrofossil record primarily by compressions assigned to the form-genera *Achaenites* Braun and *Cypselites* Heer (Turner, 1977). A compression supposed to represent a capitulum (*Viguiera cronquistii* Becker) may actually be an immature gymnosperm strobilus (Crepet & Stuessy, 1978). All are no older than Oligocene. Pollen unequivocally referable to Asteraceae also makes its first appearance in Oligocene rocks (Muller, 1981). The only other candidate taxon represented in the fossil record is Goodeniaceae. *Poluspissusites digitatus* Salard-Cheboldaeff from the Oligocene of Cameroon is very similar to pollen of *Scaevola sericea* (Muller, 1981). Thus, there is no evidence at present for the existence of any Campanulales prior to the Oligocene, approximately 40 million years ago.

CIRCUMSCRIPTION

In this section, two aspects of circumscription will be addressed. First, what is the best circumscription of the order, i.e., which of the 12 candidate taxa should be included in Campanulales and which should be removed to other orders? Second, what is the best circumscription and rank for each of these taxa, e.g., should Campanulaceae include Lobeliaceae as a subfamily, or should the latter be recognized as a distinct family? The goal throughout is to delimit natural (i.e., monophyletic) groups. Ideally, these groups should be relatively homogeneous in their various features and sharply distinct from other such groups, due to pronounced gaps in the spectrum of variation and the possession of one or more uniquely derived character states (i.e., synapomorphies). This ideal may not always be attainable, given the present state of our knowledge.

The discussion will proceed in a stepwise manner. Rules of nomenclature dictate that Campanulaceae remain in the order as long as it is recognized, no matter what else is removed. For this reason, the first step is to examine relationships within the core group of families. Next, the relationships of each of the five satellites will be examined.

THE CORE GROUP

The traditional broad circumscription of Campanulaceae (Schönland, 1889; Takhtajan, 1980) results in a family that is heterogeneous and possibly not monophyletic. A more homogeneous group, with a greater likelihood of being monophyletic, results from a narrower circumscription (Kovanda, 1978; Shetler & Morin, 1986), in which the family includes only those genera encompassed by the following description.

Perennial herbs (less often annual or woody), with articulated lactifers, producing 14-carbon polyacetylenes and caffeic acid but no iridoids and few if any alkaloids, storing carbohydrate as inulin; sieve-elements with S-type plastids. Leaves exstipulate, commonly alternate and simple; stomates anomocytic. Inflorescences variously monotelic or polytelic, predominantly racemose, or flowers solitary and axillary. Flowers tetracyclic, commonly perfect, with a specialized method of proterandrous secondary pollen presentation. Calyx synsepalous, commonly pentamerous, the odd lobe dorsal. Corolla sympetalous, commonly pentamerous, actinomorphic, the lobes valvate. Stamens equaling the number of corolla lobes, antisepalous; filaments distinct, inserted atop the ovary (on the rim of the free hypanthium in *Cyananthus*); anthers tetrasporangiate, dithecal, basifixed, connivent, dehiscent introrsely via longitudinal slits, the wall development dicotyledonous; endothecium with fibrous thickenings; tapetum glandular, the cells binucleate; pollen spheroidal, oblate, or prolate, commonly triaperturate and spinuliferous, binucleate or trinucleate when shed. Ovary syncarpous, inferior and fully adnate to hypanthium (superior and free in *Cyananthus*), commonly 3–5-loculed; placentation commonly axile; ovules anatropous, unitegmic, tenuinucellar, commonly numerous; embryo sac *Polygonum*-type, with an integumentary tapetum; embryogeny Solanad; embryo dicotyledonous, straight; endosperm copious, commonly oily, with equally aggressive terminal haustoria, its development ab initio cellular; style 1, with a ring of invaginating hairs near the apex; stigmatic lobes typically equaling the locules in number; fruit a loculicidal or poricidal capsule, or a berry. Of these features, the unique invaginating stylar hairs are the only evident synapomorphy for the family.

Approximately 46 genera, comprising some 950 species, match this description and are here included in Campanulaceae. Though nearly cosmopolitan in its distribution, the family is best developed in the temperate zones of the Old World:

over 60% of the species are native to Eurasia, and another 30% are African.

Lobeliaceae. This taxon, whatever its rank, is typically circumscribed (Wimmer, 1943, 1953; Wagenitz, 1964; Takhtajan, 1987) to include genera identical to Campanulaceae except for the following characters: plants producing chelidonic acid and pyridine alkaloids, but no caffeic acid; flowers resupinate, but the odd sepal ventral prior to resupination; corolla zygomorphic; filaments connate for at least part of their length; anthers connate; pollen never spinuliferous; ovary 2-loculed; stylar hairs noninvaginating. The resupinate flowers and connate anthers are evident synapomorphies uniting these genera.

This circumscription would encompass more than 1,200 species in 30 genera. The group is nearly cosmopolitan in its distribution but is most diverse in the tropics and subtropics (commonly at higher elevations): 55% of the species occur in Latin America and the Caribbean, 20% in Africa, and 10% in Polynesia (primarily the Hawaiian Islands).

A few authors (McVaugh, 1943; Hegnauer, 1966b; Hutchinson, 1973; Thulin, 1978; Thorne, 1983) have included one or more of the genera segregated here as Cyphiaceae in the Lobeliaceae at various ranks. These genera do share some features that differentiate Lobeliaceae from Campanulaceae: odd sepal ventral, corolla zygomorphic, ovary 2-loculed; some of the genera also have filaments connate for at least part of their length and most have a bilobed stigma. However, including these genera in Lobeliaceae disrupts the latter's homogeneity by introducing several novel character states: flowers nonresupinate, lacking a specialized pollen presentation mechanism; stamens epipetalous; filaments and anthers distinct; style topped by a laterally uniaperturate fluid-filled stigmatic cavity. These novel states rob the family of its defining synapomorphies. Furthermore, chromosome numbers in Lobeliaceae are clearly based on seven, while those of Cyphiaceae apparently are based on nine. For these reasons, the five genera of Cyphiaceae are excluded from this group.

The question of appropriate rank remains. No author has doubted that the Lobeliaceae are closely related to Campanulaceae. Among the numerous characters shared by both taxa, the presence of articulated lactifers, specialized proterandrous pollen presentation, equally aggressive terminal endosperm haustoria, and similar 14-carbon polyacetylenes are perhaps most indicative of a close relationship. Such a relationship is also supported by the molecular data. In all analyses performed thus far, representatives of the Lobeliaceae and Campanulaceae consistently form a clade distinct from other clades, undoubtedly due to the extensive rearrangements found in the chloroplast genomes of both families.

However, Lobeliaceae also differs from Campanulaceae in a number of significant characters, listed above. These differences are similar in degree and kind to the differences that distinguish many other dicot families. Furthermore, the chloroplast genome of Lobeliaceae is not as extensively rearranged as that of Campanulaceae. For these reasons, it is appropriate to recognize Lobeliaceae as a family distinct from Campanulaceae, following Kovanda (1978), Takhtajan (1987), and others.

Cyphiaceae. Whatever its rank, this taxon in its broadest circumscription (Schönland, 1889; Wagenitz, 1964; Wimmer, 1968; Takhtajan, 1980) comprises five genera. All are poorly understood and little studied. *Cyphia* is the largest, with approximately 60 species in southern and tropical Africa. *Cyphocarpus* comprises three species endemic to northern Chile. *Nemacladus* includes 13 species, while both *Parishella* and *Pseudonemacladus* are monospecific. These last three genera, all endemic to western North America, are very closely related and could be treated as a single genus (Munz, 1924).

Although there is no question that the Cyphiaceae belong to Campanulales, there are questions regarding their precise relationships within the order. Most authors have considered them a link connecting plesiomorphic Campanulaceae to apomorphic Lobeliaceae (Cronquist, 1981). Indeed, they resemble both families overall, and the exceptions appear intermediate. With Lobeliaceae, they share a ventral odd sepal, zygomorphic corolla, connate filaments (some genera), bilocular ovary, and bilobed stigma (some genera); the unique sepal position may well be a synapomorphy uniting the two. Like Campanulaceae, they lack alkaloids and floral resupination, and the anthers are not connate. In common with both families, they produce latex; articulated lactifers probably are a synapomorphy uniting all three. However, there are additional characters not found in either family: the unique stigmatic cavity of *Cyphia* and the epipetalous stamens of *Cyphocarpus*. Furthermore, all five genera appear to lack specialized mechanisms for proterandrous pollen presentation.

There are also similarities between some of these genera and Goodeniaceae. The tricolporate pollen of Goodeniaceae, with its spinules lacking roots and its perforated tectum (Dunbar, 1975b), resembles that of *Nemacladus*. *Cyphia*, *Nemacladus*, and Goodeniaceae have chromosome numbers based on nine. Goodeniaceae differ in the absence of latex, the dorsal origin of the odd sepal, and the presence of a stylar indusium; the latter, however, could be homologous to the stigmatic cavity of *Cyphia*.

Furthermore, there are fundamental questions regarding whether these five genera constitute a natural group (Bentham, 1875; Thulin, 1978; Dunbar, 1975b, 1984; Dunbar & Wallentinus, 1976). For example, Hutchinson (1973) included *Cyphocarpus* in Campanulaceae but placed the remaining four genera in Lobeliaceae. Similarly, Thorne (1983) segregated *Cyphia* as the sole member of Cyphioideae, but placed the others in Lobelioideae. Finally, Takhtajan (1987) divided the genera among three families: Cyphiaceae (*Cyphia*), Cyphocarpaceae (*Cyphocarpus*), and Nemacladaceae (the remaining three genera). Cyphiaceae and Nemacladaceae were positioned between Campanulaceae and Lobeliaceae, but Cyphocarpaceae followed Lobeliaceae.

Implicit in these classifications is the idea that one or more of the genera may not share an origin with the others. These five genera are indeed heterogeneous in various morphological features, more so than might be expected in so small a group. The corolla of *Cyphocarpus* has a four-lobed ventral lip with a gibbose palate and a one-lobed dorsal lip; the others have two ventral and three dorsal lobes and lack any sort of palate. The stamens are epipetalous in *Cyphocarpus*, but inserted atop the ovary in the others. The filaments are distinct in *Cyphocarpus* and some species of *Cyphia*, but connate in the remainder of the group. In *Cyphia*, the style is topped by a unique, laterally uniaperturate fluid-filled stigmatic cavity, while the others have a bilobed stigma.

These genera are likewise heterogeneous palynologically (Dunbar, 1975b, 1984; Dunbar & Wallentinus, 1976). *Parishella* has 6-colpate pollen, while the others are 3-colporate. In *Nemacladus*, the colpi are oriented obliquely at varying angles to the equatorial plane, while in others they are perpendicular to it. In both *Parishella* and *Nemacladus*, the sexine is covered with spinules 1 μm tall, lacking roots; the intervening tectum is pitted. No other genus has spinules or tectal pits. Pollen of *Cyphia* is nano-granulate, almost smooth, while that of *Cyphocarpus* is reticulate, with the muri in high relief and with protrusions in the lumina.

On the basis of morphology, palynology, and geography, the five genera fall into three apparently natural groups: African *Cyphia*, Chilean *Cyphocarpus*, and the three genera of western North America. Whether these three cyphioid groups can be tied together as a single taxon is an open question. As shown above, there are no obvious synapomorphies uniting them. Their characters are either shared with other families, or restricted to single genera. It is possible that all three groups should be recognized at familial rank, as Takhtajan (1987) has done.

Several questions regarding the three cyphioid groups must be answered before we can reach a conclusion on their relationships to other families and to each other. First, do they produce iridoids, particularly simple seco-iridoids such as seco-loganin? If so, it would support a relationship to Goodeniaceae. Second, are the tapetal cells binucleate or multinucleate? The former would favor Campanulaceae and Lobeliaceae, the latter Goodeniaceae. Third, do terminal haustoria form in the endosperm? Such structures would suggest a relationship to Campanulaceae and Lobeliaceae. Fourth, is there structural or developmental homology between the indusium of Goodeniaceae and the stigmatic cavity of *Cyphia*? Fifth, are fibrillar protein inclusions found within cell nuclei? Their presence could indicate a close relationship with certain Campanulaceae. If different genera were to yield different answers to any of these questions, this would be additional evidence that the five genera do not form a monophyletic group. Inclusion of all five genera in a phylogeny derived from molecular data could provide good evidence of their true affinities.

Based on our present knowledge, none of the three cyphioid groups can be assigned to Campanulaceae or Lobeliaceae without disrupting the naturalness and homogeneity of those families; none share the unique stylar hairs of Campanulaceae or the resupinate flowers and connate anthers of Lobeliaceae. I am unwilling to follow Takhtajan (1987) in elevating all three to familial rank, due to the conspicuous gaps in our knowledge of their embryology, chemistry, and molecular biology, and to their general phenetic similarity. For these reasons, I recommend that all five genera be recognized provisionally as members of a single, possibly unnatural family Cyphiaceae, as Kovanda (1978) has done. A final disposition can be proposed once the studies outlined above have been completed.

Sphenocleaceae. This taxon includes only *Sphenoclea* Gaertner, a genus of two species: pantropical *S. zeylanica* Gaertner and *S. pongatium* DC. of western Africa. These species differ from the description of Campanulaceae given above in the following characters: annual herbs with abundant aerenchyma but no network of articulated lactifers; stomates tetracytic; inflorescence a dense terminal spike; flowers lacking a specialized method of pollen presentation; corolla lobes imbricate; filaments inserted on corolla tube; anthers distinct; pollen subprolate, never spinuliferous, trinucleate when shed; ovary 2-loculed; seeds exalbuminous; style glabrous; stigma unlobed; capsule circumscissile.

A close relationship between *Sphenoclea* and Campanulaceae has been widely recognized (Subramanyam, 1950; Bhattacharyya, 1972; Hutchinson, 1973; Monod, 1980; Takhtajan, 1980; Cronquist, 1981; Thorne, 1983). Only Airy Shaw (1948, 1973) seriously questioned it, calling such a relationship "illusory." On the basis of similarities in habit and unspecified anatomical characters, he suggested a close relationship to Phytolaccaceae (Caryophyliidae). However, the Phytolaccaceae and their allies differ from *Sphenoclea* in their anomalous secondary growth, sieve-element plastids with unique (P-III) protein inclusions, storage of carbohydrate as starch, betalain (vs. anthocyanin) pigments, bitegmic crassinucellar campylotropous ovules, lack of an integumentary tapetum, Caryophyllad or Onagrad embryogeny, curved embryo, and nuclear endosperm development (Rodman et al., 1984), as well as in the numerous floral features (e.g., distinct petals, superior ovary) noted previously (Hutchinson, 1969; Monod, 1980; Rosatti, 1986). Certainly the gap evident in this comparison is much wider than the one separating *Sphenoclea* from Campanulaceae.

Some authors (Schönland, 1889; Hutchinson, 1973; Takhtajan, 1980; Dahlgren, 1983; Thorne, 1983) have included *Sphenoclea* within Campanulaceae. Doing so, however, disrupts the homogeneity of that family. *Sphenoclea* lacks the unique stylar hairs that help define Campanulaceae, as well as the articulated lactifers that unite Campanulaceae, Cyphiaceae, and Lobeliaceae into a clade. For this reason, it seems best to assign *Sphenoclea* to its own family Sphenocleaceae, following Wagenitz (1964), Cronquist (1981), and others.

Pentaphragmataceae. This taxon includes only *Pentaphragma* Wallich ex G. Don, a genus of approximately 30 species endemic to southeastern Asia, the Malay Archipelago (excluding Java and Nusa Tenggara), and New Guinea. As with *Sphenoclea*, most authors (Schönland, 1889; Kapil & Vijayaraghavan, 1965; Hutchinson, 1973; Dunbar, 1978; Takhtajan 1980) have recognized a close relationship between *Pentaphragma* and Campanulaceae. The following differences distinguish the former: stems never woody, often fleshy or succulent, without lactifers; leaves strongly asymmetric at base; inflorescence an axillary sympodial helicoid cyme; flowers lacking any specialized mechanism for proterandrous secondary pollen presentation; corolla polypetalous in some species; filaments inserted on corolla tube (atop ovary in polypetalous species); anthers distinct, the wall development basic; pollen trilobate, never spinuliferous, binucleate when shed; ovary adnate to the hypanthium only via 5 longitudinal septa, 2-loculed; endosperm with a micropylar haustorium only; style glabrous; stigma unlobed; fruit a berry. The asymmetric leaves, distinctive inflorescence, trilobate pollen, and unique hypanthium may serve as defining synapomorphies.

Only Airy Shaw (1942, 1954, 1973) questioned the presumed relationship with Campanulaceae, suggesting affinities with Begoniaceae (Dilleniidae). He cited the asymmetrical leaf base and unspecified anatomical characters as supporting his suggestion. However, such a relationship does not seem likely, as Begoniaceae differ from *Pentaphragma* in their bitegmic crassinucellar ovules, Onagrad embryogeny, and nuclear endosperm formation, as well as in numerous floral features noted previously (Kapil & Vijayaraghavan, 1965). Again, the gap separating *Pentaphragma* from Begoniaceae is much wider than the one that separates it from Campanulaceae.

Some authors (Schönland, 1889; Hutchinson, 1973; Takhtajan, 1980) have included *Pentaphragma* within Campanulaceae. As in the previous taxon, this disrupts the homogeneity of that family by introducing a significant number of new character states. *Pentaphragma* likewise lacks the distinctive invaginating stylar hairs of Campanulaceae, and the articulated lactifers that serve as a synapomorphy for the clade comprising Campanulaceae, Cyphiaceae, and Lobeliaceae. Differences in details of the pollen also support exclusion of *Pentaphragma* from Campanulaceae (Dunbar, 1978). Although there are a few similarities to *Sphenoclea*, the more numerous differences and lack of any synapomorphies preclude assigning these two genera to one family. For these reasons, it seems best to assign *Pentaphragma* to its own family Pentaphragmataceae, following Wagenitz (1964), Cronquist (1981), and others.

BRUNONIACEAE AND GOODENIACEAE

The Goodeniaceae, excluding *Brunonia* Smith (Krause, 1912a, b; Wagenitz, 1964; Cronquist, 1981), comprise approximately 325 species in 16 genera. Over 95% of the species are endemic to Australia and Tasmania. Two species are widely dispersed on tropical shores of the Atlantic and Indian oceans, while the remainder extend north and east in the Pacific as far as China, the Philippines, the Hawaiian Islands, New Zealand, and Chile.

Goodeniaceae have been dissociated from Campanulales only by Dahlgren (1975a, 1977, 1980, 1983), primarily on chemical grounds. Dahlgren accepted the hypothesis that the ability to synthesize iridoids is a synapomorphy uniting many sympetalous dicots into a single clade, and that taxa unable to synthesize iridoids cannot be accommodated within this clade (Hegnauer, 1964; Bate-Smith & Swain, 1966; Frohne & Jensen, 1973; Jensen et al., 1975; Kaplan & Gottlieb, 1982; Gershenzon & Mabry, 1983). However, the ability to synthesize iridoids could have arisen more than once among Asteridae. Alternatively, their absence from certain taxa could be explained as a loss of the necessary biosynthetic pathways; a single point mutation affecting a critical enzyme could easily shut down iridoid production (Jensen et al., 1975; Cronquist, 1977; Gershenzon & Mabry, 1983).

Goodeniaceae differ from the core group of Campanulales in the following characters only: plants producing iridoids, tapetal cells multinucleate, endosperm lacking haustoria, and style with a cuplike indusium below the unlobed or bilobed stigma. The indusium is unique and serves as a synapomorphy for these genera. Furthermore, although polyacetylenes have been isolated from both, those in Campanulaceae and Lobeliaceae have 14 carbon atoms, while those of Goodeniaceae have 13. Overall, this gap does not seem sufficient to justify removal of the Goodeniaceae from the order. Furthermore, phylogenies reconstructed from molecular data consistently place Goodeniaceae in the sister group of the clade comprising Campanulaceae and Lobeliaceae. For these reasons, the Goodeniaceae are retained within Campanulales.

There remains the question of the affinities of *Brunonia*, a genus that has been variously included in or excluded from Goodeniaceae. It comprises a single species, *B. australis* Smith of Australia and Tasmania, that is distinguished by its involucrate capitulate inflorescence, actinomorphic corolla, connate anthers, superior ovary with a single ovule attached to the base of the single locule, and unlobed stigma. However, virtually all these features occur in various genera of Goodeniaceae, e.g., superior ovary in *Velleia*, connate anthers in *Dampiera*, solitary basal ovule in *Verreauxia*. The only thing unique about *Brunonia* is the co-occurrence of these traits in one genus.

Clearly, the phenetic gap separating *Brunonia* from Goodeniaceae is much smaller than those separating Campanulaceae from Lobeliaceae, Pentaphragmataceae, or Sphenocleaceae. In fact, Thorne (1976) commented that *Leschenaultia*, a genus unequivocally assigned to Goodeniaceae, is much more distinct than *Brunonia*. Furthermore, *Brunonia* possesses the unique stylar indusium that defines Goodeniaceae, but lacks clear synapomorphies of its own. For these reasons, *Brunonia* is here retained within Goodeniaceae.

This conclusion may be tested by addressing several questions regarding the chemistry and embryology of *Brunonia*. First, does *Brunonia* produce iridoids (particularly simple seco-iridoids such as seco-loganin) and 13-carbon polyacetylenes? Second, is the tapetum glandular with multinucleate cells? Third, are the ovules anatropous, unitegmic, and tenuinucellar, with a *Polygonum*-type embryo sac and Solanad embryogeny? Fourth, is endosperm formation ab initio cellular, and are terminal haustoria lacking? Affirmative answers to any of these questions would support the proposed relationship with Goodeniaceae. Incorporating *Brunonia* in a phylogeny generated from molecular data should provide definitive evidence.

CALYCERACEAE

This distinctive family includes approximately 60 species in six genera endemic to temperate South America. The group has been little studied, and there are conspicuous gaps in our knowledge of its chemistry and embryology.

Although the Calyceraceae were assigned to Campanulales in traditional Englerian classifications (Höck, 1889; Wagenitz, 1964), most recent authors (Thorne, 1976; Dahlgren, 1980; Cronquist, 1981) have placed them in or near Dipsacales. However, that order differs in its storage of carbohydrate as starch, and in possessing glandular hairs, opposite leaves, centrifugal inflorescences, flowers with an epicalyx, imbricate corolla lobes, distinct stamens, amoeboid tapetum, trinucleate pollen, and Asterad embryogeny (Davis, 1966; Cronquist, 1981; Pollard & Amuti, 1981). Furthermore, molecular studies have placed representatives of Dipsacales at some distance from Calyceraceae.

From the core group, Calyceraceae differ primarily in the production of iridoids, possession of multinucleate tapetal cells, and lack of endosperm haustoria. Other characteristic features occur in certain genera, e.g., involucrate capitula of actinomorphic flowers in *Jasione* (Campanulaceae), connate filaments with free anthers in *Nemacladus*

(Cyphiaceae), uniovulate ovaries (though with basal placentation) in *Merciera* (Campanulaceae) and *Unigenes* (Lobeliaceae), and apical placentation in *Siphocodon* (Campanulaceae).

The Calyceraceae are even more similar to Goodeniaceae, differing primarily in their epipetalous stamens and lack of an indusium. Several characteristic features of the Calyceraceae occur sporadically among the Goodeniaceae: involucrate capitula of actinomorphic flowers (*Brunonia*), uniovulate ovary (*Brunonia, Verreauxia*), and apical placentation (*Catosperma*). Especially notable is the presence in both families of seco-loganin and specialized mechanisms for secondary presentation of pollen. Furthermore, molecular studies have placed Calyceraceae and Goodeniaceae together as a clade within the sister group of Campanulaceae and Lobeliaceae. These data support the traditional Englerian assignment of Calyceraceae to Campanulales.

MENYANTHACEAE

This family includes five genera and approximately 35 species of aquatic and wetland plants of scattered distribution throughout the world. As discussed earlier, recent authors have assigned it to Gentianales or Solanales. However, Gentianales differ in the production of L−(+)-bornesitol, flavones, C-glycoflavones, indole alkaloids, and cardenolides, but not simple seco-iridoids; storage of carbohydrate as starch; the possession of intraxylary phloem, opposite leaves, convolute or imbricate corolla lobes, and nuclear endosperm development; and the lack of an integumentary tapetum (Davis, 1966; Jensen et al., 1975; Schilling, 1976; Gornall et al., 1979; Cronquist, 1981; Pollard & Amuti, 1981; Gershenzon & Mabry, 1983). Furthermore, molecular data group Gentianaceae with Apocynaceae, Rubiaceae, and Spigeliaceae at a substantial distance from Menyanthaceae. Similarly, Solanales differ primarily in their lack of iridoids, storage of carbohydrate as starch (except Polemoniaceae), and intraxylary phloem (Jensen et al., 1975; Cronquist, 1981; Pollard & Amuti, 1981); once again, they lie at some distance from Menyanthaceae in the molecularly derived phylogenies. Of the two proposed assignments, Menyanthaceae are nearer overall to Solanales.

The family is closer yet to Campanulales, however. It differs from the core of that order only in its production of iridoids; possession of heterostyly, aposepalous calyx, multinucleate tapetal cells, and Asterad embryogeny; and lack of endosperm haustoria. Several distinctive features characteristic of the Menyanthaceae are found sporadically among the core families, e.g., superior ovary (*Cyananthus,* Campanulaceae) and unilocular ovary with two parietal placentae (*Apetahia* Baillon, *Downingia,* Lobeliaceae).

Menyanthaceae differ from Goodeniaceae in their lack of an indusium and specialized mechanism of pollen presentation; possession of heterostyly, aposepalous calyx, actinomorphic corolla, distinct stamens, trinucleate pollen, parietal placentation, and Asterad embryogeny. The characteristic superior ovary occurs in some genera (*Brunonia, Velleia*).

From Calyceraceae, the Menyanthaceae differ in never having an involucrate capitulum; in possessing heterostyly, aposepalous calyx, distinct stamens, parietal placentation, and Asterad embryogeny; and in lacking a specialized method of proterandrous pollen presentation.

As can be seen, Calyceraceae, Goodeniaceae, and Menyanthaceae share many features. Especially suggestive of a close relationship among them are the production of seco-loganin, storage of carbohydrate as inulin, the possession of multinucleate tapetal cells, and the lack of endosperm haustoria. The chromosome numbers of all three are based on $x = 8$ or 9. Most convincing are the molecular data, which place Menyanthaceae as the sister group of the clade that contains Asteraceae, Calyceraceae, and Goodeniaceae. For these reasons, it is recommended that Menyanthaceae be dissociated from Gentianales and Solanales, and assigned to Campanulales.

ASTERACEAE

The cosmopolitan Asteraceae are the largest family of dicotyledons, with membership estimated at more than 1,100 genera and 20,000 species (Cronquist, 1981). In the phylogenetic trees generated by molecular studies, Asteraceae are embedded firmly among campanulalean families, at a substantial distance from Apiales, Cornales, Dipsacales, Rubiales, and other supposed relatives. These molecular data are supported by the other data reviewed here. Asteraceae differ from the core group of Campanulales in the following characters: plants producing sesquiterpene lactones and a more diverse array of polyacetylenes; calyx reduced to a pappus or absent; tapetum often amoeboid, its cells multinucleate; embryo sac sometimes bisporic or tetrasporic; embryogeny Asterad; and endosperm lacking haustoria, its development sometimes nuclear. Several distinctive features characteristic of the Asteraceae occur sporadically among the core families: involucrate capitula (*Ja-*

sione, Campanulaceae); epipetalous stamens (polypetalous Pentaphragmataceae, Sphenocleaceae); exalbuminous seeds (Sphenocleaceae); and uniovulate ovaries with basal placentation (*Merciera*, Campanulaceae; *Unigenes*, Lobeliaceae).

The molecular data suggest that Asteraceae are even closer to the group comprising Calyceraceae, Goodeniaceae, and Menyanthaceae. They form the sister group to the clade comprising Calyceraceae and Goodeniaceae; Menyanthaceae is then the sister group to this larger clade. From these three families, Asteraceae differ in producing sesquiterpene lactones and a more diverse array of polyacetylenes but no iridoids, and in having the calyx pappose or absent. In particular, the Calyceraceae seem very similar by virtue of their involucrate capitula, specialized pollen presentation mechanism, epipetalous stamens, and uniovulate ovary; details of the pollen, particularly the presence of unusual intercolpar concavities in both Calyceraceae and Barnadesiinae, also support a close relationship (Skvarla et al., 1977). All these data support the Englerian assignment of Asteraceae to a position near Calyceraceae at the apex of Campanulales.

DONATIACEAE AND STYLIDIACEAE

The Stylidiaceae, excluding *Donatia* Forster & G. Forster (Carlquist, 1969c; Cronquist, 1981; Takhtajan, 1987), include five genera and approximately 175 species. Over 95% are restricted to Australia and Tasmania; the remainder are distributed to the north and east as far as Ceylon, southern China, the Philippines, New Guinea, New Zealand, and Tierra del Fuego.

Morphologically and chemically, the Stylidiaceae are the most discordant members of the Campanulales, bringing to that order a significant number of character states found nowhere else in the order: plants producing carbocyclic iridoids; secondary growth anomalous; flowers solitary and terminal; stamens 2, wholly adnate to the style, forming a gynandrium that is commonly irritable; anther thecae divergent and apically confluent. The unique gynandrium with its divergent thecae is clearly a synapomorphy uniting these five genera. Regrettably, the family has not yet been represented in a phylogenetic reconstruction based on molecular data.

Three characteristics of Stylidiaceae are of limited distribution among dicots, and thus may serve as an indication of their affinities. First, there is the storage of carbohydrate as inulin, a trait used to support their inclusion in Campanulales. Only a handful of other families store inulin (Pollard & Amuti, 1981): Boraginaceae (Lamiales); Clethraceae, Monotropaceae, and Pyrolaceae (Ericales); and Polemoniaceae (Solanales).

Second, there is the production of iridoids, which might be used to support a relationship with Goodeniaceae, Calyceraceae, and Menyanthaceae. However, these families produce seco-iridoids, while Stylidiaceae produce monotropein, a carbocyclic iridoid. Monotropein has been detected in only a few other families (Jensen et al., 1975; Kaplan & Gottlieb, 1982): Altingiaceae (Hamamelidales); Cornaceae (Cornales); Ericaceae, Monotropaceae, and Pyrolaceae (Ericales); Globulariaceae (Scrophulariales); and Rubiaceae (Rubiales).

Third, there is the development of terminal endosperm haustoria, a feature that might suggest a relationship with Campanulaceae, Lobeliaceae, and Sphenocleaceae. However, terminal endosperm haustoria characterize several other dicots with ab initio cellular endosperm formation (Davis, 1966; Dahlgren, 1975b; G. Dahlgren, 1989a): Acanthaceae, Bignoniaceae, Gesneriaceae, Globulariaceae, Lentibulariaceae, Myoporaceae, Orobanchaceae, Pedaliaceae, and Scrophulariaceae (Scrophulariales); Bruniaceae (Rosales); Callitrichaceae (Callitrichales); Clethraceae, Cyrillaceae, Empetraceae, Epacridaceae, Ericacaeae, Grubbiaceae, and Monotropaceae (Ericales); Lamiaceae and Verbenaceae (Lamiales); Loasaceae (Violales); and Plantaginaceae (Plantaginales).

The Ericales are the only order in which all three of these unusual character states are found; even the Campanulales share only two. Numerous other characteristics of Stylidiaceae are found in at least some members of Ericales: sieve-tubes with S-type plastids; leaves alternate, simple; stomates anomocytic; corolla sympetalous, zygomorphic (*Rhododendron* L., Ericaceae), the lobes valvate (*Kalmia* L., Ericaceae); stamens two (*Oligarrhena* R. Br., Epacridaceae); anthers tetrasporangiate, dehiscent via longitudinal slits (*Oxydendrum* DC., Ericaceae), development of the wall dicotyledonous, the endothecium with fibrous thickenings; tapetum glandular, the cells binucleate; ovary inferior, bicarpellate, with axile placentation, and crowned by an intrastaminal nectary disc; ovules numerous, anatropous, unitegmic, tenuinucellar, with an integumentary tapetum; embryo sac *Polygonum*-type; embryogeny Solanad; fruit capsular; endosperm copious, its development ab initio cellular. Even their ecology is suggestive. Carlquist (1969c: 15) hypothesized that Stylidiaceae are derived from "ancestors which prefer acidic or mineral-poor soils," a statement that fits more Ericales than it does Campanulales. The bryoid or cushion-plant habit of many Stylidiaceae is likewise more common among Ericales than Campanulales.

A distinctive feature of many Ericales is their unusual anthers. Commonly, these are inverted during their development (i.e., the morphologically basal portion is uppermost at anthesis) and poricidal. The distinctive gynandrium of Stylidiaceae might be less out of place in Ericales, given this tendency toward structural modification and rearrangement of the anthers, than it is in Campanulales.

Some authors (Thorne, 1976; Dahlgren, 1980) have suggested a relationship with Hydrangeaceae and its allies in the Cornales–Saxifragales alliance. However, none of these plants stores inulin or develops terminal endosperm haustoria. Dahlgren later realized this, and transferred Stylidiaceae to its own order near Ericales in the Ericanae (G. Dahlgren, 1989a, b).

In summary, the only alternative placement of Stylidiaceae that seems credible is in or near Ericales. Aside from the unique gynandrium, the family has no features that could not be accommodated within that order as it is commonly circumscribed. At the very least, it would be no more out of place than among Campanulales, an order in which carbocyclic iridoids are totally foreign. Consequently, Stylidiaceae should be removed from Campanulales to a position in or near Ericales, pending further data from molecular phylogenetic studies.

There remains the question of the affinities of *Donatia*, a genus variously included in or excluded from the Stylidiaceae. The genus comprises two widely disjunct species, *D. novae-zelandiae* of Tasmania and New Zealand and *D. fascicularis* of Tierra del Fuego. Nothing is known of their embryology or chemistry, aside from the fact that inulin is stored. On morphological grounds, *Donatia* also should be removed from Campanulales. The solitary sessile terminal flower, dimerous or trimerous androecium, and distinct styles are unknown elsewhere in the order. The apopetalous corolla is matched by only a few species of Pentaphragmataceae, and paracytic stomates are otherwise found only in *Brunonia* (Goodeniaceae).

Most authors have considered *Donatia* to be closely related to Stylidiaceae; only Hutchinson (1969, 1973) has totally divorced the two. The perception of a relationship with Stylidiaceae is due primarily to the remarkable similarity of *Donatia* to *Phyllachne* in habit and ecology (Carlquist, 1969c). However, the habital similarities are underlain by significant differences in vegetative anatomy, and may well represent parallellism or convergence induced by the rigors of their antarctic cushion-bog habitat (Rapson, 1953).

Donatia differs from Stylidiaceae in its paracytic stomates, apopetalous corolla, free and distinct stamens, colinear anther thecae, smooth pollen, and free and distinct styles. Its inclusion in that family would not only increase the morphological heterogeneity of an already heterogeneous family, but would deprive that family of its defining synapomorphies. For these reasons, it is recommended to continue recognition of Donatiaceae as a family distinct from Stylidiaceae (Rapson, 1953; Hutchinson, 1973; Cronquist, 1981).

Is it possible that Donatiaceae still deserve a position somewhere near Stylidiaceae, or are they only distantly related? The distinct styles would seem to argue for the latter; this feature is as unknown among Ericales as it is among Campanulales. Carlquist (1969c) commented that there is no compelling evidence of a relationship, aside from the common occurrence of inulin. However, Carolin (1960b) found floral structure and anatomy to be quite similar, and expressed no hesitation in treating *Donatia* as the ancestor of the Stylidiaceae.

Several questions regarding chemistry and embryology must be answered before a conclusion on the relationship of *Donatia* to Stylidiaceae can be reached. First, does *Donatia* produce iridoids, particularly carbocyclic iridoids such as monotropein? Second, is the tapetum glandular with binucleate cells? Third, are the ovules anatropous, unitegmic, and tenuinucellar, with a *Polygonum*-type embryo sac and Solanad embryogeny? Fourth, is endosperm formation ab initio cellular, and do terminal haustoria form? Negative answers to any of these questions would weaken the case for a relationship with Stylidiaceae. The inclusion of *Donatia* in a phylogeny generated from molecular data should provide definitive evidence. Pending the results of such studies, it is recommended to maintain the status quo and consider Donatiaceae to be a more primitive relative of Stylidiaceae.

SUMMARY

The available data support the inclusion of the following candidate taxa at familial rank: Asteraceae, Calyceraceae, Campanulaceae, Cyphiaceae, Goodeniaceae (including *Brunonia*), Lobeliaceae, Menyanthaceae, Pentaphragmataceae, and Sphenocleaceae. With this circumscription, the Campanulales comprise nine families, more than 1,200 genera, and approximately 21,650 species, distributed throughout the world. Donatiaceae and

Stylidiaceae are removed from the order and assigned provisionally to a position in or near Ericales.

The following description summarizes the character states found in the order. Perennial herbs (less often annual or woody), producing polyacetylenes, simple seco-iridoids, sesquiterpene lactones, or alkaloids (seldom with more than one class of compound in a given species), storing carbohydrate as inulin; sieve-elements with S-type plastids. Leaves exstipulate, commonly alternate and simple; stomates anomocytic (rarely paracytic or tetracytic). Inflorescences variously monotelic or polytelic, predominantly racemose, often condensed into a tight capitulum subtended by an involucre, or sometimes the flowers solitary and axillary. Flowers tetracyclic, perfect or imperfect, sometimes heterostylous, resupinate in Lobeliaceae, commonly with a specialized method of proterandrous secondary pollen presentation. Calyx synsepalous (rarely aposepalous), commonly pentamerous, pappose or absent in Asteraceae. Corolla sympetalous (rarely polypetalous), commonly pentamerous, actinomorphic or variously zygomorphic, the lobes valvate (rarely imbricate). Stamens (4–)5, antisepalous; filaments distinct or connate, inserted atop the ovary or on the corolla tube (rarely on the rim of the free hypanthium or the floral receptacle); anthers tetrasporangiate (rarely bisporangiate), dithecal, basifixed, distinct, connivent or connate, dehiscent introrsely (less often extrorsely) via longitudinal slits, the wall development dicotyledonous (rarely basic); endothecium with fibrous thickenings; tapetum glandular (rarely amoeboid), the cells binucleate or multinucleate; pollen spheroidal, oblate, or prolate (rarely trilobate), commonly triaperturate, binucleate or trinucleate when shed. Ovary syncarpous, inferior (rarely superior), 1–5(–10)-loculed; placentation axile or basal (rarely parietal or apical); ovules 1–many, anatropous, unitegmic, tenuinucellar; embryo sac *Polygonum*-type (rarely *Allium*-type or variously tetrasporic) with an integumentary tapetum; embrogeny Solanad or Asterad; embryo dicotyledonous, straight; endosperm development ab initio cellular, with or without haustoria; style 1, often with a ring of hairs or cup subtending the unlobed or 2–5(–10)-lobed stigma; fruit a capsule, berry, achene, or cypsela. Chromosome numbers commonly $x = 7$, 8, or 9.

Two facts are apparent from the above description. First, the Campanulales, despite their diversity, are relatively homogeneous when compared to other angiosperm orders. Second, while the order may be defined on the basis of a suite of correlated features, there are no evident nonmolecular synapomorphies that define it rigorously.

PHYLOGENY

Reconstructing the phylogeny of a group of families on the basis of morphology and other phenotypic data is rife with the potential for error, due to difficulties in correctly assessing homologies (Cronquist, 1987b; Stuessy, 1990). Missing data also reduce the confidence that can be placed in such phylogenetic trees. Fortunately, very low levels of such homoplasy characterize phylogenies inferred from the results of chloroplast DNA restriction fragment analysis and *rbc*L sequence data. Attempts are under way in various laboratories to incorporate all families of Asteridae into these molecular studies. Once such studies have been completed, as well as additional chemical and embryological investigations recommended above, it will be possible to examine phenotypic character state trends and changes in a more satisfactory manner, by integrating the data reviewed here into the framework provided by the molecular phylogeny. Then, a comprehensive understanding of phylogenetic relationships among Campanulales, as well as a sound revision of their classification, will be possible.

For these reasons, no diagram purporting to show phylogenetic relationships among the families of Campanulales is proffered at this time. Meanwhile, the following preliminary notes toward an integrated phylogeny of the order are appropriate. These may be considered hypotheses to be tested by the accumulation of additional data.

PHYLOGENETIC PATTERNS

The molecular phylogeny indicates that the Campanulales, as here circumscribed, are indeed a monophyletic group. Unfortunately, there are no evident nonmolecular synapomorphies to support this clade. The ability to store inulin, which occurs in but does not characterize three other orders, may be the closest approach to one. Note that if Asteraceae and/or Calyceraceae were to be segregated as discrete orders, the Campanulales that remained would clearly be paraphyletic.

The sparse fossil record suggests that the order arose no later than the Oligocene, some 40 million years ago. Given that the earliest fossils are of rather advanced families (Asteraceae, Goodeniaceae), origin earlier in the Tertiary or even in the late Cretaceous is not improbable (P. R. Crane, pers. comm.).

The molecular phylogeny shows the Campanulales dividing into two clades. This basal dichotomy is supported by three nonmolecular characters, none of them morphological. Taxonomically, the two clades might be recognized as suborders; alternatively, it might be advantageous to recognize each at ordinal rank in a revised classification of Asteridae. Phylogenetic relationships within each clade are confused by the combination of plesiomorphic and apomorphic states in several of the families.

The asterad clade comprises Asteraceae, Calyceraceae, Goodeniaceae, and Menyanthaceae. These families have multinucleate tapetal cells, lack endosperm haustoria, and produce deterrent chemicals via the mevalonate pathway (either seco-iridoids or sesquiterpene lactones, but not both). Menyanthaceae might be the most primitive family in this clade (and perhaps in the order), judging by their greater diversity of iridoid compounds, lack of a specialized mechanism for secondary pollen presentation, free and often distinct sepals, actinomorphic corolla, and superior ovary. However, their heterostylous flowers, trinucleate pollen, and unilocular ovary with two parietal placentae would appear to be relatively advanced features. The Goodeniaceae seem relatively advanced in their zygomorophic corolla and stylar indusium, as do Calyceraceae by virtue of their involucrate capitula, epipetalous stamens, uniovulate ovaries, and apical placentation. Undeniably, Asteraceae are the most specialized group morphologically, both within the order, and within the Asteridae as a whole.

The campanulad clade comprises Campanulaceae, Cyphiaceae, Lobeliaceae, Pentaphragmataceae, and Sphenocleaceae. These families have binucleate tapetal cells, terminal endosperm haustoria, and apparently are unable to synthesize deterrent chemicals by the mevalonate pathway. The Campanulaceae would appear to be plesiomorphic, on the basis of their radially symmetric flowers and multilocular ovaries; in particular, *Cyananthus*, with its 5-locular ovary free from the hypanthium, has been suggested to be the most primitive extant genus in the family (Hutchinson, 1969; Carolin, 1978; Takhtajan, 1980; Dunbar, 1984). However, the production of latex and the specialized pollen presentation mechanism, including the unique invaginating stylar hairs, most likely are derived features.

The absence from Sphenocleaceae and Pentaphragmataceae of lactifers and any sort of specialized pollen presentation mechanism suggests that these families might be even more primitive than Campanulaceae. The sometimes polypetalous corolla, partially adnate hypanthium, and micropylar haustoria of the latter might be primitive features as well. However, these two families also exhibit several apparently advanced characters, including the trinucleate pollen grains, circumscissile capsule, and exalbuminous seeds of the former; the asymmetric leaves, unique inflorescence, and trilobate pollen of the latter; and the epipetalous stamens and bilocular ovaries of both.

The Lobeliaceae clearly are more advanced than Campanulaceae, based on their resupinate flowers with the odd sepal ventral prior to resupination, zygomorphic corolla, connate heteromorphic anthers, and bilocular ovary. In as much as Cyphiaceae likewise have the odd sepal ventral and the corolla zygomorphic, they, too, seem to be more advanced than Campanulaceae. Their nonresupinate flowers and apparent lack of secondary pollen presentation mark them as less advanced than Lobeliaceae, however.

MORPHOLOGICAL TRENDS

This section examines the distribution of various morphological characters employed in the classification of Campanulales against the framework of this preliminary hypothetical phylogeny. For example, it is obvious that there has been an evolutionary reduction in the syncarpous gynoecium, involving both a reduction in the number of locules and in the number of ovules per locule. The two trends vary independently, as evidenced by the existence of several possible permutations, e.g., unilocular ovaries with numerous ovules and bilocular ovaries with a solitary ovule in each locule. The two trends converge at their respective culminations, producing a unilocular ovary with solitary ovule. Such ovaries occur among campanulads (*Merciera*, Campanulaceae; *Unigenes*, Lobeliaceae) and asterads (*Brunonia* and *Verreauxia*, Goodeniaceae; Calyceraceae; Asteraceae), suggesting that the uniovulate ovary has evolved more than once within Campanulales.

Epigyny likewise appears to have had multiple origins, because genera with superior ovaries are found among asterads and campanulads. Furthermore, there are significant differences in the nonepigynous flowers of these clades. In the putatively most primitive genus of the campanulad clade, *Cyananthus* (Campanulaceae), the flower is perigynous. The superior ovary is surrounded by (but free from) a cuplike hypanthium, upon which are inserted the corolla and filaments. By contrast, in the putatively most primitive members of the asterad line, the Menyanthaceae, the flower is hypogynous. There is no adnation among the floral whorls surrounding the superior ovary, all of which arise from the floral receptacle. These observations correlate well with Carolin's (1959, 1960b, 1978) observations on anatomy and ontogeny in epigynous flowers of Campanulaceae and Goodeniaceae. These studies showed that in Campanulaceae, the outer floral whorls coalesced into a free hypanthium prior to adnation of the ovary, while the inferior ovary of Goodeniaceae formed by the sequential adnation of the outer floral whorls to the ovary. These facts suggest that inferior ovaries evolved independently in the asterad and campanulad clades.

Zygomorphy likewise appears to have arisen more than once and in different ways, because it occurs in derived taxa of both the campanulad (Cyphiaceae and Lobeliaceae) and the asterad (Asteraceae and Goodeniaceae) clades. As discussed previously, the bilabiate flowers of Goodeniaceae and Lobeliaceae may look very similar at anthesis, but are fundamentally different, due to differences in the position of the odd lobe and resupination. Even within a clade, zygomorphy may have multiple origins. Bremer (1987) considered the zygomorphic florets of Asteraceae to be derived from actinomorphic florets.

Even the distinctive mechanisms for secondary pollen presentation that characterize most members of the order also appear to have had multiple origins, as evidenced by detailed study of the structures involved (Carolin, 1960a; Erbar & Leins, 1989; Leins & Erbar, 1990) and their distribution among the families. Connate anthers occur among both campanulads (Lobeliaceae) and asterads (Asteraceae, some Goodeniaceae); likewise, connate filaments with distinct anthers occur in both clades (Cyphiaceae, Calyceraceae).

If these interpretations are correct, it means that any attempt to utilize these distinctive morphological features as synapomorphies in a cladistic analysis of Campanulales would be fraught with frustration. Assuming that a feature has evolved once when in fact it has had multiple origins would introduce considerable homoplasy to the phylogeny and indicate close relationships where none exist.

CHEMICAL TRENDS

The integrated phylogeny shows the sesquiterpene-producing Asteraceae to be derived from iridoid-producing families. The monoterpenoid structure of seco-iridoids is not very different from the basic skeleton of sesquiterpene lactones, and both classes of compounds are synthesized via the mevalonate pathway. From these observations, I hypothesize that mutations affecting one or more enzymes in the mevalonate pathway interrupted iridoid production in ancestral Asteraceae and that the chemical precursors or intermediates were shunted into the production of sesquiterpene lactones. Such a hypothesis fits in with Cronquist's (1977) view that the evolutionary success of Asteraceae was due primarily to biochemical innovation.

This hypothesis also helps explain the oft-cited chemical similarity between Asteraceae and Apiaceae. These two families have been hypothesized to be closely related, because they are among the few angiosperms capable of producing sesquiterpene lactones (Hegnauer, 1964, 1977; Bate-Smith & Swain, 1966; Herz, 1977; Gershenzon & Mabry, 1983). However, the molecular data indicate that they are only distantly related. As discussed earlier, Apiaceae and Araliaceae form a clade, the apiads, that is the sister-group of the dipsacad clade. All dipsacads produce seco-iridoids; the apiads do not. Once again, it appears that a family rich in sesquiterpene lactones is related to iridoid producers. Apparently, there have been parallel mutations in the mevalonate pathways of Apiaceae and Asteraceae, shutting down the synthesis of seco-iridoids and initiating the production of sesquiterpene lactones in both families. Thus, the production of sesquiterpene lactones, while a derived character state, cannot be used as a synapomorphy to unite Apiaceae and Asteraceae.

From the above two cases, it might appear that the production of sesquiterpene lactones is the natural consequence of blockage of iridoid synthesis. However, it does not appear to be an obligate outcome, because Araliaceae, Campanulaceae, and Lobeliaceae produce neither iridoids nor sesquiterpene lactones. Rather, these families deter predators and pathogens with polyacetylenes and/or alkaloids, which are biogenetically unrelated to deterrents from the mevalonate pathway. Further study is needed to explain this pattern. The co-occurrence of polyacetylenes with sesquiterpene lactones in many Apiaceae and Asteraceae, and with seco-iridoids in some Goodeniaceae, may be significant in the elucidation of this problem.

RELATIONSHIPS TO OTHER ORDERS

Given the present state of our knowledge, it is difficult to draw any firm conclusions regarding the relationships of Campanulales to other orders. The difficulties with inferring phylogeny from morphological and chemical data, which cause such frustration for interfamilial comparisons, become even more insufferable at the ordinal level. It is expected that molecular studies will eventually resolve these problems, but at this time, not enough taxa have been included in these studies to permit a confident conclusion. Until a more complete phylogeny is available, the following brief comment is offered.

As noted above, the molecular data indicate that the sister group of Campanulales is the apiad–dipsacad clade. The sister group of this combined clade includes Cornaceae and Philadelphaceae. These data support the hypothesis that the Campanulales ultimately take their origin very near the ancestry of the Asteridae, in the complex of families comprising the Cornales and woody Saxifragales (Thorne, 1976; Dahlgren, 1980). This complex is poorly understood, and much more study is required before a definitive statement can be made on its role in the ancestry of Campanulales.

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A NEW SUBFAMILY OF THE ASTERACEAE[1]

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ABSTRACT

The Asteraceae are generally divided into two large subfamilies, the Cichorioideae (syn. Lactucoideae; tribes Mutisieae, Cardueae, Lactuceae, Vernonieae, Liabeae, Arctoteae) and the Asteroideae (Inuleae, Astereae, Anthemideae, Senecioneae, Calenduleae, Heliantheae, Eupatorieae). Recent phylogenetic analyses based on morphological and chloroplast DNA data show that the Mutisieae–Barnadesiinae are the sister group to the rest of the family. The Mutisieae–Barnadesiinae are here excluded from the Mutisieae and elevated to the new subfamily Barnadesioidae.

Until the 1970s the tribe Lactuceae was considered to be distinct from all other Asteraceae and it was classified in its own subfamily, the Liguliflorae. The other tribes were placed together in the Tubuliflorae (e.g., Hoffmann, 1890). During the 1970s there was a growing understanding that all the tribes, including the Lactuceae, could be arranged in two large groups (Robinson & Brettell, 1973; Carlquist, 1976; Wagenitz, 1976), foreshadowed by diagrams in Carlquist (1961) and Poljakov (1967). Carlquist (1976) treated these two groups as the subfamilies Cichorioideae and Asteroideae. Their precise circumscription was modified by later authors (Robinson, 1977, 1981, 1983; Thorne, 1983).

Since 1985 cladistic analyses of molecular and morphological data have clarified the phylogeny and classification of the Asteraceae. Jansen & Palmer (1987) reported the presence of a 22 kb cpDNA inversion in *Lactuca* and several other Asteraceae. The inversion was found to be absent in three genera of the Mutisieae–Barnadesiinae, suggesting a basal dichotomy between the Barnadesiinae and the rest of the family. Subsequently, Jansen & Palmer (1988) undertook an analysis of cpDNA restriction site data from 13 genera of the Mutisieae (including the Barnadesiinae) and 9 representatives from other tribes. Later Jansen et al. (1990, 1991a) sampled 57 genera from 15 tribes in an extended study of cpDNA restriction site data. These studies corroborated the sister-group relationship between the Barnadesiinae and the rest of the family. To date, Jansen et al. (1991b) have examined more than 250 Asteraceae genera for the cpDNA inversion, which has proved to be present in all genera except those of the Barnadesiinae. The sister-group relationship between the Barnadesiinae and the rest of the family is supported also by analysis of *rbc*L sequences (Kim et al., 1992).

Simultaneously with Jansen & Palmer's cpDNA investigations, Bremer (1987) conducted a cladistic analysis of tribal interrelationships based on morphological data. The study included 27 tribes and subtribes and 47 phylogenetically informative characters, one of them being the cpDNA inversion. The sister-group relationship between the Mutisieae–Barnadesiinae and the rest of the family, revealed by the cpDNA inversion, was supported also by several morphological characters, such as presence of the typical Asteraceae twin hairs on the fruits and spiny pollen.

All available data sets strongly support the sister-group relationship between the Mutisieae–Barnadesiinae and the rest of the family (Jansen & Palmer, 1987, 1988; Bremer, 1987; Jansen et al., 1990, 1991a, b; Karis et al., 1992; Kim et al., 1992). The subtribe Barnadesiinae should now receive formal subfamilial status, as Barnadesioideae. It is a small subfamily of nine genera and nearly 90 species, distributed in South America mainly along the Andes. The Barnadesioideae genera share a number of morphological and molecular synapomorphies. Hence, the subfamily is a strongly supported monophyletic group. Its members are characterized by unique axillary spines and by a unique indumentum of long, unicellular, barnadesioid hairs on the corollas, cypselas, and pappus (Cabrera, 1959, 1961, 1977; Bremer, 1987).

The large subfamily Asteroideae is also a monophyletic group, with synapomorphies both in mor-

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phology and cpDNA. Members of the Asteroideae are characterized by shallowly lobed corollas, style branches with stigmatic areas separated in two parallel lines, and caveate pollen (Bremer, 1987). Among the molecular synapomorphies there is a length mutation at the 3′ end of the *rbc*L gene involving a six bp repeat, which is repeated four times, in all examined Asteroideae taxa (Kim et al., 1992).

The status of the subfamily Cichorioideae (excluding Barnadesioideae) remains unresolved, and the interrelationships among its tribes are not clearly understood from our hitherto published analyses. The morphological and the cpDNA trees are incongruent in several of the groupings, especially if Bremer's (1987) tree is compared to those based on cpDNA. The more detailed analysis of Karis et al. (1992) has removed some of the conflicts, whereas others persist. Karis et al. propose that a large part of the Mutisieae form a monophyletic group, excluding a number of Mutisieae–Gochnatiinae genera, which form a more or less unresolved paraphyletic grade at the base. Jansen et al. (1990, 1991a, b) suggested that the Mutisieae are monophyletic; all taxa sampled consistently group together. Further studies are necessary to evaluate the status of the subfamily Cichorioideae and to resolve tribal interrelationships within the two subfamilies Cichorioideae and Asteroideae.

Barnadesioidae (Bentham & Hooker) Bremer & Jansen, subfam. stat. nov. Barnadesieae (Bentham & Hooker) Bremer & Jansen, trib. stat. nov. Basionym: Mutisieae–Barnadesiinae Bentham & Hooker, Gen. Pl. 2: 168, 1873. Type: *Barnadesia* Mutis ex L. f.

Spinae axillares frequenter presentes. Corallae, cypselae pappusque villosae pilis longis unicellularibus. Stylus breviter bilobus, glaber vel papillosus. Pollen laeve vel granulare, non spinosum.

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PHYLOGENETIC ANALYSIS OF THE CICHORIOIDEAE (ASTERACEAE), WITH EMPHASIS ON THE MUTISIEAE[1]

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ABSTRACT

We present a cladistic analysis of 53 taxa from Asteraceae using 72 characters of mainly morphological data. Results reveal subfamily Cichorioideae is paraphyletic. The Mutisieae constitute a basal grade that contains monophyletic groups with *Mutisia* and Cardueae sensu lato. The Arctotideae, Liabeae, Vernonieae, and Lactuceae form a clade together with subfamily Asteroideae. Our results show some inconsistencies with those from cladistic analyses of molecular data.

The relationships within the Asteraceae, discussed since Cassini and Lessing in the early nineteenth century, have been scrutinized using cladistic methods (Bremer, 1987; Jansen & Palmer, 1987, 1988; Jansen et al., 1990). Many results of cladistic analyses were inconsistent with the intrafamilial systems proposed by other authors (e.g., Carlquist, 1976; Cronquist, 1977, 1981; Jeffrey, 1978; Wagenitz, 1976). Jansen & Palmer (1987) demonstrated that Mutisieae–Barnadesiinae (Cabrera, 1961, 1977) form a sister group to the rest of the family, a finding that was corroborated by an apomorphic cpDNA inversion in the latter group. Bremer (1987) also came to this conclusion in his cladistic analysis of the family, noting strong morphological support for this dichotomy. Bremer's (1987) analysis further supported the monophyly of the subfamily Asteroideae, and the subfamily Cichorioideae emerged as a paraphyletic assemblage. The analyses of Jansen et al. (1990) yielded quite different topologies. The only monophyletic groupings established in all trees, both Wagner and Dollo analyses, are the subfamily Asteroideae, the Vernonieae as the sister group to the Liabeae, and the Eupatorieae as a subclade within a paraphyletic Heliantheae sensu lato. Dollo analysis always supported a monophyletic Cichorioideae, but the Wagner analysis resulted in a paraphyletic Cichorioi-

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FIGURE 1. One of the two final cladograms. Character distributions are given below. Note that genera in the shaded area are all assigned to Mutisieae–Gochnatiinae. All apomorphies/reversals are listed for each node and each terminal taxon. Apomorphies with subsequent reversals/parallelisms are without further labeling, parallelisms are marked =, reversals are marked − with the change in multistate characters indicated within brackets. Multistate characters have the state in question indicated within parentheses. Under the terminal taxa all characters are parallelisms unless otherwise indicated.

Node 1: 28(0→1), 37, 65; =33(0→1); *Node 2:* 5, 58(0→1), 68; *Node 3:* 4, 30, 38(0→1), 42, 60; *Node 4:* 27(0→1), 29(0→1), 55; *Node 5:* −38(1→0); *Node 6:* 50, 51; *Node 7:* 15, =−42(1→0); *Node 8:* =16(0→1), =17, −29(1→0); *Node 9:* −4, −55; *Node 10:* =21, =48(0→3), =49(0→2); *Node 11:* −30; *Node 12:* =9, =16(1→2), =48(3→1), 59; *Node 13:* =1, =45, =46(0→2), =49(2→4), =58(1→3); *Node 14:* =66; *Node 15:* −15; *Node 16:* =29(0→1), =58(3→0); *Node 17:* −5, =23, =38(0→1); *Node 18:* −50, −55; *Node 19:* =1; *Node 20:* =5, =27(1→3), −28(1→0), =42(0→2), 64; *Node 21:* 8, =20; *Node 22:* =16(1→2); *Node 23:* =46(0→1), 48(3→4),

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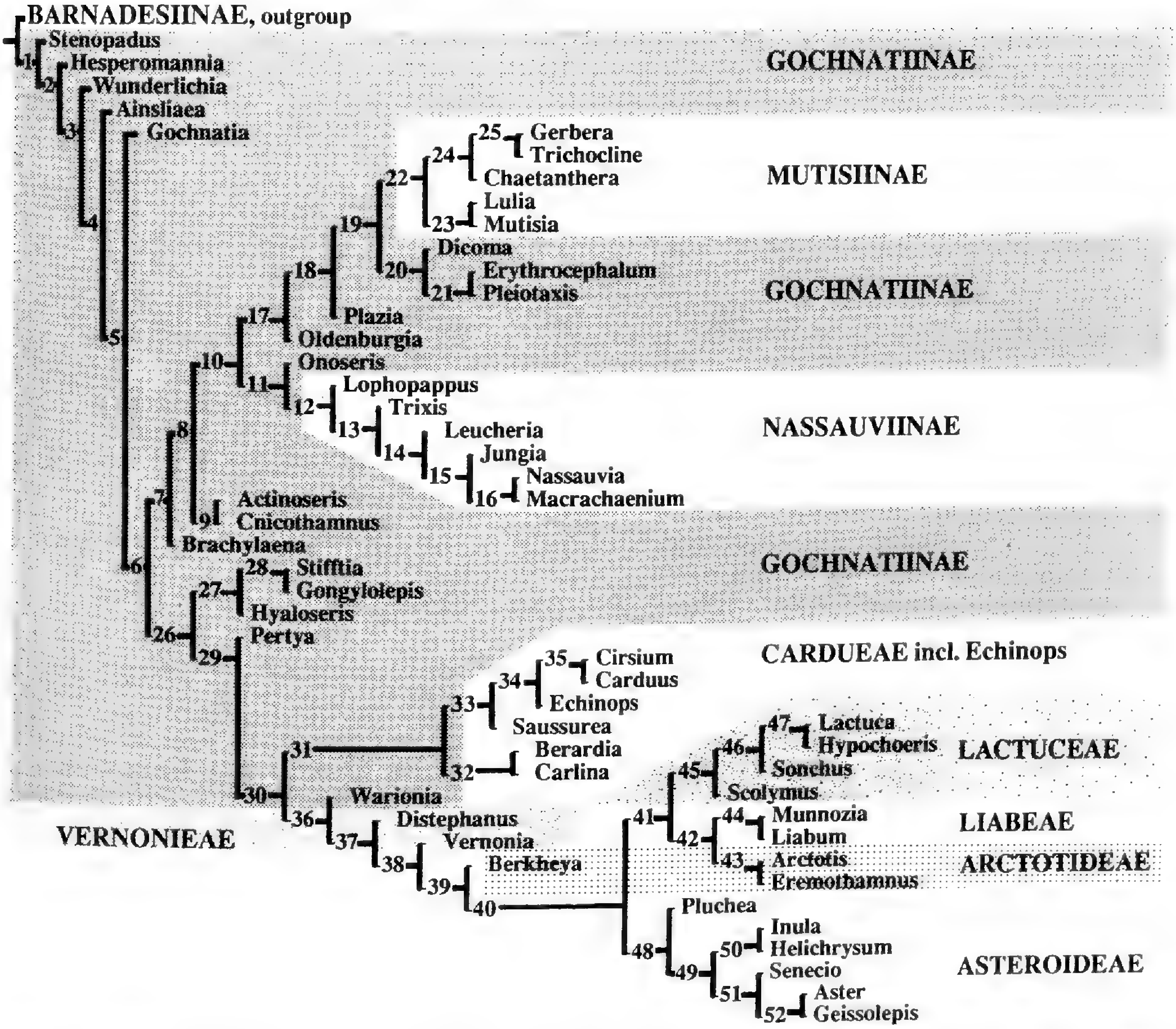

−58(1→0); *Node 24:* =18(0→1), −30; =58(1→3), −68; *Node 25:* =2(0→2), −60; *Node 26:* =21, =45, =46(0→1); *Node 27:* −5, −29(1→0); *Node 28:* −4, =12, −58(1→0), =69; *Node 29:* =38(0→1), =49(0→1), −68; *Node 30:* −28(1→0), =48(0→3); *Node 31:* =1, −60; *Node 32:* =19, −45, −46(1→0); *Node 33:* =20, =49(1→5), −55; *Node 34:* =3, =58(1→0); *Node 35:* 33(1→3), =39; *Node 36:* −4, −30, =42(1→2); *Node 37:* =32(0→1); *Node 38:* =1, 34, =68; *Node 39:* =15, =26, =29(1→2), 41, =48(3→2), =67; *Node 40:* 16(0→3); *Node 41:* −51, −55; *Node 42:* =4, =17, =18(0→1); *Node 43:* =32(1→2), −33(1→0), =48(2→3), −60, −68; *Node 44:* =24, −37; *Node 45:* =10, 13, −15, =16(3→4), 25(0→3), =32(1→2), 43, 54, =71(0→1); *Node 46:* =31, −33(1→0), =35, −58(1→0), −68, =70; *Node 47:* =55, 57; *Node 48;* =18(0→1), =19, −33(1→0), =48(2→1), 47(0→2), 72; *Node 49:* =36, 44, =49(1→4), −50; *Node 50:* −58(1→0), −60, =63; *Node 51:* =17, −37, −68; *Node 52:* =10, 28(1→2), =49(4→2), 53; *Actinoseris:* 1, 2(0→2), 25(0→1), 29(0→1), 45, 67, 69; *Ainsliaea:* 1, 18(0→1), −42(1→0), 66; *Arctotis:* 10, 19, −21, −26, 27(1→2), 28(0→1), −37, −38(1→0), 42(2→1), 49(1→5), 51, 52; *Aster:* −36, 50, 61; *Berardia:* 2(0→2), 20, −21, 26, 27(1→2), −58(1→0), 67, 71(0→1); *Berkheya:* 3, 4, 16(0→5), 18(0→2), 24, 28(0→1), 31; *Brachylaena:* 26, 27(1→3), −28(1→0), −68; *Carduus:* −4, −27(1→0), 42(1→2), −50, 52, 56, 62, 71(0→2); *Carlina:* 3, −4, 11, 14, 22, 23, 49(1→5), −50, 66, 71(0→2); *Cirsium:* 36, 66, 67, 68; *Chaetanthera:* 10, 43(0→3); *Cnicothamnus:* −29(1→0), 36, 42(0→1); *Dicoma:* 18(0→1), 69; *Distephanus:* 29(1→2), −38(1→0), 48(3→1); *Echinops:* 24, −38(1→0), 52; *Eremothamnus:* −1, 3, 22, 29(2→1), 31, 35, −67; *Erythrocephalum:* 14, 29(0→1), 45, 46(0→1), 50, 58(1→2), 66, 67; *Gerbera:* 5, 29(0→1), 46(0→1), 50, 67; *Gochnatia:* 21; *Gongylolepis:* 6, 7, 16(0→2), 17, −46(1→0); *Helichrysum:* 4, −5, 11, 16(3→6), 46(1→2), 61; *Hesperomannia:* 32(0→1), 45, 48(0→1), 49(0→1); *Hyaloseris:* 10, 16(0→4), −30, −51, 58(1→2); *Hypochoeris:* 2(0→2), 14, −54, 66; *Inula:* 17, −21, 25(0→2), −32(1→0), 47(2→1), 48(1→3), 49(4→3), −67, 62; *Jungia:* 14, 32(0→1); *Lactuca:* 9, −25(3→0), 63; *Leucheria:* 25(0→2), 38(0→2); *Liabum:* 9, 22, −41, 55, 70; *Lophopappus:* 3, −5, −15, −50; *Lulia:* 18(1), 24, −37, −38(1→0), 39, 50, 61; *Macrachaenium:* 2(2), 32(1), 36, −46(2→1), −49(4→2); *Munnozia:* 27(2), 58(0), 71(1); *Mutisia:* −1, 25(1), 40, 45, −60, 66; *Nassauvia:* 3, −4, 38(2), −55, −66, 67, −68; *Oldenburgia:* 7; *Onoseris:* 18(1), 19, 24, 38(1), 39, 40, 42(1), 45, 62, −68; *Pertya:* 48(4), −50; *Plazia:* 22, 42(0→1), 45, 49(2→3); *Pleiotaxis:* 10, −15, −16(1→0), −17, −21, −23, 36, 49(2→3), 55, −68; *Pluchea:* −5, 16(3→6), 25(2), −32(1→0), −67; *Saussurea:* 56, 61, 70; *Scolymus:* 14, 24, 37, 67(2); *Senecio:* −5, 9, 38(1→2), 46(1→2); *Sonchus:* 3, 9, 24, 69; *Stenopadus:* 6, 7, 12, 22, 51, 55; *Stifftia:* 9, −42(1→0), −50, −68; *Trichocline:* −1, 39, 40, 48(3→4); *Vernonia:* −5, 22, −37, 66, 70; *Warionia:* 24, 27(1→3), 40, −50, −55, 62, 71(0→1); *Wunderlichia:* 22, 25(0→1).

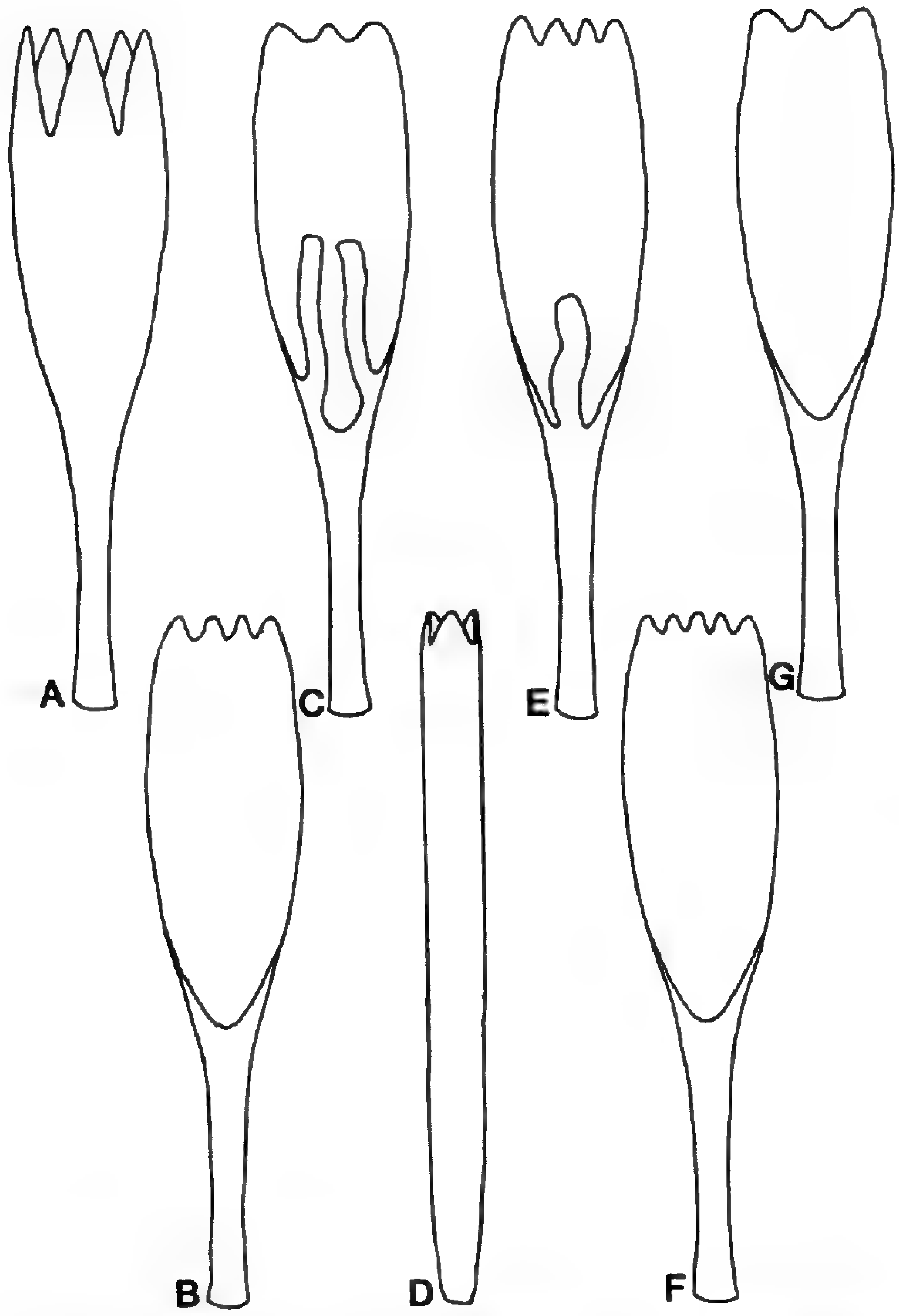

FIGURE 2. Corollas in Asteraceae.—A. Actinomorphic.—B. Gorteriinae ray.—C. Bilabiate.—D. Tubular.—E. Pseudobilabiate.—F. Ligule.—G. True ray.

deae similar to that from Bremer's analysis. The status of the Cichorioideae thus requires further investigation.

Our aim with this study is to clarify the relationships in the basal part of the family. This is important because these relationships were not resolved with certainty by Bremer (1987). Further, the relationships based on molecular data (Jansen et al., 1990) seem unstable.

Relationships of the tribe Mutisieae (excluding the Mutisieae–Barnadesiinae) are crucial for understanding the basal diversification of the family (Bremer, 1987).

MATERIAL AND METHODS

The study is based on herbarium material, but we also gathered a large amount of information (used as characters, Appendix II) from the literature. Our emphasis is on morphological features, and especially large is the number of characters gained from florets, including many microcharacters. We investigated numerous genera of Mutisieae with selected genera from other cichorioid tribes and selected Asteroideae representatives.

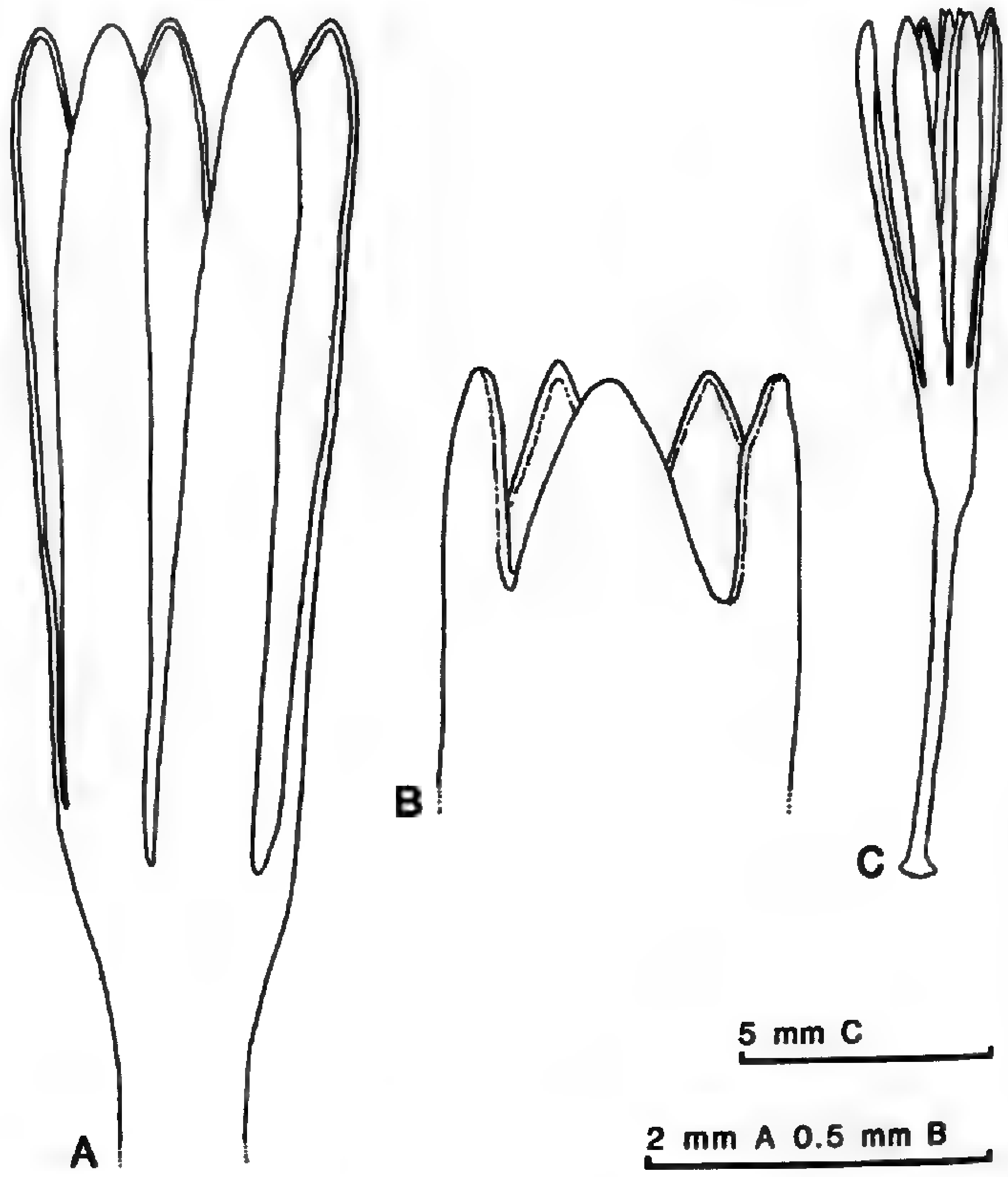

FIGURE 3. Corolla characters.—A. Actinomorphic, deeply 5-lobed, typical for most Mutisieae and Cardueae.—B. Shortly lobed actinomorphic, typical for most Asteroideae.—C. Corolla with a long slender tube typical for Cardueae. (A, *Dicoma galpinii, Germishuizen 294*; B, *Helichrysum auriceps, Ross 2099*; C, *Carduus argyroa, Segelberg 16460/3.*)

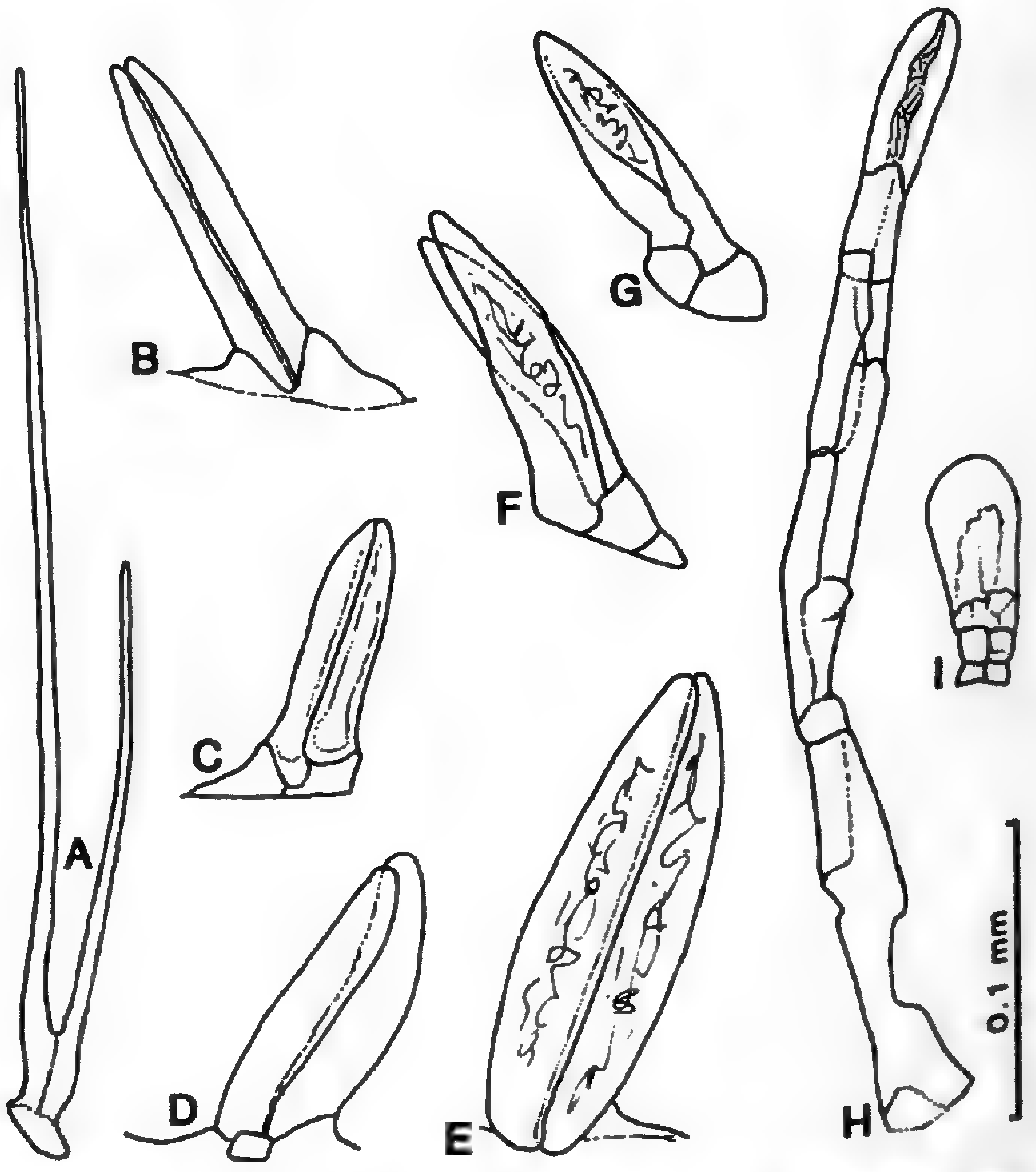

FIGURE 4. Twin trichomes.—A. Deeply cleft twin hair.—B. Short ovoid twin hair, nonmyxogenic.—C–G. Short ovoid twin hairs, myxogenic.—H. Long glandular hair.—I. Short glandular hair. (A, *Erythrocephalum zambesiacum, Faulkner 110*; B, *Acourtia glomeriflora, Asplund 148*; C, *Trixis brasiliensis, Malme 1124*; D, *Trixis cacalioides, Asplund 10832*; E, *Trixis californica, Dillon et al. 997*; F, G, *Jungia axillaris, Chavez 3260*; H, I. *Munnozia hastifolia, Asplund 12510.*)

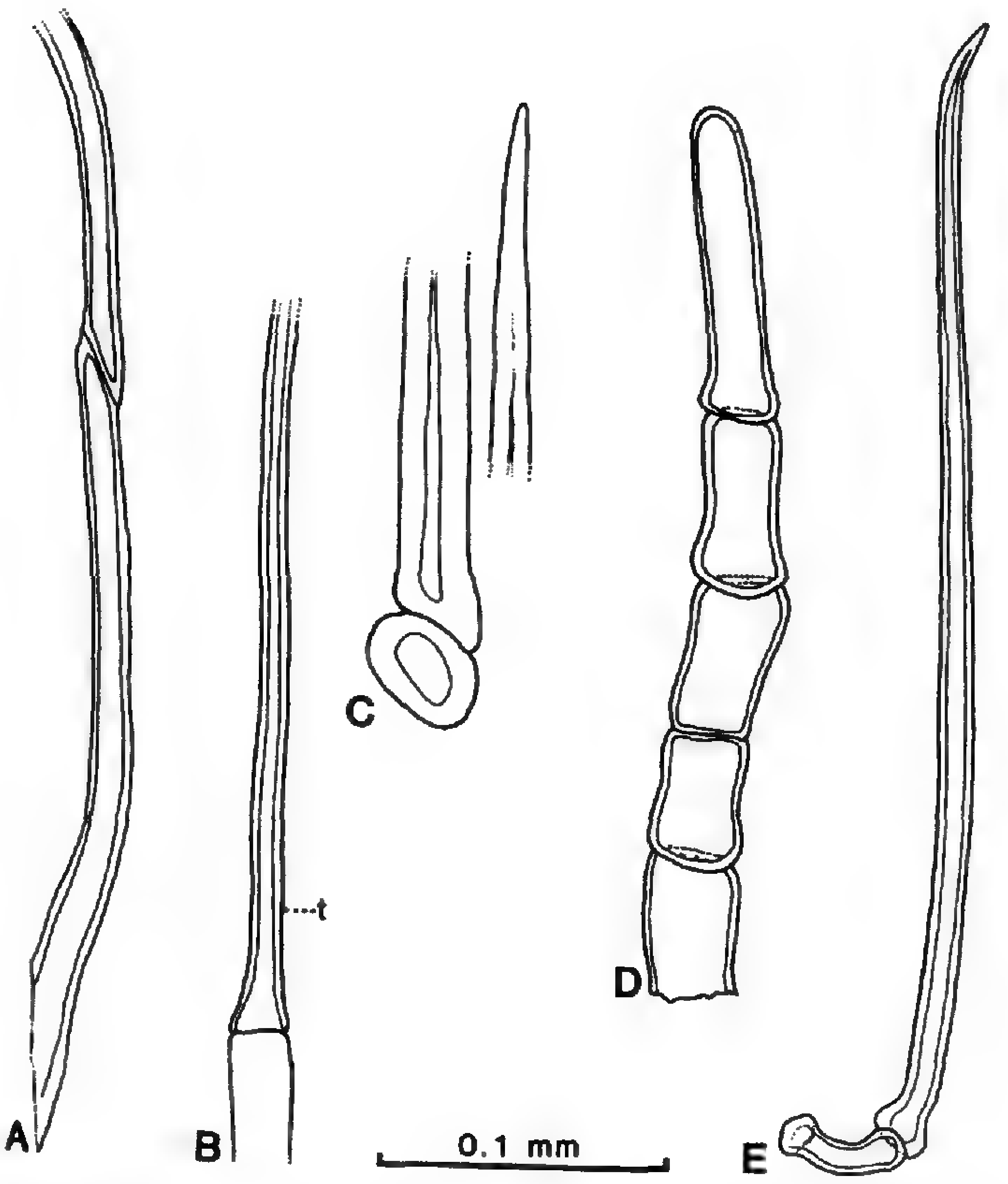

FIGURE 5. Simple corolla hairs.—A. Cell walls oblique.—B. Walls in ultimate cell much thicker than in the cell below, marked t.—C. With basal cell.—D, E. Walls straight. (A. *Mutisia clematis, Killip & Smith 19600*; B, *Scolymus hispanicus, Starbäck 119*; C, *Dasyphyllum reticulatum, Hatschbach 27243*; D, *Pluchea camphorata, Jansson s.n.*; E, *Pluchea lanceolata, Meebold 11036.*)

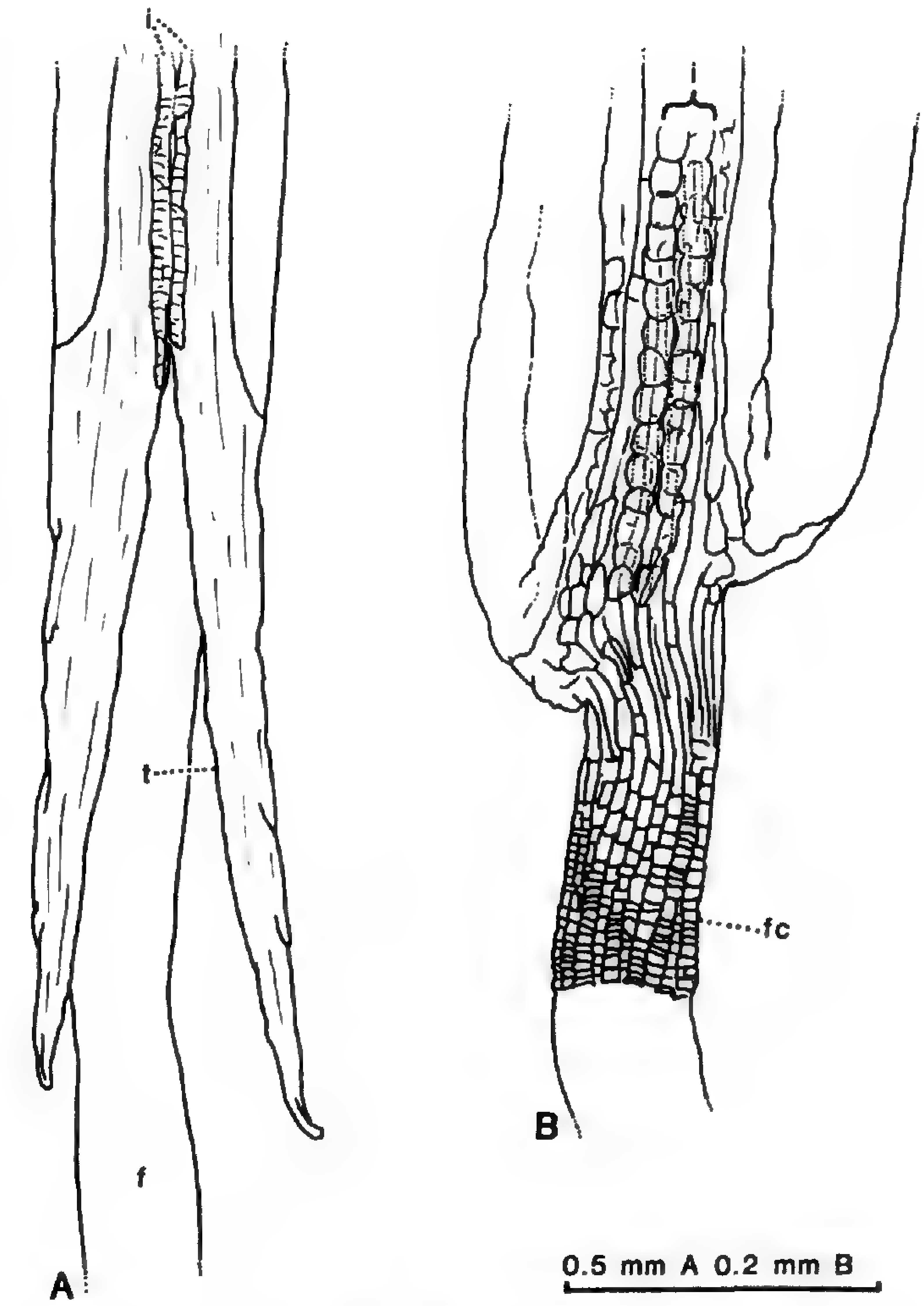

FIGURE 6. Features of anther bases.—A. Calcarate, caudate, i = inner pollen sacs, opened, oriented toward the observer, t = sterile tail, f = filament.—B. Ecalcarate, ecaudate, i = inner pollen sacs, oriented toward the observer, fc = filamental collar. (A, *Lycoseris latifolia, Breteler 4414*; B, *Geissolepis suadaefolia, Pringle 3762.*)

Some poorly understood genera were included to refine hypotheses about their placement.

Genera used as a basis for coding terminal taxa are given in Appendix I. A list of specimens examined is available from P. O. Karis. All material cited in the figure legends is housed in S, except for a specimen of *Inula inuloides*, which is housed in K.

Wagner parsimony analyses were performed using HENNIG 86 (Farris, 1988). In all analyses, options mhennig* and bb* were applied to provide the most extensive heuristic option available. All multistate characters are treated as unordered. Some multistate characters include states that may be correlated. The details of the analyses are discussed further below. Polarization was determined by the outgroup comparison method (Stevens, 1980; Maddison et al., 1984).

DATA ANALYSIS AND RESULTS

Running our entire initial matrix causes a computer memory overflow because of numerous equally parsimonious solutions. Therefore, we have performed a series of more than 100 analyses with reductions of taxa, in order to explore the phylogenetic information in the matrix (similar to those of Doyle & Donoghue, 1986). Using this approach (detailed below), we hypothesize relationships of the Cichorioideae tribes, although generic relationships remain uncertain.

Numerous equally parsimonious trees are a major problem with analyses of large data matrices. Strict consensus trees of these equally parsimonious trees may be uninformative. A single unstable taxon may cause the strict consensus tree to collapse. Adams's (1973) consensus trees are less sensitive to unstable taxa, but conceptually more difficult to evaluate in a phylogenetic context. For example, an Adams consensus tree may contain branching sequences that are not present in any of the equally parsimonious cladograms.

Initially, eight genera of Mutisieae–Barnadesiinae were included as the outgroup, but various equally parsimonious arrangements among these genera multiplied the number of ingroup solutions. The outgroup was replaced subsequently with a hypothetical ancestor based on these Barnadesiinae. In cases of variation among the outgroup genera, coding followed the states of Calyceraceae, Goodeniaceae, Campanulaceae, and Lobeli-

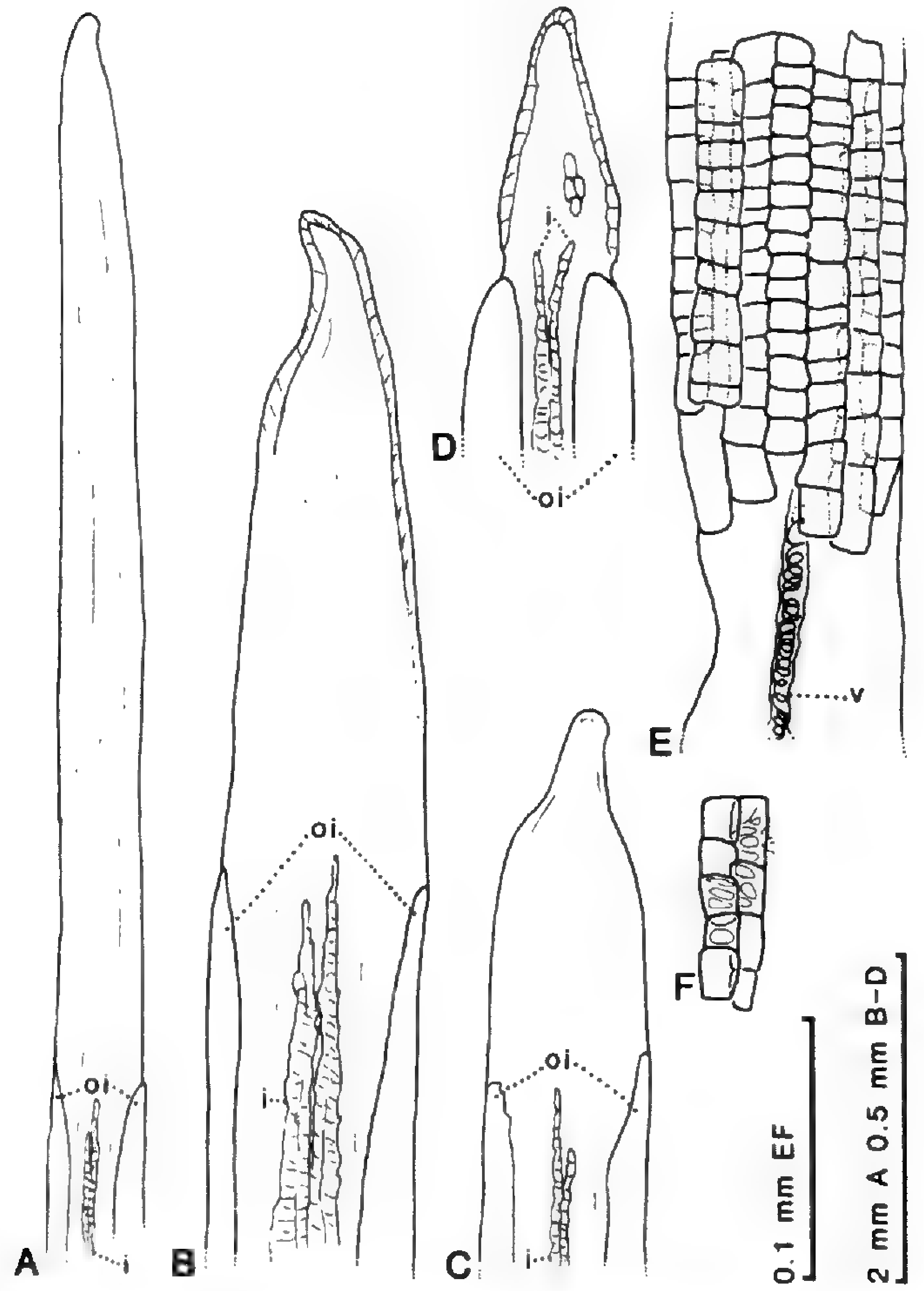

FIGURE 7. Features of anther appendages and collar, i = inner pollen sacs, opened and faced toward the observer, oi = outer and inner pollen sacs, without a distinct limit in between.—A, B. Long appendage.—C. Medium appendage.—D. Short appendage.—E. Conspicuous collar, v = vein.—F. Collar cells with transverse thickenings. (A, *Mutisia acuminata, Hutchison 1044*; B, *Dicoma picta, Dinter 8253*; C, *Gochnatia rupestris, Malme 2417*; D, *Aster simplex, Jones 32876*; E, *Inula helenium, Wall s.n.*; F, *Lactuca muralis, Karis & Källersjö s.n.*)

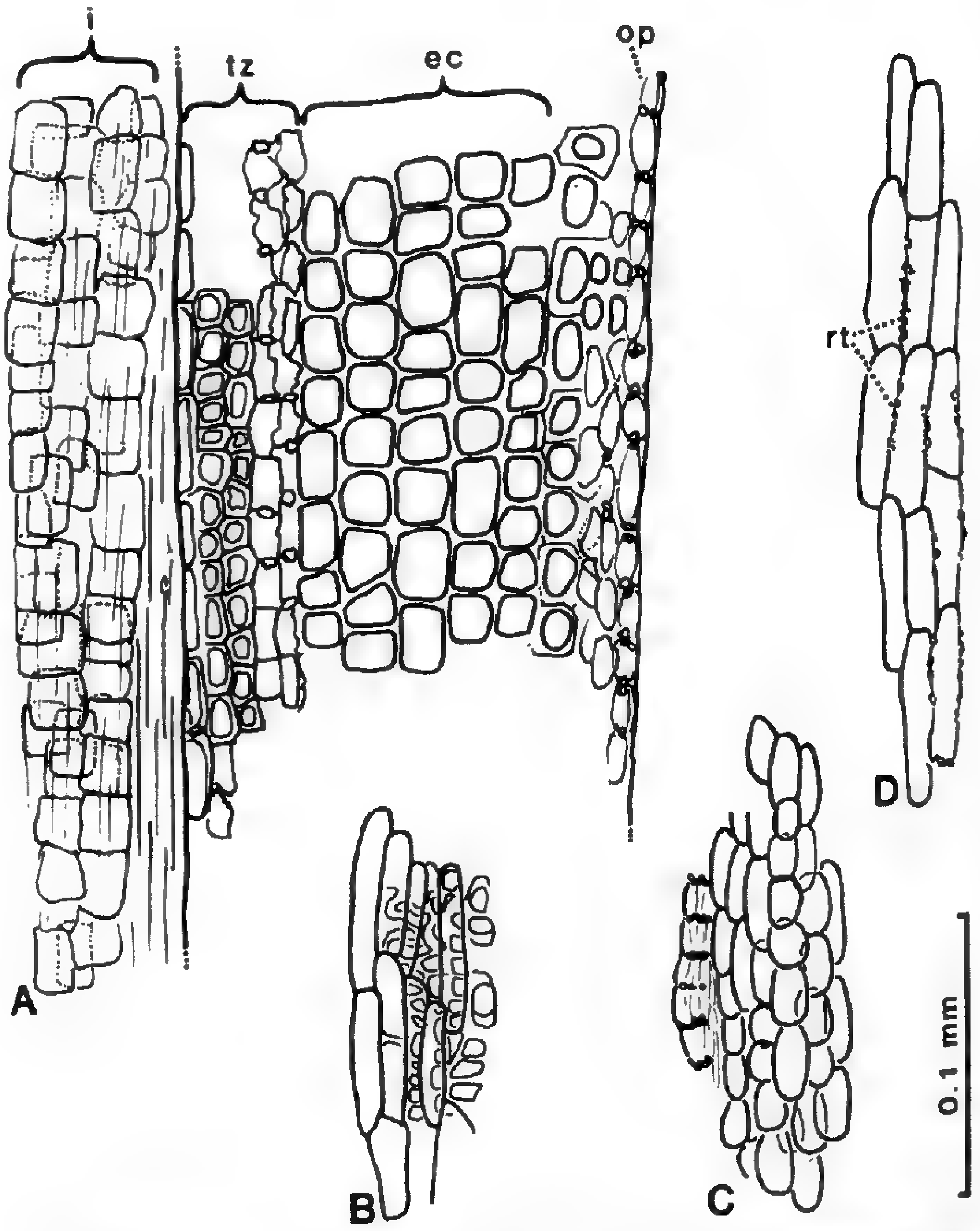

FIGURE 8. Endothecial tissues.—A. Cardueae-Carduinae, i = inner pollen sacs, opened, faced toward the observer, tz = transition zone between connective and pollen sacs, partly seemingly polarized, ec = endothecial cells typical for the Cardueae-Carduinae, op = outer pollen sac, polarized at the edge.—B. Lactuceae, transversal bands.—C. Mutisieae and Cardueae sens. lato, with polarized thickenings at the edges of the pollen sacs.—D. Barnadesiinae, rt = radial thickenings. (A, *Carduus nutans, Wall s.n.*; B, *Lactuca muralis, Karis & Källersjö s.n.*; C, *Gochnatia rupestris, Malme 2417*; D, *Dasyphyllum candolleanum, Irwin, Souza & dos Santos 7960.*)

aceae. When families outside Asteraceae could not be used to decide among coding variants for the hypothetical ancestor, character states were coded as "inapplicable" in the outgroup. Analysis using the hypothetical ancestor continued to result in large numbers of trees in which taxa moved within the same subclade of the different cladograms.

We ascertained stable configurations of taxa and unstable genera that were subsequently excluded. Finally, some genera, e.g., *Senecio, Aster, Geissolepis,* and *Cirsium,* were added in order to stabilize the Asteroideae and the Cardueae; in previous analyses the position of clades such as Asteroideae and Cardueae (sens. str.) was influenced by the choice and number of genera included.

Following experimental taxon deletion and addition, the data matrix consisted of 53 genera and 72 characters (with taxon reduction some characters became uninformative and were deleted). Two equally parsimonious cladograms (one shown in Fig. 1), 419 steps long, resulted from this matrix. The two cladograms differ only in the position of *Onoseris,* which is placed as the sister group of the taxa above node 17 in the alternative. The consistency index is 0.24 and the retention index 0.57.

Our cladogram (Fig. 1) is obviously partly in conflict with earlier schemes. Alternative topologies consistent with prior classifications and earlier cladistic analyses (e.g., Bremer, 1987; Jansen et al., 1990) were investigated using the xx-command in HENNIG 86. More complicated rearrangements, such as forcing monophyly of Mutisieae (excluding the Barnadesiinae) and the entire Cichorioideae, were achieved using heavily weighted dummy characters to produce the desired topology (the steps added by the dummy character were deleted in computing tree length).

Forcing monophyly of the entire subfamily Ci-

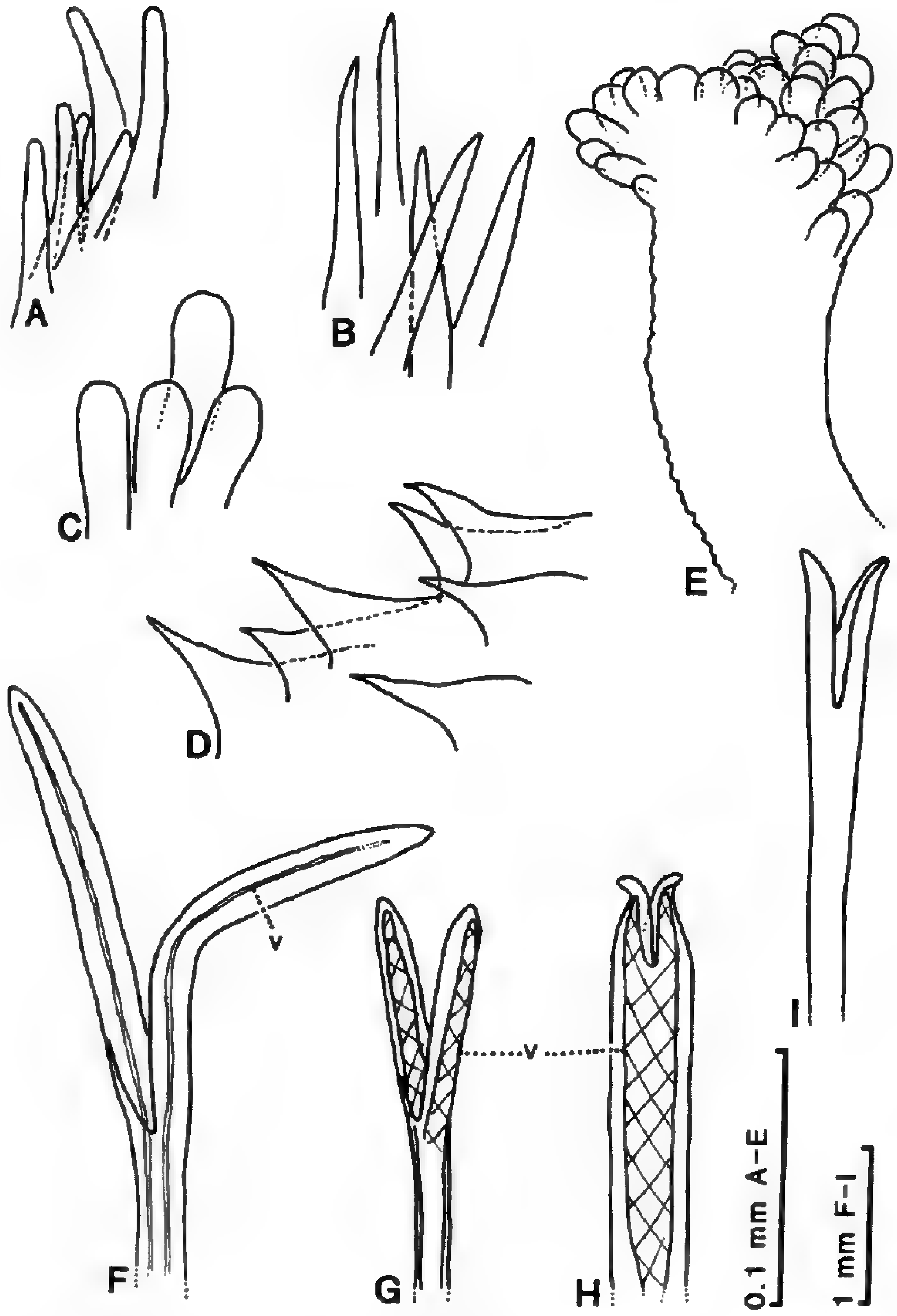

FIGURE 9. Features of styles and nature of sweeping hairs, v = vein.—A. Narrow obtuse sweeping hairs.—B. Narrow acute sweeping hairs.—C. Broad obtuse sweeping hairs.—D. Broad acute sweeping hairs.—E. Anthemoid style, with sweeping hairs only apically, typical for Nassauviinae and many Asteroideae.—F. Style with long, gradually tapering branches with narrow veins.—G. Style with long branches with thick veins (hatched).—H. Style with short branches with thick veins (hatched).—I. Style with short branches. (A, I, *Lulia nervosa, Hatschbach 23205*; B, *Chaetanthera elegans, Eyerdam 10725*; C, F, *Distephanus aurantiacus, La Croix 3024*; D, *Scolymus hispanicus, Starbäck 119*; E, *Helichrysum aureolum, Hilliard & Burtt 14369*; G, *Inula inuloides, Davis 24353* [K]; H, *Dicoma burmannii, Hafström & Acocks 2284.*)

chorioideae, in agreement with Jansen et al.'s (1990) results, requires 12 extra steps. Making the tribe Mutisieae monophyletic, excluding *Pertya* and *Warionia*, requires nine extra steps. Moving *Warionia* or *Pertya* to the main Mutisieae branch, below *Brachylaena* in Figure 1, requires ten and five extra steps, respectively. Moving *Arctotis* to the Cardueae sensu lato, in agreement with Bremer's (1987) results, requires five extra steps, and moving *Berkheya* to *Arctotis*, making the Arctotideae monophyletic, requires four extra steps.

Most of Jansen et al.'s Wagner trees are similar in outline to our cladogram, with the Cichorioideae paraphyletic and Mutisieae and Cardueae sensu

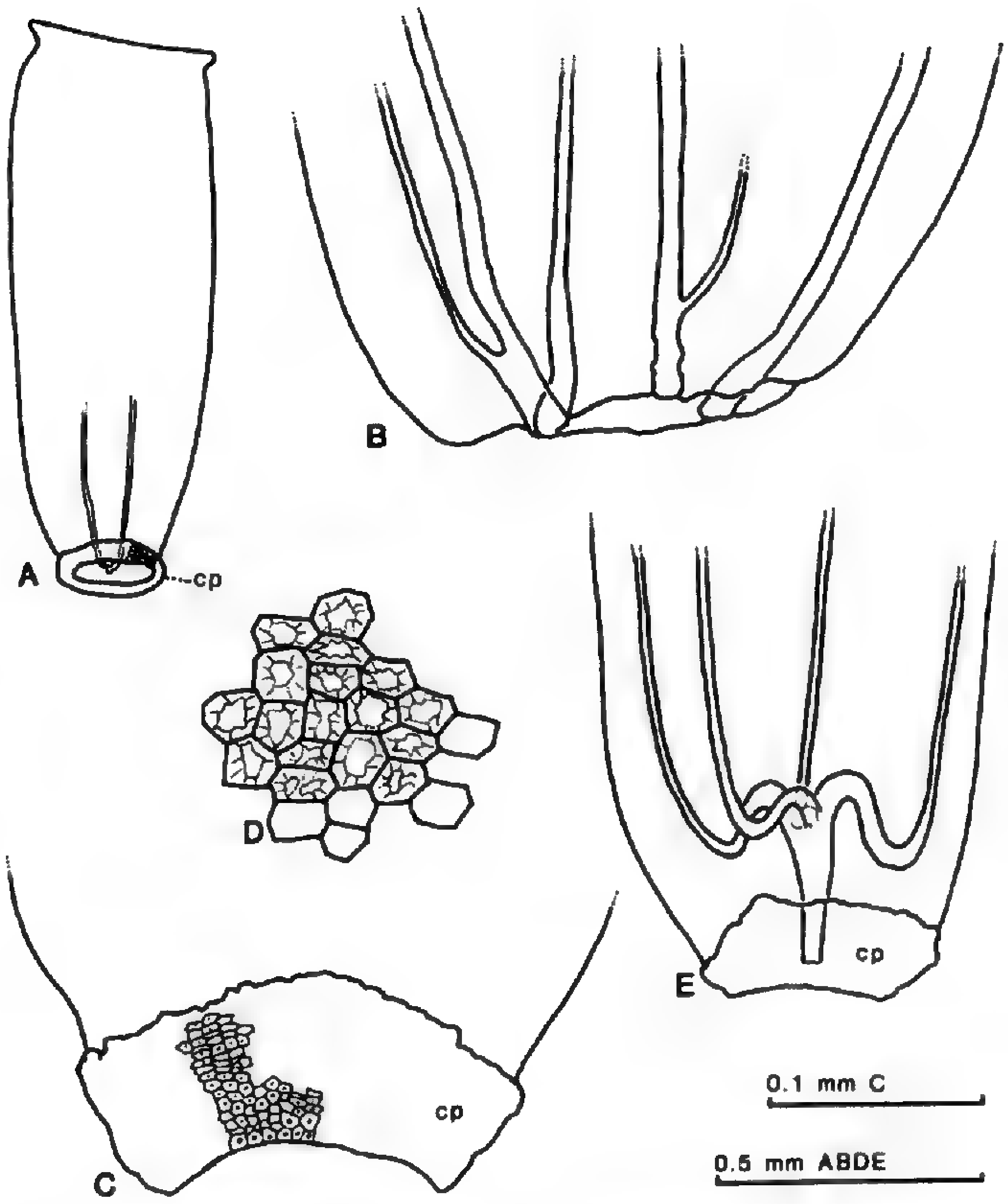

FIGURE 10. Features of cypselas, cp = carpopodium.—A. Two-veined cypsela with a small carpopodium, veins uniting within the base.—B. Cypsela without a carpopodium, veins uniting below the cypsela base.—C. Well-developed carpopodium consisting of sclerified cells.—D. Magnification of cells in C.—E. 5-veined cypsela, veins uniting within the base, carpopodium well developed. (A, *Helichrysum arenarium, Rechinger 666*; B, *Dasyphyllum candolleanum, Irwin, Souza & dos Santos 7960*; C, D, *Pertya scandens, Furuse s.n.*; E, *Vernonia novaboracensis, Wilkens 4255.*)

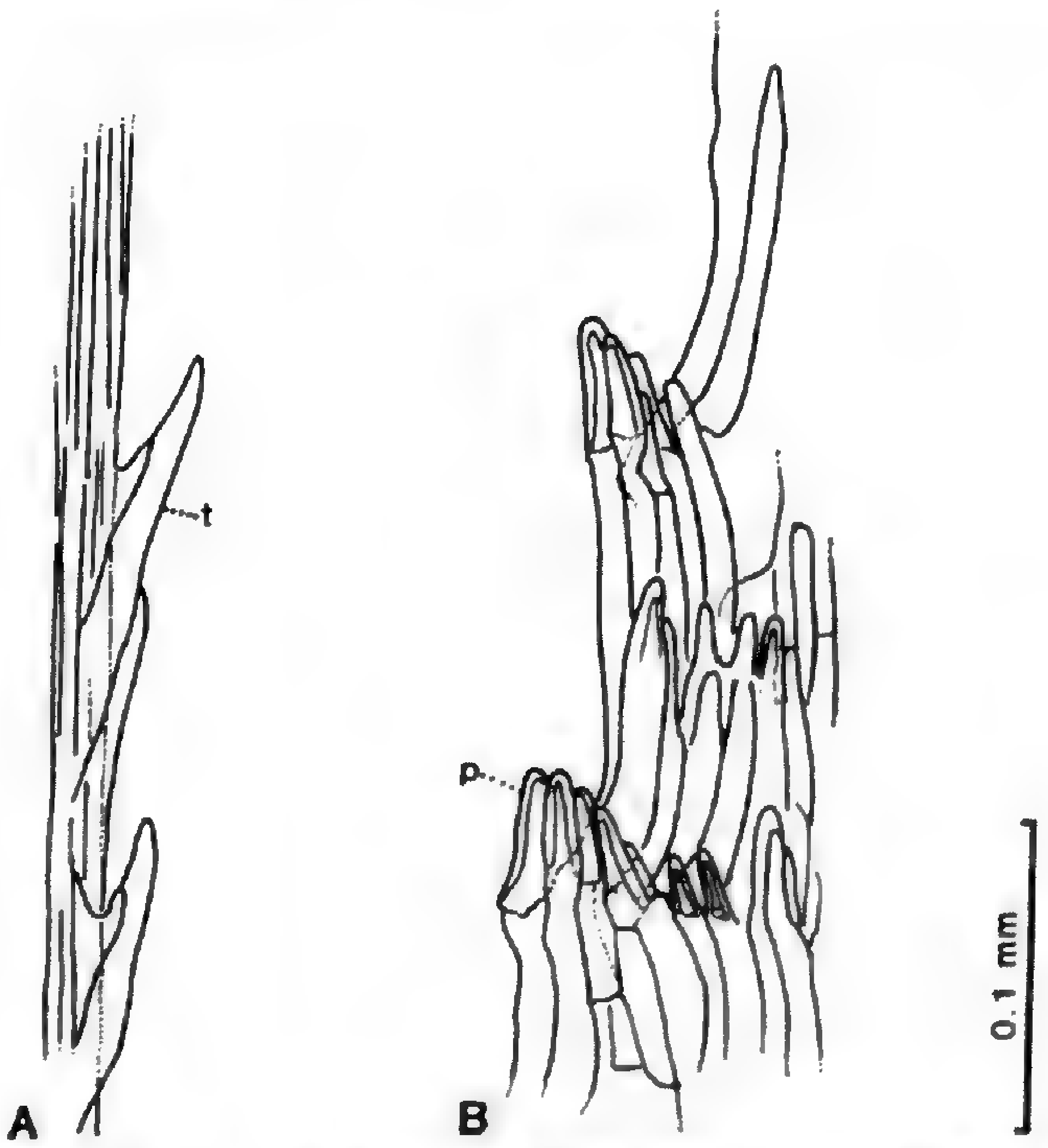

FIGURE 11.—A. Pappus bristle teeth consisting of the top of one cell together with the base of the adjacent marginal cell, t = tooth.—B. Epicarp with finlike arranged papillae, p = papillae. (A, *Actinoseris radiata, Hatschbach 27447*; B, *Hypochoeris glabra, Klackenberg & Lundin 253.*)

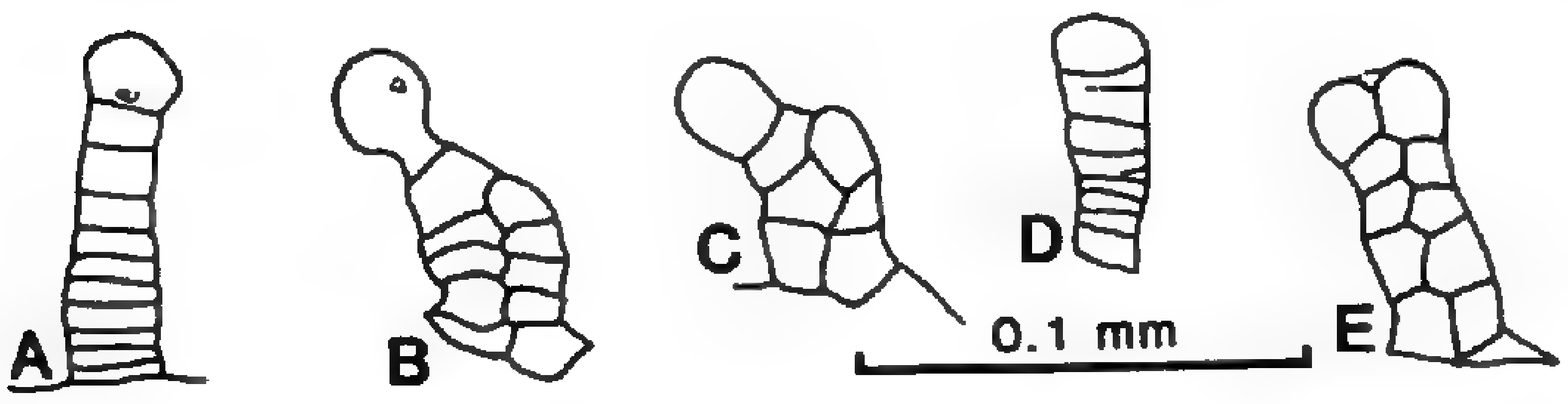

FIGURE 12. Glands of the Nassauviinae.—A. *Trixis divaricata* (*Mexia 8110*).—B. *Jungia axillaris* (*Chavez 3260*).—C. *Leucheria leontopodioides* (*Santesson 469*).—D. *Acourtia vanillosma* (*Ekman 43034*).—E. *Trixis brasiliensis* (*Malme 1124*).

lato at the base. Eight of their Wagner trees and the Dollo trees, with the Cichorioideae monophyletic, are incongruent with our results. The cause for the difference between Jansen et al.'s Dollo trees and the Wagner trees based on morphology and cpDNA data (i.e., 12 out of 20) remains obscure. We find no morphological or chemical features to corroborate the monophyly of Cichorioideae.

CONCLUSIONS

Our analyses support the placement of Mutisieae as a basal assemblage of the family, but the tribe is paraphyletic even without the Barnadesiinae. A monophyletic Mutisieae is an unparsimonious solution using morphological data. A large part of the Mutisieae, including the Nassauviinae, most of the Mutisiinae, and part of the Gochnatiinae, form a monophyletic group, but its exact circumscription requires study.

The placement of the genera cannot be established with certainty because the most parsimonious cladogram differs from other alternatives only few steps longer. However, all Mutisieae genera included in the analyses consistently form a basal assemblage; hence there is no basis for transfer of any Mutisieae except *Warionia* to other tribes. Moving *Warionia* to the Mutisieae branch in the cladogram is highly unparsimonious, but it cannot immediately be assigned to any other tribe.

The subtribe Nassauviinae is monophyletic, and part of the Mutisiinae also forms a monophyletic group. The Gochnatiinae are paraphyletic and form a basal complex in the family. This complex includes several isolated genera that presumably evolved early in the history of the family. These genera include *Stenopadus* and discoid derivatives (the bilabiate *Gongylolepis* and its satellite genera may or may not be immediately related) from the Guyana Highlands, *Hesperomannia* from Hawaii, *Wunderlichia* from Brazil, *Ainsliaea* from East Asia, the presumably artificial genus *Gochnatia* (cf. Appendix I) from Central and South America and Southeast Asia, and *Brachylaena* (with *Tarchonanthus*) from Africa. The scattered distributions of these elements also suggest that they represent ancient relicts from the early evolution of the family. It is not surprising that these genera form a basal grade, since they share numerous symplesiomorphies with the Barnadesiinae.

The Cardueae sensu lato, including *Berardia*, *Carlina*, *Echinops*, and their relatives (Carlineae and Echinopeae of Dittrich, 1977) form a monophyletic group. Many similarities between the Cardueae and the Mutisieae are symplesiomorphies, including pluriseriate involucral bracts, actinomorphic and deeply 5-lobed corollas, and anthers with long, sclerified, sometimes acuminate, apical appendages. The Arctotideae are not closely related to the Cardueae sensu lato as assumed by earlier authors. They form a monophyletic group consisting of four tribes, Arctotideae, Lactuceae, Liabeae, and Vernonieae, as well as the subfamily Asteroideae. Relationships within this group cannot be resolved with certainty. Hence the sister group of the subfamily Asteroideae cannot be identified, although our data strongly indicate that it is to be found among the tribes Arctotideae, Lactuceae, Liabeae, and Vernonieae. Placing a monophyletic Cichorioideae as the sister group of Asteroideae is highly unparsimonious for morphological data.

The Liabeae and the Vernonieae do not form a clade in this study, but this may result from sampling problems and the choice not to code "liaboid pollen" for these taxa (as was done by Bremer, 1987, referring to Skvarla et al., 1977).

Significantly, our results show the basal position and the paraphyly of Mutisieae, the position of the Cardueae, and the presence of the monophyletic group mentioned above, consisting of the tribes Arctotideae, Lactuceae, Liabeae, and Vernonieae, as well as the subfamily Asteroideae. Our analyses did not focus on the sister group relationship of the Asteroideae but did indicate that it is not to be found within the Mutisieae or the Cardueae. We consider a new classification based on this analysis premature because tribal relationships above the basal Mutisieae–Cardueae remain uncertain.

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APPENDIX I. Genera used as terminal taxa in the analysis and species used as the basis for coding. Generic types are marked with an asterisk (*).

Mutisieae–Barnadesiinae.

Barnadesia Mutis in L. f.: *B. dombeyana* Less., *B. horrida* Muschler, *B. parviflora* Spruce ex Benth. & Hook. f., *B. rosea* Lindl.

Chuquiraga Juss.: *C. aurea* Skottsberg, **C. jussieui* J. F. Gmel., *C. kingii* Ball, *C. macrocephala* Baker, *C. rotundifolia* Wedd.

Dasyphyllum HBK: *D. candolleanum* (Gardn.) Cabr., *D. ferox* (Wedd.) Cabr., *D. leptacanthum* (Gardn.) Cabr., *D. reticulatum* (DC.) Cabr., *D. velutinum* (Baker) Cabr.

Mutisieae–Gochnatiinae.

Actinoseris (Endl.) Cabr.: *A. angustifolia* (Gardn.) Cabr., **A. radiata* (Vell.) Cabr.

Ainsliaea DC.: *A. acerifolia* Sch.-Bip., *A. pteropoda* DC.

Cnicothamnus Griseb.: **C. lorentzii* Griseb.

Dicoma Cass.: *D. anomala* Sond., *D. antunesii* O. Hoffm., *D. argyrophylla* Oliv., *D. burmannii* Less., *D. capensis* Less., *D. galpinii* F. C. Wilson, *D. picta* (Thunb.) Druce, *D.* (*Hochstetteria*) *schimperi* (DC.) Baill., **D. tomentosa* Cass.

Erythrocephalum Benth. in Benth. & Hook. f.: **E. zambesiacum* Oliv. & Hiern.

Gochnatia HBK: *G. argentina* Cabr., *G. argyrea* (Dusén ex Malme) Cabr., *G. avicenniifolia* (DC.) Cabr., *G. barrosoii* Cabr., *G. cordata* Less., *G. cowellii* (Britt.) Jervis & Alain, *G. discoidea* (Less.) Cabr., *G. microcephala* (Griseb.) Jervis & Alain, *G. paniculata* (Less.) Cabr., *G. picardae* (Urb.) Jiménez.

Gongylolepis R. H. Schomb.: **G. benthamiana* R. H. Schomb., *G. paniculata* Maguire & Phelps.

Hesperomannia A. Gray.: **H. arborescens* A. Gray.

Oldenburgia Less.: *O. grandis* (Thunb.) Baill., **O. paradoxa* Less., *O. papionum* DC.

Onoseris Willd.: *O. gnaphalioides* Muschler, *O. odorata* H. & A., *O. onoseroides* B. L. Robinson, *O. speciosa* HBK.

Pertya Sch.-Bip.: *P. glabrescens* Sch.-Bip., *P. phylicoides* J. F. Jeffrey, **P. scandens* Sch.-Bip.

Plazia Ruiz & Pavon: *P. daphnoides* Wedd.

Pleiotaxis Steetz: **P. pulcherrima* Steetz, *P. racemosa* O. Hoffm., *P. rugosa* O. Hoffm.

Stenopadus Blake: *S. campestris* Maguire & Wurdack, *S. chimantensis* Maguire, Steyermark & Wurdack.

Stifftia Mikan: **S. chrysantha* Mikan.

Wunderlichia Riedel: *W. crulziana* Taub., *W. tomentosa* Glaziou.

Mutisieae–Mutisiinae.

Chaetanthera Ruiz & Pavon: *C. acerosa* (Remy.) Benth. & Hook., *C. elegans* Phil., *C. euphrasioides* Meigen, *C. glabrata* (DC.) Meigen, *C. pentacaenoides* Hauman, **C. villosa* D. Don.

Gerbera L.: *G. ambigua* (Cass.) Sch.-Bip., *G. jamesonii* Bolus ex Adlam, **G. linnaei* Cass.

Hyaloseris Griseb.: *H. camataquensis* Hieron. ex Koster, *H. cinerea* (Griseb.) Griseb.

Lulia Zardini: **L. nervosa* (Less.) Zardini.

Mutisia L. f.: *M. acerosa* Poepp. ex Less., *M. acuminata* Ruiz & Pavon, *M. clematis* L. f., *M. ledifolia* Decne ex Wedd.

Trichocline Cass.: *T. auriculata* (Wedd.) Hieron.

Mutisieae–Nassauviinae.

Jungia L. f.: *J. axillaris* (DC.) Sprgl, *J. floribunda* Less., *J. paniculata* (DC.) Gray.

Leucheria Lag.: *L. cerberoana* Remy, *L. floribunda* DC., *L. leontopodioides* (O. Kuntze) K. Schumann.

Lophopappus Rusby: *L. blakei* Cabr., **L. foliosus* Rusby.

Macrachaenium Hook. f.: **M. gracile* Hook. f.

Nassauvia Comm. ex Juss.: *N. abbreviata* Dusén, *N. acerosa* (Meyen) Wedd., *N. darwinii* O. Hoffm. & Dusén, *N. lagascae* Meigen, **N. magellanica* Gmel.

Trixis P. Browne: *T. auriculata* Hook., *T. brasiliensis* DC., *T. cacalioides* (HBK) D. Don, *T. californica* Kellogg.

Arctotideae.

Arctotis L.: **A. angustifolia* L., *A. hirsuta* (Harv.) Beauv., *A. venusta* T. Norl.

Berkheya Ehrh.: *Berkheya* represents the Arctotideae–Gorteriinae (Roessler, 1959). *B. armata* (Vahl) Druce, *B. bipinnatifida* (Harv.) Roessler ssp. *bipinnatifida*, *B. canescens* DC., *B. heterophylla* (Thunb.) O. Hoffm.

Cardueae.

Carlina L.: *C. acaulis* L., *C. corymbosa* L., *C. salicifolia* Cav., **C. vulgaris* L.

Carduus L.: *C. argyroa* Biv., *C. carpetanus* Boiss. & Reuter, *C. crispus* L., **C. nutans* L.

Cirsium L.: *C. pitcheri* Torr. & Gray, *C. vulgare* L.

Echinops L.: *E. angustilobus* S. Moore, *E. longifolius* A. Rich., **E. sphaerocephalus* L., *E. strigosus* L.

Saussurea DC.: **S. alpina* L., *S. amabilis* Kitamura, *S. chondrilloides* C. Winkl.

Vernonieae.

Distephanus Cass.: *D. divaricatus* (Steetz) H. Robinson & H. Kahn.

Vernonia Schreb. sens. str.: *V. glabra* (Steetz) Vatke, **V. nova-boracensis* (L.) Willd.

Liabeae.

Liabum Adans.: *L. igniarium* (HBK) Less., *L. solidagineum* (HBK) Less.

Munnozia Ruiz & Pavon: *M. hastifolia* (Poepp. & Endl.) H. Robinson & R. D. Brettell, *M. lanceolata* Ruiz & Pavon, *M. senecionidis* Benth.

Lactuceae.

Hypochoeris L.: *H. glabra* L., *H. maculata* L.

Lactuca L.: *L. canadensis* L., *L. muralis* L., **L. sativa* L.

Scolymus L.: *S. grandiflorus* Desf., *S. hispanicus* L., **S. maculatus* L.

Sonchus L.: *S. arvensis* L., *S. congestus* Willd.

Inuleae.

Inula L.: **I. helenium* L.

Gnaphalieae.

Helichrysum Mill.: *H. arenarium* (L.) Moench, *H. areolum* Hilliard, *H. auriceps* Hilliard, **H. orientale* (L.) Gaertn.

Plucheeae.

Pluchea Cass.: *P. camphorata* DC., *P. lanceolata* Oliv. & Hiern, *P. odorata* Cass.

Astereae.

Aster L.: *A. simplex* Willd., *A. tripolium* L.
Geissolepis B. L. Robinson: **G. suaedaefolia* B. L. Robinson.

Senecioneae.

Senecio L.: **S. vulgaris* L.

Taxa of uncertain position.

Berardia Vill.: **B. subacaulis* Vill.
Brachylaena R. Br.: **B. neriifolia* (L.) Less.
Eremothamnus O. Hoffm.: **E. marlothianus* O. Hoffm.
Warionia Benth. & Coss.: **W. saharae* Benth. & Coss.

APPENDIX II. Characters. The plesiomorphic states are coded as 0, apomorphic states as 1, 2, etc.

1. Habit: woody (0), perennial/annual herbs (1).
2. Leaf position: alternate (0), opposite (1), rosulate (2).
3. Leaves: not spiny (0), spiny (1). The spinulose leaf margins in many Lactuceae are not coded as spines.
4. Leaf trichomes: without woolly hairs (0), with woolly hairs ("type B" of Drury & Watson, 1966) (1).
5. Leaf margin: entire (0), serrate to dentate or pinnatisect (1).
6. Leaf texture: herbaceous (0), coriaceous, glossy (1).
7. Leaf shape: ovate to lanceolate (0), broadly obovate, obtuse-cuneate (1).
8. Leaf veins: even with leaf surface (0), submerged (1).
9. Involucral bracts: pluriseriate (0), 1–3 seriate (1).
10. Involucral bract margins: not scarious (0), scarious (1).
11. Involucral bract morphology: homogeneous (0), divided into a basal stereome and an apical lamina (1).
12. Involucral bract apex: acute (0), rounded, obtuse and ± broad (1).
13. Involucral bract texture/venation: coriaceous to herbaceous, thick, venation inconspicuous (0), thin, with several parallel veins (1).
14. Receptacle: epaleate (0), paleate (1).
15. Floret dimorphism: absent (0), present (1). We interpret the occurrence of two kinds of florets in the same head as a synapomorphy, regardless whether the florets are rays, actinomorphic, bilabiate, etc. Since the Barnadesiinae vary in this instance, the condition in adjacent outgroups was taken into consideration (Watrous & Wheeler, 1981; Maddison et al., 1984). It is important to remember that the Asteraceae heads are inflorescences, and as such are comparable to other inflorescences. The different kinds of florets are distinguished in the multistate character 16.
16. Marginal/central floret organization: only actinomorphic (0), bilabiate/actinomorphic (Fig. 2C/A) (1), bilabiate/bilabiate (Fig. 2C/C) (2), true rays/actinomorphic (Fig. 2G/A) (3), ligules (Fig. 2F) (4), Gorteriinae-rays/actinomorphic (Fig. 2B/A) (5), tubular/actinomorphic (Fig. 2D/A) (6). This multistate character is formulated in such a way as to separate nondiscoid heads into distinct groups. Actinomorphic deeply 5-lobed corollas (Fig. 3A, C) are interpreted as plesiomorphic, following Bremer's (1987) argument. Gorteriinae-rays (Fig. 2B) are an autapomorphy for the Arctotideae–Gorteriinae (Bremer, 1988).
17. Floret morphology: bilabiate (Fig. 2C) or true rays (Fig. 2G) absent (0), bilabiate or true rays present (1). Rays are often thought to have evolved from bilabiate corollas, where the two ventral lobes are reduced (Jeffrey, 1977; Bremer, 1987, 1988), but ligules presumably have evolved directly from actinomorphic corollas.
18. Marginal floret sex: hermaphroditic (0), female (1), neuter (2).
19. Disc corolla lobes: long, narrowly triangular (Fig. 3A, C) (0), short, ± deltoid (Fig. 3B) (1).
20. Disc corolla tube: short, thick (0), long, slender (Fig. 3C, Dittrich, 1977) (1).
21. Disc corolla vein bifurcation: well below the lobes (0), adjacent to the lobes (1).
22. Disc corolla lobe venation: without a midvein (0), with a midvein (1).
23. Disc corolla lobe venation: without thick-bundled apical veins (0), with thick-bundled apical veins (1).
24. Long corolla glandular hairs (Fig. 4H, cf. 4I): absent (0), present (1).
25. Corolla hairs: absent (0), simple multicellular with oblique walls (Fig. 5A) (1), simple multicellular with straight walls (Fig. 5D, E) (2), simple multicellular, ultimate cell with much thicker walls (Fig. 5B) (3).
26. Zygomorphic marginal floret (rays, bilabiate, ligules) epidermal cell outline (Baagøe, 1977a, b, 1978): narrowly oblong (0), tabular (1), rounded (2).
27. Zygomorphic marginal floret (rays, bilabiate, ligules) epidermal cell cuticle ornamentation (Baagøe, 1977a, b, 1978): none (0), transversely striate (1), longitudinally striate (2), intestinelike (H. V. Hansen, Copenhagen, unpublished) (3).
28. Zygomorphic marginal floret (rays, bilabiate, ligules) epidermal cell surface (Baagøe, 1977a, b, 1978): flat (0), crested (1), papillose (2).
29. Apical anther appendage length: at least three times as long as wide (Fig. 7A, B) (0), at least twice as long as wide (Fig. 7C) (1), up to twice as long as wide (Fig. 7D) (2).
30. Apical anther appendage outline: rounded to acute (0), acuminate to apiculate (1).
31. Filament collar cell wall thickenings (King & Robinson, 1987; Fig. 7F): absent (0), present (1).
32. Apical anther appendage texture: sclerified (0), nonsclerified (1), soft (2).
33. Endothecial cell wall thickening organization: on the lateral walls (radial, Fig. 8D; Dormer, 1962; Nordenstam, 1978, Vincent & Getliffe, 1988; Thiele, 1988) or with transverse bands (Fig. 8B) (0); with thickenings on the cell ends (polarized, with or without vertical bands, Robinson, 1977; Fig. 8A, C, at the edge of the pollen sacs) (1), without thickenings (2), outer pollen sacs with large rectangular cells with semicircular to elliptic inner walls (Fig. 8A) (3).
34. Endothecial cell wall thickening organization: polarized (0), with vertical bands (1).
35. Endothecial cell wall thickening organization: radial (0), with transverse bands (1).
36. Anther thecae base morphology (Robinson, 1983; Bremer, 1987): calcarate (0), ecalcarate (Fig. 6B) (1).
37. Anther thecae base morphology (Robinson, 1983; Bremer, 1987): ecaudate (0), caudate (1).
38. Filament collar: inconspicuous or absent (0), conspicuous (Figs. 6B, 7E) (1), swollen (2).
39. Filament surface: smooth (0), papillose or hairy (1).

40. Filament vein arrangement: running throughout, uninterrupted (0), in distinct groups without connection in between (1).
41. Pollen exine (Leins, 1971; Skvarla et al., 1977; Bolick, 1978): ecaveate (0), caveate (1).
42. Pollen surface: smooth (0), granular (1), spiny (2).
43. Pollen surface sculpturing: smooth to echinate (0), lophate to echinolophate (1).
44. Pollen exine columellae anatomy (Skvarla et al., 1977): unperforated (0), with internal foramina (1).
45. Style branch length: short (Fig. 9H, I) (0), long (Fig. 9F, G) (1). Some genera in the Cardueae have clearly secondarily fused style branches and have been coded as having long branches.
46. Style apex outline: rounded (0), tapering gradually toward the top (Fig. 9F) (1), truncate (Fig. 9E) (2).
47. Stigmatic surface: entire (0), in two apically confluent lines (1), in two separate lines (2).
48. Stylar sweeping hair shape: styles papillose or without sweeping hairs (0), broad, obtuse (Fig. 9C, E) (1), broad, acute (Fig. 9D) (2), narrow, acute (Fig. 9B) (3), narrow, obtuse (Fig. 9A) (4).
49. Stylar sweeping hair position: without sweeping hairs (0), reaching below the bifurcation (1), ± covering the abaxial surface of style branches, not reaching below the bifurcation (2), in a subapical tuft of style branches (3), in an apical tuft (4), in a ring below the bifurcation (5).
50. Style branch veins: very thick (Fig. 9G, H) (0), narrow (9F) (1).
51. Style base: not swollen (0), swollen (1).
52. Style apex: as wide as the rest of the style (0), conspicuously thickened (1).
53. Style apical appendage: absent (0), present (1).
54. Cypsela shape: terete to prismatic (0), compressed (1).
55. Cypsela carpopodium (Fig. 10A, D, E): absent (0), present (1).
56. Cypsela pericarp: not rugose (0), rugose (1).
57. Cypsela epicarp papillae arrangement: papillae absent or individually arranged (0), finlike (Fig. 11B) (1).
58. Cypsela twin hairs: absent (0), ± long (1), deeply cleft (Fig. 4A) (2), short, narrowly ovoid (myxogenic) (Fig. 4C–G) (3).
59. Cypsela glands: biseriate with a collapsing head (0), compact, persistent, uni- or biseriate, generally with a spherical ultimate cell (Fig. 12) (1).
60. Cypsela vein union: below the base (Fig. 10B) (0), at the base (Fig. 10A, E) (1).
61. Cypsela vein number: 5–10 (Fig. 10B, E) (0), 2–3 (Fig. 10A) (1).
62. Cypsela epicarp crystals (Anderberg, 1982, 1989): absent (0), present (1).
63. Testa (Grau, 1980; Dittrich 1977): persistent, often reinforced (0), collapsed (1).
64. Testal epidermis strengthening pattern (Grau, 1980): none or diffuse (0), stalagmitelike (1).
65. Pappus: terete bristles with unicellular hairs (0), true bristles, or bristlelike scales (1). The Barnadesiinae pappus consists of terete bristles with unicellular hairs with a basal cell, exactly like those on florets and fruits as well. They therefore have a superficial resemblance to plumose bristles that are found in various tribes in the family. The Barnadesiinae bristles also seem to be of quite another texture than the bristles in the rest of the family. It is possible that they are of another origin than the pappus bristles outside the Barnadesiinae, and the conclusion is that true bristles is an evolutionary novelty for the ingroup. Most of the pappus characters are therefore scored as inapplicable in the outgroup.
66. Pappus bristle margins: scabrid to barbellate (0), plumose (1).
67. Pappus base fusion: present (0), absent (1).
68. Pappus setae cell thickenings (Karis, 1989): absent (0), present (1).
69. Pappus bristle teeth organization (Karis, 1989, 1990): of one cell (0), of the top of one cell together with the base of the adjacent marginal cell (Fig. 11A) (1).
70. Pappus element dimorphism: absent (0), present (1).
71. Laticiferous tissue (Col, 1899–1901): absent (0), present (1), with latex-resin (2).
72. Chemistry: benzofurans and benzopyrans absent (0), present (Proksch, 1985; Proksch & Rodrigues, 1983) (1).

Appendix III. Datamatrix. Inapplicable or unknown character states are coded -

	1	10		20		30		40		50		60		70	
OUTGROUP	00000	00000	00000	00000	00000	——00	000–0	00000	00000	00000	00000	00000	00000	——0	00
MUTISIEAE-GOCHNATIINAE															
Actinoseris	12001	00000	00001	11000	00001	01111	0010–	01000	–00–1	00001	10000	00101	00–01	01110	00
Ainsliaea	100–1	00000	00000	00100	00000	01111	0010–	01100	–00–0	00000	00001	00101	00001	10100	00
Brachylaena	00011	00000	00001	00–00	00000	13011	0010–	01000	00000	00001	10001	00101	00001	00000	00
Cnicothamnus	00001	00000	00001	11000	00000	01101	0010–	11000	–10–0	00001	00000	00101	00001	00100	00
Dicoma	10011	00000	–0001	11100	10100	03001	0010–	01100	–20–0	00320	10000	00101	00011	00110	00
Erythrocephalum	10011	00100	00011	11001	10100	03011	0110–	01100	02001	10321	00000	00201	00011	11100	00
Gochnatia	00011	00000	00000	00000	10000	01111	0010–	01000	01000	00000	00001	00101	00001	001–0	00
Hesperomannia	00001	00000	00000	00000	00000	00100	012—	01100	01001	10110	00000	00100	00001	00100	00
Oldenburgia	00010	01000	00001	11000	10100	01101	0010–	01100	–00–0	00321	00001	00101	00–01	00100	00
Onoseris	–0011	00000	00001	11110	10010	01100	0010–	01111	01001	00321	10001	00101	01001	00000	00
Pertya	00011	00000	00000	00000	10000	01111	0010–	01100	–10–1	10410	10001	00101	00001	00000	00
Plazia	000–0	00000	00001	11000	11100	01101	0010–	01100	01001	00330	10000	00101	00001	00100	00
Pleiotaxis	10011	00101	00000	00001	00000	03001	0010–	11100	–20–0	00330	00001	00101	00011	00000	00
Stenopadus	00000	11000	010–0	00000	–1000	00100	0010–	01000	–00–0	00000	10001	00000	00001	00000	00
Stifftia	00000	00010	01000	00000	10000	01101	0010–	01–00	–00–1	10000	10001	00001	00001	00010	00
Warionia	00001	00000	00000	00000	10010	03010	0010–	01101	–20–1	10310	10000	00101	01–01	00000	10
Wunderlichia	00010	00000	00000	00000	01001	00101	0010–	01100	–10–0	00000	00000	00101	00001	00100	00
MUTISIEAE-MUTISIINAE															
Chaetanthera	10010	00001	–0001	211–0	—00	01100	0010–	01100	00000	00330	00000	00301	00001	00000	00
Gerbera	12011	00000	00001	211–0	—00	01110	0010–	01100	00000	10321	00000	00300	00001	01000	00
Gongylolepis	00000	11000	01000	210–0	—00	0—01	0010–	01000	–10–1	00001	10001	00001	00001	00110	00
Hyaloseris	00010	00001	00000	400–0	—00	01100	0010–	01000	–10–1	10001	00001	00201	00001	00100	00
Lulia	10010	00000	00001	211–0	—10	01101	0010–	00010	–00–0	10421	00000	00001	10–01	00100	00
Mutisia	00010	00000	00001	210–0	—01	01101	0010–	01101	00001	10420	00000	00000	00001	10100	00
Trichocline	02010	00000	00001	211–0	—00	01100	0010–	01111	00000	00420	00000	00300	00001	00000	00
MUTISIEAE-NASSAUVIINAE															
Jungia	–0011	00010	00010	210–0	—00	01100	0110–	01000	00001	20141	10001	00311	00001	10100	00
Leucheria	10011	00010	00001	210–0	—02	01100	0010–	01200	00001	20141	10001	00311	00001	10100	00
Lophopappus	00110	00010	00000	21000	–0000	01100	0010–	01000	00000	00120	10001	00111	00001	–0100	00
Macrachaenium	12011	00010	00000	210–0	—00	0—10	0110–	11000	00001	10121	10001	0000–	00–01	10100	00
Nassauvia	10101	00010	00000	210–0	—00	01110	0010–	01200	00001	20141	10000	00001	–0001	01000	00
Trixis	10011	00010	00001	210–0	—00	01100	0–10–	01000	00001	20141	10001	00311	00001	00100	00
ARCTOTIDEAE															
Arctotis	10011	00001	00001	31110	00000	02120	020–0	00000	11001	10351	11000	00100	00–01	–1000	00
Berkheya	10111	00000	00001	50200	10010	01120	1111–	01100	12001	10211	10001	00101	00–01	01100	00
Eremothamnus	00111	00000	00001	31100	11000	10010	120–1	01100	120–1	10311	00000	00100	00–01	00000	00
CARDUEAE sensu lato															
Berardia	12011	00000	000–0	00011	00000	12011	0010–	01100	–10–0	00311	1000–	00000	00001	01000	10
Carduus	10101	00000	00000	00001	10000	00011	003—	01110	–20–1	10350	11000	10000	01001	00000	20
Carlina	10101	00000	10010	00010	11100	—11	0010–	01100	–10–0	00350	10001	00100	00001	10000	20
Cirsium	10111	00000	00000	00001	10000	—01	003—	11110	01001	10351	10000	00000	00001	11100	00
Echinops	10111	00000	0000–	00–01	10010	—11	0010–	01000	–10–1	10351	11000	00000	00001	00000	00
Saussurea	10011	00000	00000	00001	10000	—11	0010–	01100	–10–1	10351	10000	10100	10001	–0001	00
VERNONIEAE															
Distephanus	00000	00000	00000	00000	10000	—20	0111–	01000	–20–1	10111	10001	00101	00–01	00000	00
Vernonia	10001	00000	00000	00000	11000	—10	0111–	00100	02001	10311	10001	00101	00–01	10101	00
LACTUCEAE															
Hypochoeris	12001	00001	00110	400–0	—03	—20	120–1	01100	–21–1	10211	00001	01001	00–01	11001	10
Lactuca	10001	00011	00100	400–0	—01	—20	120–1	01100	–21–1	10211	00011	01001	–0101	010–0	10
Scolymus	10101	00001	00110	400–0	—13	—20	0210–	00100	–21–1	10211	00010	00101	00001	—100	10
Sonchus	10001	00011	00100	400–0	—13	—20	120–1	01100	–21–1	10211	00010	00001	00001	01011	10
LIABEAE															
Liabum	11011	00010	00001	31100	11010	10020	0110–	00100	02001	10211	00001	00101	00–01	01101	00
Munnozia	11011	00000	00001	31100	10010	12020	0110–	00100	–20–1	10211	00000	0000–	00–01	01100	10
ASTEROIDEAE															
Helichrysum	10010	00000	10001	60110	10000	—20	0110–	11100	12011	22140	10001	00000	10101	01100	01
Inula	10001	00000	00001	311-0	00002	11020	000–0	11100	12011	11330	10001	00000	01101	00100	01
Pluchea	10000	00000	00001	60110	10002	—20	000–0	01100	120–1	10111	10001	00101	00001	00100	01
Aster	10001	00001	00001	31110	10000	11220	010–0	00100	12011	12121	10101	00101	10001	01000	01
Geissolepis	10001	00001	00001	31110	10000	11220	010–0	10100	12011	12120	1010–	00101	00001	01000	01
Senecio	10000	00010	00001	31110	10000	11020	010–0	10200	12011	22140	10001	00101	00–01	01000	01

PHYLOGENETIC IMPLICATIONS OF *rbc*L SEQUENCE VARIATION IN THE ASTERACEAE[1]

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ABSTRACT

Complete nucleotide sequences of the *rbc*L gene were obtained for 25 species of Asteraceae representing 15 of the currently recognized tribes and three outgroup families. A total of 345 variable nucleotide positions was identified, 170 of which were phylogenetically informative. Phylogenetic analyses of the *rbc*L data generated eight equally parsimonious trees with a consistency index of 0.47. Three major monophyletic clades that correspond to the subfamilies Barnadesioideae, Cichorioideae, and Asteroideae were identified in the most parsimonious cladograms; however, support for these groups was not strong. Relationships among tribes were not supported strongly except for the close affinity of the Tageteae, Coreopsideae, Heliantheae, and Eupatorieae. These results are congruent with chloroplast DNA restriction site comparisons with respect to the subfamilial circumscription in the Asteraceae and the sister group relationship of the Heliantheae and Eupatorieae. In contrast, morphological cladograms indicated the paraphyly of the Cichorioideae and a closer relationship of the Eupatorieae to the Astereae. Parsimony analyses were also performed on data sets combining *rbc*L and cpDNA restriction site mutations and DNA and morphological characters. These phylogenies provide moderate to strong support for the monophyly of the Asteroideae and Cichorioideae and the sister-group relationship of the Eupatorieae and Heliantheae. Comparisons of trees generated from restriction site and sequence data also indicate that cpDNA restriction site data from the entire chloroplast genome are more useful for phylogenetic studies in the Asteraceae than sequences from the highly conserved *rbc*L gene. This is due to the sampling of more sequence variation in the restriction site comparisons and the higher incidence of homoplasy in the sequence data.

Recent studies of phylogenetic relationships of the Asteraceae at higher taxonomic levels using both chloroplast DNA (cpDNA) (Jansen & Palmer, 1987a, 1988; Jansen et al., 1990, 1991a, b; Keeley & Jansen, 1991; Watson et al., 1991) and morphological (Bremer, 1987; Harris, 1991; Karis et al., 1992) data have clarified many controversial systematic issues involving this large angiosperm family. Both *rbc*L sequence data (H. Michaels et al., unpublished; Jansen et al., 1991b) and morphology (Harris, 1991) provided strong evidence that the Calyceraceae and Goodeniaceae are sister taxa of the Asteraceae. This finding appears to resolve a phylogenetic controversy that has puzzled synantherologists for over 150 years. Within the Asteraceae phylogenetic trees generated from cpDNA restriction site and morphological data are congruent in three areas: (1) the Barnadesioideae are the sister group to the rest of the family; (2) the Asteroideae are monophyletic; and (3) 14 of the 17 currently recognized tribes (Jansen et al., 1991b) are monophyletic. The primary incongruence between morphology and cpDNA concerns the placement of the tribe Eupatorieae and the monophyly of the Cichorioideae. Morphological trees (Bremer, 1987) placed the Eupatorieae closest to the Astereae and indicated that the Cichorioideae are paraphyletic. In contrast, cpDNA restriction site studies (Jansen et al., 1990, 1991a; K.-J. Kim, B. Turner and R. Jansen, unpublished)

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indicated that the Eupatorieae are most closely allied to the Heliantheae and that there is moderate support for the monophyly of the Cichorioideae.

In this paper we present the results of phylogenetic analyses of sequences of the chloroplast gene encoding the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (*rbc*L) from 25 species of Asteraceae and three outgroup families. This gene is currently being used to examine evolutionary relationships in a wide diversity of plant groups. Several studies have demonstrated the potential of *rbc*L for resolving phylogenetic relationships at the interfamilial level (Olmstead et al., 1992; Donoghue et al., 1992), but its utility at the intrafamilial level has only been examined in the Poaceae and Saxifragaceae (Doebley et al., 1990; Soltis et al., 1990). In the study of grasses (Doebley et al., 1990), insufficient sequence variation was encountered to decide reliably among alternative tree topologies. The goals of our study were: (1) to examine *rbc*L sequences in the Asteraceae to provide additional characters for resolving incongruencies between phylogenies generated in previous morphological and cpDNA restriction site studies: (2) to perform phylogenetic comparisons of combined DNA and morphological characters to provide a comprehensive and broadly based assessment of evolutionary relationships in the Asteraceae; and (3) to evaluate the utility of cpDNA restriction site and *rbc*L sequence data for phylogenetic comparisons at the intrafamilial level.

MATERIALS AND METHODS

We obtained complete sequences of *rbc*L for 24 species of Asteraceae and two closely related outgroup families (Appendix 1). Data for two taxa (*Nicotiana tabacum* and *Flaveria trinervia*) come from previously published reports (Shinozaki et al., 1986; Hudson et al., 1990). Species names and voucher information for all taxa examined except *Cichorium intybus* L. are provided in Jansen & Palmer (1987a) and Jansen et al. (1990, 1991a). The new sequences have been submitted to Genbank and may also be obtained directly from R. Jansen.

A cloning strategy was employed for generating sequence data. Chloroplast DNAs were isolated from each species using the sucrose gradient method of Palmer (1986). Previous restriction site comparisons within the Asteraceae identified two conserved sites for BamHI and SacI (Jansen & Palmer, 1987b; R. Jansen, unpublished data). These enzymes produced a 2.0–2.6 kilobase (kb) fragment that contained the entire *rbc*L gene and associated noncoding regions at the 3′ and 5′ end of the gene (Fig. 1). Restriction fragments containing *rbc*L were excised from 1.2% Sea-Plaque low melting temperature agarose (FMC) and ligated directly to BamHI/SacI- digested bacteriophage M13mp18 DNA or the phagemid pBlueScript II (Stratagene). The entire cloned fragment was sequenced by the dideoxy chain termination method (Sanger et al., 1977) using Sequenase (US Biochemicals) and a series of 14 overlapping synthetic primers and universal primers for M13mp18 DNA and pBlueScript II (Fig. 1). Nine of the synthetic primers (provided by G. Zurawski, DNAX) were based on the *rbc*L sequences of maize and spinach, and the others were constructed at the University of Connecticut Biotechnology Center using sequences from the Asteraceae. The M13mp18 clones were sequenced from single-stranded DNA, and pBlueScript II clones were sequenced from double-stranded template. Although sequences were obtained for a single strand only, the sequence data are accurate because we used cloned single or double stranded template and because the 14 sequencing primers (Fig. 1) have considerable overlap.

Sequences were aligned manually and only the coding region up to 1428 basepairs (bp) was used in phylogenetic analyses because of length mutations at the 3′ end of *rbc*L and in the noncoding regions (K.-J. Kim, R. Jansen & R. Wallace, unpublished). Phylogenies were constructed using parsimony, and the most parsimonious trees were searched for on a MacIntosh IIcx using PAUP version 3.0q (developed by D. Swofford) with the Tree Bisection Reconnection (TBR) and mulpars options. One hundred random entries of the data were performed for all phylogenetic analyses in an attempt to locate all equally parsimonious trees (Maddison, 1991).

The bootstrap method (Felsenstein, 1985) was employed to evaluate the reliability of phylogenetic estimates. One hundred replicates were performed using parsimony and the TBR option (without mulpars) of PAUP. The topological constraints option of PAUP was used to determine the number of additional steps required to break up the monophyly of selected groups.

All *rbc*L trees were rooted using multiple outgroups from the families Solanaceae, Campanulaceae, and Goodeniaceae. The close phylogenetic relationship of the latter family is supported by recent comparisons of *rbc*L sequences (Jansen et al., 1991b; H. Michael et al., unpublished) and features of inflorescence and floral development (Harris, 1991).

The *rbc*L sequence data were combined with

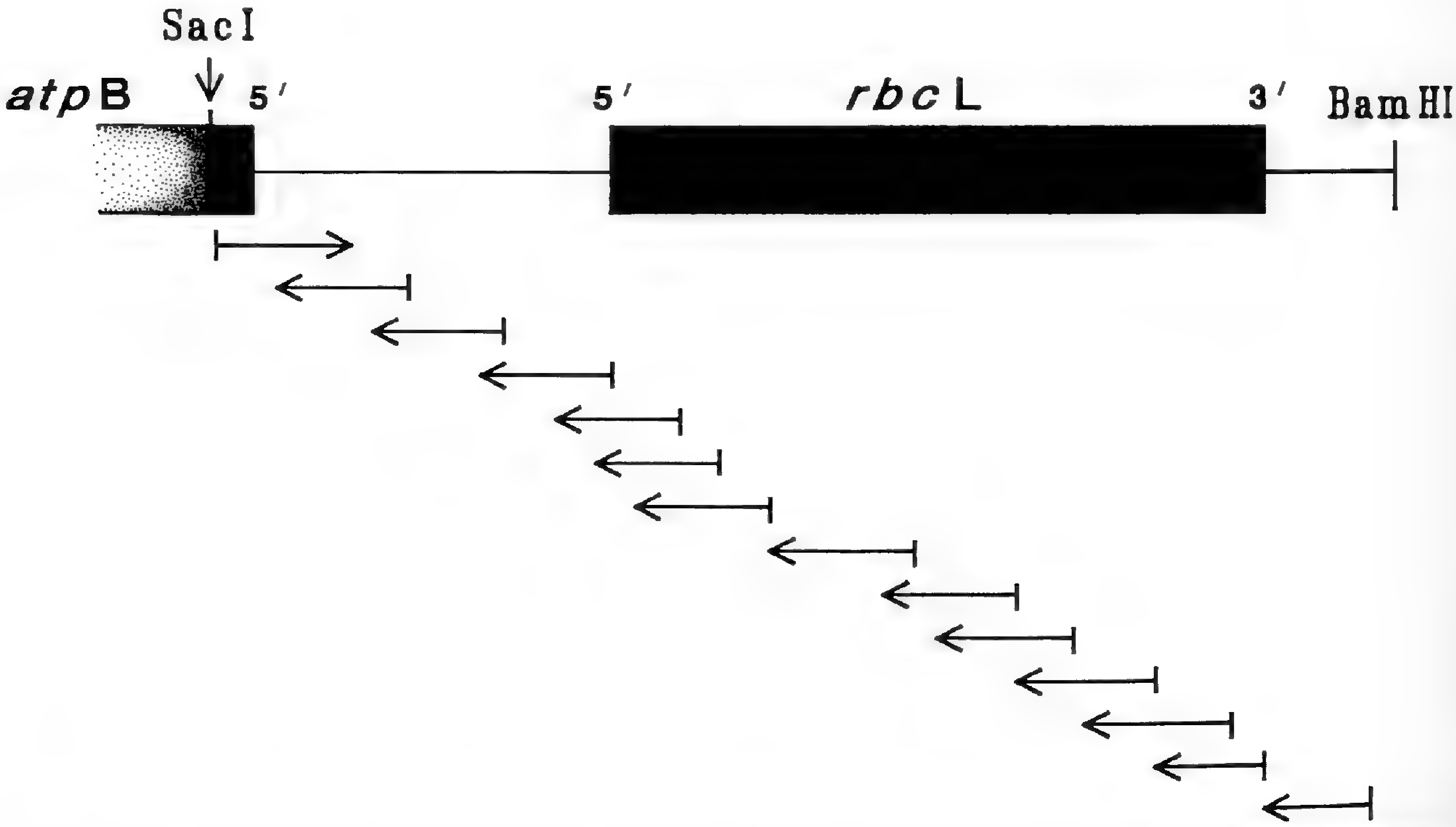

FIGURE 1. Cloning and sequencing strategy for *rbc*L. BamHI and SacI restriction sites used in cloning strategy are indicated. Arrows show the location of the 14 overlapping primers used in dideoxy sequencing.

data derived from cpDNA restriction site mutations (Jansen et al., 1990, 1991a) and morphology (Bremer, 1987). The combined data set for *rbc*L sequences and restriction site mutations included a single species from each of 22 genera representing 15 tribes of Asteraceae (Appendix 1, asterisks). One restriction site mutation (number 235 in Jansen et al., 1990) was excluded in phylogenetic analyses of this combined data set because it occurs in the *rbc*L gene. The combined morphology and DNA data set included 17 taxa (Appendix 1, plus signs) representing 15 tribes. All analyses of the two combined data sets used unweighted parsimony and the Barnadesieae as the outgroup (Bremer, 1987; Jansen & Palmer, 1987b, 1988; Jansen et al., 1991b). Copies of both combined data sets are available from R. Jansen.

RESULTS

PHYLOGENETIC ANALYSES OF *RBC*L SEQUENCES

The length of the *rbc*L coding region in the Asteraceae is 1428, 1431, 1434, or 1458 bp. All of this length variation occurs at the 3′ end of the gene and is due to small insertions/deletions and frameshift mutations (K.-J. Kim, R. Jansen & R. Wallace, unpublished). For phylogenetic analyses sequence data were truncated at 1428 bp, the shortest length of *rbc*L in the family.

A total of 345 variable nucleotide positions was identified and 73, 45, and 227 of these occurred at the first, second, and third codon positions, respectively. Of the variable positions, 170 were phylogenetically informative (Appendix 1). The ratio of informative mutations by codon position was 39 : 18 : 113. Parsimony analyses of the phylogenetically informative base substitutions resulted in eight equally parsimonious trees of 704 steps (including autapomorphies) and a consistency index of 0.47 (excluding autapomorphies). The strict consensus tree is shown in Figure 2.

The *rbc*L data do not provide strong support for most clades as indicated by the low bootstrap percentages (Fig. 2). The amount and distribution of homoplasy is the most likely explanation for this result. An overall consistency index of 0.47 is not particularly low for a data set with 28 taxa (Sanderson & Donoghue, 1989); however, a more detailed examination of the distribution of homoplasy in *rbc*L characters showed that 78% of the phylogenetically informative base substitutions exhibit homoplasy. Furthermore, examination of the number of character state changes over the three codon positions (Fig. 3) showed a similar pattern at the first, second, and third codon positions. It is particularly noteworthy that the second codon position, in which all base substitutions result in amino acid changes, has the highest percentage of homoplastic mutations (90%; 18 of 20 changes are homoplastic).

In spite of these problems, the *rbc*L tree does

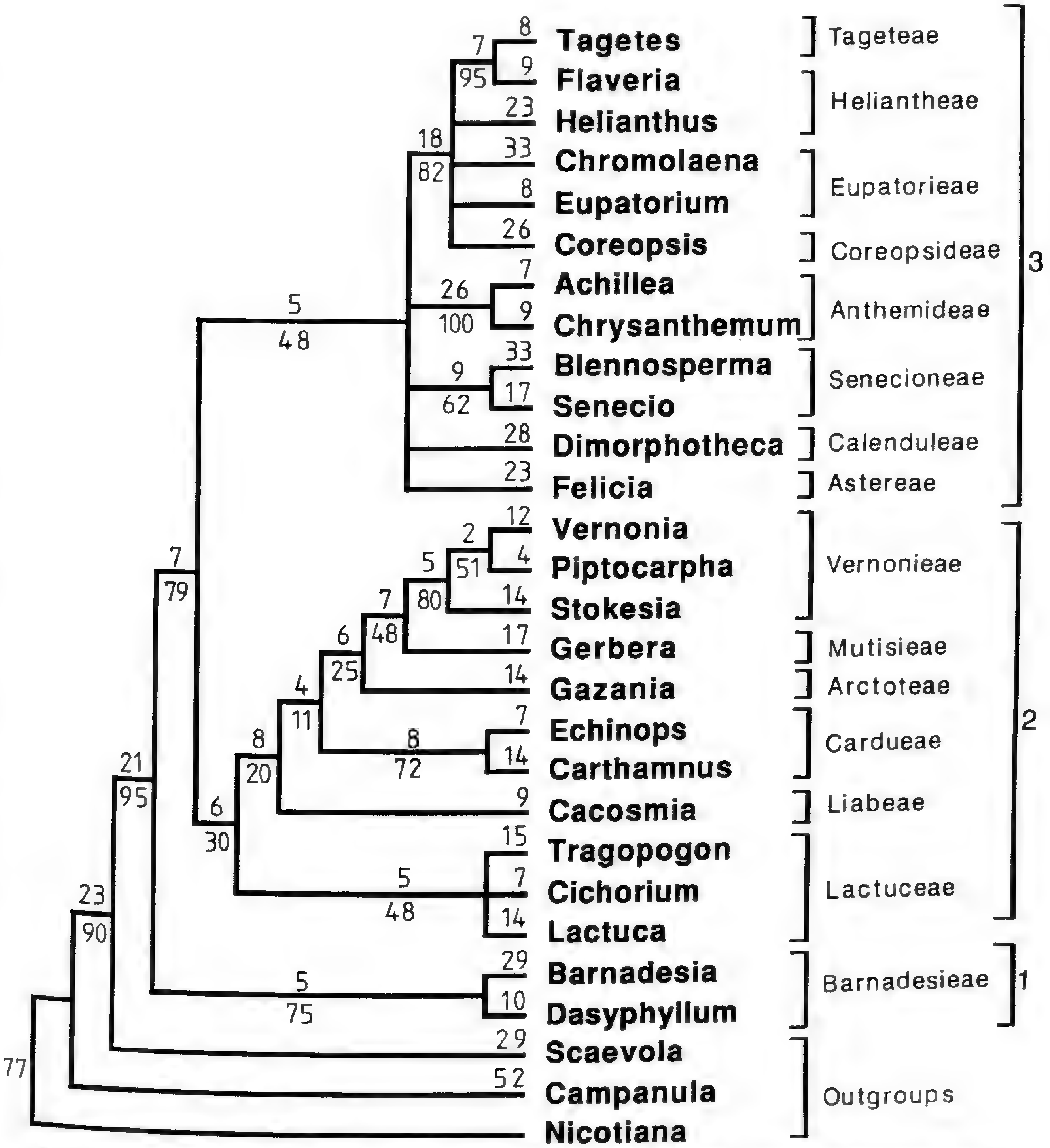

FIGURE 2. Strict consensus tree of eight equally parsimonious trees based on 345 variable nucleotide positions of *rbc*L, 170 of which are phylogenetically informative (Appendix 1). Numbers above the nodes indicate the number of mutations supporting each monophyletic group. Numbers below nodes indicate the number of times that a monophyletic group occurred in 100 bootstrap replicates. Brackets show the tribal and subfamilial circumscriptions in the Asteraceae (sensu Jansen et al., 1991a, b); 1 = Barnadesioideae, 2 = Cichorioideae, and 3 = Asteroideae.

provide some resolution of phylogenetic relationships in the Asteraceae. The tree provides moderate support for an initial dichotomy separating the Barnadesieae from the remaining tribes of Asteraceae, and this group occurs in 79 of the 100 bootstrap replicates (Fig. 2). Although both the subfamilies Asteroideae and Cichorioideae are monophyletic in the most parsimonious trees, statistical support for their monophyly is weak (48% and 30%, respectively; Fig. 2). All of the tribes for which multiple species were examined are monophyletic except the Heliantheae and Eupatorieae (Fig. 2). One genus of the Heliantheae (*Flaveria*) forms a strongly supported monophyletic group with the Tageteae (seven synapomorphies and 95% of the bootstrap replicates). Only one tribal grouping is well supported, the Tageteae, Coreopsideae, Heliantheae, and Eupatorieae, which has 18 synapomorphic base

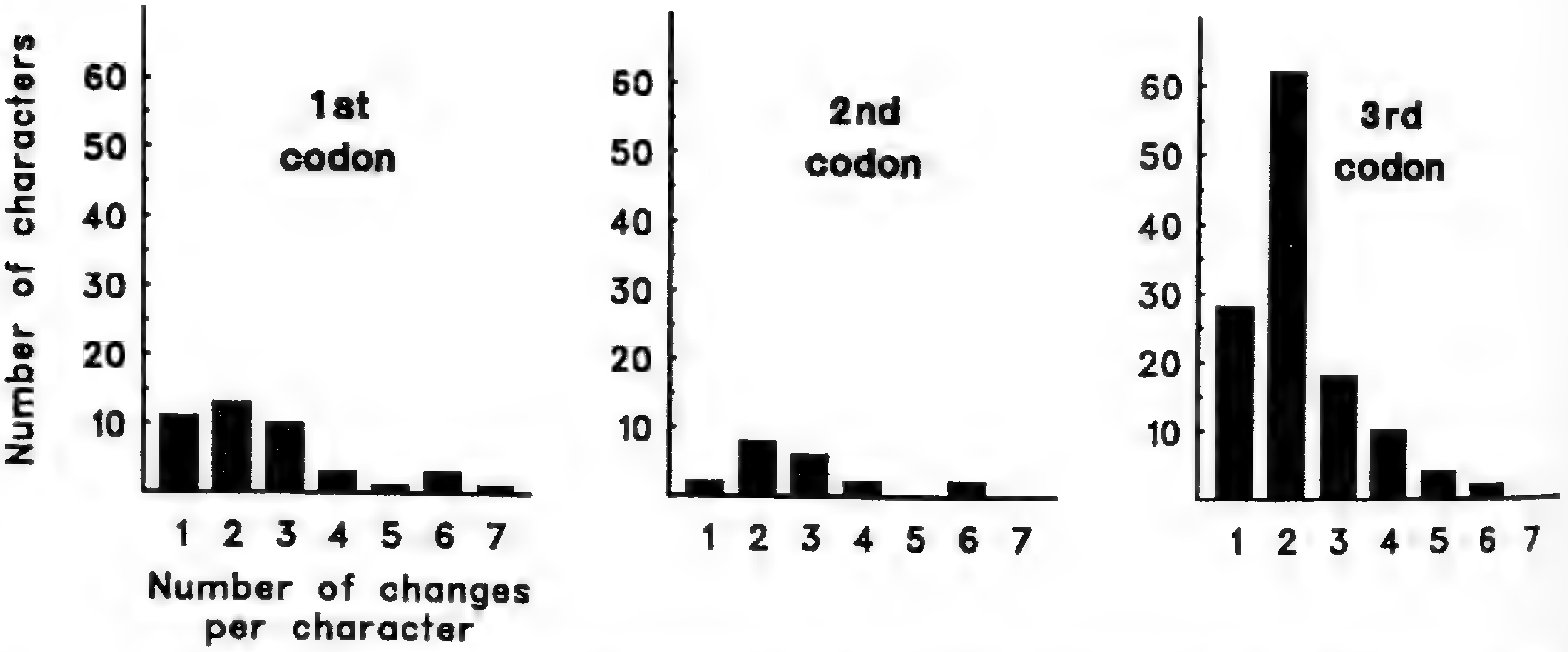

FIGURE 3. Histogram showing the number of character state changes at each of the codon positions for the 170 phylogenetically informative nucleotide positions based on one of the eight equally most parsimonious trees.

substitutions, and it occurs in 82% of the bootstrap replicates (Fig. 2). All other tribal clades in both subfamilies are supported by fewer synapomorphies, and they occur in less than 50% of the bootstrap replicates.

Three of the tribal groupings in the *rbc*L tree are incongruent with tribal relationships suggested in previous phylogenetic studies of the Asteraceae using morphology (Bremer, 1987; Karis et al., 1992) or cpDNA restriction site mutations (Jansen et al., 1990, 1991a). We explored the robustness of these groups formed in the tree generated from sequence data by determining the number of additional steps required to fit the sequence data to the alternative tribal groups in the other data sets. Restriction site studies provided moderate support for the monophyly of the subfamily Cichorioideae (Jansen et al., 1990, 1991a), whereas morphological data (Bremer, 1987; Karis et al., 1992) indicate that this is a paraphyletic group. Only one additional step is required to force the paraphyly of the Cichorioideae in the sequence data. This result, combined with the fact that this group occurs in only 30 of the 100 bootstrap replicates (Fig. 2), suggests that the sequence data provide weak support for the monophyly of the Cichorioideae. Although initial restriction site (Jansen et al., 1990, 1991a) and morphological (Bremer, 1987) studies supported a sister-group relationship of the tribes Liabeae and Vernonieae, more recent molecular (Keeley & Jansen, 1991) and morphological (Karis et al., 1992) data cast some doubt on their close relationship. The *rbc*L tree (Fig. 2) does not support a sister-group relationship for the Liabeae and Vernonieae, and forcing their monophyly requires four additional steps. Another incongruence between morphological and cpDNA restriction site phylogenies concerned the placement of the Eupatorieae. The *rbc*L tree is in agreement with the restriction site data, which place the Eupatorieae close to the Heliantheae. The fact that eight additional steps are required to group the Eupatorieae with the Astereae as suggested by Bremer (1987) provides additional convincing evidence in favor of their strong phylogenetic affinity with the Heliantheae.

PHYLOGENETIC ANALYSES OF COMBINED DATA SETS

rbcL sequences and chloroplast DNA restriction site mutations. The combined *rbc*L and cpDNA restriction site data set, which included a single species of each of 22 genera representing 15 tribes of Asteraceae (Appendix 1, asterisks), consists of 498 characters (170 *rbc*L base substitutions for 28 taxa (this paper) and 328 cpDNA restriction site mutations for 57 taxa (Jansen et al., 1990)). The elimination of taxa that were not shared among the two data sets reduced the number of phylogenetically informative characters for the 22 taxa held in common to 278 (169 restriction site mutations and 109 sequence positions). Phylogenetic analyses resulted in two equally parsimonious trees of 634 steps and a consistency index of 0.50. A strict consensus tree (Fig. 4) shows that the two trees differ in the relative placement of the tribe Liabeae in the Cichorioideae. In one of the shortest trees the Liabeae are the sister tribe of the Mutisieae and Vernonieae, whereas in the second equally parsimonious tree the Liabeae are positioned outside the clade that includes the tribes

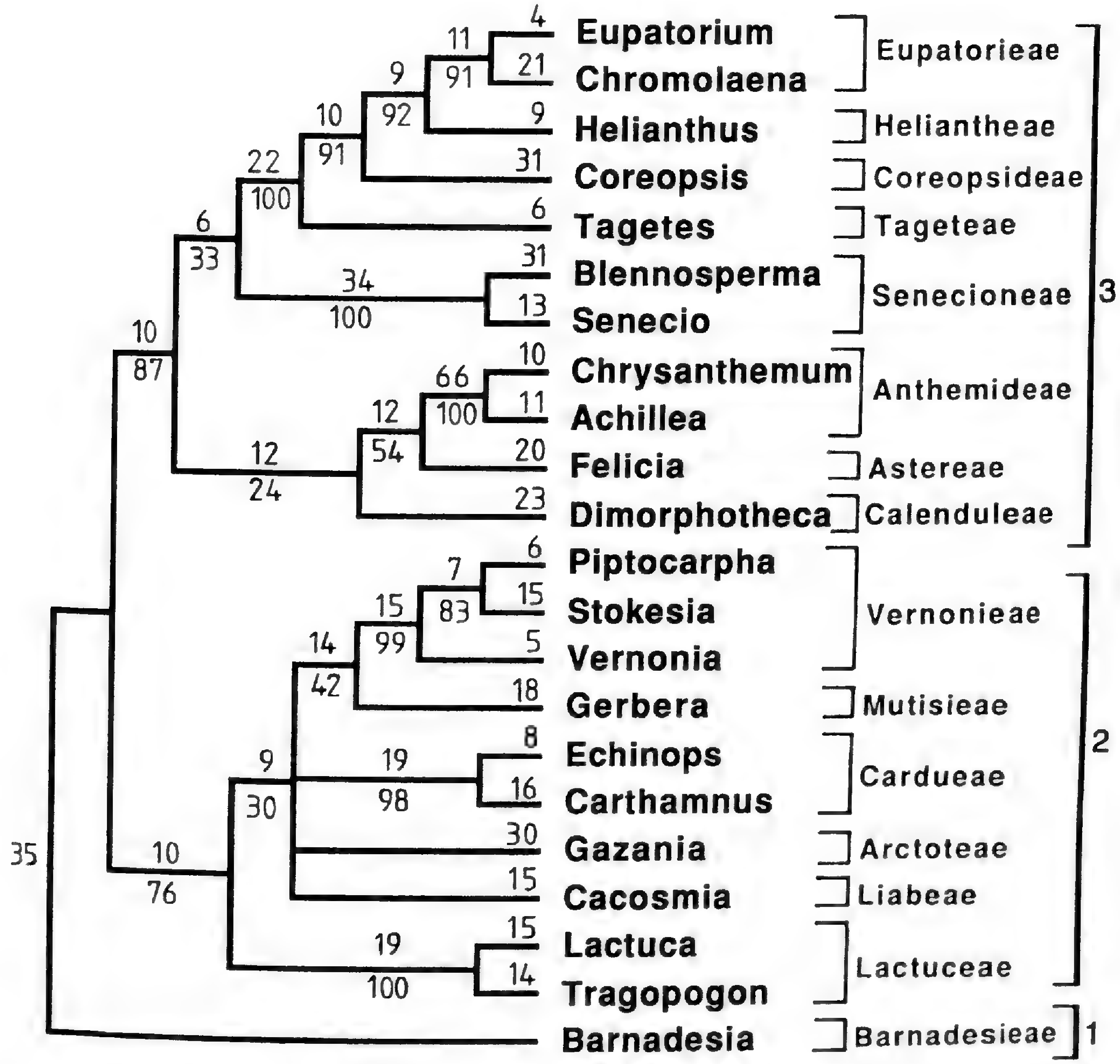

FIGURE 4. Strict consensus tree of two equally parsimonious Wagner trees based on 498 cpDNA restriction site and *rbc*L mutations, 278 of which were phylogenetically informative. Numbers above nodes indicate the number of mutations supporting each monophyletic group. Numbers below nodes indicate the number of times that a monophyletic group occurred in 100 bootstrap replicates. Brackets show the tribal and subfamilial circumscriptions in the Asteraceae (sensu Jansen et al., 1991a, b); 1 = Barnadesioideae, 2 = Cichorioideae, and 3 = Asteroideae.

Cardueae, Arctoteae, Mutisieae, and Vernonieae. Thus in the strict consensus tree (Fig. 4) relationships among all five of these cichorioid tribes are unresolved. Both equally parsimonious trees indicate the same relationships among tribes in the Asteroideae.

The tree from the combined cpDNA data sets provides considerable support for the monophyly of both the subfamilies Cichorioideae and Asteroideae (Fig. 4). Both subfamilies are characterized by 10 synapomorphic characters and moderate to high bootstrap percentages (76% and 87%). It requires two (636 total steps) and four (638 total steps) additional steps to force the paraphyly of the Cichorioideae and Asteroideae, respectively. The level of support for the monophyly of the two subfamilies is similar to that found in the Dollo analysis of cpDNA restriction site characters alone (Jansen et al., 1990). Wagner parsimony analysis of restriction site data for 57 taxa resulted in only weak support for the monophyly of the Cichorioideae; the subfamily was present in only eight of 20 trees and had very weak statistical support (Jansen et al., 1990). The Cichorioideae are paraphyletic in Wagner analyses of the 22 taxon restriction site data set. In this case only a single most parsimonious tree with 411 steps (including autapomorphies) and a CI of 0.56 (excluding autapomorphies) is generated (not shown). Thus, in the combined cpDNA data, support for the mono-

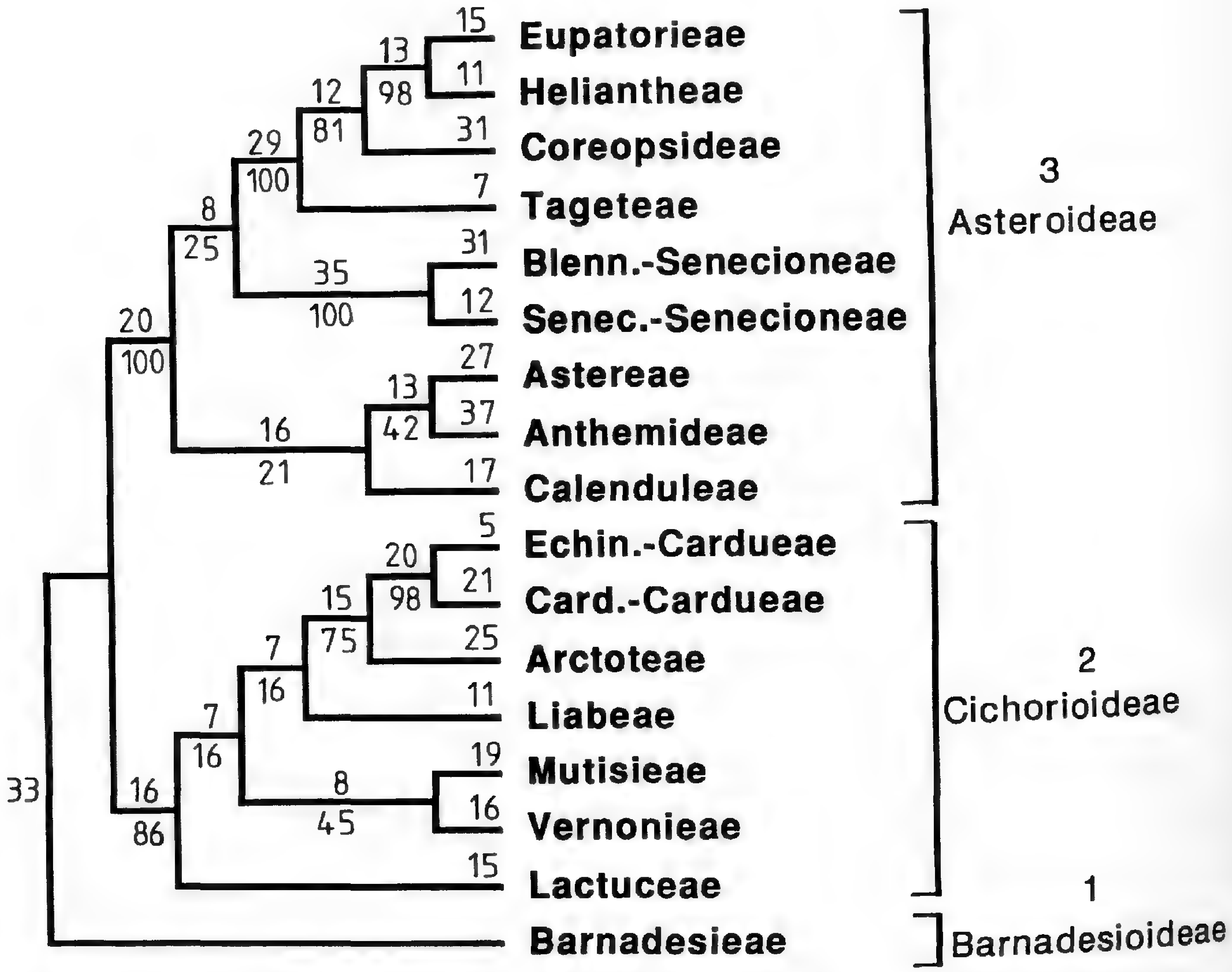

FIGURE 5. Single most parsimonious tree based on the combined data set of 579 DNA and morphological characters, 235 of which were phylogenetically informative. Numbers above nodes indicate the number of characters supporting a monophyletic group. Numbers below nodes indicate the number of times that a monophyletic group occurred in 100 bootstrap replicates. Brackets show the subfamilial circumscriptions in the Asteraceae (sensu Jansen et al., 1991a, b). Abbreviations for the two lineages in the Senecioneae and Cardueae are: Blenn. = Blennospermatinae, Senec. = Senecioninae, Echin. = Echinopsideae, and Card. = Cardueae.

phyly of the Cichorioideae is enhanced even when all characters are weighted equally.

Within the Asteroideae several tribal groupings are evident in the tree produced by the combined restriction site and sequence data. It is no surprise that the clade including the Tageteae, Coreopsideae, Heliantheae, and Eupatorieae is supported strongly since this group had substantial support when these data sets were analyzed separately (Fig. 2 and Jansen et al., 1990). Bremer's (1987) morphologically based cladistic analysis suggested that the Eupatorieae are the sister tribe of the Astereae. This is very unlikely because 28 additional steps (662 total steps) are required to constrain the monophyly of these two tribes.

DNA and morphology. The combined DNA and morphology data set included 17 taxa (Appendix 1, plus signs) and 579 characters (170 *rbc*L characters for 28 taxa (this paper), 328 cpDNA restriction site mutations for 57 taxa (Jansen et al., 1990), and 81 morphological characters for 29 taxa (Bremer, 1987)). The elimination of taxa that were not shared among all three data sets reduced the number of phylogenetically informative characters to 235 (93 sequence characters, 108 restriction site changes, and 34 morphological features) because 344 characters became autapomorphic or invariant.

Phylogenetic analyses resulted in one most parsimonious tree with 552 steps and a consistency index of 0.49 (Fig. 5). The tree has a topology similar to trees generated from the combined *rbc*L and cpDNA restriction site data (Fig. 4). The phylogeny shows the strongest support yet obtained for the monophyly of the Cichorioideae and Asteroideae. Both subfamilies have numerous synapomorphies (16 or 20) and high bootstrap confidence intervals (86% or 100%). Furthermore, four and ten additional steps were required to force the paraphyly of the Cichorioideae and Asteroideae, respectively.

Several tribal clades are evident in the combined DNA and morphological phylogeny (Fig. 5). Monophyly of the clade that includes the Tageteae, Coreopsideae, Heliantheae, and Eupatorieae is strongly supported by 29 synapomorphies, and this group occurs in 100% of the bootstrap replicates. Within this clade the sister-group relationship of the Eupatorieae and Heliantheae is evident (13 synapomorphies and 98% bootstrap confidence interval). Forcing the monophyly of the Eupatorieae and Astereae requires 32 additional steps. There is also overwhelming support for the close affinity of two lineages in the Cardueae (Cardueae and Echinopsideae) (20 synapomorphies and 98% confidence interval) and Senecioneae (Senecioninae and Blennospermatinae) (35 synapomorphies and 100% confidence interval). Less strongly supported groups include the Mutisieae and Vernonieae (eight synapomorphies and 45% confidence interval) and the Arctoteae and Cardueae (including Echinopsideae) (15 synapomorphies and 75% confidence interval). Parsimony analyses that constrain the monophyly of the Liabeae and Vernonieae generate three trees with 554 steps (two steps longer than the most parsimonious tree).

The reduction in the number of taxa in the combined DNA and morphology data set could affect the outcome of the phylogenetic analyses. Furthermore, because there are many more DNA characters in the combined data set, it is possible that the DNA characters could swamp out the morphological characters (see Miyamoto, 1985; Hillis, 1987; Donoghue & Sanderson, 1991). We explored these phenomena by performing Wagner parsimony analyses of the three reduced individual data sets (*rbc*L sequences, cpDNA restriction sites, and morphology) separately and compared the tribal groupings formed from each of these with those formed from each of the complete data sets as well as from the combined data sets. In general, the tree topologies generated by the reduced data sets were very similar to those produced by the original data sets.

All three reduced data sets provide some support for the monophyly of the Cichorioideae. This group occurred in 40 of the 60 equally parsimonious morphological trees and all four of the shortest *rbc*L trees. The two most parsimonious Wagner trees from the cpDNA restriction site data indicated paraphyly of the Cichorioideae. However, only one additional step was required to constrain the monophyly of this subfamily. The Asteroideae were monophyletic in trees generated from both morphological and cpDNA restriction site data, in agreement with phylogenetic comparisons of the complete data sets (Bremer, 1987; Jansen et al., 1990, 1991a). In this case six additional steps were required to force the monophyly of this subfamily using the reduced sequence data set. This is surprising because the Asteroideae were monophyletic in the most parsimonious trees generated from the complete *rbc*L data set. Tribal groupings in trees generated from each of the three reduced data sets were very similar to those depicted in comparisons including all taxa. Most of the incongruence occurred in groups that were only weakly supported in the original data sets.

DISCUSSION

PHYLOGENETIC IMPLICATIONS OF *RBC*L SEQUENCES

The *rbc*L data provide some resolution of tribal relationships in the Asteraceae; however, support for many groups is limited. The sequence data alone do not provide strong evidence to clarify most of the remaining phylogenetic issues at higher taxonomic levels in the family. Tribal clades in the *rbc*L phylogeny show substantial congruence with those indicated in cpDNA restriction site comparisons (Jansen et al., 1990, 1991a), but there is some incongruence with morphological trees (Bremer, 1987; Karis et al., 1992). Thus, we believe that it is best to consider the implications of the *rbc*L data in conjunction with these other data sets in order to provide a balanced view of the higher level phylogeny of the Asteraceae.

Subfamilial circumscriptions. The *rbc*L tree (Fig. 2) confirms the position of the Barnadesieae as the sister group to the rest of the family, which was suggested previously by a cpDNA inversion (Jansen & Palmer, 1987a, b), cpDNA restriction site data (Jansen & Palmer, 1988), and morphology (Bremer, 1987). Independent support from four different types of data for this ancient evolutionary split in the Asteraceae justifies the formal recognition of the Barnadesieae as a separate subfamily (Bremer and Jansen, 1992). The systematic implications of this dichotomy have been discussed in detail elsewhere (Jansen & Palmer, 1987b, 1988; Jansen et al., 1991b). Certainly one of the more important implications is that the Barnadesioideae can be used as an outgroup for cladistic analyses in the family.

The *rbc*L phylogeny (Fig. 2) provides support for the recognition of two additional subfamilies in the Asteraceae, the Asteroideae and Cichorioideae. Support for the monophyly of both subfamilies is weak as indicated by the low bootstrap percentages (48% and 30%) and the fact that only one additional step is required to force the paraphyly of the Cichorioideae and Asteroideae. Monophyly of the Asteroideae is supported strongly in cladistic analyses of cpDNA restriction site mutations (Jansen et al., 1990, 1991a), morphology (Bremer, 1987; Sanderson, 1989), and the combined DNA and morphological tree (Fig. 5). The composition of this subfamily in the *rbc*L tree is in agreement with the circumscription of the Asteroideae by Robinson (1981), Thorne (1983), Bremer (1987), and Jansen et al. (1991a, b).

The monophyly of the Cichorioideae is currently the most controversial issue in the higher classification of the Asteraceae. Bremer's (1987) morphologically based cladistic analysis indicated that the subfamily is paraphyletic. This hypothesis was not strongly supported, however, because the monophyly of the subfamily could be attained by adding only one step to the morphological tree. A more recent morphological cladistic analysis by Karis et al. (1992) also suggested that the Cichorioideae are paraphyletic. Phylogenetic analyses of cpDNA restriction site data provided some support for the monophyly of the Cichorioideae (Jansen et al., 1990, 1991a, b). In Wagner parsimony analyses of restriction site data, eight of the 20 equally parsimonious trees supported their monophyly. All 16 Dollo and weighted parsimony trees (sensu Holsinger & Jansen, 1992) also indicated the monophyly of the Cichorioideae, but this group was only moderately supported in bootstrap analyses (74 of 100 replicates; Jansen et al., 1990). These results led to the conclusion that the combined Wagner and Dollo analyses of cpDNA restriction site data provide substantial, but not overwhelming, support for the monophyly of the Cichorioideae.

Our combined cpDNA evidence (Fig. 4) provides substantial support for the monophyly of the Cichorioideae. In fact, the level of support for this subfamily (10 synapomorphies and 76% of the bootstrap replicates) is comparable to the support for the Asteroideae (10 synapomorphies and 87% of bootstrap replicates). Furthermore, combining the DNA data with the morphological data of Bremer (1987) provides even stronger support for both subfamilies (Fig. 5). We believe that the question of whether the Cichorioideae are monophyletic is still an open one, but that the available evidence supports their monophyly. One of our labs (R. Jansen) is continuing restriction site and sequence comparisons in the Asteraceae to provide further resolution of this important issue.

Tribal relationships. Tribal relationships are not fully resolved in the strict consensus *rbc*L tree (Fig. 2). The strongest clade includes *Flaveria* (Heliantheae, subtribe Flaveriinae) and *Tagetes* (Tageteae). This sister-group relationship of the subtribe Flaveriinae and Tageteae is also supported by cpDNA restriction site comparisons (K.-J. Kim, B. Turner & R. Jansen, unpublished) and the presence of thiophenic acetylenes (Rodriguez & Mabry, 1977).

The clade that includes the Coreopsideae, Tageteae, Heliantheae, and Eupatorieae had 18 synapomorphies and occurred in 82 of the 100 bootstrap replicates. The close relationship of these four tribes is in agreement with cpDNA restriction site phylogenies (Jansen et al. 1990, 1991a; K.-J. Kim, B. Turner & R. Jansen, unpublished) but is not congruent with Bremer's (1987) morphological cladogram, where the Eupatorieae are placed outside this clade as a sister tribe to the Astereae. Support for the sister-group relationship of the Eupatorieae and Heliantheae is now overwhelming, especially since 32 additional steps are required to obtain a sister-group relationship of the Astereae and Eupatorieae in the combined DNA and morphology tree (Fig. 5).

The *rbc*L tree (Fig. 2) does not support a close relationship between the Liabeae and Vernonieae; four additional steps are required to force their monophyly. A sister-group relationship was indicated between these tribes in initial cpDNA restriction site (Jansen et al., 1990, 1991a) and morphological (Bremer, 1987) studies. In spite of this congruence, the combined DNA and morphological tree (Fig. 5) did not group the Liabeae with the Vernonieae; two extra steps were required to make them sister tribes. This result is not surprising because expanded restriction site (Keeley & Jansen, 1991) and morphological (Karis et al., 1992) studies have raised some doubts concerning the close relationship of the Liabeae and Vernonieae. Further work is required to test their monophyly.

Two morphologically anomalous genera, *Echinops* and *Blennosperma*, were included in the *rbc*L comparisons. *Echinops* has been described as being intermediate between the Cardueae and Arctoteae and is not easily accommodated in either tribe. Several workers have recognized the genus as a separate tribe (Dittrich, 1976; Bremer, 1987). The sister-group relationship of the Echinopsideae with the Cardueae is supported by the *rbc*L tree, but the Arctoteae are not included in this clade (Fig. 2). This agrees with the results of cpDNA restriction site comparisons (Jansen et al., 1990, 1991a).

Several morphological characters indicate a close relationship between the cichorioid tribes Arctoteae and Cardueae (Cronquist, 1955; Bremer, 1987). It is noteworthy that the combined DNA and morphological tree (Fig. 5) is in agreement with the morphological data and supports the monophyly of the Cardueae, Arctoteae, and Echinopsideae. *Blennosperma* has been previously placed in four separate tribes (Ornduff et al., 1973). The *rbc*L tree is in agreement with both cpDNA restriction site (Jansen et al., 1990, 1991a) and morphological data (Bremer, 1987), which indicate that *Blennosperma* and the Senecioneae form a monophyletic group.

PHYLOGENETIC ANALYSES OF COMBINED DATA SETS

Integration of molecular and morphological data is a controversial issue (Miyamoto, 1985; Cracraft & Mindell, 1989; Hillis, 1987; Sytsma, 1990; Donoghue & Sanderson, 1991; Doyle, 1992). We agree with Donoghue & Sanderson (1991) that the best approach is to combine directly the different data sets so that all of the characters can be considered at the same time. We have examined two combined data sets, one using *rbc*L sequences and cpDNA restriction site mutations from Jansen et al. (1990) and a second that combines the two DNA data sets with the morphological characters of Bremer (1987). We have not treated the molecular trees as a single multistate character as recommended by Doyle (1992), because we believe that the assumption of independence of characters is valid at these higher taxonomic levels.

Comparisons of trees generated by the combined DNA and morphological character set and trees produced from each of these three data sets alone indicate two things. First, there are no apparent artifacts caused by reducing the number of taxa to 17. Tree topologies in the reduced data sets are nearly identical to those generated by the original data sets. Second, the DNA data do not overwhelm the morphological data and thus dictate the resulting tree topologies. This latter phenomenon is exemplified by the presence of the clade including the Arctoteae, Cardueae, and Echinopsideae. This group only occurs in morphological trees and the combined tree; there is no support for the monophyly of these tribes in the most parsimonious trees derived from either the restriction site or *rbc*L data. Thus, when the three different data sets are combined they reinforce each other to give a more fully resolved pattern of tribal relationships in the Asteraceae.

UTILITY OF *RBC*L SEQUENCE DATA AT THE INTRAFAMILIAL LEVEL

Two previous studies in the Poaceae (Doebley et al., 1990) and the Saxifragaceae (Soltis et al., 1990) used *rbc*L sequences for assessing phylogenetic relationships at the intrafamilial level. Both studies included fewer taxa (nine and eight species, respectively) and in neither case were cpDNA restriction site data available for the same species. Two factors indicate that cpDNA restriction site data are more useful than *rbc*L sequences for phylogenetic analyses within the Asteraceae. First, there are more phylogenetically informative restriction site mutations (169) than base substitutions (109). The difference is probably the result of examining more sequence variation (3,498 bp, based on examining 583 variable sites with 11 six-base-pair restriction enzymes (this does not include the invariant sites sampled) versus 1,428 bp in *rbc*L), much of which probably resides in more variable noncoding regions. These empirical data support recent suggestions from simulation studies of the animal mitochondrial genome that restriction site data provide more accurate phylogenetic estimates than those derived from conserved and short (500 bp or less) DNA sequences (Jin & Nei, 1991). Second, the consistency index for the restriction site data (0.56) is higher than the CI for the sequence data (0.47). The distribution of homoplasy by codon position is interesting because the pattern of base substitutions at all three codon positions is similar (Fig. 3). The cause of this pattern may relate to functional constraints on certain regions of *rbc*L. For example, it is possible that amino acid substitutions in certain regions of the protein have little if any effect on its function. Certainly our results raise some doubts concerning the phylogenetic utility of *rbc*L sequences versus restriction site data in the Asteraceae and possibly within other angiosperm families with highly conserved chloroplast genomes. In families with more divergent cpDNAs, such as the Fabaceae (Palmer et al., 1983), *rbc*L sequences should provide sufficient numbers of informative characters for clarifying phylogenetic relationships.

Overall, our comparisons suggest that restriction site data from the entire chloroplast genome are more useful than conserved *rbc*L sequences in families with low levels of sequence divergence. The phylogenetic utility of *rbc*L sequences at the intrafamilial level was also found to be limited in the Poaceae (Doebley et al., 1990), where it was not possible to choose reliably among alternative tree topologies. In these families restriction site analyses and comparative sequencing of much more divergent and/or longer chloroplast genes may prove more appropriate for phylogenetic analyses.

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APPENDIX 1. Species of Asteraceae and related families examined for *rbc*L sequence comparisons. All sequences are new except for *Nicotiana* (Shinozaki et al., 1986) and *Flaveria* (Hudson et al., 1990). Species names and voucher information are given in Jansen & Palmer (1987a) and Jansen et al. (1990, 1991a). * indicates those taxa included in the combined *rbc*L sequence and cpDNA restriction site data set; + indicates those taxa included in the combined DNA and morphological data set.

	Nucleotide position																			
Taxa	21	25	27	29	30	39	42	48	69	81	84	88	102	108	120	138	147	168	207	219
Nicotiana	T	G	A	G	T	C	A	T	T	T	G	C	T	A	C	T	A	G	A	A
Campanula	G	G	A	A	A	T	G	T	T	G	C	G	G	T	T	C	C	A	G	G
Scaevola	G	G	A	A	A	T	G	T	T	T	C	G	T	C	C	T	A	A	G	A
**Stokesia*	T	G	A	G	T	C	A	T	T	G	C	A	T	C	T	T	G	A	G	A
*+*Dimorphotheca*	T	G	A	G	T	C	A	T	T	T	C	A	T	C	T	T	G	A	G	A
*+*Tagetes*	T	G	A	G	T	C	A	T	T	T	A	G	T	C	T	T	A	A	A	A
*+*Gazania*	T	G	A	G	T	C	A	T	T	T	C	G	T	C	T	T	T	A	G	A
*+*Felicia*	T	G	A	G	T	C	A	T	T	T	A	G	T	C	T	T	G	T	A	A
**Chromolaena*	T	G	A	G	T	C	A	T	T	T	A	G	T	C	T	T	G	A	A	A
*+*Achillea*	T	G	A	G	T	C	A	G	T	T	G	G	T	C	T	T	G	A	G	A
*+*Coreopsis*	T	G	A	G	T	C	A	T	T	T	A	G	T	C	T	T	G	A	A	A
*+*Gerbera*	T	G	A	G	T	C	A	T	T	T	C	G	T	C	T	T	G	A	G	A
*+*Cacosmia*	T	G	A	G	T	C	A	T	T	T	C	G	T	C	T	T	G	A	G	A
*+*Blennosperma*	T	G	G	G	T	C	A	T	T	T	C	G	G	C	T	A	A	T	G	A
*+*Vernonia*	T	G	A	G	T	C	A	T	T	T	G	G	T	C	T	T	G	A	G	A
**Tragopogon*	T	G	A	G	T	C	A	T	T	T	A	G	T	T	T	T	G	A	G	A
**Chrysanthemum*	T	G	A	G	T	C	A	G	T	T	G	G	T	C	T	T	G	A	G	A
*+*Eupatorium*	T	G	A	G	T	C	A	T	T	T	A	G	T	C	T	T	G	A	A	A
*+*Echinops*	T	A	A	G	T	C	A	T	T	T	C	A	T	C	T	T	G	A	G	A
**Piptocarpa*	T	G	A	G	T	C	A	T	T	T	C	G	T	C	T	T	G	A	G	A
Cichorium	T	G	A	G	T	C	A	T	T	T	A	G	T	T	T	T	G	A	G	A
*+*Senecio*	T	G	G	G	T	C	A	T	T	T	C	G	T	C	T	A	G	A	G	A
*+*Lactuca*	T	G	A	G	T	C	A	T	T	T	G	G	T	T	T	T	G	A	G	A
*+*Helianthus*	T	G	A	G	T	C	A	T	T	T	A	G	T	C	T	T	G	A	A	A
Flaveria	T	G	A	G	T	C	A	T	T	T	A	G	T	C	T	T	G	A	A	A
*+*Carthamnus*	T	A	A	G	T	C	A	T	T	T	C	A	T	C	T	T	G	A	G	G
*+*Barnadesia*	T	G	A	G	T	C	A	T	G	T	C	G	T	C	T	T	A	A	G	A
Dasyphylum	T	G	A	G	T	C	A	T	G	T	C	G	T	C	T	T	A	A	G	A

	Nucleotide position																			
Taxa	225	246	247	249	256	258	261	267	271	272	282	283	284	290	312	360	369	372	378	387
Nicotiana	C	G	C	A	C	C	C	T	G	T	A	G	A	A	T	T	C	A	G	C
Campanula	G	G	A	A	C	C	T	C	G	C	A	A	A	A	A	T	T	A	T	A
Scaevola	G	G	C	A	G	A	T	C	C	C	A	A	A	A	A	T	T	T	G	?
**Stokesia*	C	G	C	A	G	A	C	T	C	C	A	A	G	T	A	T	T	A	G	C
*+*Dimorphotheca*	G	A	A	A	G	A	C	T	C	T	A	A	A	A	A	T	T	A	G	C
*+*Tagetes*	G	C	C	A	G	A	C	T	C	C	C	A	A	T	A	T	T	A	G	C
*+*Gazania*	C	G	C	A	G	A	C	T	C	C	A	A	G	T	A	T	T	A	G	T
*+*Felicia*	G	C	C	A	G	A	C	T	C	T	A	A	A	A	A	T	T	A	G	C
**Chromolaena*	G	C	C	A	G	A	C	T	C	C	C	A	A	A	A	T	T	A	G	C
*+*Achillea*	G	G	C	C	G	A	T	T	C	T	G	A	A	A	A	G	C	A	T	C
*+*Coreopsis*	G	C	C	A	G	C	C	T	C	C	A	A	G	T	A	T	T	A	G	C
*+*Gerbera*	C	G	C	A	G	A	C	T	C	C	A	A	G	T	A	T	G	A	G	C

APPENDIX 1. Continued.

Taxa	Nucleotide position 225	246	247	249	256	258	261	267	271	272	282	283	284	290	312	360	369	372	378	387
*+*Cacosmia*	C	G	C	A	G	A	C	T	C	C	A	G	G	T	A	T	T	A	G	C
*+*Blennosperma*	G	G	C	A	G	A	C	T	C	C	A	A	A	A	T	T	T	T	G	C
*+*Vernonia*	C	G	C	A	G	A	C	T	C	C	A	A	G	T	A	T	T	A	G	C
**Tragopogon*	G	C	C	A	G	A	C	T	C	C	A	A	A	T	A	T	T	A	G	C
**Chrysanthemum*	G	G	C	A	G	A	T	T	C	T	G	A	A	A	A	G	C	A	T	C
*+*Eupatorium*	C	C	C	A	G	A	C	T	C	C	C	A	A	A	A	T	T	A	G	C
*+*Echinops*	C	G	C	A	G	A	C	T	C	C	A	A	G	T	A	T	T	A	G	C
**Piptocarpa*	G	G	C	A	G	A	C	T	C	C	A	A	G	T	A	T	T	A	G	C
Cichorium	G	G	C	C	G	A	C	T	C	C	A	A	A	A	A	T	T	A	G	C
*+*Senecio*	G	C	C	A	G	A	C	T	C	T	A	A	A	T	A	T	T	A	G	C
*+*Lactuca*	G	G	C	A	G	A	C	T	C	C	A	A	A	A	A	T	T	A	G	C
*+*Helianthus*	C	C	C	A	G	A	C	T	C	C	C	A	A	T	A	T	T	A	G	C
Flaveria	G	C	C	A	G	A	C	T	C	C	C	A	A	A	A	T	T	A	G	C
*+*Carthamnus*	C	G	C	A	G	A	C	T	C	C	A	A	C	T	A	T	T	A	G	C
*+*Barnadesia*	A	G	A	A	G	A	C	T	C	T	A	A	A	A	A	T	T	A	G	A
Dasyphylum	C	G	C	A	G	A	C	T	C	C	A	A	A	A	A	T	T	A	G	C

Taxa	Nucleotide position 393	405	408	412	420	424	425	427	445	447	453	455	462	474	504	507	513	528	537
Nicotiana	C	G	A	C	C	C	C	G	C	A	G	C	G	A	C	G	A	T	G
Campanula	C	A	T	T	C	C	C	G	C	A	G	C	C	C	C	G	A	A	G
Scaevola	T	G	A	C	C	A	C	T	C	A	G	C	C	G	C	G	A	T	G
**Stokesia*	T	G	A	T	C	A	C	G	C	A	C	G	C	G	C	G	A	T	G
*+*Dimorphotheca*	T	G	A	T	T	A	C	G	C	A	G	C	T	G	C	G	A	T	G
*+*Tagetes*	T	A	A	T	C	A	C	G	G	A	G	C	T	G	C	G	A	T	G
*+*Gazania*	T	G	A	T	C	A	C	G	C	A	C	G	C	G	C	G	A	T	G
*+*Felicia*	T	G	A	T	C	A	C	G	C	A	G	C	T	G	C	G	C	T	G
**Chromolaena*	T	G	A	T	C	A	T	G	G	C	G	C	T	G	C	G	A	T	G
*+*Achillea*	T	G	A	T	T	A	C	G	C	A	G	C	T	A	T	G	A	T	G
*+*Coreopsis*	T	G	A	T	T	G	T	G	G	C	G	C	T	G	C	G	A	A	G
*+*Gerbera*	T	G	A	T	C	A	T	G	C	A	C	G	C	G	C	G	A	G	G
*+*Cacosmia*	T	G	A	T	C	A	C	G	C	A	C	G	C	G	C	G	A	T	G
*+*Blennosperma*	T	A	A	T	T	A	C	G	C	A	G	C	T	A	T	A	A	A	G
*+*Vernonia*	T	G	A	T	C	A	T	T	C	A	C	G	C	G	C	G	A	T	G
**Tragopogon*	T	G	A	T	C	A	C	G	C	A	C	G	C	G	C	G	A	T	A
**Chrysanthemum*	T	G	A	T	T	A	C	G	C	A	G	C	T	A	T	G	A	T	G
*+*Eupatorium*	T	G	A	T	C	A	C	G	G	T	G	C	T	G	C	G	A	T	G
*+*Echinops*	T	G	A	T	C	A	C	G	C	A	C	G	C	G	C	G	A	T	G
**Piptocarpa*	T	G	A	T	C	A	T	G	C	A	G	G	C	G	C	G	A	A	G
Cichorium	T	G	A	T	C	A	C	G	C	G	C	G	C	A	C	G	A	A	G
*+*Senecio*	G	G	A	T	C	A	C	G	C	A	G	C	T	G	T	A	A	T	T
*+*Lactuca*	T	G	T	T	C	G	C	G	C	A	C	G	C	G	C	G	A	T	G
*+*Helianthus*	T	G	A	T	C	A	C	G	G	C	G	C	T	A	C	G	A	G	G
Flaveria	T	G	A	T	C	A	C	G	G	G	G	C	T	G	C	G	C	T	G
*+*Carthamnus*	T	G	A	T	C	A	C	G	C	A	?	?	C	G	C	G	A	T	G
*+*Barnadesia*	T	G	A	T	C	A	C	G	C	G	G	C	C	C	C	G	A	G	A
Dasyphylum	T	G	A	T	C	A	C	G	C	A	?	?	C	G	C	G	A	T	A

APPENDIX 1. Continued.

	Nucleotide position																			
Taxa	538	564	565	566	573	582	588	612	618	630	648	672	673	677	682	687	690	711	747	751
Nicotiana	T	C	G	T	A	C	A	G	G	A	T	A	C	A	G	G	T	G	A	A
Campanula	T	A	G	T	A	C	A	G	C	C	T	A	C	A	G	G	T	G	A	A
Scaevola	T	T	G	T	A	T	C	G	C	A	C	T	C	A	G	G	T	A	A	A
**Stokesia*	T	T	G	T	A	T	C	G	G	A	C	T	A	T	T	A	C	G	C	A
*+*Dimorphotheca*	T	T	G	T	A	T	C	G	G	A	C	T	A	A	G	A	C	G	A	A
*+*Tagetes*	T	T	T	G	A	T	C	G	G	A	C	T	A	A	G	A	T	G	A	C
*+*Gazania*	T	T	G	T	A	T	C	G	G	A	C	T	C	A	G	A	T	G	A	A
*+*Felicia*	T	T	G	T	A	T	C	G	G	A	C	T	A	A	T	A	T	G	T	A
**Chromolaena*	T	T	T	G	A	T	C	G	A	G	C	T	A	A	G	A	T	G	A	A
*+*Achillea*	T	T	G	T	A	T	C	G	G	A	C	T	A	T	T	A	T	G	A	A
*+*Coreopsis*	T	T	T	G	A	T	C	G	G	A	C	T	A	A	T	A	T	G	A	A
*+*Gerbera*	T	T	G	T	A	T	C	G	G	A	C	T	C	T	G	A	T	G	A	A
*+*Cacosmia*	T	T	G	T	A	T	C	G	G	A	C	T	A	A	T	A	T	G	A	A
*+*Blennosperma*	C	T	G	T	G	T	C	A	G	A	C	T	A	A	G	A	T	A	T	A
*+*Vernonia*	T	T	G	T	A	T	C	T	G	A	C	T	C	T	G	A	T	G	A	A
**Tragopogon*	T	T	G	T	A	T	C	G	G	A	C	T	A	T	T	A	T	G	A	A
**Chrysanthemum*	T	T	G	T	A	T	C	G	G	A	C	T	A	T	T	A	T	G	C	A
*+*Eupatorium*	T	T	T	G	A	T	C	G	G	G	C	T	C	A	G	A	T	G	C	A
*+*Echinops*	T	T	G	T	A	T	C	G	G	A	C	T	A	A	T	A	T	G	A	A
**Piptocarpa*	T	T	G	T	A	T	C	G	G	A	C	T	C	T	G	A	T	G	A	A
Cichorium	T	T	G	T	A	T	C	G	G	A	C	T	A	T	T	A	T	G	A	A
*+*Senecio*	C	T	G	T	G	T	C	A	G	A	C	T	A	A	T	A	T	G	A	A
*+*Lactuca*	T	T	G	T	A	T	C	G	G	A	C	T	A	T	T	A	T	G	A	A
*+*Helianthus*	T	T	T	G	A	T	C	G	G	A	C	T	C	A	G	A	T	G	T	A
Flaveria	T	T	T	G	A	T	C	G	G	A	C	T	A	A	G	A	T	G	A	C
*+*Carthamnus*	T	T	G	T	A	T	C	G	G	A	C	T	A	A	G	A	T	G	C	A
*+*Barnadesia*	T	C	G	T	A	T	C	G	G	G	C	C	A	A	G	A	T	G	A	A
Dasyphylum	T	T	G	T	A	T	C	G	G	A	C	T	C	A	G	A	T	G	A	A

	Nucleotide position																			
Taxa	753	763	771	777	793	808	813	816	825	836	840	841	846	861	864	865	885	897	921	927
Nicotiana	C	G	T	A	G	T	G	G	C	G	G	G	T	T	T	C	T	G	T	C
Campanula	T	G	C	G	A	A	C	G	T	G	G	G	T	T	T	C	C	A	T	A
Scaevola	A	G	C	A	G	T	G	G	C	G	G	G	T	T	C	C	C	A	T	A
**Stokesia*	G	G	C	A	G	C	A	G	T	G	G	G	T	T	C	C	C	A	T	G
*+*Dimorphotheca*	G	G	C	A	G	C	A	T	T	G	G	G	T	T	C	C	C	A	T	C
*+*Tagetes*	T	G	C	A	G	C	A	G	T	G	G	T	T	C	C	C	C	A	C	G
*+*Gazania*	G	A	C	A	G	C	A	G	T	G	G	G	T	T	A	C	C	A	T	A
*+*Felicia*	G	G	C	A	G	C	A	G	T	G	A	G	T	T	C	C	T	A	T	G
**Chromolaena*	G	A	C	A	G	C	T	G	T	G	G	G	T	T	T	C	C	A	T	G
*+*Achillea*	G	A	C	A	G	C	A	T	T	G	G	G	T	T	C	C	C	A	T	A
*+*Coreopsis*	G	A	C	A	G	C	A	G	T	G	G	T	G	T	C	C	T	A	C	G
*+*Gerbera*	G	G	C	A	A	C	A	G	T	C	G	G	T	T	C	C	C	A	T	G
*+*Cacosmia*	C	G	C	A	G	A	A	G	T	G	G	G	T	T	C	C	C	A	T	G
*+*Blennosperma*	G	A	C	A	G	C	A	G	T	G	G	G	T	T	C	T	C	A	T	A
*+*Vernonia*	G	A	C	A	G	C	A	G	T	G	G	G	T	T	C	C	C	A	T	G
**Tragopogon*	G	A	C	A	G	C	A	G	T	G	G	G	T	T	C	C	C	A	T	A
**Chrysanthemum*	G	G	C	A	G	C	A	G	T	C	G	G	T	T	C	T	C	A	T	A
*+*Eupatorium*	G	G	C	A	G	C	A	G	T	G	G	G	T	T	T	C	C	A	T	G
*+*Echinops*	G	A	C	A	G	C	A	G	T	G	G	G	T	T	C	C	C	A	T	A
**Piptocarpa*	G	G	C	A	G	C	A	G	T	G	G	G	T	T	C	C	C	A	T	G

APPENDIX 1. Continued.

	Nucleotide position																			
Taxa	753	763	771	777	793	808	813	816	825	836	840	841	846	861	864	865	885	897	921	927
Cichorium	G	A	C	A	G	C	A	G	T	G	G	G	T	T	C	C	C	A	T	A
*+Senecio	G	A	C	A	G	C	A	G	T	G	G	G	T	T	C	C	C	A	T	G
*+Lactuca	G	A	C	A	G	C	A	G	T	G	G	G	T	T	T	C	C	A	T	A
*+Helianthus	G	G	T	A	G	C	A	T	T	G	G	T	G	T	T	C	C	G	T	G
Flaveria	T	G	C	A	A	C	A	G	T	G	G	T	T	C	C	C	C	A	T	T
*+Carthamnus	G	G	C	A	G	C	A	G	T	C	G	G	T	C	C	C	C	A	T	G
*+Barnadesia	G	G	C	A	G	C	A	G	T	G	A	G	T	T	C	C	C	A	T	G
Dasyphylum	G	G	C	G	G	C	A	G	T	G	G	G	T	T	C	C	C	A	T	A

	Nucleotide position																			
Taxa	930	933	940	951	963	975	978	981	982	984	1020	1045	1047	1050	1060	1062	1063	1066	1072	1088
Nicotiana	C	C	T	G	T	T	T	C	T	T	C	C	G	T	G	T	G	C	C	A
Campanula	C	T	T	C	T	T	T	C	T	G	G	C	G	C	G	G	G	A	C	A
Scaevola	?	C	T	C	T	T	T	C	T	T	G	C	A	T	A	T	G	A	C	A
*Stokesia	C	T	C	A	T	T	T	T	G	C	A	T	G	T	A	T	A	A	A	T
*+Dimorphotheca	C	T	C	G	T	T	T	T	T	C	G	T	G	T	A	T	G	C	G	A
*+Tagetes	C	C	C	G	T	C	T	T	T	C	A	C	G	T	A	G	G	A	A	A
*+Gazania	C	T	C	G	T	T	C	T	T	C	A	T	G	T	A	T	G	A	C	T
*+Felicia	C	T	C	C	T	T	T	T	G	C	G	C	G	T	A	T	G	A	A	A
*Chromolaena	C	C	C	G	T	C	T	T	G	C	A	T	G	T	A	T	A	A	A	A
*+Achillea	C	C	C	G	T	T	C	T	G	C	A	C	A	T	A	T	G	A	A	A
*+Coreopsis	C	C	C	G	T	C	T	T	T	C	A	C	A	T	A	T	G	A	A	T
*+Gerbera	C	T	C	G	T	T	T	T	T	C	A	C	G	T	A	T	G	A	C	A
*+Cacosmia	C	T	C	G	T	T	T	T	T	C	T	C	G	T	A	T	G	A	A	A
*+Blennosperma	C	T	C	G	T	T	T	T	T	C	G	C	G	T	A	T	G	A	A	A
*+Vernonia	C	T	C	A	T	T	T	T	G	C	A	C	G	T	A	T	G	A	A	T
*Tragopogon	C	T	C	G	T	T	T	T	T	C	A	C	G	T	A	T	G	A	A	A
*Chrysanthemum	C	C	C	G	T	T	C	T	G	C	G	T	A	T	A	T	G	A	A	A
*+Eupatorium	C	C	C	G	T	C	T	T	T	C	A	C	G	T	A	T	G	A	A	A
*+Echinops	C	T	C	G	C	T	T	T	T	C	G	C	G	T	A	T	G	A	C	A
*Piptocarpa	C	T	C	A	T	T	T	T	G	C	A	C	G	T	A	T	G	A	A	T
Cichorium	C	T	C	G	T	T	T	T	T	C	A	C	G	T	A	T	G	A	A	A
*+Senecio	C	T	C	G	T	T	T	T	G	C	G	C	G	C	A	T	G	A	C	A
*+Lactuca	C	C	C	G	T	T	T	T	T	C	A	C	G	T	A	T	G	A	A	A
*+Helianthus	C	C	C	G	C	C	T	T	T	C	A	C	G	T	A	T	G	A	A	A
Flaveria	C	C	C	G	T	C	T	T	T	C	A	T	G	T	A	T	G	A	A	A
*+Carthamnus	C	T	C	G	C	T	T	T	T	C	G	C	G	T	A	T	G	A	C	A
*+Barnadesia	T	T	C	G	T	T	T	T	G	C	G	C	G	T	A	T	A	A	C	A
Dasyphylum	T	T	C	G	T	T	T	T	T	C	G	C	G	T	A	T	G	A	C	A

	Nucleotide position																			
Taxa	1095	1106	1111	1123	1125	1129	1131	1137	1140	1170	1176	1185	1194	1206	1212	1224	1227	1235	1236	1245
Nicotiana	T	C	T	C	A	C	G	A	A	G	G	G	C	C	A	A	T	G	T	A
Campanula	T	C	C	C	G	C	G	A	C	G	G	G	C	C	A	A	T	G	A	C
Scaevola	T	C	C	C	G	C	G	G	G	G	G	G	C	C	A	G	C	G	A	C
*Stokesia	C	C	C	A	A	T	A	G	C	G	G	G	C	C	A	G	C	G	A	C
*+Dimorphotheca	C	C	C	C	G	G	A	G	G	G	G	C	C	C	A	G	C	G	A	C

APPENDIX 1. Continued.

Taxa	1095	1106	1111	1123	1125	1129	1131	1137	1140	1170	1176	1185	1194	1206	1212	1224	1227	1235	1236	1245
*+Tagetes	C	C	C	C	G	T	A	G	G	G	G	G	C	C	A	G	C	G	G	T
*+Gazania	C	C	C	C	G	T	A	G	C	G	G	G	T	C	A	G	C	G	A	C
*+Felicia	C	C	C	C	G	G	A	G	G	G	G	G	T	T	C	G	C	G	A	A
*Chromolaena	C	C	C	C	A	T	A	A	G	A	G	G	C	T	A	G	C	G	A	T
*+Achillea	C	G	C	C	G	G	A	G	C	G	G	G	C	C	T	C	C	G	A	T
*+Coreopsis	C	C	C	C	G	T	A	G	A	G	G	G	C	C	A	G	C	G	A	T
*+Gerbera	C	C	C	C	G	C	A	G	G	G	G	G	C	C	A	G	C	G	A	C
*+Cacosmia	C	C	C	C	G	T	A	G	C	G	G	G	C	C	A	G	C	G	A	T
*+Blennosperma	C	C	C	C	A	C	A	T	G	G	A	G	C	C	C	G	C	G	A	C
*+Vernonia	C	C	C	A	A	T	A	G	C	G	G	G	C	C	A	G	C	G	A	T
*Tragopogon	C	C	C	C	G	T	A	G	C	G	G	G	C	C	A	G	C	G	A	C
*Chrysanthemum	C	G	C	C	G	G	A	G	C	G	G	A	C	C	C	C	C	G	A	T
*+Eupatorium	C	C	C	C	G	T	A	G	G	A	G	G	C	C	A	G	C	G	A	T
*+Echinops	C	C	C	C	A	C	A	G	G	G	A	G	C	C	A	G	C	G	A	C
*Piptocarpa	C	C	C	A	A	T	A	G	C	G	G	G	C	C	A	G	C	G	A	T
Cichorium	C	C	C	C	A	T	A	G	C	G	G	G	C	C	A	G	C	G	A	C
*+Senecio	C	C	T	C	G	A	A	G	T	G	G	G	T	C	A	G	C	G	T	G
*+Lactuca	C	C	C	C	G	T	A	G	C	G	G	A	C	C	A	G	C	A	A	C
*+Helianthus	C	C	C	C	G	T	A	G	G	A	G	G	C	C	A	G	C	A	A	T
Flaveria	C	C	C	C	G	T	A	G	G	G	G	G	C	C	A	G	C	G	G	T
*+Carthamnus	C	C	C	C	A	C	A	G	C	G	A	G	C	C	C	G	C	G	A	T
*+Barnadesia	C	C	C	C	G	C	G	A	G	G	G	G	C	C	A	G	T	G	A	C
Dasyphylum	C	C	C	C	G	C	G	G	G	G	G	G	C	C	A	G	C	G	A	C

Taxa	1260	1296	1299	1305	1306	1315	1316	1317	1318	1320	1337	1338	1341	1342	1345	1346	1389	1404	1407	1408
Nicotiana	T	T	A	T	G	C	A	G	G	A	G	C	G	G	T	G	A	T	T	G
Campanula	T	T	G	T	G	C	G	T	G	G	G	G	G	G	G	C	A	G	T	G
Scaevola	T	T	G	C	G	A	T	T	G	G	C	G	G	G	A	G	A	G	T	C
*Stokesia	T	T	G	C	G	A	A	G	C	G	G	T	G	G	G	C	G	G	T	G
*+Dimorphotheca	T	C	G	C	A	A	C	T	G	A	G	C	G	G	G	C	G	A	C	C
*+Tagetes	T	T	G	C	G	A	C	T	G	G	G	T	G	G	A	C	G	G	C	C
*+Gazania	C	T	G	C	G	G	T	T	G	G	G	T	G	G	A	C	G	G	T	G
*+Felicia	T	C	G	C	A	T	C	T	G	G	G	C	G	G	A	C	G	G	C	G
*Chromolaena	T	T	G	C	G	A	C	T	G	G	G	T	G	G	G	C	G	G	C	G
*+Achillea	C	T	G	C	G	A	C	C	G	G	G	C	A	G	A	C	G	A	C	C
*+Coreopsis	T	T	G	C	G	G	T	T	G	G	G	T	G	G	A	C	G	A	C	G
*+Gerbera	T	T	G	C	G	A	G	G	G	G	G	T	G	G	G	C	G	G	T	A
*+Cacosmia	T	T	G	C	G	G	T	T	G	G	G	T	G	G	G	C	G	G	T	C
*+Blennosperma	T	T	A	C	G	A	C	T	G	G	G	C	G	G	A	C	G	G	C	C
*+Vernonia	T	T	G	C	G	A	G	G	G	G	C	T	G	G	G	C	G	G	T	A
*Tragopogon	T	T	G	C	G	A	T	T	G	G	G	T	G	G	G	C	G	G	T	A
*Chrysanthemum	C	T	G	C	G	A	C	C	G	G	G	C	A	G	A	C	G	A	C	C
*+Eupatorium	T	T	G	C	G	A	C	T	G	G	G	T	G	G	A	C	G	G	C	C
*+Echinops	T	T	G	C	G	A	C	T	G	G	G	T	G	G	A	C	G	G	T	G
*Piptocarpa	T	T	G	C	G	A	G	G	G	G	G	T	G	G	G	C	G	G	T	G
Cichorium	C	T	G	C	G	A	C	T	G	G	G	T	G	G	G	C	G	G	T	C
*+Senecio	T	T	G	C	G	A	C	T	G	G	G	T	G	C	C	C	G	G	C	C
*+Lactuca	T	T	G	C	G	A	C	T	G	G	G	T	G	G	A	C	G	G	T	C

APPENDIX 1. Continued.

Taxa	Nucleotide position 1260	1296	1299	1305	1306	1315	1316	1317	1318	1320	1337	1338	1341	1342	1345	1346	1389	1404	1407	1408
*+*Helianthus*	C	T	G	C	G	A	C	T	G	G	G	T	G	C	A	G	G	G	C	C
Flaveria	T	T	G	T	G	A	C	T	G	G	G	T	G	G	A	C	G	G	C	C
*+*Carthamnus*	T	T	G	C	G	A	C	T	G	G	G	T	G	G	A	C	G	G	T	G
*+*Barnadesia*	T	T	C	C	G	A	T	T	C	T	G	T	G	G	T	G	G	G	T	C
Dasyphylum	T	T	G	C	G	A	A	T	G	G	G	T	G	G	A	G	G	G	T	G

Taxa	Nucleotide position 1409	1410	1411	1414	1420	1421	1423	1425	1426	1427	1428
Nicotiana	C	A	G	G	G	T	T	G	G	A	T
Campanula	C	C	G	A	A	C	T	A	T	A	A
Scaevola	A	G	G	A	A	C	T	G	G	A	T
**Stokesia*	C	T	C	G	A	C	A	T	G	A	C
*+*Dimorphotheca*	A	G	G	A	A	C	T	G	G	A	T
*+*Tagetes*	A	G	G	A	A	C	T	G	G	A	T
*+*Gazania*	C	T	C	G	A	C	A	T	T	G	A
*+*Felicia*	A	G	G	A	A	C	T	G	G	A	T
**Chromolaena*	A	G	G	A	G	T	T	G	G	A	T
*+*Achillea*	A	G	G	A	A	C	T	G	G	A	T
*+*Coreopsis*	C	T	C	G	A	C	A	T	G	A	T
*+*Gerbera*	A	T	C	G	A	C	T	G	G	A	T
*+*Cacosmia*	A	G	G	A	A	C	A	T	T	A	A
*+*Blennosperma*	A	G	G	A	A	C	T	G	G	A	T
*+*Vernonia*	A	G	C	G	A	C	A	T	G	A	C
**Tragopogon*	A	G	C	G	A	C	T	G	G	A	T
**Chrysanthemum*	A	G	G	A	A	C	T	G	G	A	T
*+*Eupatorium*	A	G	G	A	A	C	T	G	G	A	T
*+*Echinops*	A	G	G	C	A	C	A	T	T	G	A
**Piptocarpa*	C	G	C	G	A	C	A	T	G	A	C
Cichorium	A	G	G	A	A	C	T	G	G	A	T
*+*Senecio*	A	G	G	A	A	C	T	G	G	A	T
*+*Lactuca*	A	G	G	A	A	C	T	G	G	A	T
*+*Helianthus*	A	G	G	A	A	C	T	G	G	A	T
Flaveria	A	G	G	A	A	C	T	G	G	A	T
*+*Carthamnus*	A	G	G	A	A	C	T	G	G	A	T
*+*Barnadesia*	C	G	G	T	A	C	T	C	G	T	C
Dasyphylum	C	T	G	A	A	C	T	G	G	A	T

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THE LYCOPSIDA: A SYMPOSIUM

William A. DiMichele[1] *and*
Judith E. Skog[2]

The lycopsids are among the most morphologically bizarre and, consequently, fascinating group of "lower" vascular plants. The extant orders, Lycopodiales, Selaginellales, and Isoetales, are ancient lineages, all extending back in time well into the Paleozoic. Among the defining characters, exarch protoxylem maturation, adaxial, laterally or foliar borne eusporangia with distal dehiscence, and "microphyllous" leaves are the most conspicuous and tie the lycopsids to the zosterophylls of the Early Devonian, either as direct descendants or as codescendants from a common ancestor (see Sporne, 1975; Niklas & Banks, 1990; Gensel, 1992). It is the linkage of the extant lycopsids to a long and elaborate fossil history that provides perspective on the importance of this group to studies of plant evolution: the lycopsid–zosterophyll clade appears to be the sister group to all other vascular plants (Fig. 1; Banks, 1975; Crane, 1990).

A morphologically distinct lycopsid lineage was unquestionably present in the Early Devonian (Niklas & Banks, 1990; Hueber, 1992) and may have occurred as early as the Late Silurian (Andrews, 1961; Tims & Chambers, 1984), in either case millions of years prior to the appearance of any other extant classes or orders of vascular plants. From simple beginnings, with plants organized much like modern *Lycopodium*, there appeared a great diversity of structural form and ecological specialization, reaching a zenith in the Late Carboniferous, which included the giant tree lycopsids of the coal forests (see Bateman et al., 1992, and Phillips & DiMichele, 1992, for reviews). Throughout the history of land plants, lycopsids have been present on every land mass; today *Lycopodium* sens. lat. (see Wagner & Beitel, 1992; Øllgaard, 1992) is the most widely distributed of the lower vascular plants, found on every major continent except Antarctica and almost every major island group in the world.

In the course of this extensive radiation the lycopsids evolved many characteristics that, on first examination, appear to be homologous with attributes of other tracheophytes: leaves, centralized root systems and bipolar development (Rothwell & Erwin, 1985), secondary xylem, secondary protective tissues, siphonosteles (Schmid, 1982), strobili, and seedlike organs (Phillips, 1979), among other characters. In some cases the distinctiveness and evolutionary independence of the lycopsid organs have been recognized (see Andrews, 1961, for an early discussion), as indicated by names such as microphyll (as opposed to megaphyll) for lycopsid leaves, rhizomorph for "rooting" organs in the Isoetales, and rhizophore for roots in some Selaginellales (Webster, 1992). Overall, however, the

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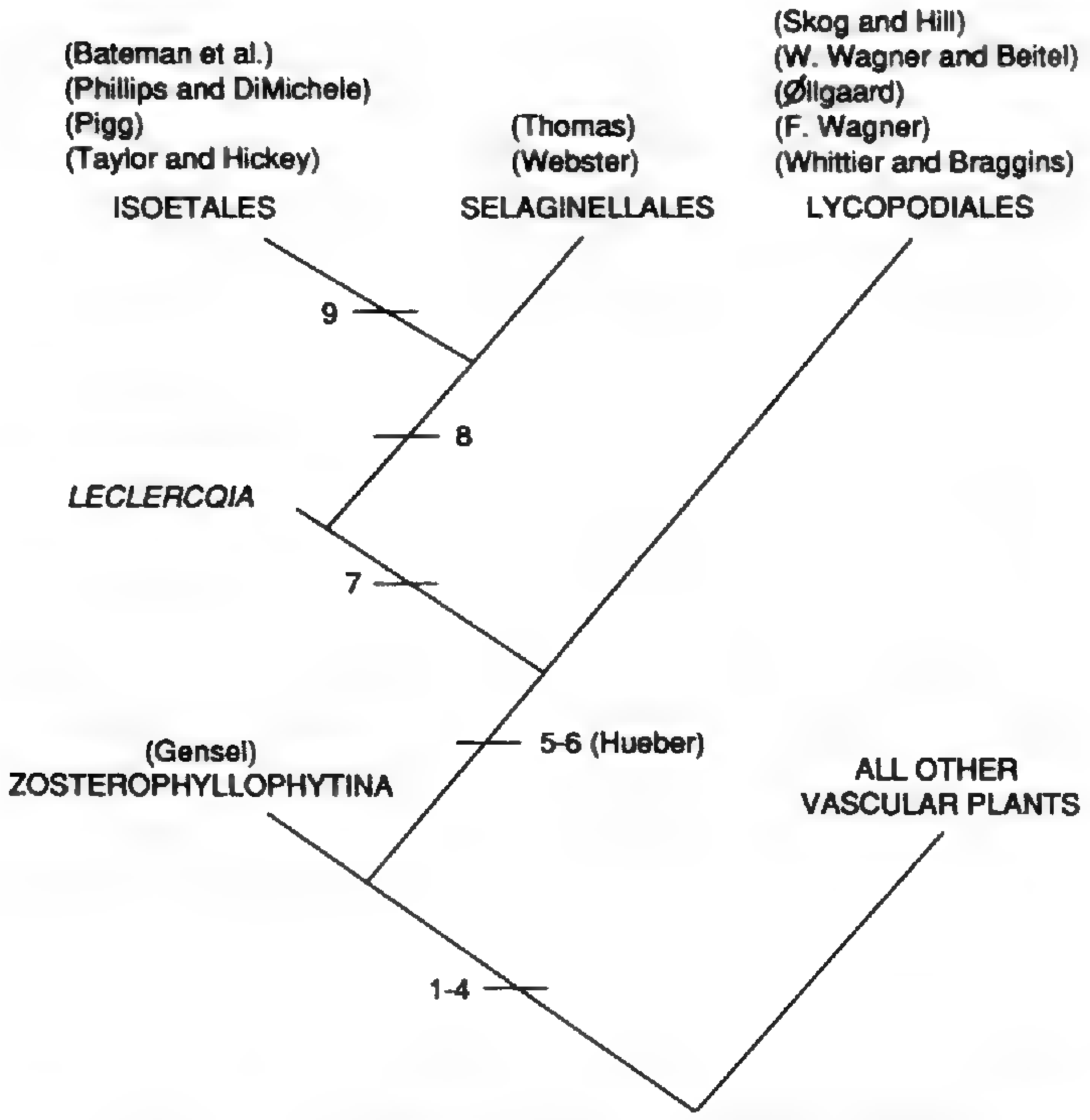

FIGURE 1. Phylogenetic relationships of major groups of lycopsids and zosterophylls. The genus *Leclercqia* is included as an important intermediate form. Authors of papers in this volume are noted in parentheses above the relevant taxonomic group. Major characters are noted on the tree: The zosterophyll–lycopsid clade is delimited by the presence of (1) exarch protoxylem, (2) sporangia borne laterally on the stem, (3) reniform sporangial shape, (4) complete distal dehiscence of sporangia. This clade is distinct from all other vascular plant groups. The Class Lycopsida is delimited by (5) microphyllous leaves, and (6) adaxial, foliar-borne or axillary sporangia. *Leclercqia*, and the orders Isoetales and Selaginellales are united into a clade by (7) the presence of a foliar ligule. The Selaginellales and Isoetales are united further by (8) heterospory. The Isoetales are distinguished by (9) rhizomorphic rooting structures. This is not a rigorous cladistic analysis, but the characters shown are synapomorphies for the clades they delimit. Compiled by W. A. DiMichele and F. M. Hueber.

unique phylogenetic position of this group, while recognized and discussed, has not been exploited as a vehicle to study either apparent convergent structural evolution in vascular plants, or limits on structural solutions to common problems such as light interception, propagule dispersal, and nutrient acquisition. The lycopsids have been treated consistently as "pteridophytes," "fern allies," or "lower vascular plants" (e.g., Jermy et al., 1973; Sporne, 1975), and as such have been lumped on the basis of symplesiomorphies with the phenetically similar clades of the "other" branch of vascular plant life history.

The work of E. C. Jeffrey (1902, 1910, 1917) is, in a historical sense, perhaps the most important to identify the phylogenetic and morphological distinctiveness of the lycopsids. Jeffrey recognized two lineages of vascular plants, the Lycopsida (lycopsids, sphenopsids, and Psilotales), and the Pteropsida (ferns and seed plants), but based this distinction almost entirely on stelar anatomy and his conception of stelar evolution, ideas now discredited (see Beck et al., 1982). The failure of Jeffrey's system was not so much in his phylogenetic perspective, but in the weakness of his arguments on stelar evolution. His broader intuition about vascular plant phylogeny, which undoubtedly played a role in the development of his formal arguments, was more nearly correct—Jeffrey was close to being right even if for the wrong reasons.

Unfortunately, it is now fashionable to inflate every order of non-angiospermous seed plants to divisional rank (in order to accommodate inflation of the angiosperms to divisional status). This necessitates similar inflation of lycopsids, sphenopsids, and ferns, and serves the botanical community no better than lumping lycopsids with the other free-sporing plants as a "pteridophyte" grade group (but see Knoll & Rothwell, 1981, for a beacon in the current taxonomic fog). Jeffrey's insights, in spite of their flaws, at least provided a point of departure that could have served to foster recognition and exploitation of the fundamental phylogenetic split between lycopsids and all other plants.

The modern awareness of the unique phylogenetic position of the lycopsids can be traced to fossil evidence demonstrating not only the antiquity of the lineage but the many unique aspects of development and morphology in extinct forms (Andrews, 1961). This was followed by the dismemberment of the Early Devonian "psilophytes" by Banks (1975), who demonstrated and discussed early divergence of lycopsids from the rest of the vascular plants. This problem has lain in need of further analysis until recently; readers drawn to the results of this symposium should see papers by Crane (1990) and Kenrick & Crane (1991) that present and discuss hypotheses for the relationships among land plants. The analysis of sporogenesis by Crane (1990) is based on a cladistic analysis of land-plant phylogeny that demonstrates explicitly a split between a lycopsid–zosterophyll clade and a clade including all other extant vascular-plant lineages. Relationships among basal Devonian elements of this phylogeny are considered further by Kenrick & Crane (1991). Such phylogenies are central to developing research agendas that propose using the lycopsids to investigate more basic, mechanistic questions about plant evolution including studies of physiology, population biology, and structural evolution.

The papers in this volume originated from a symposium jointly sponsored by the Paleobotanical Section of the Botanical Society of America and

the American Fern Society on 8 August 1989 at their annual meeting, which was held in Toronto, Canada. The symposium was partially funded by The Botanical Society of America and by the National Science Foundation; we thank them for their sponsorship and support. We are grateful to the numerous scientists who assisted with prompt, thoughtful reviews of the papers. Amy Scheuler of the Missouri Botanical Garden was instrumental in shepherding us and the papers to final publication, and we thank her for her patience and help. Lastly, we thank the contributors for willingness to participate and for prompt preparation and modification of manuscripts.

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NOTE ADDED IN PROOF

Recently, Raubeson & Jansen (1992) found a major difference in the chloroplast DNA gene order between lycopsids and all other vascular plants, supporting the view that the lycopsids are a sister group to other tracheophytes.

RAUBESON, LINDA A. & ROBERT K. JANSEN. 1992. Chloroplast DNA evidence on the ancient evolutionary split in vascular land plants. Science 255: 1697–1699.

PHYLOGENETIC RELATIONSHIPS OF THE ZOSTEROPHYLLS AND LYCOPSIDS: EVIDENCE FROM MORPHOLOGY, PALEOECOLOGY, AND CLADISTIC METHODS OF INFERENCE[1]

Patricia G. Gensel[2]

ABSTRACT

Zosterophylls have been considered the probable ancestors of lycopsids since the establishment of the group in 1968 by Banks. Both share the characters of exarch protosteles and reniform sporangia, and it is argued that characters separating the two, e.g., microphylls and leaf-associated sporangia, could easily be derived by modification of zosterophyll emergences and sporangial position. Recently, different opinions concerning the derivation of lycopsid features have been proposed and an earlier time of occurrence of lycopsids has been suggested. The purpose of this paper is to evaluate the position of zosterophylls relative to lycopsids employing current information and considering prevailing theories. Aspects of morphology and ecology of zosterophylls and lycopsids are summarized, various evolutionary theories are evaluated, and a preliminary phylogenetic analysis involving zosterophylls, lycopsids, and selected other types of early land plants is presented. The cladograms suggest that zosterophylls and lycopsids are monophyletic based on the characters employed in the study. However, critical information is lacking that would allow a more precise estimate of affinity among all early land plants and between zosterophylls and lycopsids. Determining homologies is difficult, and early land plants exhibit extensive homoplasy.

The subdivision Zosterophyllophytina was erected by Banks (1968) for leafless plants of Devonian age with exarch protosteles and laterally borne sporangia with transverse dehiscence. He suggested that these plants possibly gave rise to the lycopsids, based on similarity of xylem maturation and sporangium morphology. Since then, more than 14 genera (Table 1) have been assigned to the group, some being monotypic and others encompassing several species. The geographic and stratigraphic distribution of the group, last reviewed in depth by Banks (1975), has been extended. As presently known, zosterophylls range from late Silurian (?) or earliest Devonian (Gedinnian or Pragian) to late Devonian (Frasnian) (Fig. 1) and occur worldwide.

Circumscription of the zosterophylls has remained fairly clear and the group has been considered "natural." A close relationship with lycopsids still can be argued, given their morphological and anatomical similarities and the presence of possible intermediates between the two groups. Recently however, Stewart (1983), building on the suggestion that *Leclercqia* leaves are branchlike (Bonamo & Grierson, 1981), suggested that lycopsids might be diphyletic, with only some lycopsids being derived from a zosterophyll ancestor. In these, microphylls may have evolved via vascularization of enations, and leaf-borne sporangia perhaps via "phyletic slide" (Stewart, 1983). Early lycopsids with forked leaves, such as *Leclercqia*, may have arisen from a rhyniophyte ancestor, by reduction of branch systems containing both fertile and vegetative components. Bonamo et al. (1988), however, noted several inconsistencies between *Leclercqia* and its putative ancestors and interme-

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[1] I thank Brent Mishler, Duke University, Mark Chase, University of North Carolina–Chapel Hill, and Victor Albert, University of North Carolina–Chapel Hill for their advice and assistance with the phylogenetic analysis; Susan Whitfield for preparation of the line drawings; Katherine Rankin and Mitchell Sewell for careful technical assistance; and the National Science Foundation for research support under NSF grant BSR-8800432.

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diates that suggest Stewart's hypothesis is untenable.

A number of plants exhibit a zosterophyll type of sporangium, i.e., one that is stalked, reniform or globose in shape, and with transverse dehiscence (Fig. 2). However, these lack one or more critical characters that would permit unequivocal assignment to the group. Of these, *Hicklingia* (Fig. 2A) is included in the zosterophylls on the basis of its sporangial characters, even though its anatomy is unknown (Edwards, 1976). *Renalia* Gensel, 1976, *Hsua* Li, 1982, and perhaps *Huia* Geng, 1985, more likely represent rhyniophytes with more extensive, strongly anisotomous branching than normally is attributed to that group (Fig. 2B–D). The presence of centrarch protosteles in the latter two taxa may support that affinity. *Eophyllophyton* Hao, 1988, is not known well enough to permit assignment to a major group, but is intriguing in possessing globose or reniform sporangia located within possible leaflike structures (Fig. 2F). More information is needed on aspects of its morphology and anatomy. Conducting cells in *Nothia* El-Saadawy & Lacey, 1979, apparently lack secondary thickenings (Fig. 2E), as do some axes referred to *Taeniocrada dubia* by Hueber (1982), and these presently may constitute, with other fossils, one or more separate, nontracheophytic land plant lineages.

Some plants known only from anatomy also may represent zosterophylls. *Euthursophyton hamperbachense* Mustafa, 1978, and *Stolbergia spiralis* Fairon, 1967, are Middle Devonian plants based mainly on permineralized axes that exhibit an exarch haplostele (Fig. 7C), but they lack evidence of leaf traces and attached reproductive structures. While this suggests zosterophylls, one should be cautious since stelar characters alone do not define the group and many possible combinations of anatomy and morphology are becoming evident among early land plants.

The early history of lycopsids is more problematic, both in terms of definition of the group (division or class) when one considers early fossil taxa, and first appearance of the group. If one accepts that a lycopsid must have microphyllous leaves and leaf-associated sporangia (borne in leaf axils or on a leaf surface), then undoubted representatives from the Lower Devonian include only *Leclercqia*, because sporangial attachment in *Baragwanathia* may be cauline (Lang & Cookson, 1935; Rayner, 1984; Edwards & Fanning, 1985; Kenrick & Edwards, 1988b).

Other Lower Devonian plants often regarded as lycopsids include *Drepanophycus*, *Kaulangiophyton*, and *Asteroxylon*. Rayner (1984) grouped *Drepanophycus*, *Baragwanathia*, and questionably *Asteroxylon* in a separate class of plants, the Drepanophycopsida, which he characterized as exhibiting lycopsid vegetative features, e.g., microphylls (*Asteroxylon* is tentatively placed here because in its axes, vascular tissue extends only to the base of the leaflike structures) and zosterophyll reproduction (sporangia cauline, not associated with leaves). Niklas & Banks (1990) removed *Baragwanathia* from the Drepanophycopsida sensu Rayner because it is unknown whether the sporangia are stalked. There is as yet no evidence of vascularization in the emergences (leaflike appendages) of *Kaulangiophyton*, a plant that strongly resembles some specimens of *Drepanophycus*, so the status of this taxon is unclear. If the appendages are unvascularized, it would best be considered a zosterophyll. For convenience, I will refer to *Kaulangiophyton*, *Drepanophycus*, and *Asteroxylon* collectively by the grade-level designation of "prelycopsid" (= intermediate between zosterophyll and lycopsid) as has been done previously (Gensel & Andrews, 1984; Niklas & Banks, 1990, and others cited therein).

TABLE 1. Plants assigned to the zosterophylls or with some characteristics of zosterophylls.

Genera of zosterophylls	Selected references
Anisophyton	Remy et al. (1986)
Bathurstia	Hueber (1971b)
Crenaticaulis	Banks & Davis (1969)
Deheubarthia	Edwards et al. (1989)
Discalis	Hao (1989)
Gosslingia	Heard (1927), Edwards (1970)
Hicklingia	Edwards (1976)
Koniora	Zdebska (1982)
Margophyton	Zakharova (1981)
Oricilla	Gensel (1982b)
Rebuchia	Hueber (1970, 1972)
Sawdonia	Hueber (1971a), Gensel et al. (1975)
Serrulacaulis	Hueber & Banks (1979)
Tarella	Edwards & Kenrick (1986)
Thrinkophyton	Kenrick & Edwards (1988b)
Zosterophyllum	Penhallow (1892), Edwards (1975), Gensel & Andrews (1984)
Possible Zosterophylls: Taxa based on anatomy—show exarch protostele; lack vascularized leaves and reproductive structures	
Euthursophyton hamperbachense	Mustafa (1978)
Stolbergia spiralis	Fairon (1967)

			Zosterophylls																	Prelycopsids			Lycopsids					
			Zosterophyllum	*Sawdonia*	*Gosslingia*	*Crenaticaulis*	*Koniora*	*Thrinkophyton*	*Rebuchia*	*Oricilla*	*Serrulacaulis*	*Bathurstia*	*Tarella*	*Margophyton*	*Anisophyton*	cf. *Psilophyton princeps* Croft & Lang	*Discalis*	unnamed zosterophylls - Australia	*Hicklingia*	*Asteroxylon*	*Kaulangiophyton*	*Drepanophycus*	*Baragwanathia*	*Leclercqia*	*Colpodexylon*	*Archaeosigillaria*	*Haskinsia*
DEVONIAN	Upper	Famennian																									
		Frasnian		●							●											●			●	●	●
	Middle	Givetian									●								●?					●	●	●	●
		Eifelian																				●			●	●	
	Lower	Emsian	●	●		●	●		●	●				●	●?						●	●	●	●		●?	
		Siegenian	●	●	●			●	●			●	●	●	●?	●	●			●		●	●?				
		Gedinnian	●		●																						
SILURIAN	Upper	Pridolian																									
		Ludlovian																●?					●?				
	Lower	Wenlockian																									
		Llandoverian																									

FIGURE 1. Stratigraphic occurrence of zosterophyll, pre-lycopsid, and lycopsid genera in Silurian–Devonian strata.

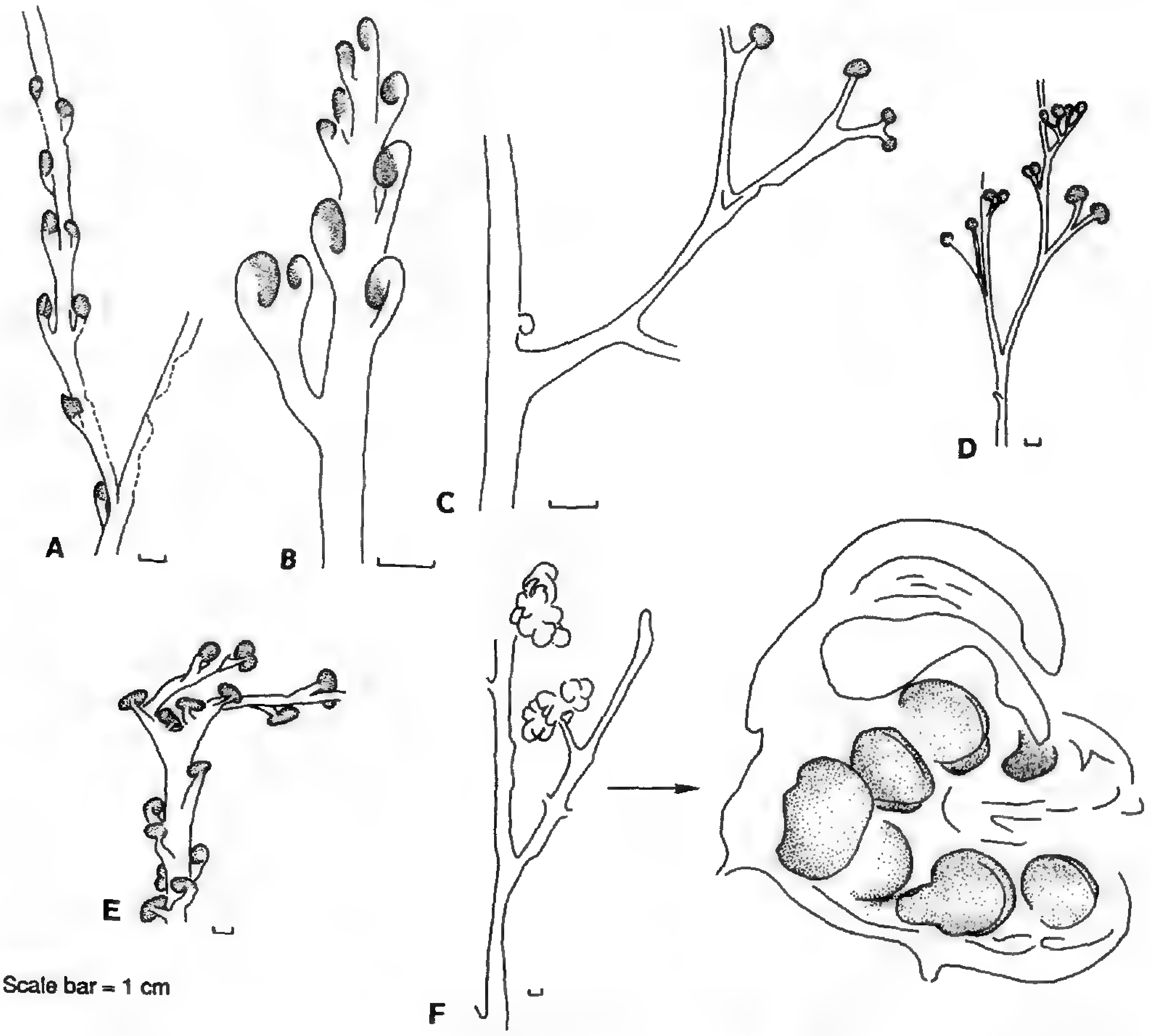


FIGURE 2. Line drawings of plants with zosterophyll-like sporangia. Sporangia are stippled.—A. *Hicklingia edwardii*—assigned to the zosterophylls by Edwards (1976). B–D. Probable rhyniophytes.—B. *Huia recurvata* Geng, 1985.—C. *Hsüa robusta* Li, 1982.—D. *Renalia hueberi* Gensel, 1976. E, F. Incertae sedis.—E. *Nothia aphylla* El-Saadawy & Lacey, 1979.—F. *Eophyllophyton bellum* Hao, 1988.

Even though the earliest undoubted lycopsid, *Leclercqia*, is found in Emsian and Givetian strata, uncertainty about the time of appearance of lycopsids remains. If *Baragwanathia* is a lycopsid, and if the Ludlow age of some Australian *Baragwanathia* is correct, lycopsids would have existed in the mid–late Silurian. As yet undescribed zosterophylls are reported from comparable age sediments in Australia (Tims & Chambers, 1984), and thus the two groups may have co-occurred in the late Silurian.

In light of these developments, and despite the constraints of imperfect representation in the fossil record, it is appropriate to evaluate the position of zosterophylls relative to lycopsids once again. Specifically, how do zosterophylls relate to the lycopsids—do they represent a paraphyletic group with respect to the lycopsids (i.e., are they ancestral?), or might they be a monophyletic sister group, or do they have only a distant relationship to lycopsids? This paper will consider these questions by (1) characterizing zosterophylls, putatively related taxa, and selected lycopsids in terms of their structural organization, growth habit, reproduction, and ecology, and (2) considering prevailing theories concerning how lycopsids may have arisen. This is followed by an analysis of relationships of zosterophylls, pre-lycopsids, and lycopsids within the context of major pteridophyte lineages using cladistic methods of phylogenetic reconstruction. Some specific questions to be dealt with in the course of this evaluation are the following: (1) Is the morphology of these plants complex enough to allow such a question to be answered definitively? (2) Do the patterns of diversity and directions of morphological change differ significantly between these two groups? (3) Do ecological patterns of zosterophylls differ from those of early lycopsids? (4) Do the differences in their morphologies and ecologies constrain them into different evolutionary directions?

GENERAL FEATURES OF ZOSTEROPHYLLS

If one surveys the array of plants assigned with some assurance to zosterophylls, the following are characteristics common to the majority of them: plants with a rhizomatous habit, in which axes bifurcate isotomously and/or anisotomously (Fig. 3A, C, D) at frequent to infrequent intervals. Some exhibit H or K branching, in either prostrate and aerial, or only aerial, portions of the plant. H and K branching has been variously interpreted in the

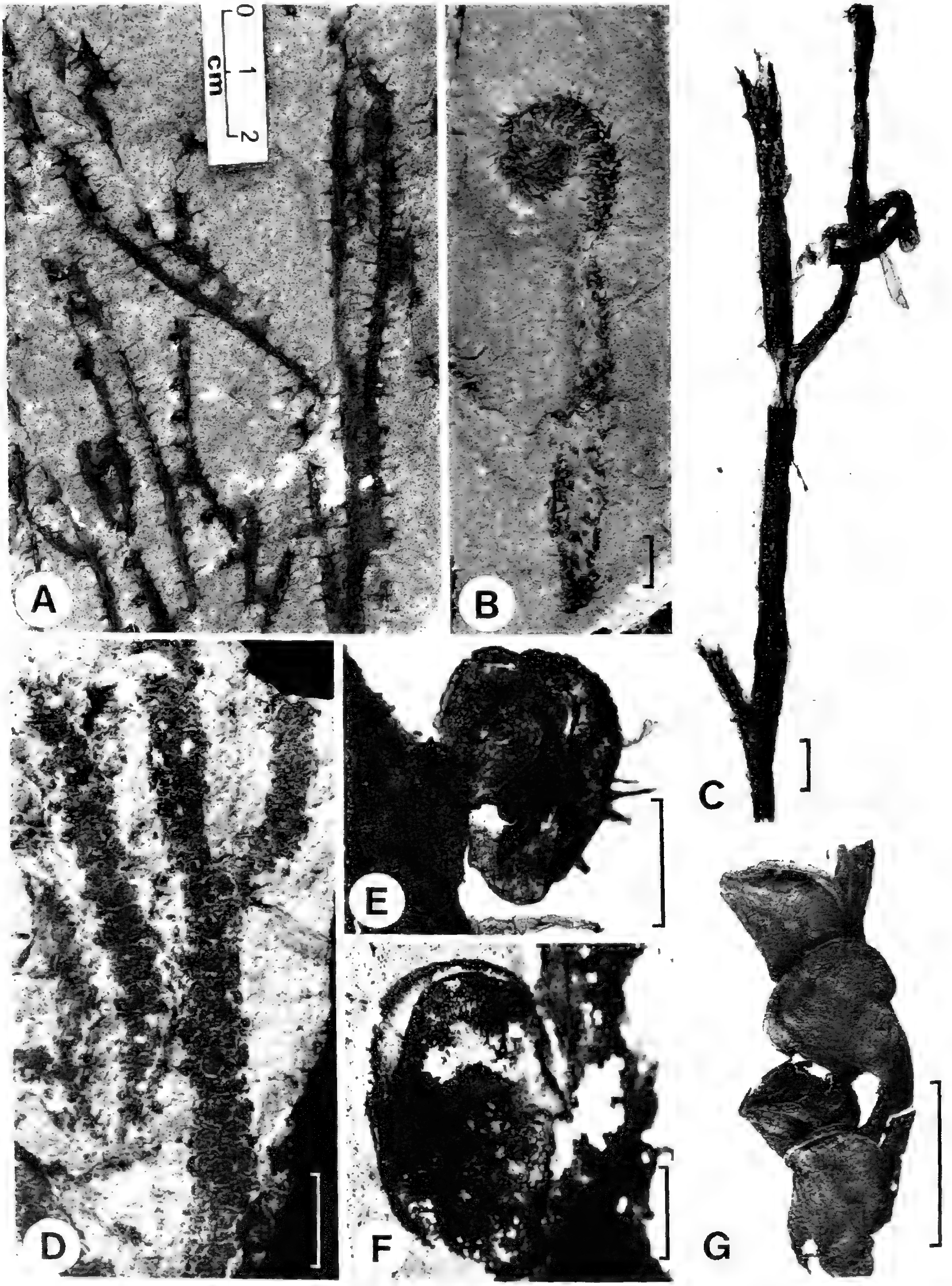


FIGURE 3. A. Several axes of *Sawdonia ornata* from Gaspé, Canada. Central one bears sporangia.—B. Circinate axis of *Sawdonia ornata* from New Brunswick, Canada.—C. Branched axis of *Crenaticaulis verruculosus*, with subaxillary branch at upper right.—D. Sparsely branched new zosterophyll from New Brunswick covered with globose emergences.—E. Sporangium of *Sawdonia ornata* from Gaspé showing short stalk, two valves and emergences on outer valve.—F. Sporangium of *Oricilla bilinearis* from New Brunswick illustrating short stalk, horizontal orientation relative to axis.—G. Several sporangia of *Zosterophyllum divaricatum* from New Brunswick, illustrating upright orientation. Note the thickened area adjacent to dehiscence region. F from Gensel (1982b). G from Gensel (1982a). B–D, G scale bars = 5 mm. E, F scale bars = 1 mm.

literature; I view it as a result of flattening during fossilization of branched axes of a plant consisting of a prostrate, dichotomizing rhizome from which upright branches depart. Certain types of dichotomy in upright axes also could produce this pattern when flattened, as demonstrated by Gerrienne (1988) and Edwards & Kenrick (1986).

Several taxa exhibit subaxillary tubercles, branches (Fig. 3C), or scattered protuberances ranging from small stubs to branched axes (discussed in detail by Edwards & Kenrick, 1986). These suggest some instability in developmental patterns of shoot apices. Circinate vernation of axes (Fig. 3B) is known for several genera.

Axes are either smooth or covered with emergences that vary in morphology and arrangement depending on the taxon (Figs. 5, 6). A few taxa exhibit emergences on sporangia (*Sawdonia*—Fig. 3E, *Discalis, Koniora,* and a new taxon from New Brunswick).

Where known, anatomy consists of an exarch, round to elliptical haplostele (Fig. 7A, C). Protoxylem, recognized mainly on the basis of smaller cell diameter, consists either of a single layer or of several clusters of a few small tracheids located around the periphery of the xylem strand. The outline of the stele is smooth in contrast to the ridged or lobed appearance of steles in early lycopsids. Tracheid wall pattern according to Kenrick & Edwards (1988a) is annular, helical, indirectly connected annular or helical, and possibly scalariform to bordered pitted (*Koniora*). Kenrick & Edwards (1988a) also demonstrated the presence of irregular perforations on walls in between the annular thickenings (not considered an artifact of preservation) in *Gosslingia, Thrinkophyton,* and *Deheubarthia* and noted that some other zosterophylls, pre-lycopsids, and early lycopsids may show a similar condition (Fig. 10B). Figure 7B confirms the same pattern for *Crenaticaulis.* The outer cortex in several taxa consists of thickened cells just below the epidermis (Fig. 7A).

Cuticular features are known to different extents among the zosterophylls. Epidermal cell shape varies from elongate-rectangular to nearly isodiametric in *Zosterophyllum* (Lele & Walton, 1961) and in some other genera. Several genera in which cuticles have been studied exhibit the distinctive "rosette cell" pattern (Fig. 7D, E) first noted in *Sawdonia ornata* by W. N. Edwards (1924). Papillae occur on epidermal cells in *Sawdonia* (Fig. 8B) and *Crenaticaulis.* Both of these features are absent in *Zosterophyllum,* however. Stomata are interpreted as consisting of two guard cells surrounded by epidermal cells (Figs. 7F, 8A), even though the cuticular impressions do not delimit two guard cells. The basis for this interpretation is the presence of T-shaped thickenings at the stomatal poles, and the occasional presence of a faint dividing line that would delimit guard cells in the cuticle of *Zosterophyllum myretonianum* (Lele & Walton, 1961; Edwards et al., 1982). In some taxa stomata appear sunken.

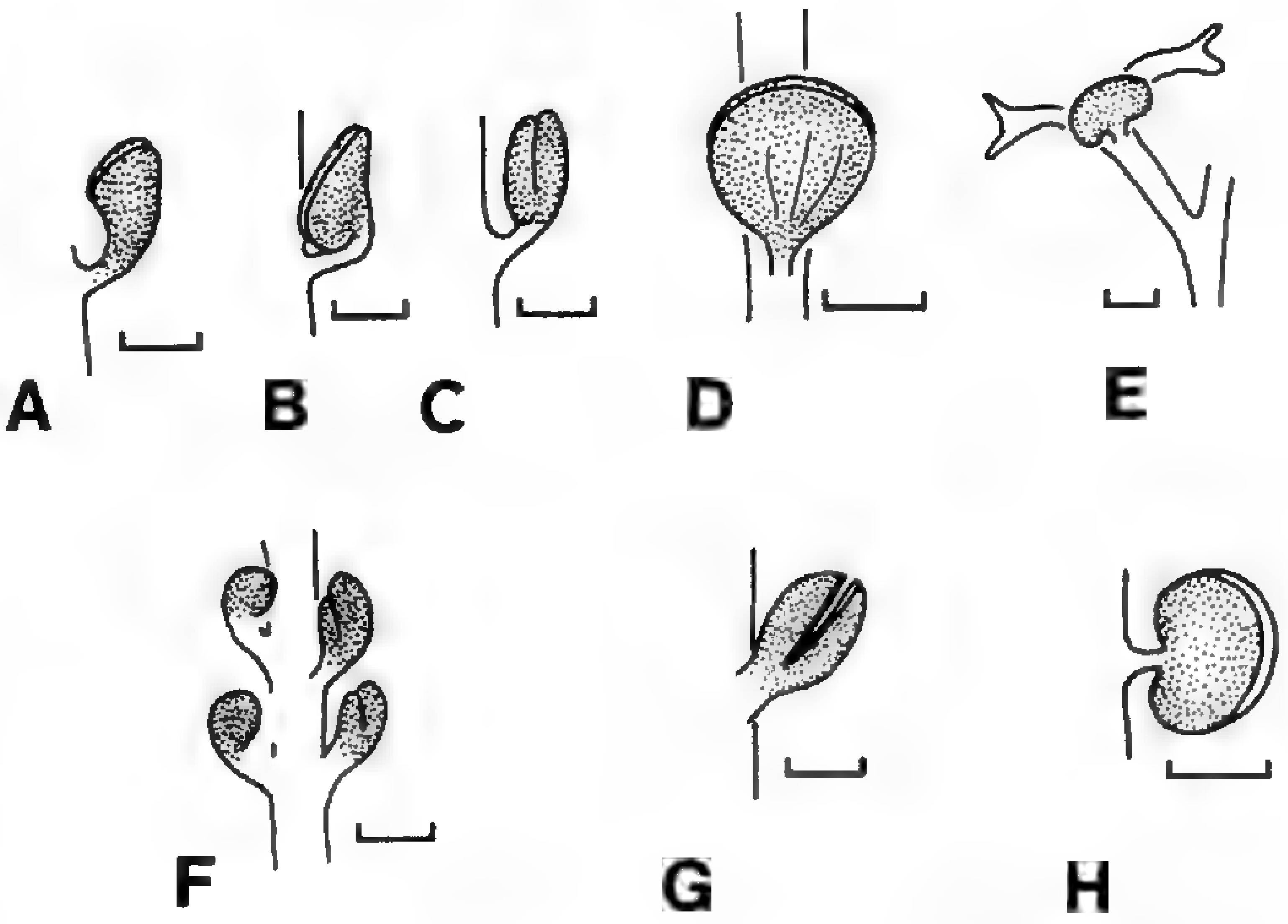


FIGURE 4. Sporangial orientation in zosterophylls. A–G. Upright orientation.—A–D. *Zosterophyllum.*—E. *Koniora.*—F. *Crenaticaulis.*—G. *Sawdonia.*—H. Horizontal orientation. *Oricilla.* Also present in *Tarella, Gosslingia,* perhaps *Anisophyton* and *Margophyton.* Scale bars = 2 mm.

Sporangia are borne laterally on axes and terminate stalks ranging from less than 1 mm to 4 mm long. Sporangial stalks in *Zosterophyllum* are reported to be vascularized. Sporangia are reniform or occasionally globose in outline and dehisce along their distal margins (transverse dehiscence) into equal or unequal valves. In several taxa, compression remains of sporangia exhibit a thickened border adjacent to the dehiscence line (an annulus?). Anatomy of *Zosterophyllum llanoveranum* sporangia (Edwards, 1969) shows the thickened margins to consist of up to nine layers of elongate, thick-walled cells; in between these borders are some thin-walled cells, some of which probably broke down to cause sporangium opening.

Sporangia are oriented with respect to the axes in one of two ways: (1) upright—their stalks are parallel or at an acute angle to the axis such that their dehiscence lines are perpendicular to the axis bearing them (Figs. 3E, G, 4A–G); or (2) horizontal—their stalks are perpendicular to the axes so that their dehiscence line parallels the axis (Figs. 3F, 4H). Spores are trilete, smooth or slightly granular, sometimes with curvaturae perfectae. They are very similar throughout the group (Fig. 8C, D). *Zosterophyllum myretonianum, Z. divaricatum, Gosslingia, Sawdonia, Crenaticaulis, Thrinkophyton,* and *Deheubarthia* are among the

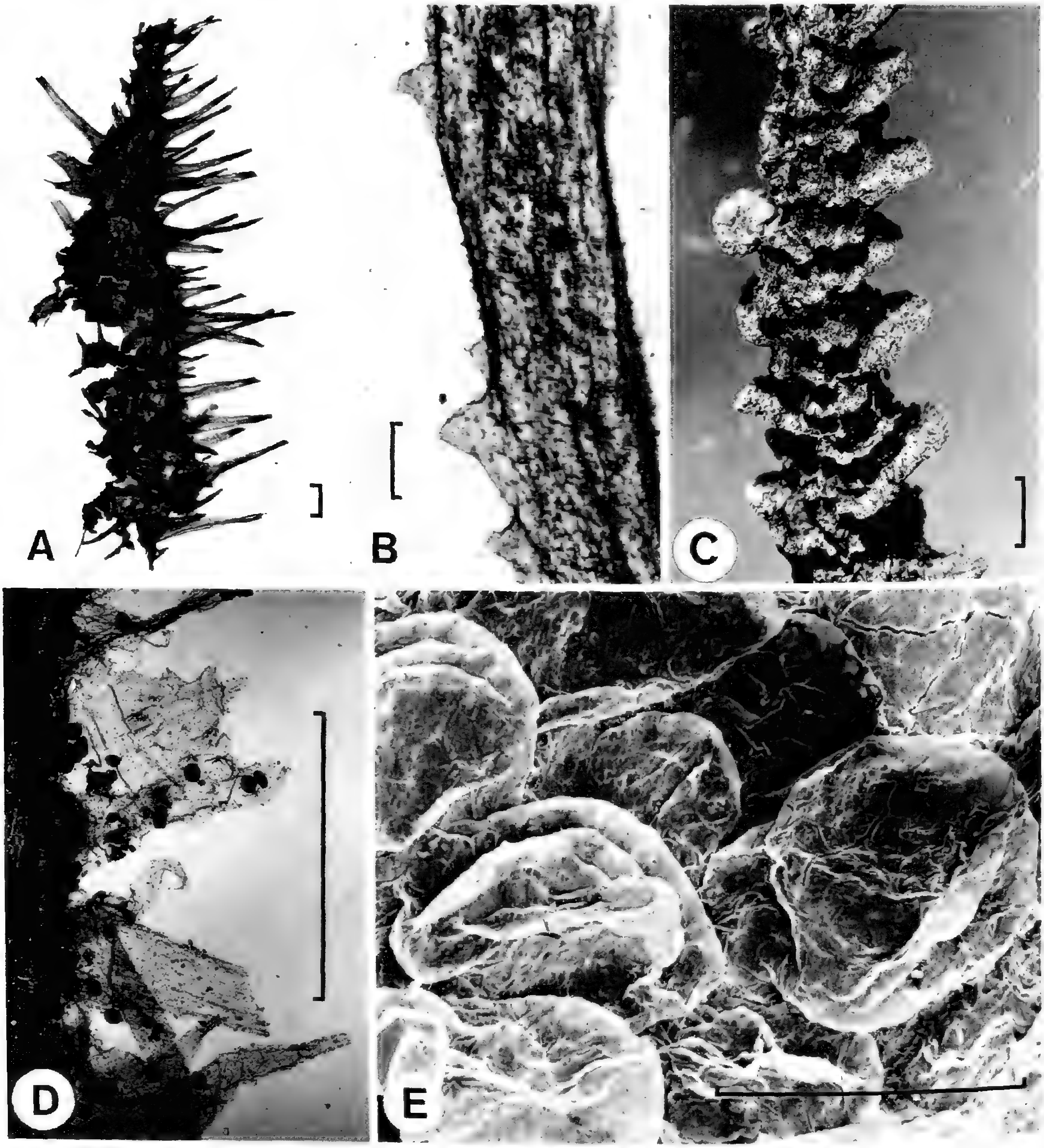


FIGURE 5. Emergence types in zosterophylls.—A. Tapered spinelike emergences of *Sawdonia ornata*.—B. Papillae and short deltoid emergences (teeth) in opposite rows on axis of *Crenaticaulis verruculosus*.—C. New zosterophyll type b from New Brunswick with flattened wedgelike emergences.—D. Forked and entire spinelike emergences of *Sawdonia acanthotheca* from New Brunswick. One near the top has eight tips.—E. Scanning electron micrograph of globose emergences in a new zosterophyll type from New Brunswick; general view is in Figure 4D. Scale bars = 1 mm.

more completely known zosterophylls: they exhibit several branching orders, at least some aspects of anatomy, and bear sporangia.

Zosterophylls vary greatly while retaining a basic sporangium morphology and attachment that unite the group. An assessment of the characters useful in recognizing genera is presented by Kenrick & Edwards (1988b) and Edwards et al. (1989). The former note that each new taxon presents a new "concatenation of overlapping characters" with the others. The characters they regard as useful are: (1) sporangium distribution on axes; (2) sporangium arrangement (spiralled, linear, variable, singly); (3) sporangium orientation, e.g., sporangium upright or horizontal; (4) sporangial valves equal or unequal; (5) branching pattern isotomous versus pseudomonopodial with distal isotomy possible; (6) aerial branch systems spiralled or planar; (7) axillary tubercles present versus absent or presence of other lateral branch-related projections; (8) non-vascularized emergences present versus absent. Some of these are included in the phylogenetic

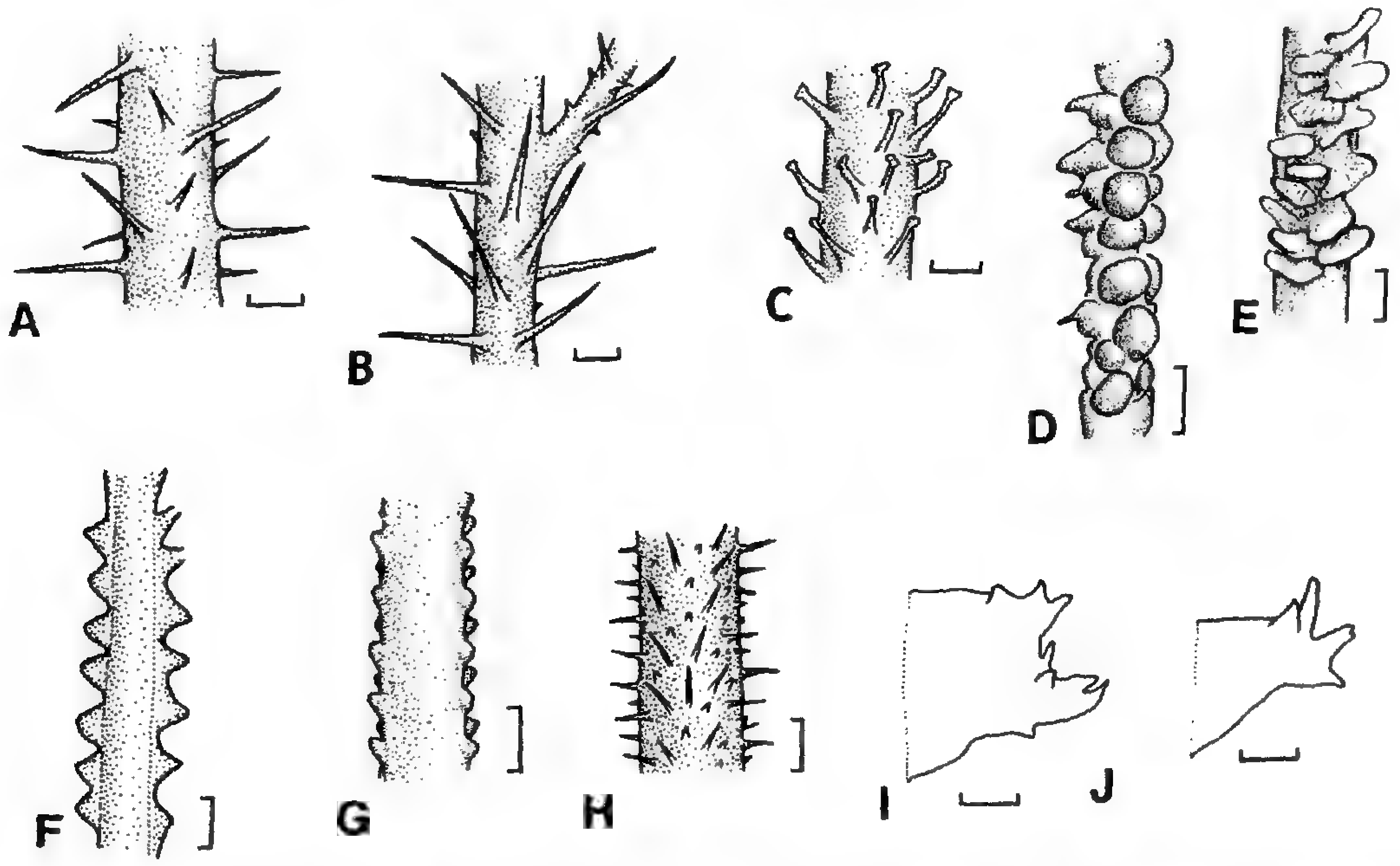


FIGURE 6. Line drawings interpreting emergence types in zosterophylls.—A. *Sawdonia ornata.*—B. *Koniora andrychoviensis.*—C. *Discalis longistipa.*—D. New zosterophyll type a.—E. New zosterophyll type b.—F. *Serrulacaulis furcatus.*—G. *Crenaticaulis verruculosus.* Papillae not shown. H–J. *Sawdonia acanthotheca.*—H. Unforked, spinelike emergences.—I., J. Forked emergences. A–H scale bars = 2 mm. I, J scale bars = 0.2 mm.

analysis discussed later, while others are too incompletely known or represent autapomorphies and could not be included as markers of phylogenetic relationships.

Emergence type is not in the above list and is excluded from the analysis to follow, because it is quite variable and autapomorphic. Several genera lack emergences entirely (*Zosterophyllum, Gosslingia, Tarella, Oricilla*). Among those with emergences, some have axes and sporangia covered with emergences while others exhibit distinct patterns such as opposite double rows in *Crenaticaulis,* or opposite and in single rows in *Serrulacaulis* (Fig. 6). The importance of emergences as a taxonomic character varies; considering several plant groups, in some cases it is used at the generic level (*Sawdonia,* the monotypic genera *Serrulacaulis, Crenaticaulis*), in others to distinguish species (*Psilophyton, Anisophyton*).

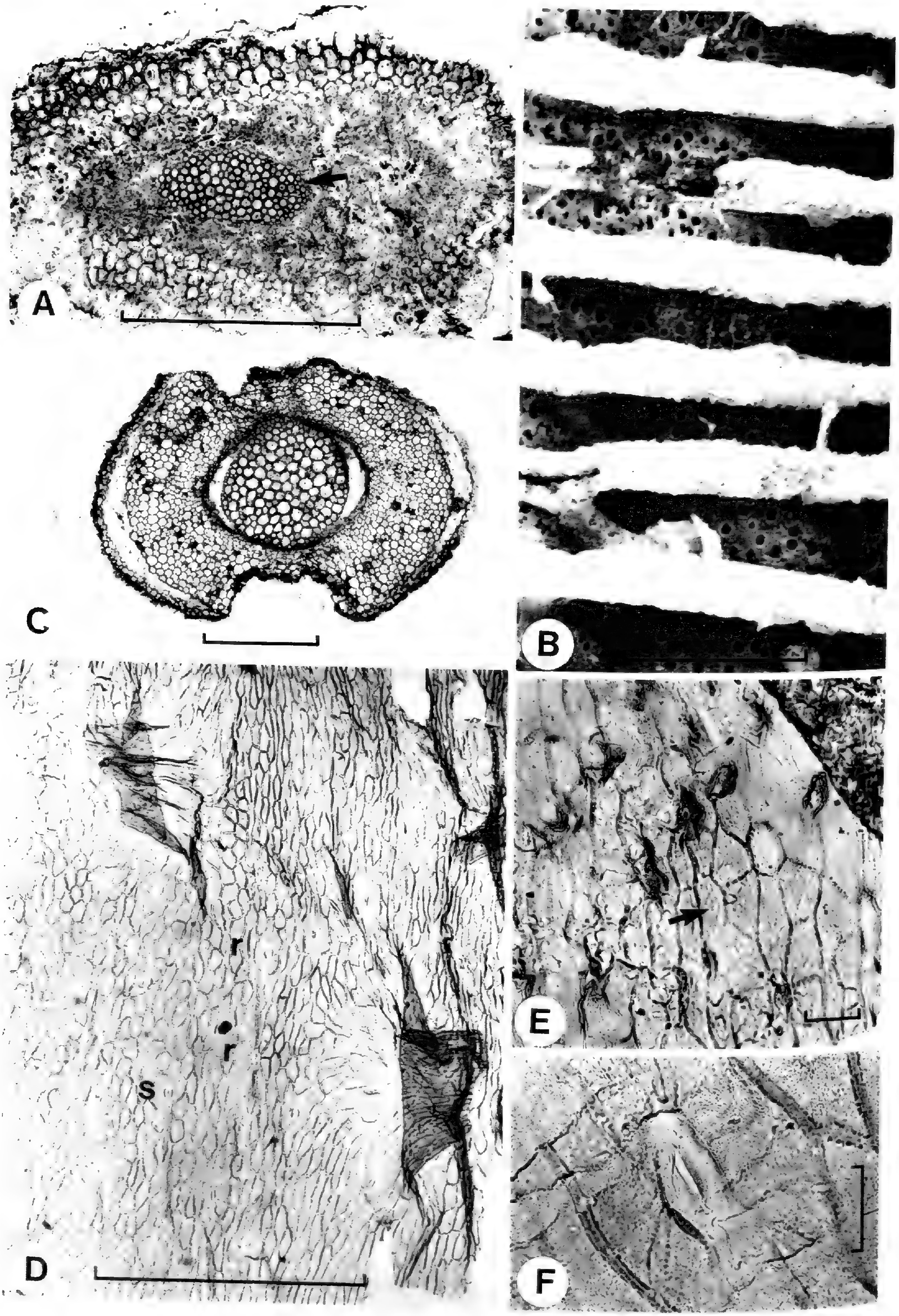
Banks (1968) and Banks & Davis (1969) proposed dividing the subdivision Zosterophyllophytina into two families, the Zosterophyllaceae and the Gosslingiaceae. Hueber (1972), Edwards (1970), Gensel et al. (1975), and several other workers have questioned whether this proposal was reasonable, and as more taxa have been added to the subdivision, it has been dropped, with the family Zosterophyllaceae being retained.

A recent assessment of characteristics of zosterophylls led Niklas & Banks (1990) to propose that two major types of zosterophylls could be recognized. One is characterized by axes that terminate in sporangia (terminate axes) and exhibit predominantly radial symmetry (although symmetry varies greatly in some taxa included here). *Zosterophyllum, Rebuchia,* and *Hicklingia* represent this group. The other type is characterized by axes not terminating in sporangia and exhibiting predominantly bilateral symmetry and encompasses the remainder of genera. Associated with this latter group is the presence of emergences, circinate axes, and possibly planar branching. The nonterminate character is somewhat problematic because axes are incomplete for several taxa included in that group. The proposition that emergences and sporangia are homologous to each other in the nonterminate group also needs further consideration, in part because sporangia can bear emergences.

Niklas & Banks (1990) suggest that the two types still are closely related, as only minor morphogenetic change is necessary to derive the second type from the first. Further, they propose that lycopsids arose, via the "pre-lycopsid complex," from the second type of zosterophyll, with a major reversal in symmetry (bilateral to radial). These hypotheses are worth further testing in that they are based on a dynamic concept of developmental aspects of the plants, and they build on previous observations concerning symmetry of sporangial arrangement and branching of several types of zosterophylls.

MORPHOLOGIC FEATURES OF PRE-LYCOPSIDS AND LYCOPSIDS

As previously noted, Gensel & Andrews (1984) and other workers have used the term "pre-lycop-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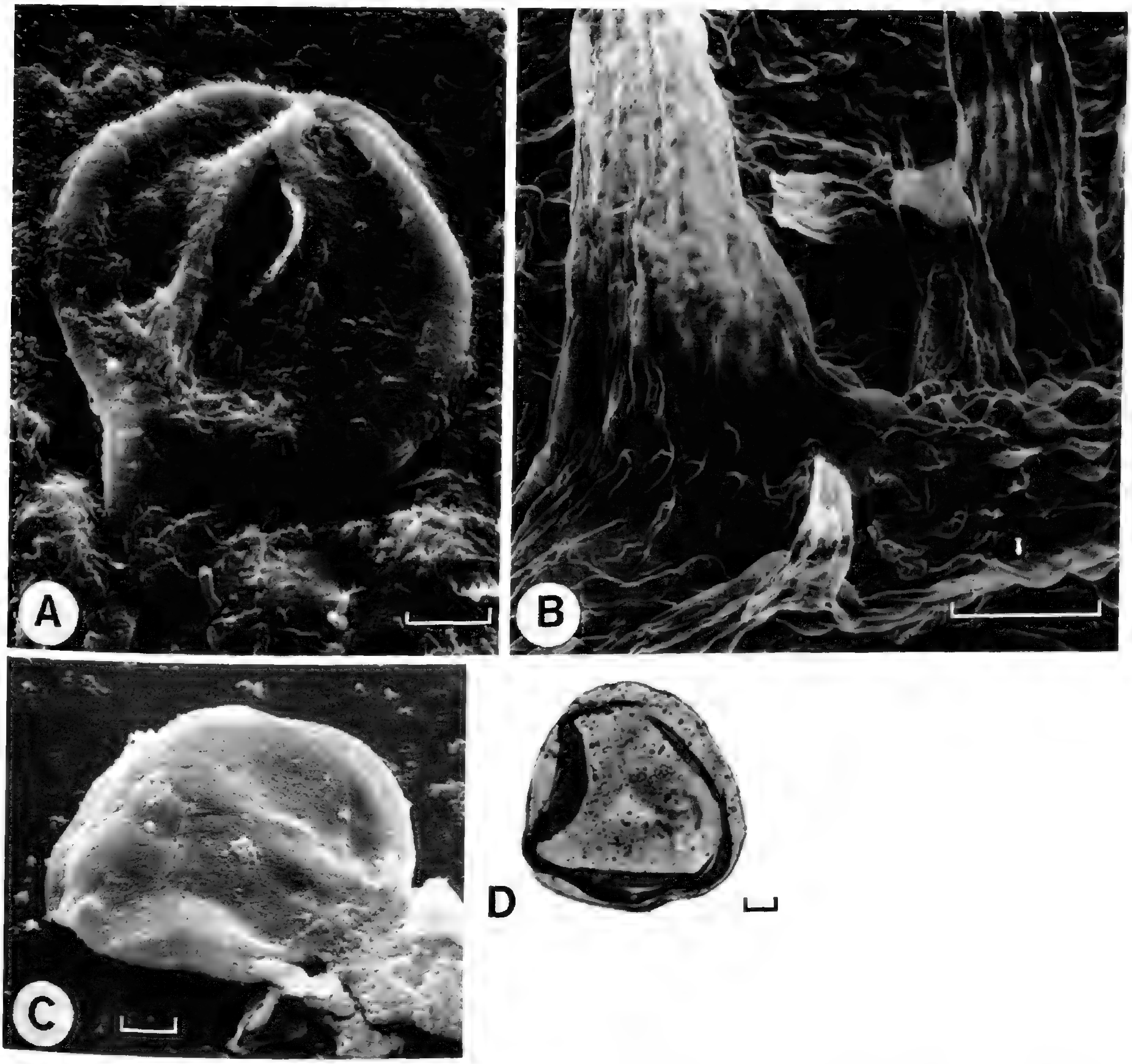

FIGURE 8. Cuticular and spore features of zosterophylls.—A. SEM of stomate of *Sawdonia ornata*, viewed from the inside. Ridge may be region where guard cells connect.—B. SEM of stem surface showing papillae and spine bases of *Sawdonia ornata*.—C, D. SEM and light micrograph (LM) of spores obtained from *Zosterophyllum divaricatum* sporangia. Note curvaturae, chagrenate surface. A, C, D scale bars = 10 μm. B scale bar = 100 μm.

sid" for some Devonian taxa (*Asteroxylon*, *Drepanophycus*, *Kaulangiophyton*) that are believed to be close to lycopsids in most of their characters but lack either a vascularized leaf or leaf-associated sporangia. They all are similar in exhibiting a rhizomatous habit, with prostrate axes producing aerial ones by dichotomy. The latter two exhibit H and K branching, and *Asteroxylon* and *Drepanophycus* bear adventitious roots (zosterophylls probably have these too). All of these taxa differ from

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FIGURE 7. Anatomical and cuticular features of zosterophylls.—A. Cross section through stem of *Crenaticaulis verruculosus*. Note thickened cells in outer cortex and elliptic, exarch haplostele. An arrow indicates presumed protoxylem.—B. SEM of tracheid of *Crenaticaulis* in longitudinal view. This has directly and indirectly connected annular to helical thickenings and a perforated secondary wall in between.—C. Cross section of a stem of *Stolbergia* from the Middle Devonian of Maine illustrating an exarch haplostele, suggesting this plant may be a zosterophyll.—D. Cuticle of *Sawdonia ornata* showing papillate epidermal cells, stomata (s), and rosette cell pattern (r).—E. Cuticle of *Crenaticaulis verruculosus*—note the rosette cell pattern at the right.—F. Stomate of *Sawdonia ornata*. A, C, D scale bars = 1 mm. B scale bar = 10 μm. E, F scale bars = 0.1 mm.

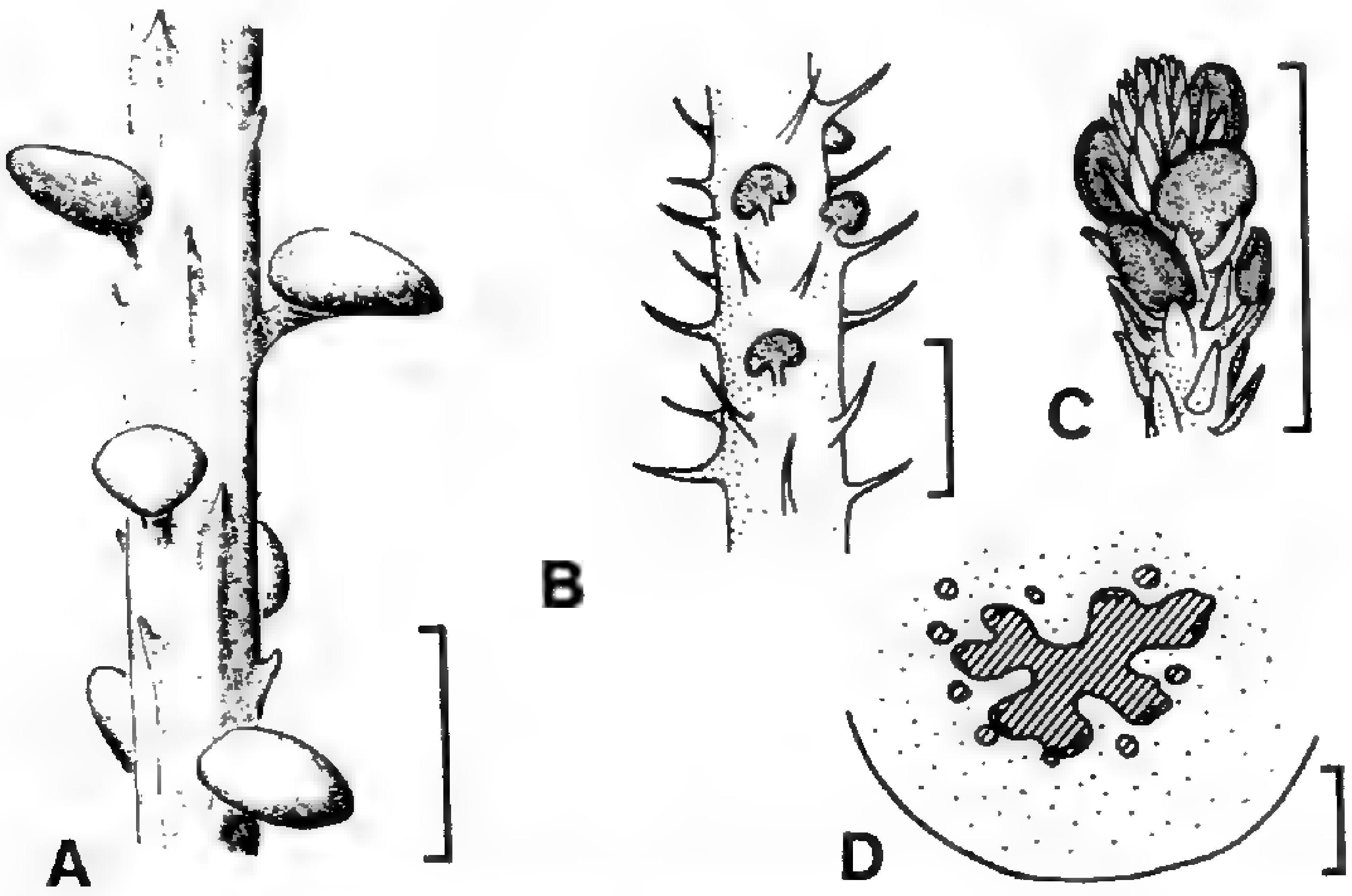

FIGURE 9. Line drawings of pre-lycopsids.—A. *Kaulangiophyton akantha.*—B. *Drepanophycus spinaeformis.* C, D. *Asteroxylon mackiei.*—C. Restoration of "leafy" shoot with sporangia interspersed among "leaves."—D. Diagram of actinostele with traces. A redrawn from Gensel et al. (1969); B modified from Schweitzer (1980); C, D redrawn from Chaloner and MacDonald (1980). A–C scale bars = 10 mm. D scale bar = 1 mm.

lycopsids in that their sporangia are cauline, i.e., attached to stems by short stalks (Fig. 9A–C), rather than being associated with microphylls. *Asteroxylon* and *Drepanophycus* exhibit deeply lobed actinosteles (Fig. 9D) from which lateral traces emanate; anatomy is unknown for *Kaulangiophyton.* The lateral traces extend to the base of leaflike appendages in *Asteroxylon. Drepanophycus* has vascularized microphylls. There is no evidence of vascularization in the thornlike emergences of *Kaulangiophyton,* even though they are very similar to those of some axes attributed to *Drepanophycus spinaeformis* (Fig. 10A). Circinate axes are not evident. The sporangial stalks of *Asteroxylon* are vascularized.

Baragwanathia traditionally is considered the oldest undoubted lycopsid, exhibiting a deeply lobed actinostele with lateral traces supplying microphylls. Its sporangia have been presumed to occur in the axils of the microphylls, but sporangial attachment could be cauline as noted previously. There is no evidence of a stalk. The sporangia apparently occur in zones along the stem, and both microphylls and sporangia are radially arranged. At the very least, *Baragwanathia* is more similar to lycopsids than the preceding taxa, in that sporangia seem to be associated with leaves.

Leclercqia and several other genera present in Middle and Upper Devonian sediments are the best known early lycopsids (Fig. 11). These plants have exarch protosteles exhibiting ridges or variable depth of lobing, microphyllous leaves, and sporangia (where known) located adaxially on microphylls (Fig. 11B). Early lycopsids vary mostly in leaf morphology, with those of *Leclercqia, Protolepidodendron scharyanum,* and *Colpodexylon* being five, two, and three times forked, respectively. Sporangia are attached to a small pad of sterile tissue on the microphyll surface. In *Leclercqia,* the attachment site is located near one end of the sporangium and is only one cell layer thick. Bonamo et al. (1988) did not recognize *Leclercqia* sporangia as stalked. However, when coding aspects of sporangial attachment for cladistic analysis, I regarded such pads in lycopsids as homologous to stalks.

Other lycopsids, such as *Haskinsia* and *Archaeosigillaria,* exhibit leaves with a distinctive shape (sagittate) or lobing (Fig. 11C, D). Their fertile parts are unknown. Many Middle Devonian lycopsids are much larger than most zosterophylls, although *Baragwanathia* and *Drepanophycus* can have axes 3 cm or more wide. Small tree-sized lycopsids appear by Late Devonian times. By the Carboniferous, a trend toward greater size and arborescence in some lineages, protection of sporangia, and their aggregation into strobili was well established.

POSSIBLE ANCESTRY OF ZOSTEROPHYLLS

It has been suggested that the zosterophylls arose from a rhyniophyte ancestor, although Banks (1968) did not indicate a relationship between the two lineages. Such a derivation would involve a shift from terminal to laterally borne sporangia (which could result from increasingly anisotomous branching) and from centrarch to exarch protoxylem maturation. How the latter might have occurred is unclear, especially in apparently "leafless" plants, unless by means of a change in developmental cues such as hormone distribution. Considering protoxylem maturation sequences among fossil and extant pteridophytes, I cannot think of any instances where such a shift has been documented. The closest might be in the changes in relative position of proto- and metaxylem in the so-called shoot-root transition zone in seed plants, where metaxylem differentiation changes from centripetal to laterally divergent to centrifugal in the zone between root and cotyledons (Esau, 1965).

Chaloner & Sheerin (1979) modified this scenario slightly to suggest both zosterophylls and rhynialean rhyniophytes may have arisen from *Cooksonia.* They further suggested that lycopsids arose from some zosterophylls and trimerophytes arose from rhyniophytes. Taylor (1988) noted that plants now included in *Cooksonia* may encompass vascular and nonvascular plants and suggested that

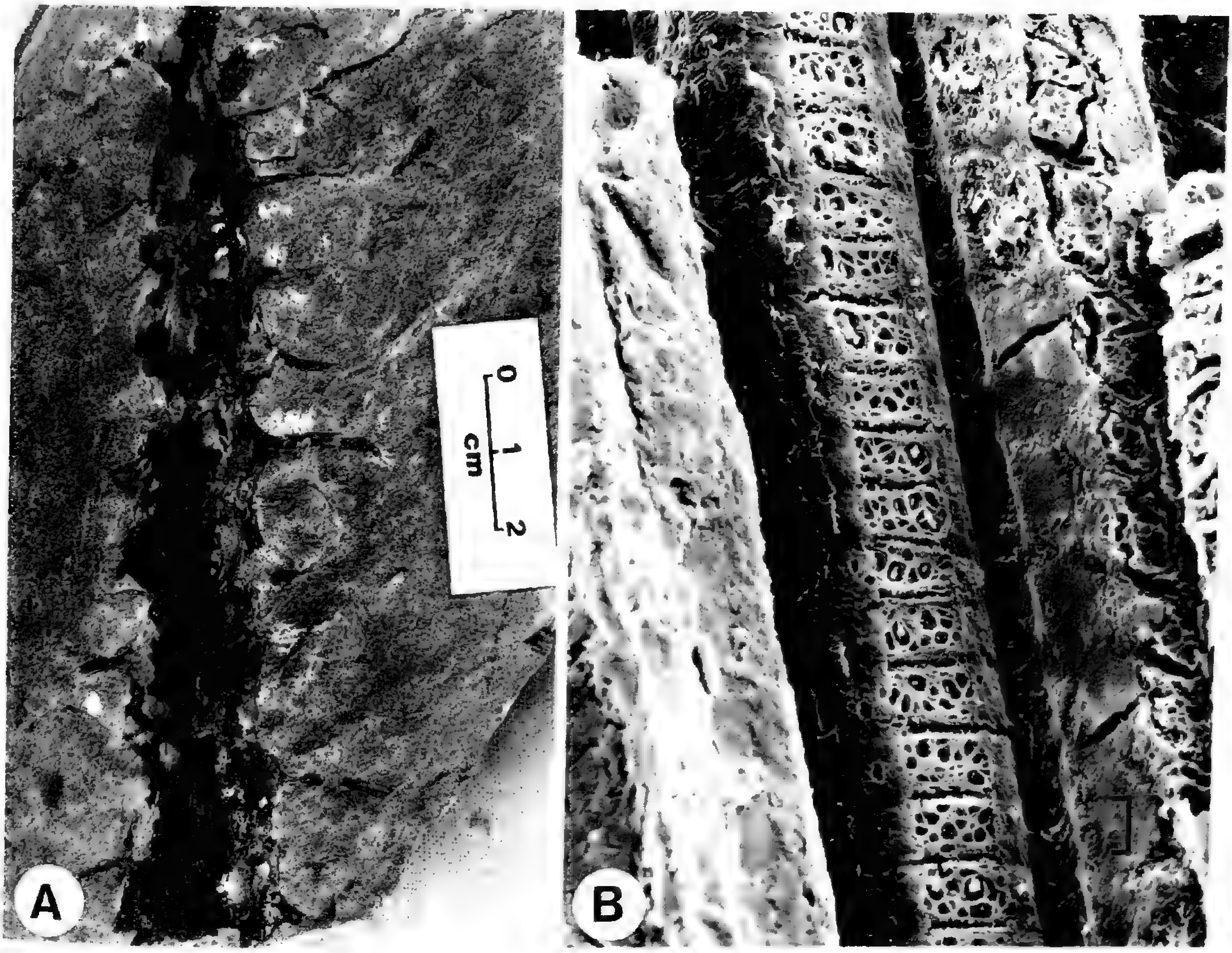

FIGURE 10. A. General view of *Drepanophycus spinaeformis* leafy stem. Leaves are long, falcate, and spinelike. Unfortunately, this specimen does not show leaf venation.—B. SEM of tracheid of cf. *Drepanophycus gaspianus* from New Brunswick, illustrating perforated secondary wall between scalariform thickenings. B scale bar = 10 μm.

the origin of zosterophylls, rhyniophytes, trimerophytes, and the major groups of bryophytes centered on a cladistically unresolved complex of poorly understood, highly variable plants with either no conducting cells or ones lacking secondary wall patterns—his so-called cooksonioid complex. This scenario obviates the need to explain a shift from centrarchy to exarchy and also implies the possibility of polyphyletic origin of conducting cells and possibly of tracheophytes. Unfortunately, no putative lineage in his study was supported by specific characters or character-state transformations (but see Kenrick & Crane, 1991).

Current research also has resulted in questions concerning which plants truly conform to the definition of a rhyniophyte. Edwards & Edwards (1986) adopted a fairly broad definition of rhyniophytes, especially in terms of types of branching pattern, but retained two original features, the occurrence of sporangia terminating infrequently branched axes and a centrarch haplostele. Taxa included in rhyniophytes by them are *Rhynia gwynne-vaughanii*, *Renalia*, *Taeniocrada decheniana*, and some specimens assigned to *Aphyllopteris*, *Hostinella*, and *Taeniocrada*. *Uskiella* Shute & Edwards, 1989, may also represent a rhyniophyte.

Other plants originally assigned to the rhyniophytes either lack tracheids with obvious secondary wall patterns or are problematic with regard to some necessary characters. The major issue is how to define a tracheid, and thus a tracheophyte. Currently, the presence of lignified secondary wall thickenings is regarded as distinctive of tracheids. In such plants as *Aglaophyton*, *Nothia aphylla*, *Taeniocrada dubia*, and more recently, *Rhynia gwynne-vaughanii* (coded in this paper as a vascular plant), it is difficult to determine if the absence of secondary thickenings, or the presence of other types of patterns or wall layers, is an intrinsic feature or the result of preservational factors. These differences have been interpreted as intrinsic in many of these taxa and not homologous to tracheids, and all of these taxa except *Rhynia gwynne-vaughanii* have been formally removed from the rhyniophytes. Recent studies of Kenrick & Crane (1991) suggest that the conducting cell structure

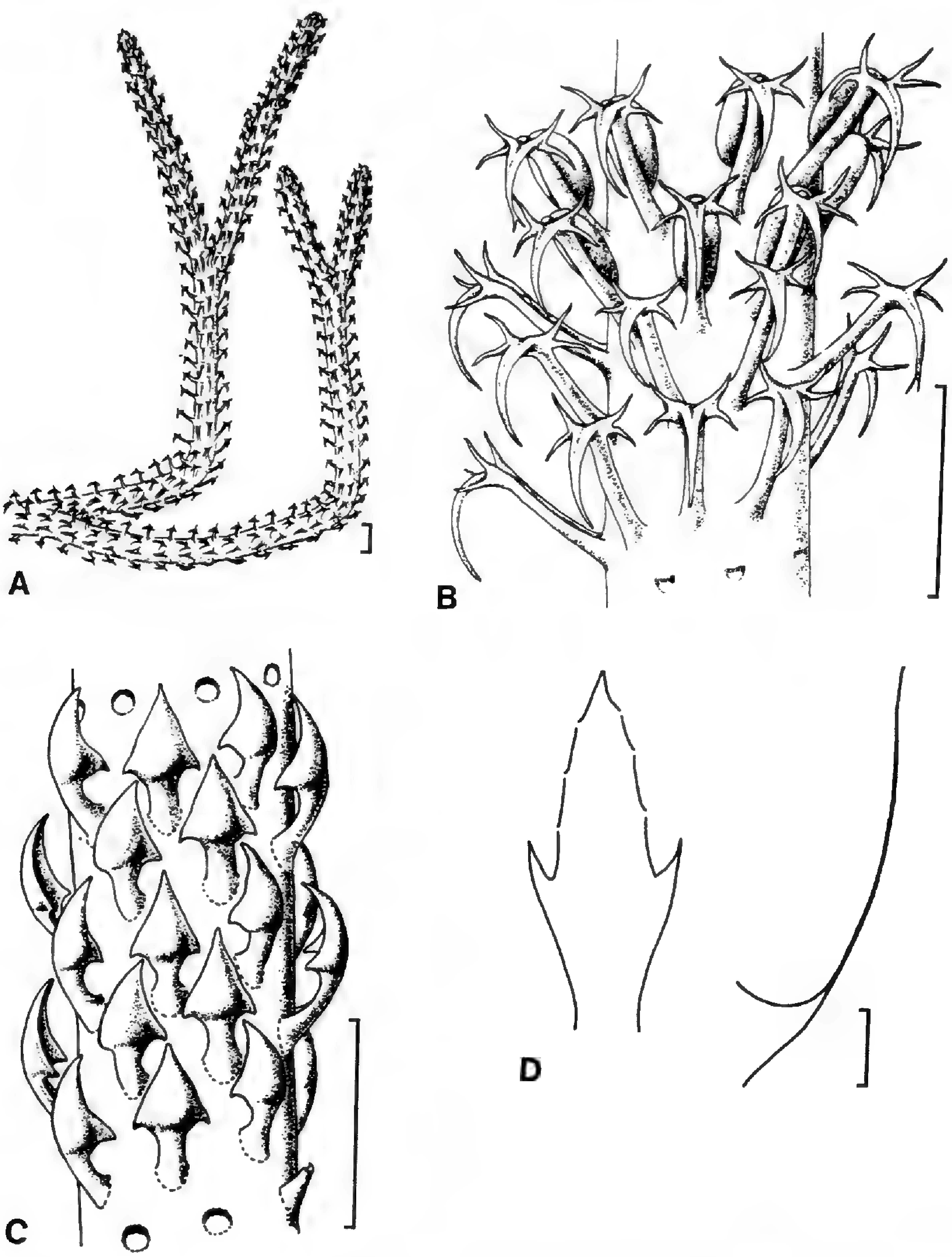

FIGURE 11. Line drawings of early lycopsids.—A. *Leclercqia complexa*, general habit.—B. Detail of *Leclercqia complexa* showing sporophylls and abaxial sporangia.—C. *Haskinsia colophyllus* showing sagittate leaves.—D. Diagram of leaf in front and side view of *Archaeosigillaria vanuxemii*. A–C redrawn from Bonamo et al. (1988). D redrawn from Fairon-Demaret & Banks (1978). A–C scale bars = 5 mm. D scale bar = 1 mm.

in *R. gwynne-vaughanii* also is more similar to *Sennicaulis* and *Taeniocrada*, and they present hypotheses concerning the possible affinities of these taxa. This obviously is important in considering rhyniophytes as a sister group or source of ancestor for any plant lineage and in assessing homology among conducting cells.

PATTERNS OF DIVERSIFICATION AND MORPHOLOGIC VARIATION

Examining the diversity (Fig. 1) of the zosterophylls and lycopsids shows that zosterophylls clearly diversified in the Siegnian–Emsian, with more than 14 genera represented, whereas the number of lycopsids present prior to the Middle Devonian is very low, being one or two, with an increase in numbers in the Middle and Upper Devonian. A few zosterophylls are recorded in the Eifelian–Givetian (*Hicklingia*, perhaps *Stolbergia*, *Euthursophyton hamperbachense*) and a few genera extend into the Upper Devonian (*Sawdonia*, *Serrulacaulis*, *Drepanophycus*). Thus, no matter when the group first appeared, diversification of lycopsids, on the basis of present evidence, lagged behind that of zosterophylls. The reason is unknown. Perhaps early members were somehow constrained by ecological parameters (e.g., competition for the same habitat?).

There are some parallels in morphologic variation between the two groups. Emergences in zosterophylls and microphylls in pre-lycopsids and lycopsids are quite variable. Both may have performed similar functions—i.e., protection of the stem from desiccation, mechanical damage, or herbivory, and increased surface area for photosynthesis and gas exchange. It is assumed that vascularized microphylls would be more efficient both in providing water for photosynthesis and in transporting photosynthate away from its source. Early and Middle Devonian lycopsids are more or less similar in size to zosterophylls, but some younger lycopsids are much larger.

Sporangial attachment is different in the two groups, ranging from cauline, with vascularized stalks (in some zosterophylls at least, and *Asteroxylon*), to foliar, either axillary or epiphyllous (lycopsids). In some lycopsids, sporangial stalks are unvascularized. In younger lycopsids, sporophylls are modified to enclose sporangia more completely and differ anatomically. For example, sporophylls of some extant *Lycopodium* species have a mucilage cavity at their base or adjacent to the vascular strand (Bruce, 1976). Its function is unknown but might be to aid in moisture retention, store excess metabolites, or to aid spore dispersal by causing the sporophyll to reflex when dried. Sporangial stalks, although unvascularized, show patches of lignified cells (probable transfusion tissue) that are in contact with those surrounding the vascular strand of the sporophyll (Sykes, 1908). The ligule in extant *Selaginella* is regarded as aiding in moisture retention during early ontogeny or producing mucilage (Bilderback, 1987). The outer sporangium wall often is lignified.

Although anatomy is known for only about two-thirds of the zosterophyll genera, it is stereotypical, differing only in shape (terete or ellipsoidal to strap-shaped), which may correlate with arrangement of branches and/or sporangia. Anatomy in lycopsids varies mainly in depth of lobes, from deeply lobed to slightly ridged actinosteles. Tracheary wall patterning is circular to oval pitted in *Leclercqia* in contrast to the indirectly connected annular or helical patterns of most zosterophylls (*Koniora* also exhibits reticulate pitting) and pre-lycopsids. Tracheid diameter is similar in zosterophylls and lycopsids of comparable age, or in some cases greater in zosterophylls (Niklas, 1984). By the Middle Devonian, xylem cross-sectional area is greater in lycopsids than in zosterophylls, which might suggest increased water-conducting capacity (Niklas, 1984, 1985).

Nothing is known about the gametophytes of zosterophylls (Schweitzer (1979, 1983) has suggested that a *Sciadophyton* may be the gametophyte of *Zosterophyllum*, but definite proof is lacking) or of extinct Devonian lycopsids other than their spores. The only notable difference in spores of homosporous Devonian members of the two groups is that those known in *Leclercqia* have a coarser ornament. Some Devonian lycopsids (e.g., *Cyclostigma*) are heterosporous, a reproductive syndrome not present among zosterophylls.

To what extent might these morphological differences lead to different evolutionary pathways? The lycopsids survived and zosterophylls did not. Is this chance, or might lycopsids have had a greater developmental potential? Did their more integrated and extensive vascularization confer survival advantage? No clear answers exist, but these questions should be pursued.

ECOLOGICAL PATTERNS

Evidence thus far does not suggest major differences in the habitat preferences of zosterophylls and lycopsids during the Devonian. Sedimentological analyses of plant-rich strata suggest both groups inhabited floodplain or channel margin environments, usually adjacent to streams or lakes. Within a deposit, a taxon may be represented by abundant, parallel aligned axes, or by closely intermingled specimens. Thus, it seems likely that they formed dense stands and that many were buried at or close to their site of growth. *Tarella* Edwards & Kenrick, 1986, is interpreted as living on an exposed point bar subjected to periodic flooding, which preserved parts of the stand during each episode. *Sawdonia ornata* in Gaspé occurs in a sandstone containing marine fossils immediately below the plant-rich layer; the sedimentary environment thus is interpreted as representing a tidally influenced floodplain (D. Lawrence, pers. comm.). *Leclercqia* is regarded as inhabiting a more distal floodplain habitat (Banks et al., 1985). The distribution of fossils in several Early and Middle Devonian deposits suggests only one type occurred in any given area; perhaps in the Lower Devonian, zosterophylls, pre-lycopsids, and *Leclercqia* competed for similar sites, and only one type predominated as might be expected of clonal or "turfing-in" types of organisms.

Edwards & Kenrick (1986) suggested that the occurrence of dormant apices (subaxillary protuberances of various degrees of development) may have been an adaptation to unstable environments, allowing the plant to begin growing again after damage (or partial burial) or to become reestablished after being uprooted. Zosterophylls also show some cuticular features that could be interpreted as adapted for periodic water unavailability, for example: (1) their cuticles are quite robust and resistant to destruction (in contrast to those of trimerophytes or rhyniophytes); (2) many exhibit epidermal cells with papillae (thickened regions of cuticle); and (3) their stomata in some cases appear sunken (*Sawdonia*, *Deheubarthia*). Several also exhibit the distinctive, epidermal "rosette cell" arrangement (Fig. 7D, E), which has been considered to represent either hair bases (although hairs never have been seen), mini-lenses for concentrating sunlight for photosynthesis (Rayner, 1983), an unknown function in plant water relations (Edwards et al., 1982), or salt glands. *Drepanophycus* often has a very large diameter axis with a narrow vascular strand, leading to the suggestion that it was possibly succulent.

EVOLUTIONARY CONSIDERATIONS

Despite abundant new evidence, particularly of zosterophylls and earliest land plants, it still is not possible to resolve how microphylls and leaf-associated sporangia arose. Evidence from fossil plants and extant lycopsids seems to favor the vascularization of enations theory more extensively than the telome reduction theory (see also Niklas & Banks, 1990). The presence of forked microphylls in some early lycopsids is not necessarily problematic because they too could have evolved from emergences. In a paper submitted elsewhere (Gensel, 1991), I demonstrate the occurrence of emergences that fork up to eight times in *Sawdonia acanthotheca*. One could suggest on that basis that the genetic potential for forked emergences existed in the putative ancestral plants, which could be coopted or expressed during leaf development in some putative descendants.

The traditional views of the origin of foliar-associated sporangia are that either the sporangium became associated with the leaf through "phyletic slide," perhaps via developmental changes that reduced the distance between leaf and sporangium, or through modification of a branch truss with both vegetative and fertile components (the telome theory).

Evidence supporting either of these hypotheses is inconclusive. Reports concerning development of sporangia in extant lycopsids are conflicting; in some cases the sporangial initials originate on the stem and in others on leaves (Eames, 1936). Sykes (1908) noted that sporangia primordia in *Lycopodium selago* originated separately from leaf primordia, the developing sporangia becoming associated with leaves later. Bower (1935), however, described sporangial initiation as foliar for the same species. Eames also noted that where sporangia originate is not necessarily where they are located at maturity, although those originating on leaves usually stay positioned on leaves. Additional studies of sporangial and leaf development in extant lycopsids are needed to clarify this variability. Such studies might shed light on how the lycopsid sporangium/sporophyll affiliation came about. If the sporangium-leaf association is variable in extant lycopsids, the same might apply to fossil ones. This is significant in regard to the status of *Baragwanathia*; simply having leaf-associated sporangia may be sufficient to place it in the lycopsids without worrying about whether it attaches to the stem or the leaf.

Another explanation for the transition from cauline to foliar-borne sporangia might be heterotopy. A displacement of meristematic activity producing lateral appendages (sporangial primordia) from stem apex to leaf axil or leaf surface would result in the establishment of leaf-associated sporangia. This same process also could be invoked to explain forked emergences or microphylls. Heterotopy is considered the probable cause of epiphyllous leaves in *Begonia* by Sattler & Maier (1977). Other examples are reviewed by Sattler (1988).

Are microphyllous-associated sporangia homologous with those borne on stems or megaphylls? I have assumed so, since both originate from cauline structures. Therefore, the sporangial stalk of all zosterophylls is regarded as homologous to a stem in the phylogenetic analysis. Sporangial stalks in lycopsids also are homologous to stems, but seem to have lost vascular tissue. This phylogenetically important assumption requires further investigation.

PHYLOGENETIC ANALYSIS OF EXTINCT AND EXTANT "PTERIDOPHYTES"

To evaluate phylogenetic relationships of zosterophylls, pre-lycopsids, and lycopsids more rigorously, I have initiated a phylogenetic analysis of selected fossil and living pteridophytes using cladistic methodology. The results presented here are preliminary. Further analysis is ongoing, and a fuller treatment will be presented elsewhere (Gensel, Mishler & Albert, in prep.).

Numerous problems exist in attempting to use fossils in cladistic analysis, as summarized by Donoghue et al. (1989), but their argument, which focuses on the importance of using fossils in phylogenetic analysis of living plants, can be inverted and used to support inclusion of living taxa in phylogenetic reconstruction of fossil taxa. Discussions of the benefits and problems involved in attempting phylogenetic analysis of fossil plants via cladistics are well presented by Schoch (1986), Stein (1987), Stein & Beck (1987), Crane & Hill (1987), and Doyle & Donoghue (1987).

Problems that were faced here include some mentioned by the above workers, such as: (1) not all fossil remains present comparable sets of characters; (2) the plants mostly are of simple construction and present a comparatively low number of characters; and (3) developmental data are sparse or lacking. Combined, these result in the analysis being limited to a small set of putatively homologous characters. These problems are particularly acute when analyzing ancient lineages of land plants. In selecting characters, I attempted to include characters traditionally used in delimiting fossil and extant taxa at the generic and higher levels, but realize these represent hypotheses of homology that may be refuted as new knowledge is obtained. Because of the range of taxa, and the limitations of fossil remains, only a few character states could be judged homologous and synapomorphous (i.e., shared by two or more taxa). This limits the potential for accurate phylogenetic reconstruction because of the probable lack of resolution resulting from analysis of many taxa with few characters.

Wagner parsimony, PAUP 3.0d by D. Swofford, was used with a Macintosh computer to conduct the analysis. This program allows for coding multistate characters and for the construction of character state trees if needed. Three general modes of character evolution were used: (1) unordered, (2) ordered with linear transformational series, and (3) ordered with nonlinear transformation series (CSTREE option of PAUP 3.0d).

Twenty-five taxa and 12 coded characters were used to generate the cladograms. The taxa included genera of the major early land plant lineages, e.g., rhyniophytes, zosterophylls, the pre-lycopsids (*Asteroxylon* and *Drepanophycus*), *Baragwanathia*, *Leclercqia*, *Lepidophloios*, two extant species of *Lycopodium*, the trimerophytes *Psilophyton* and *Pertica*, the aneurophyte *Tetraxylopteris*, *Psilotum*, the extinct filicalean fern *Botryopteris*, and the extant marattialian *Angiopteris*. Taxa were selected that met one or more of the following criteria: (1) they represent a lineage, (2) they are well enough known that most of the characters can be coded, and/or (3) they are significant in evolutionary theories discussed previously. If a genus was polymorphic for the characters employed, a representative species was selected; thus, *Sawdonia* is based on *S. ornata*, *Drepanophycus* is based on *D. spinaeformis*, and *Botryopteris* is based on *B. antiqua*. In two cases, more than one species of a polymorphic genus was included in the data set (*Psilophyton, Lycopodium*). Some taxa were not included because they did not meet the above criteria. I included many more zosterophyll genera than for other lineages, because I wanted to test relationships within that group. Even so, some zosterophyll genera were omitted either because they are too incompletely known or because they score identically with a genus present in the analysis. A hypothetical moss ancestor, based on characteristics postulated by Mishler & Churchill (1985), was included in order to polarize characters.

Sporangial characters, branching patterns, and vascular anatomy distinguish not only major lineages of Devonian plants, but modern ones to some extent as well. These also are ones most readily obtained from the fossils; many of these characters are used in this analysis. However, branching patterns were difficult to code and resulted in character conflict; thus all aspects of branching except ones relating to how sporangia are borne on the plant were abandoned. Despite criticism for using characters that have questionably discrete states, I included one such character (sporangial shape) in these initial attempts since sporangial shape has been used to distinguish major groups of early land plants. Emergence shape and position are too variable (and either autapomorphous or homoplasious) to be included. Data on gametophytes, cuticular features, and spores are lacking, too incomplete, or not presently informative in the group as a whole. Of the 12 characters employed (Table 2), characters 3, 8, 9, and 11 were unordered. Character 2 was obtained as a branching character state tree, and the remainder were ordered with a linear transformation series. Explanation of these characters and their ordering follows next.

1. *Sporangial location.* Whether sporangia are attached to a stem or leaf and their location on a sporophyll distinguishes several plant lineages. Cauline sporangia occur in the hypothetical moss outgroup, rhyniophytes, zosterophylls, trimerophytes, pre-lycophytes, and aneurophytes. Other states, e.g., axillary or epiphyllous, are considered transformationally homologous on the premise that the sporangiophore in any tracheophyte is a cauline or cauline-derived structure. Epiphyllous sporangia are either abaxial or adaxial. Character 1 is thus linearly ordered a-b-c-d.

TABLE 2. List of characters used in this study and indication of type of ordering (O = ordered linear, U = unordered, CSTREE = ordering nonlinear). For details, see text.

1. Sporangial location (O)
    - a. epiphyllous, abaxial
    - b. cauline
    - c. axillary
    - d. epiphyllous, adaxial
2. Sporangial position if cauline (CSTREE)
    - a. terminal on unbranched axis
    - b. terminal on branched axis
    - c. lateral, branched axis
    - d. lateral, unbranched axis
3. Sporangial arrangement if cauline and lateral (U)
    - a. spiral
    - b. linear
    - c. singly
4. Sporangial orientation (O) (stalk or dehiscence line relative to organ bearing it)
    - a. upright
    - b. horizontal
5. Sporangial shape (O)
    - a. height greater than width
    - b. globose
    - c. width greater than height
6. Stem outgrowths (O)
    - a. emergences absent
    - b. emergences present, not vascularized
    - c. emergences present, vascularized to base
    - d. emergences present, fully vascularized
7. Megaphylls (O)
    - a. absent
    - b. present
8. Stelar type in mature state (U)
    - a. Haplostele
    - b. actinostele
    - c. plectostele
    - d. siphono- or dictyostele
9. Metaxylem wall patterning (U)
    - a. absent
    - b. annular-helical
    - c. indirectly connected annular, helical
    - d. scalariform to reticulate to some pitted
    - e. mostly pitted, including bordered pitted
10. Xylem maturation (O)
    - a. centrarch
    - b. mesarch
    - c. exarch
11. Tubercles, etc. (probably arrested apices) (U)
    - a. absent
    - b. present, scattered
    - c. present, branch-related
12. Circinate axes (O)
    - a. absent
    - b. present

One can postulate a reasonable transformation series of sporangial location, from cauline to axillary to adaxial epiphyllous, or from cauline to abaxial epiphyllous, considering the range of positions evident among extant and fossil plants and incorporating some modification of the "phyletic slide" hypothesis (Bower, 1935). Derivation of adaxially borne sporangia as in lycophytes was discussed in a previous section; abaxially borne ones are considered to be parts of a branch system that became modified to form a megaphyllous leaf.

2. *Sporangial position, if cauline.* This is used to distinguish between plants with cauline sporangia in terms of whether they are borne at the tips of axes or laterally along axes. The states recognized are terminal on unbranched axes, terminal on branched axes, lateral on unbranched axes and lateral on branched axes. Starting with the simplest condition, terminal on unbranched axes, axis dichotomy could result in terminal on branched axes. Unequal dichotomies of axes could produce either branched or unbranched lateral units. Thus, this character is ordered as a branched character state tree as follows: $a\text{–}b\begin{smallmatrix} {}^{\diagup}c \\ {}_{\diagdown}d \end{smallmatrix}$. Following the scenario presented by Mishler & Churchill (1985) concerning transformation of sporophyte characters: the hypothetical ancestor of mosses + tracheophytes consists of a stalk and sporangium borne on the gametophyte thallus. Next occur independent sporophytes with branched axes, which subsequently become more elaborately branched. Unequal dichotomies within sporophyte axes might result in either sporangia borne laterally on branched axes or sporangia borne laterally on unbranched axes (stalks). From these can be derived the epiphyllous conditions coded in the previous character.

These first two characters were kept separate; any attempt to combine them into a more complex series of states resulted in constraining how states could change more than I deemed reasonable.

3. *Sporangial arrangement, if cauline and lateral.* This refers to the pattern of lateral sporangia, i.e., whether spiralled, linear (in two rows

TABLE 3. Data matrix for cladistic analysis.

Taxon	Character											
	1	2	3	4	5	6	7	8	9	10	11	12
Hypothetical moss outgroup	b	a	?	?	a	a	a	a	a	?	a	a
Zosterophyllum llanoveranum	b	d	a	a	c	a	a	a	b	c	b	a
Sawdonia ornata	b	d	b	a	c	b	a	a	c	c	b	b
Crenaticaulis verruculosus	b	d	b	a	c	b	a	a	c	c	c	b
Gosslingia breconensis	b	d	b	b	c	a	a	a	c	c	c	b
Thrinkophyton formosum	b	d	b	a	c	b	a	a	c	c	c	b
Koniora andrychoviensis	b	d	c	b	c	b	a	a	d	c	a	b
Tarella trowenii	b	d	b	b	c	a	a	a	c	c	b	b
Cooksonia sp.	b	b	?	?	b	a	a	a	b	a	a	a
Rhynia gwynne-vaughanii	b	b	?	?	a	a	a	a	b	a	b	a
Renalia hueberi	b	c	a	a	c	a	a	a	b	?	b	a
Drepanophycus spinaeformis	b	d	a	a	c	d	a	b	c	c	a	a
Asteroxylon mackiei	b	d	a	a	c	c	a	b	b	c	a	a
Baragwanathia longifolia	c	?	?	a	c	d	a	b	b	c	a	a
Leclercqia complexa	d	?	?	b	c	d	a	b	e	c	a	a
Lepidophloios sp.	d	?	?	b	c	d	a	d	e	c	a	a
Lycopodium lucidulum	c	?	?	b	c	d	a	c	e	b	a	a
Lycopodium clavatum	d	?	?	b	c	d	a	c	e	b	a	a
Psilophyton dapsile	b	b	?	a	a	a	a	a	d	a	a	a
Psilophyton charientos	b	c	a	a	a	b	a	a	d	a	a	a
Pertica sp.	b	c	a	a	a	b	a	b	d	b	a	a
Tetraxylopteris schmidtii	b	c	a	a	a	a	a	b	e	b	a	a
Psilotum nudum	b	c	a	a	b	?	a	d	e	c	a	a
Botryopteris antiqua	a	?	?	b	a	b	b	a	e	b	a	b
Angiopteris evecta	a	?	?	a	a	b	b	d	d	b	a	b

or in one row), or single. This has been used especially in distinguishing zosterophyll genera, but also is useful when considering sporangial arrangement in other lineages. This character is unordered.

4. *Sporangial orientation.* This refers to the orientation of sporangial stalk and dehiscence line relative to the cauline or cauline-derived structure bearing the sporangium, as described earlier, i.e., are sporangia upright or horizontal? Indehiscent sporangia are coded with a question mark.

5. *Sporangial shape.* An attempt is made here to distinguish between plants bearing globose, reniform, or elongate (including fusiform) sporangia, because this is used in taxonomic delineation of major types of early Devonian plants. The distinctness of these states needs verification using quantitative methods. States include sporangium height greater than width, equidimensional (globose) or width greater than length. This morphocline was linearly ordered a-b-c. Sporangia that are higher than wide are regarded as basal, because that state is present in the hypothetical moss outgroup.

6. *Stem outgrowths.* This attempts to reflect some features used to differentiate within zosterophylls, or between them and other lineages. The following character states are recognized and linearly ordered as presented: emergences absent, emergences present, emergences present and vascularized to their base, and emergences present and fully vascularized. Fern scales or trichomes are considered homologous to emergences. It should be noted that this transformation series reflects one prevailing hypothesis about how microphylls are derived, and thus does not follow Stewart's hypothesis that some lycopsid leaves are not derived from emergences. This will be examined in future studies, if possible. Ordering is a-b-c-d.

7. *Megaphylls.* Absence or presence of megaphylls was coded a-b, since megaphylls are regarded as derived via modification of lateral branch systems. It is possible that not all megaphylls are homologous; in this data set, however, the only megaphyllous plants are ferns and I regard their megaphylls as being homologous.

8. *Stelar type.* Character states include a haplostele (protostele with entire outline), actinostele, plectostele, and siphono- or dictyostele (these two differ only in the spacing of leaf gaps). Each of the latter types can be derived from a haplostele

separately. Thus, the character is unordered. The hypothetical moss outgroup, and earliest presumed tracheophytes, exhibit haplosteles.

9. *Metaxylem wall patterning.* The states coded here include absence of any pattern, then the following patterns: annular to helical, indirectly connected annular-helical, scalariform to reticulate to pitted, and mostly pitted including bordered pits. Because more than one pattern may occur within a single metaxylem element, and among metaxylem elements within one taxon, each state was broadly defined. Based on known developmental sequences in many tracheophytes, transformation from annular to scalariform, or annular to helical to scalariform is possible, as are other types of changes. Thus, this character is left unordered.

10. *Xylem maturation pattern.* Maturation is considered either exarch, mesarch, or centrarch (endarch is considered not applicable in this study). Changes from one state to another could involve one or two steps. The most logical series, i.e., centrarch to mesarch to exarch, is used here. The character is ordered a-b-c.

Conducting cells of some mosses are centrarch, others undetermined (Hébant, 1977). This character is not known in *Cooksonia* so it is coded as a question mark. Traditionally, rhyniophytes with centrarch protosteles are considered basal, giving rise to lineages with either exarch or mesarch ones. However, it is not clear how exarchy is derived from centrarchy or vice versa nor if an intermediate mesarch condition is necessary (no fossil evidence exists to support this). If vascular plants arose from a rhyniophytoid ancestor, either centrarchy or exarchy could be basal.

11. *Tubercles, etc. (arrested apices).* Included here are the tubercles, or axes that arise in the same position as tubercles, that occur in several plant groups and vary in location and morphology. They seem to reflect the inability of some shoot apices to continue development in these early land plants. There is no evidence of how states are related, and this character is left unordered.

12. *Circinate axes.* Stems of zosterophylls are circinate, as are leaves of most ferns. Even though involving different organs, they are homologous structures if fern megaphylls evolved from branch systems, and thus they are coded the same. A one-step change can be invoked here. Absence of circinate vernation is considered primitive since mosses and *Cooksonia* lack it.

Table 3 shows the resulting data matrix for the 25 terminal taxa. Question marks indicate unknown data or inapplicable character states. The computer algorithm assigns character states to "unknown" entries to give the minimal number of changes when mapped onto the topology based on known character states. One needs to consider whether missing or inapplicable data are critical in the case of these simple plants, especially in ones regarded as basal to major lineages. Specific examples in this analysis are: (1) tracheids are not known with certainty in fertile *Cooksonia* axes and vascular characters, thus are coded as a question mark for that taxon; (2) similarly, while tracheids are visible in cleared axes of *Renalia*, it is not possible to determine their maturation sequence; and (3) the present interpretation of the conducting cell pattern and conducting cell homology to tracheids in *Rhynia gwynne-vaughanii* may change (see Kenrick & Crane, 1991).

PAUP 3.0d was run with the following parameters: 10 random replications, TBR (Tree bisection-reconnection branch swapping) and NNI, ACCTRAN, and MULPARS option. This resulted in 350 most parsimonious trees of 50 steps. One of the 350 most parsimonious trees is shown in Figure 12, with characters mapped on to indicate one way the various clades may be derived. The combinable component consensus tree is shown in Figure 13 and shows that most of the topology is retained. Some groups of plants are highlighted for ease of discussion, e.g., S = "*Sawdonia* clade" and A = "*Asteroxylon* clade" in Figure 12.

The consensus tree shows the following: (1) many nodes still require resolution, especially in the basal regions of the cladogram and among the plants traditionally considered as rhyniophytes, trimerophytes, ferns, and aneurophytes; (2) some parts of the tree support prevailing ideas about relationships of Devonian plants, but differences also appear; and (3) several monophyletic groups corresponding to prevailing systematic categories occur (pre-lycopsids/lycopsids; lycopsids plus zosterophylls; the ferns).

One lineage from the large basal polychotomy includes *Zosterophyllum*, the *Sawdonia* clade (rest of the zosterophylls included in this study), *Renalia*, and the *Asteroxylon* clade (pre-lycopsids and lycopsids). The position of *Zosterophyllum* as a separate line in relation to the rest of the zosterophylls (= *Sawdonia* clade) and the composition of the *Sawdonia* and *Asteroxylon* clades are constant in all trees, as are the relative positions of the pre-lycopsids. *Leclercqia*, *Lepidophloios*, and *Lycopodium* vary in their relationships, and this variation is shown in Figures 12 and 13. *Gosslingia* and *Tarella* form a clade, often sister to *Koniora*. The position of *Renalia* is variable (and in my opinion, problematical); it either appears as sister

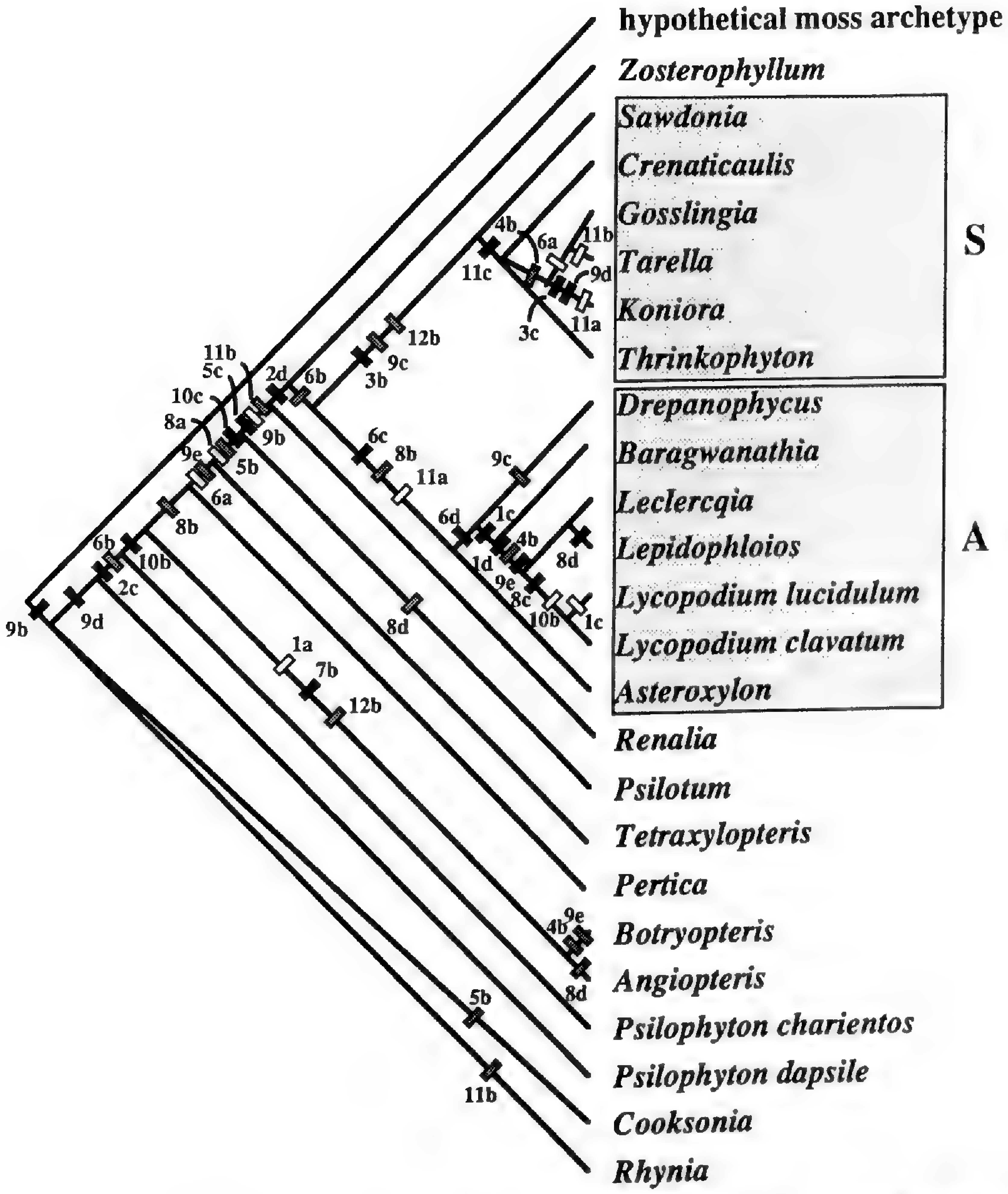

Figure 12. One of the 350 most parsimonious trees. Character states are mapped on as follows: dark rectangles indicate directional changes, stippled rectangles indicate parallelisms, and blank rectangles indicate reversals. Number and letter indicate character number and state to which it changed at that level. Categories such as *Sawdonia* clade are highlighted for ease of discussion (see text).

to *Zosterophyllum* or, as in Figure 12, it is sister to the clade giving rise to the zosterophyll-lycopsid groups. As a result it is part of the polychotomy of zosterophylls and lycopsids as shown in the consensus tree (Fig. 13). This differs from its present taxonomic placement in the rhyniophytes, indicating either that there is something significant about its relationships or that this placement is the result of incomplete knowledge of *Renalia*'s anatomy (xylem maturation unknown) and/or its very simple features.

The hypothesized relationships of zosterophylls to each other and to lycopsids are of interest in regard to Niklas & Banks's (1990) hypothesis concerning the existence of two major groups of zosterophylls, with lycopsids arising from the nonterminate group (= *Sawdonia* clade of this analysis). The presence of emergences, a linear sporangial arrangement, circinate axes, and type of metaxylem wall pattern define the *Sawdonia* clade. In many of the most parsimonious trees, the *Sawdonia* (Niklas & Banks's nonterminate group) and *Asteroxylon* clades are sister to one another; six character state changes separate the *Sawdonia* clade from the *Asteroxylon* clade (includes lycopsids). These include character state changes in emergence presence/absence and type, metaxylem wall patterning, sporangial arrangement, tubercle presence and type, and circinate apices.

Hierarchical nesting of pre-lycopsids and lycopsids occurs in the *Asteroxylon* clade to the following extent. *Asteroxylon* is sister to the line including the remainder of taxa; at the next higher level, *Drepanophycus* is sister to the remainder. *Baragwanathia* is a sister taxon to a line including *Leclercqia*, *Lepidophloios*, and *Lycopodium*. Since

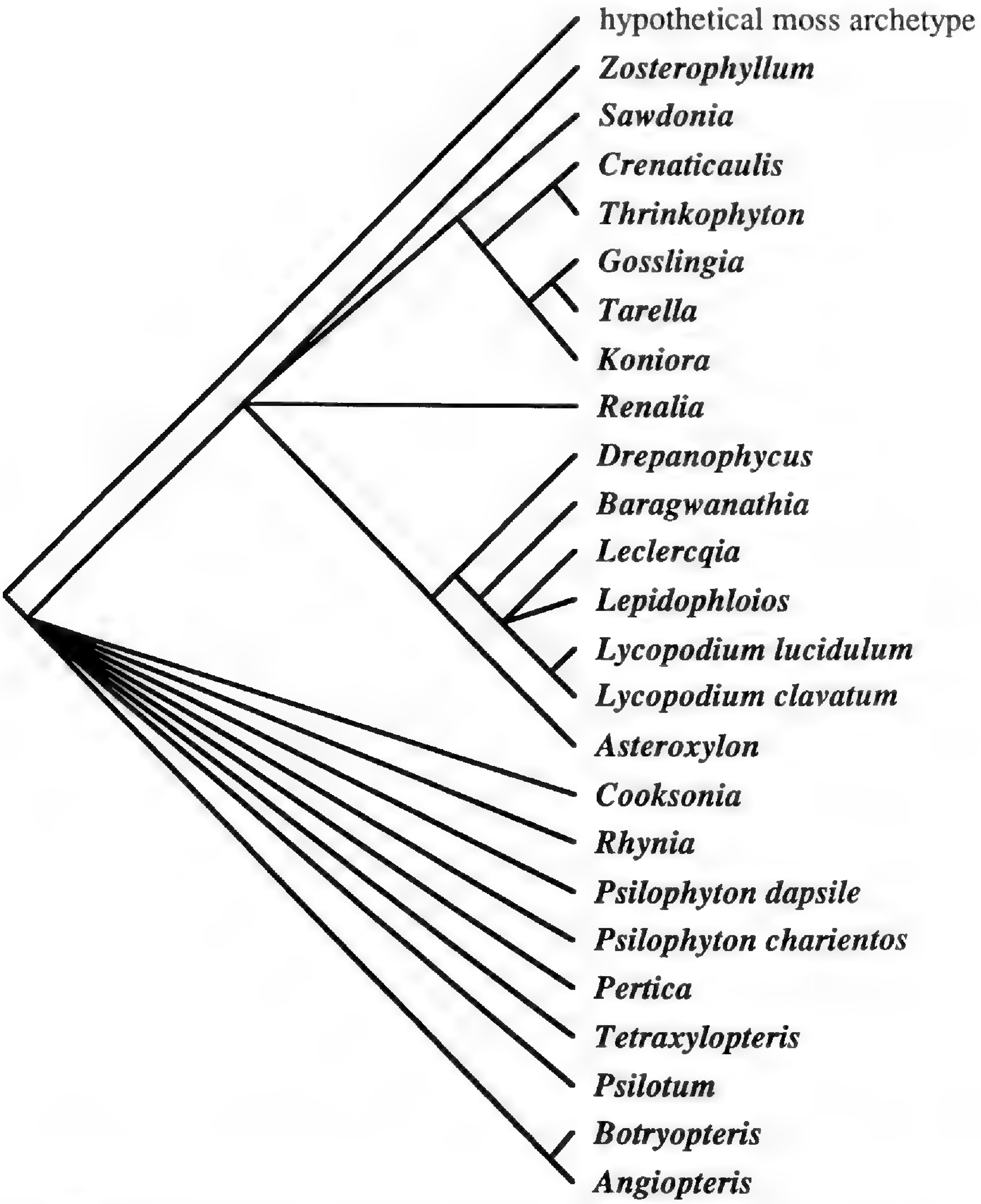

FIGURE 13. Combinable component consensus tree based on 350 most parsimonious trees. This differs only slightly from the strict consensus tree.

all are part of one clade, two alternative approaches can still be supported, namely, (1) abandon the Drepanophycales of Rayner (1984) and/or the "pre-lycopsid" concept and treat all as lycopsids in a broad sense, or (2) retain these groups as a means of recognizing some of the possible variation evident within this group (as is done throughout this paper). Better means are needed for resolving terminal taxa within the *Sawdonia* and *Asteroxylon* clades as well as within the polychotomy at the base of the cladogram.

On the consensus tree, the rhyniophytes, trimerophytes, ferns, and *Tetraxylopteris* form part of the large basal polychotomy. Again, survey of the most parsimonious trees shows that some relationships appear frequently; although details differ, the fern clade usually is most closely related to the *Psilophyton charientos* line, and *Tetraxylopteris* is more closely related to *Pertica*. *Cooksonia*, *Rhynia*, and *Psilophyton dapsile* often are more closely related to one another than to other lineages. One manifestation of these relationships is shown in Figure 12.

The lack of resolution in the more basal regions of the trees reflects at least in part the conservative coding of certain characters and the low number of characters used. Some of the postulated relationships, and lack of resolution, of the trimerophytes, *Tetraxylopteris*, and the ferns may result from inclusion of grade-level taxa. Clearly, more information is needed about the earliest representatives of several plant lineages, about transformation possibilities of some characters, and about homology of structures. Also, early land plant lineages exhibit considerable homoplasy.

The cladograms shown in Figures 12 and 13 differ mostly in details from that illustrated by Crane & Hill (1987) for some early land plants. Their cladogram shows a zosterophyll–lycopsid line and a rhyniophyte–trimerophyte–progymnosperm line. Their method of analysis differs, fewer taxa were included, and some different characters were used. The trees illustrated here agree in suggesting a fairly close relationship between *Renalia* and the zosterophyll–lycopsid group, but differ in showing less resolution of rhyniophytes, trimerophytes, and progymnosperms.

The results, while preliminary, are interesting and disappointing. They represent an assessment of relationships obtained by an alternative means to the more traditional comparative discussion in the preceding sections (even though determining transformation series of some characters includes some traditional assumptions). However, some nodes are not very robust and homoplasies exist, so it is likely that different topologies will result when new data are obtained, and character assessment and determination of homologies are refined. Better topology exists at higher hierarchical levels in the cladogram, and some of this supports relationships as predicted from other forms of analysis. I regard this analysis as particularly valuable in suggesting that the morphology of these plants is not complex enough to assess affinities easily, since character definition and determination of homology is difficult. It points out areas where more information is needed. It also supports a closer relationship between lycopsids and zosterophylls than between lycopsids and any other lineage (except perhaps the *Renalia* lineage which, as mentioned previously, may be problematical), and in fact, the two lineages are monophyletic.

SUMMARY

In conclusion, zosterophylls constitute a fairly large and well-circumscribed group of early land plants, separate from trimerophytes or rhyniophytes. They exhibit many morphologic features similar to lycopsids, or ones that could easily be modified to result in a lycopsid. They appear similar in ecological tolerances. The existing cladograms support a monophyletic relationship between zosterophylls and lycopsids.

Areas in need of resolution (not only between zosterophylls and lycopsids, but with regard to all major lines of early land plants) include analysis of: (1) all types of conducting cells, steles, and stelar maturation and their homology; (2) homology among leaves; (3) how leaf-borne sporangia arose; and (4) the extent to which homoplasies occur within the many types of early land plants that existed in the Silurian and Devonian. The time of appearance of major groups requires clarification. Definition of rhyniophytoids or cooksonioids and their putative relationship to tracheophytes is needed. Additional developmental data on extant (and extinct) lycopsids would aid in addressing questions of sporangium/sporophyll ontogeny and therefore better determine the relationship of sporangia to leaves versus stems in *Baragwanathia* and possibly some other taxa. Thus, the cladograms presented here help define the remaining problems, particularly the lack of definitive characters in several early land plant lineages that would allow better resolution of putative genealogies.

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THOUGHTS ON THE EARLY LYCOPSIDS AND ZOSTEROPHYLLS[1]

Francis M. Hueber[2]

ABSTRACT

Morphological, anatomical, and reproductive characteristics of the modern lycopsids are of great value in tracing the ancient lineage of the group. The sporangium is the principal character: lack or misinterpretation of it in fossil specimens places an investigator in a predicament. An informed choice of a group of characters must be made from all those that remain. There are, of course, pitfalls and the defining characters of fossil species of the lycopsids have become confused. Differences in ontogeny of sporangia in early land plants are suggested as a way of separating the early rhyniophytoids with terminal, fusiform, indehiscent sporangia from the cooksonioid plants with terminal, globular or reniform, dehiscent sporangia. The rhyniophytoids are the source of later plant groups other than the lycopsids. Among the cooksonioids, change in the ontogeny of the sporangium in relation to the apical meristem is suggested as the point of differentiation and separation of the zosterophyll and lycopsid lineages. A reinterpretation of *Kaulangiophyton* suggests that its sporangia are borne adaxially on the leaves rather than terminally on stalks. The apical meristem of *Asteroxylon* is illustrated and described for the first time and compared with the apical meristem seen in species of *Lycopodium*. The genus *Baragwanathia*, questionably the earliest in the lycopsid lineage, is discussed in light of specimens ostensibly dated as of Gorstian age (lower Late Silurian) in Australia. *Drepanophycus* is perhaps the earliest recognizable member of the lycopsid lineage as opposed to *Baragwanathia*. The variation in the morphology of lycopsid leaves is of taxonomic value only in differentiating genera, particularly among those in the Devonian. Lineages are suggested diagrammatically.

The adage that the present is the key to the past is one of the basic principles in paleobotanical research. Careful study of the anatomy, morphology, modes of reproduction, and habitats of the components of our modern floras is the basis for extrapolation of such study into the framework of the fossil record. Unfortunately, deficiencies in the fossil record are often barriers to orderly reconstruction of floras at many taxonomic and nomenclatural levels. We are fortunate that the ancient lineage of the lycopsids is reasonably well preserved so that reconstruction of the variations within the group through time can be made with some degree of confidence. The presence of members of the lineage in our modern floras further eases the task.

CHARACTERIZATION OF MODERN LYCOPSIDS

What is the group of characteristics used to define modern lycopsids? How many of the identifying characteristics persist or are sufficiently well preserved to identify a particular fossil with confidence as a lycopsid? The following is a summary of key characters that can be gleaned from general botany texts, taxonomic monographs, or texts on plant morphology and anatomy. The presence or absence of individual characteristics may be recorded directly from observation and preparation of a particular fossil plant or interpreted from the mode and matrix in which the plant was originally entombed. The characteristics of lycopsids are:

Vascular plants with stems, roots (not rhizoids), and leaves, reproduction vegetative and by spores; terrestrial or epiphytic; *Stems* recumbent, ascending, clambering, or twining; branching dichotomous to pseudomonopodial; herbaceous, arboreous, or arborescent (fossil record only); *Roots* adventitious, from stem (*Lycopodium*), or rhizophore (*Selaginella*); from root meristem in rhizomorph (*Isoetes*); branching dichotomously, usually monarch; *Leaves*

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microphyllous, entire, serrate, or dentate; simple, or divided (fossil record); arranged in helices, alternately, decussately, or randomly; *Eusporangiate sporangium,* borne on adaxial surface of normal leaf, or modified leaf; sessile on leaf surface; in axil of a leaf; on a "short stalk" on the stem, just above a leaf; in strobili, or in alternating fertile and sterile regions on the stem; dehiscence by a slit, distally, transversely to leaf, or distally, longitudinally to leaf, or low, outer side (distally on leaf), or low, inner side (proximally on leaf); *Vascular strand* protostelic, or siphonostelic; maturation exarch, or mesarch; terete, variously lobed, or variously dissected; traces to leaves extend upwardly from the ridges of the xylem entering the leaf as a single vein. Of all the characteristics listed here, the only one that consistently unites the Lycopsida as a group is the eusporangiate ontogeny of the sporangium and its position in relation to the microphyllous leaf. The remaining characteristics serve in the definition of the orders, families, genera and species within the class. All of these details are easily obtained from specimens of the Recent Lycopsida. However, in the study of fossilized plant remains, the absence of the principal character of the sporangium places the investigator in a predicament wherein a group of characters must be chosen from among all of those that remain. The choices, interpretations, and conclusions may not be satisfactory, and the concept of the fossil elements of the Lycopsida may become confused. As examples of a few of the pitfalls in interpreting the true morphology of leaves in the early lycopsids, Figure 1A–C illustrates three specimens of *Drepanophycus gaspianus* (Dawson) Kräusel & Weyland, 1948. The leaves as seen in lateral view in Figure 1A appear to be upwardly turned and spinelike, but in another specimen from the same horizon (Fig. 1B) the leaves appear flattened and laminate. The third specimen (Fig. 1C), from a nearby horizon, represents a partially permineralized axis in which the leaves are seen in transverse section as having a slightly flattened adaxial surface and a more rounded abaxial surface. If there were only one specimen available, the description of the leaf morphology would be unrepresentative. Occasionally a specimen will exhibit two differing morphologies of the leaves due to the mode of preservation. In Figure 1D, an unidentified lycopsid, the axis is slightly twisted and buried in the matrix in three-dimensional form such that the leaves appear spinelike in lateral view due to vertical compression, but rounded in cross section where they are not compressed. Figure 2C illustrates an axis on which the leaves appear long and acicular on the right side of the specimen but appear trifurcate along the left side. Such leaves are characteristic of *Colpodexylon* Banks, 1944 as illustrated here in Figure 2D. The morphology of the leaves alone does not identify the fossils as lycopsids, but the arrangement of the leaves in helices on axes exhibiting other characteristics attributable to the group make the identifications more credible. Axes of the type illustrated in Figure 2E, in which the vascularized spinelike appendages are widely spaced and seem not to be in any specialized arrangement, beg for classification and lack any tenable lycopsid characteristics.

Morphology of the leaves in the fossil lycopsids is of taxonomic value, but the morphology of decorticated axes among the early lycopsids, as discussed extensively by Grierson & Banks (1963) and Bonamo et al. (1988), in most instances precludes the positive identification of genera. I will not discuss the subject further here, but I will illustrate one of the peculiarities of compressed, decorticated axes of fossil lycopsids. In Figure 2A and 2B, the interpretation of the images of the fossil is directly influenced by the angle and direction of the light source used in producing the photographs. Both Figure 2A and 2B can be inverted and the effect thereby reversed. Are there "leaf bases" elevated on the surface of the specimen, or are there depressions that reflect the gaps in the hypodermis through which the vascular trace and adjunct tissues passed into the leaf? One cannot become too confident in the identification of the early lycopsids, but when the fossil material exhibits sufficient intrinsic detail and when additional details can be interpreted from the matrix and occurrence, an identification can be reached with considerable confidence.

SPORANGIA: MORPHOLOGY AND POSITION IN EARLY LAND PLANTS

Among the vascular plants in the Silurian–Early Devonian, the vegetative axes are similar in basic architecture; however, the morphologies of the sporangia are very different. All of the genera have small, naked axes, with the exception of *Baragwanathia* Lang & Cookson, 1935, which has large, leafy axes. The sporangia may be (1) fusiform or obovate, indehiscent, and borne terminally on the axes; (2) reniform, distally dehiscent, and borne terminally on primary axes; (3) reniform, distally dehiscent, and borne terminally on secondary, lateral shoots; or (4) reniform, distally dehiscent, and borne in the axil or on the adaxial surface of a leaf or on the stem immediately above a leaf. *Stegano-*

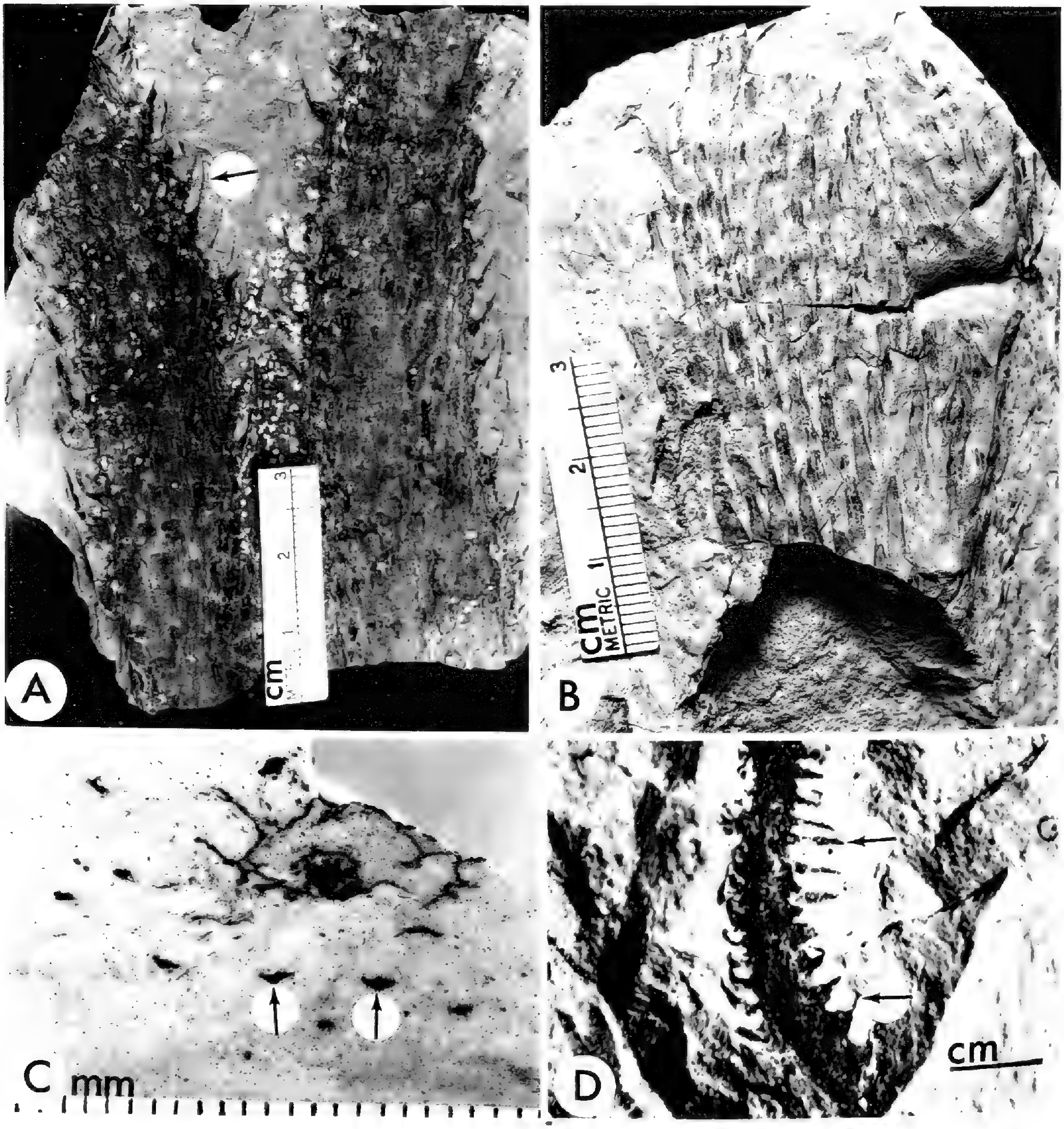

FIGURE 1. A, B, C. *Drepanophycus gaspianus* (Dawson) Kräusel & Weyland, 1948.—A. Leaves in lateral view (arrow) appear aciculate.—B. Leaves in abaxial view appear flattened and laminate.—C. Leaves in transverse section (arrows) exhibit slightly convex adaxial surfaces and more strongly convex abaxial surfaces.—D. Unidentified lycopsid in which the leaves appear to be acicular with very broad bases (arrow) or laminate; both conditions due to mode of preservation and position in the enclosing matrix. A, USNM 446319; B, USNM 446320; C, USNM 42686; D, USNM 446321.

theca Edwards, 1970 is an example of (1); *Cooksonia* Lang, 1937 (Edwards, 1970; Edwards & Feehan, 1980) is an example of (2); *Zosterophyllum* Penhallow, 1892 is an example of (3); and *Baragwanathia* is an example of (4). Other genera extant during the Late Silurian–Early Devonian with terminal, fusiform, indehiscent sporangia but without proven vascular tissue include *Salopella* Edwards & Richardson, 1974; *Hedeia* Cookson, 1935; and *Tortilicaulis* (?bryophyte) Edwards, 1979. The earliest *Cooksonia*-like sporangia from Wenlock strata (end of the late Early Silurian, see Table 1) in Ireland (Edwards & Feehan, 1980; Edwards et al., 1983) are borne on axes in which the presence of vascular tissue has not been proven. Reniform sporangia with distal dehiscence, borne laterally on axes without proven vascular structures and referred to the zosterophylls (Zosterophyllophytina, Banks, 1975) are reported in association with *Baragwanathia* in a

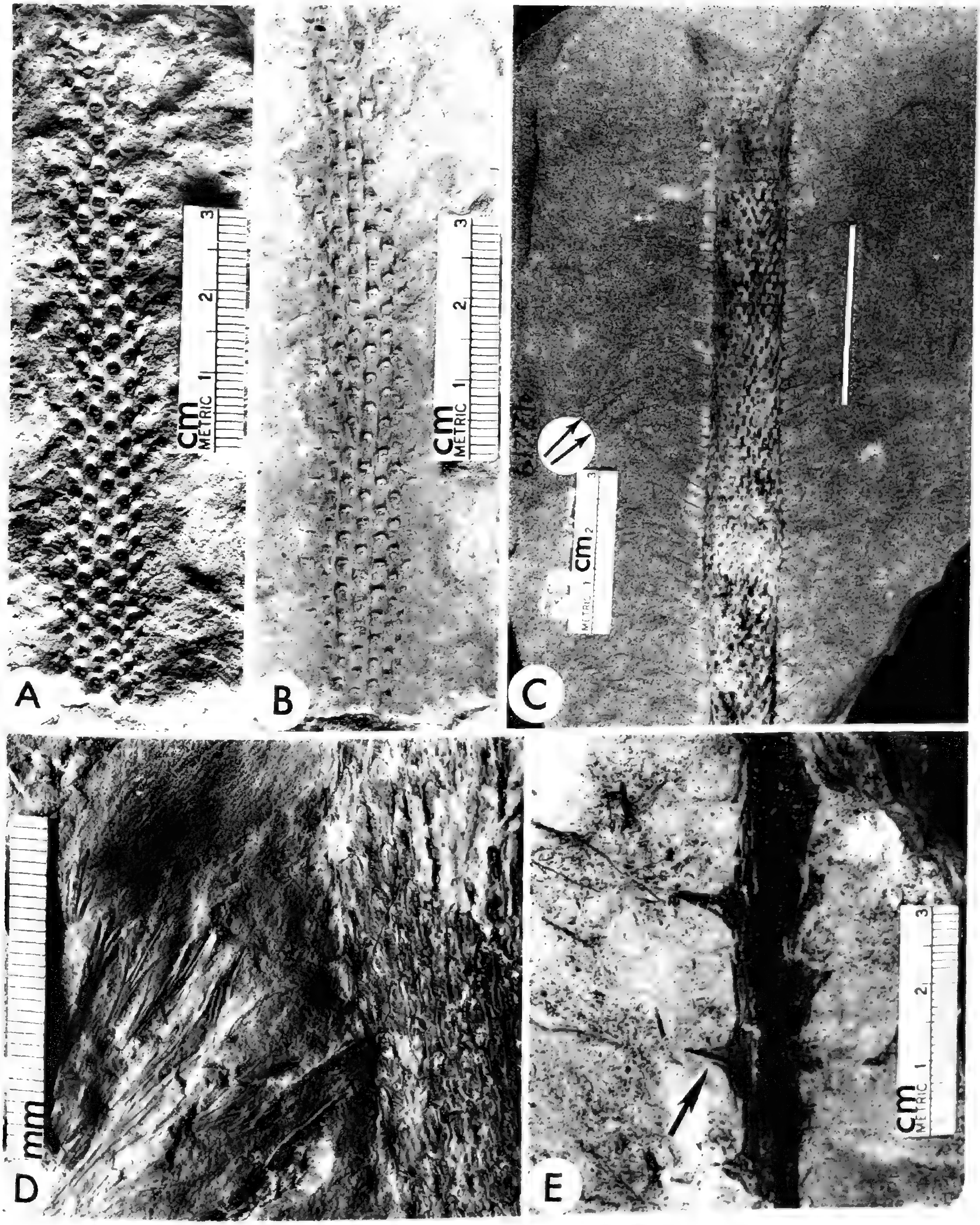

FIGURE 2. A, B. ?*Archaeosigillaria.* The lighting of specimens for photography can affect the interpretation of morphology and anatomy of decorticated lycopsid axes.—A. Specimen photographed with light source at a low angle from upper left.—B. Same specimen with light source at a low angle from the lower left. Inversion of the illustrations will exhibit the reverse effects. USNM 42217. C, D. *Colpodexylon trifurcatum* Banks, 1944. C. Specimen exhibits remains of leaves on the right margin of the axis which may be interpreted as acicular while the remains on the right are trifurcate. USNM 42219.—D. Trifurcation of the leaves clearly visible in well preserved specimen. NYSM 5240.—E. Axis with vascularized appendage (arrow) but lacking in sufficient other characteristics to allow classification with the lycopsids. USNM 422673.

TABLE 1. Silurian and Devonian time scale. Extracted from Harland et al. (1989).

Period	Epoch	Stage	Duration of intervals in millions of years			
			Began	Stage	Epoch	Period
CARBONIFEROUS						
	C_1	Tournasian	362.5			
DEVONIAN						46.0
Late	D_3	Famennian	367.0	4.5	14.9	
		Frasnian	377.4	10.4		
Middle	D_2	Givetian	380.8	3.4	8.6	
		Eifelian	386.0	5.2		
Early	D_1	Emsian	390.4	4.4	22.5	
		Pragian	396.3	5.9		
		Lochkovian	408.5	12.2		
SILURIAN						30.5
Late	S_4 Pridolian		410.7	2.2	15.5	
	S_3 Ludlovian	Ludfordian	415.1	4.4		
		Gorstian	424.0	8.9		
Early	S_2 Wenlockian	Gleedonian	425.4	1.4	15.0	
		Whitwellian	426.1	0.7		
		Sherwoodian	430.4	4.3		
	S_1 Llandoverian	Telychian	432.6	2.2		
		Aeronian	436.9	4.3		
		Rhuddanian	439.0	2.1		

plant assemblage ostensibly of Gorstian age (early Late Silurian) (Tims & Chambers, 1984; Holmes, 1988).

SPORANGIA: ONTOGENY OF THE FUSIFORM, TERMINAL SPORANGIUM

Is it possible to define the sporangia of all of the early land plants as eusporangiate and/or leptosporangiate? We can only guess at the answer because of the paucity of evidence available. Bierhorst (1971: 266), in his discussion of filicalean sporangia, states:

> An elongate sporangium, with longitudinal dehiscence, devoid of an annulus and terminally situated on an axial entity, is interpreted as the ancestral form of filicalean sporangia. This is essentially what is found in the Trimerophytaceae, which in our present state of knowledge may be ancestral to most all of the groups of ferns and fern-like plants (i.e., the Cladoxylales, the Aneurophytopsida, the coenopterid complex, the Ophioglossales and the Marattiales). It is further interpreted that the most primitive sporangium in this line had an ontogenetic history much like filicalean sporangia. That is, a single apical cell, which was also the apical cell of the axial entity upon which the sporangium was borne, ceased to produce lateral segments and divided periclinally. The outer cell produced the outer cell layer and possibly some of the cells of the inner wall layer. The inner cell produced sporogenous tissue, tapetum, and some or all of the cells of the inner wall. This would suggest that the tissue of the stalk, even if contracted and distinct, was, in part, of the same origin and continuous with the outer tissues of the axis below. This is in contradiction to some previously published interpretations but seems to fit well all the old and recently acquired evidence.

I agree completely with this interpretation of the ontogeny of the sporangium as it could apply to some early vascular plants, but can the sporangium be defined as leptosporangiate or eusporangiate? Bierhorst (1971: 267) remarked that the terms "leptosporangium" and "eusporangium" should be abandoned as too vague and presenting false impressions of their taxonomic value. He did add, however, that the "leptosporangium" is considered the most primitive among most vascular plants. I agree with that conclusion and would interpret the above ontogeny of the terminal, fusiform sporangium in early land plants as a variation of the "leptosporangium." The terminal, fusiform sporangium, as thus far documented in the fossil record, is subtended by a vascular strand; this lends more credence to the interpretation of the ontogeny of the sporangium as a modified extension of the growth of the stem apex. However, with the production of the sporangium, growth of the stem ceased, and additional vegetative growth would have required continuous branching and spreading of a rhizome or other vegetatively active portions of the plant.

A line of dehiscence was lacking in the sporangia of the Silurian vascular plants that bore elongate, fusiform sporangia. The structure appeared later in the Pragian (middle Early Devonian), if, as an example, its presence may be interpreted from the specimen of *Dawsonites subarcuatus* Tims & Chambers, 1984. The terminal sporangium with a well-developed, longitudinal line of dehiscence became particularly evident among the trimerophytes in the Emsian (upper Lower Devonian) as is clearly demonstrated in *Psilophyton dawsonii* Banks et al., 1975. In *P. dawsonii,* the outermost, thickened cortical cells of the ultimate, dichotomous divisions of the axis are continuous with the wall of the sporangium. A line of dehiscence, an "annulus," is formed as a result of a reduction in the thickening of the anticlinal and periclinal walls of two contiguous rows of cells that extend along the length of the sporangium on the inner side relative to the dichotomy of the shoot. A transverse section of a permineralized pair of such sporangia has the appearance of two letters C, one normally positioned, the other reversed, the opening in the body of the letters representing the line of dehiscence. The line of dehiscence in the terminal, fusiform sporangium arose at some time between late Wenlockian (Early Silurian) and the Pragian (middle Early Devonian), but fossil evidence that could bridge the gap is lacking. The morphology and probably the ontogeny of the terminal, fusiform, longitudinally dehiscent sporangium continue to be recognizable throughout the Devonian. The sporangium of this form is characteristic of the trimerophytes (Trimerophytina Banks, 1975) and progymnosperms (Progymnospermopsida Beck, 1960) in such genera as *Psilophyton* Dawson, 1859; *Rellimia* Leclercq & Bonamo, 1973; *Tetraxylopteris* Beck, 1957, and even *Archaeopteris* Dawson, 1871. Bierhorst's (1971) interpretation of the ontogeny of fusiform sporangia can serve as the starting point for detailed study of fossils of such sporangia. Specimens of fossil material are available that probably could provide significant ontogenetic detail if new and innovative laboratory techniques were applied to their study. The significance of such studies can only corroborate Bierhorst's interpretation and help establish the origins of what may be termed a form of the "leptosporangium."

SPORANGIA: ONTOGENY OF THE RENIFORM, TERMINAL SPORANGIUM

Interpretation of the probable ontogeny of the terminal, fusiform sporangium stimulates formulation of a hypothesis on the ontogeny of the terminal, globular or reniform sporangium as seen in late Middle Silurian and Early Devonian genera. The size and morphology of the sporangia leads to the hypothesis that the apical meristem of the subtending axes in these fossil plants comprised more than the single apical initial that has been suggested for the plants with terminal, fusiform sporangia. There may, instead, have been several apical initials that would have led to the formation of a morphologically distinct and more robust sporangium. Such a cluster of apical initials could serve as the basis in the definition of the ontogeny of a "eusporangium" as:

> . . . a group of cells, superficial in position, [that] by periclinal division forms inner and outer cells, the inner forming sporogenous cells, the outer sterile cells only. . . . The outer layer, the *primary wall cells,* by divisions both periclinal and anticlinal forms the wall, a layer of tissue when mature about three cells thick. The inner layer, the *primary sporogenous cells,* by divisions in various planes, forms a large number of *spore mother cells* or *sporocytes* (Eames, 1936: 8).

In the fossils, the wall of the sporangium is continuous with the axis that supports it, whether that axis is the main axis or a lateral shoot, and, accordingly, the sporangium lacks what may be termed a stalk. In both the reniform and fusiform sporangia, among the fossils at hand, the vascular strand of the main axis or of a lateral shoot extends into the base of the sporangium. The sporangium forms the terminus of the axis or shoot, and the formation of the sporangium depletes the apical meristem. Subsequent growth of the plant would have relied upon the rapid and steady growth and spread of the vegetative portions of the plant if such were present.

A mechanism for distal dehiscence of terminal, reniform sporangia was evident in the late Early Devonian (Dittonian Stage correlative in part to the Late Lochkovian) species *Cooksonia caledonica* Edwards, 1970. This mechanism and its position on the sporangium were also characteristic of the zosterophylls, which were represented in the ostensibly Gorstian age flora in Australia. The zosterophylls continued well up into the Devonian (Hueber & Grierson, 1961; Hueber & Banks, 1979) with a variety of morphologies and ornamentations to the axes, but at the same time the form of the sporangium was retained throughout their history. The only variation seen in the sporangium is a shifting of the line of dehiscence from distal and complete (most genera) to lateral and complete (e.g., *Crenaticaulis verruculosus* Banks & Davis, 1969). This shift of position resulted in a morphological change in the symmetry of the sporangia from equal valved (common) to unequal valved (rare). In the zosterophylls the sporangia are usu-

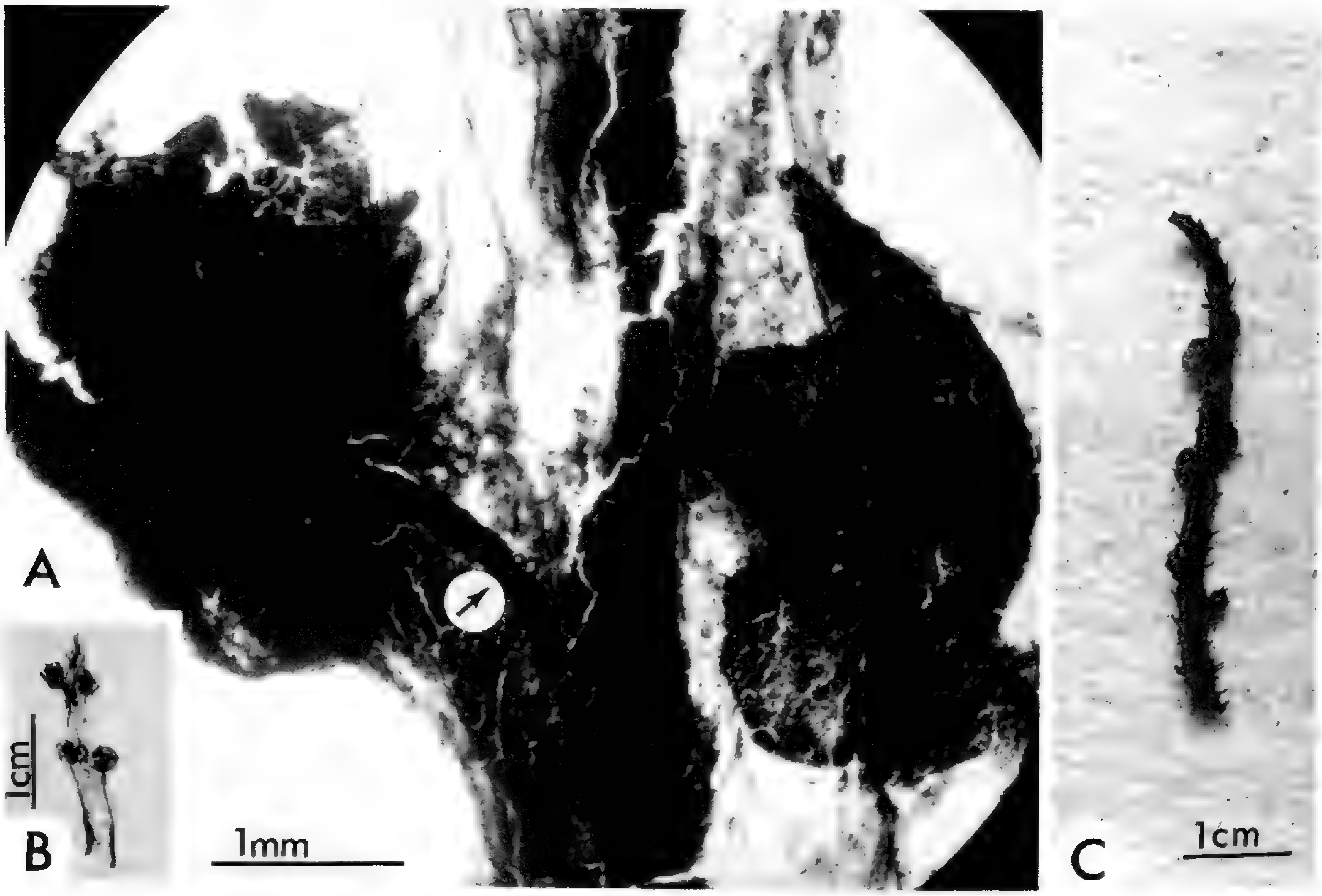

FIGURE 3. A, C. Fertile and vegetative axes of *Sawdonia ornata* (Dawson) Hueber.—A. Sporangium, as seen on upper left in B, with subtending vascular strand (arrow).—B. Portion of fertile axis, naturally retted, with subopposite sporangia.—C. Vegetative axis, isolated from matrix, with lateral buds producing the illusion of sporangia as seen in B. A, B, Geological Survey of Canada Locality 6436; C, USNM 446310.

ally described as stalked and when well preserved exhibit a vascular trace to the base of the sporangium (Fig. 3A), suggesting that the sporangia terminate a lateral, fertile shoot (Fig. 3B). There also are instances, as in specimens of *Sawdonia ornata* (Dawson) Hueber, 1971, in which a specimen of such a zosterophyll seems, at first sight, to have sporangia arranged in files along the sides of the stem. However, when the specimen is isolated by maceration of the matrix, it is found that the supposed sporangia are undeveloped or dormant lateral buds (Fig. 3C). From these few facts it is possible to review an additional line of conjecture regarding the variation in morphology of the several genera in the Zosterophyllophytina.

SPORANGIA: THE ZOSTEROPHYLLS

The zosterophylls (Zosterophyllophytina) represented a group of plants whose origins were with cooksonioid plants characterized by terminal, globular to reniform sporangia. The plants characterized by terminal, fusiform sporangia and of the same relative age as the cooksonioids represented the basis for a wholly different lineage of early land plants.

The sporangia of the cooksonioids were probably derived from the apical initials of the aerial axes, and the production of the sporangia depleted the apical initials. If the arrangement of the sporangia in the zosterophylls was a product of the loss of the apical initials of (1) the central axis, (2) the earlier formed lateral axes with subsequent atrophy of the apex of the central axis, or (3) the lateral axes only, but in combination with the continued vigorous growth of the central apex, the possibility of describing the variation of morphology of members of the group may be developed (Niklas & Banks, 1990; Gerrienne, 1988; Gensel, 1982). I repeat that a cooksonioid plant could be the progenitor of the zosterophylls and that *Renalia* Gensel, 1976, could possibly represent a zosterophyll as suggested by Niklas & Banks (1990). Interestingly, the plant now known as *Renalia* was the plant that I referred to as *Cooksonia* (Hueber, 1964) when I first began reviewing the flora of the Gaspe Sandstone. The morphology of *Renalia* resembles that of *Cooksonia hemisphaerica* Lang, 1937, as seen in the restoration of the species by Ananiev & Stepanov (1969).

My intent here is to review the interpretations of the morphology of a few of the genera represented in the Zosterophyllophytina in light of the interpretations stated above. If *Renalia* is a zosterophyll, then it clearly reflects the ancestral form of the group in which the large, reniform, distally dehiscent sporangia have been derived from apical initials and the initials have been depleted on every segment of the aerial shoots (e.g., restoration by Gensel, 1976). Additional growth of the plant would depend on rapid spreading and growth of the basal or rhizomatose regions, if such were present; otherwise the whole plant was spent in the reproductive process.

Among the genera of zosterophylls I have observed in which the sporangia are borne in compact or lax spikes, the apex of the axis is present but quite small and perhaps was abortive; examples include *Rebuchia* (Dorf) Hueber, 1972; *Zosterophyllum australianum* Lang & Cookson, 1930; and *Z. myretonianum* Penhallow, 1892. I agree with Niklas & Banks (1990) and interpret these forms as ones in which growth of each, very short, lateral shoot rather rhythmically produced by the apical meristem ended with the production of a sporangium. The development of the sporangium exhausted the apical initials of the lateral shoots. Physiological pressures may have caused the apical meristem of the main axis to cease functioning after the production of the sporangia and spores. Replacement of the heavily depleted nutrients into the system was probably controlled by the volume and development of the vegetative portions of the plant. There is also the possibility that the growth was genetically controlled, and the plant was simply determinate.

Examples of the remaining forms I will review from category 3 above are those in which the apical initials of the short, lateral branches are depleted in the production of sporangia but in which the apical meristem of the main shoot continues vigorous growth. The genera in this grouping, with which I am better acquainted through observations at collecting sites, were perhaps the most active in vegetative growth among the zosterophylls. *Sawdonia*, for example, is found as masses of intermeshing stems; however, among hundreds of stems, only one bearing sporangia might be found. Such was also the case with *Serrulacaulis* Hueber & Banks, 1979, and to a lesser degree with *Crenaticaulis*. The sporangia in these genera are borne on short, lateral "stalks," and each was supplied with a vascular trace from the central vascular strand. Their arrangement was alternate to opposite, and they formed what may be termed a fertile region along the axis. Vegetative growth beyond the fertile region generally was extensive and was terminated by a circinnate apex. One can only suggest that the large and very active vegetative growth was required to attain a concentration of auxins and nutrients that would stimulate and support reproductive activity in the stem apex. This group also had highly varied ornamentation of the stems. Some bore structures that apparently arose randomly from the protoderm and spanned the range of definition from trichome to emergence. In some genera, e.g., *Serrulacaulis* and *Crenaticaulis*, there appears to have been some influence from the apical meristem that governed an arrangement of the emergences into one or two orderly files along the margins of the stems. This characteristic may also have been influenced, at least in *Serrulacaulis*, by the morphology of the stems, which were apparently oval in cross section with the emergences borne along the opposing ridges. Any additional discussion of ornamentation requires supportive illustrative material and will have to be the subject of another paper.

The purpose in this review of sporangia and the speculations on their ontogenies in plants from the Silurian into the Devonian is so that I may express a heartfelt opinion. I do not agree with the hypothesis (Banks, 1968) that the zosterophylls are the progenitors of the lycopsids. I admit that a discussion of the ontogeny of the sporangium in the zosterophylls at this time, though sensible, is conjectural. If in the zosterophylls the apical meristem was depleted in the formation of the sporangium, I see that ontogeny of the sporangium as wholly different and separate from the ontogeny and resulting position of the sporangium in the lycopsids. The time-lapse slipping and sliding of telomic acrobatics hold little significance to me when one has evidence of the ontogeny, morphology, and anatomy of the sporangia in the Recent lycopsids as a key to the interpretation of evidence from the fossil record of the group.

SPORANGIA: INTERPRETING THE EARLY LYCOPSIDS

I suggested earlier here that the lycopsids were derived from cooksonioid stock principally on the basis of the morphology of the sporangium. My thoughts on the ontogeny of the sporangium in the zosterophylls relied upon the total activity and depletion of the apical meristem of the axis bearing the sporangium. To derive the lycopsid lineage from a stock of cooksonioid plants we need to hypothesize on what might have been the change in the growth activity of the apical meristem in the axes of the plant serving as the base stock. The suggestion was made here that the apical meristem of those plants with terminal, globose or reniform sporangia comprised several apical initial cells. That apical meristem functioned in the formation of the body of the plant, the branching of the axis, and ultimately the formation of the sporangium. At some point in the 15-million-year period between late Homerian (late Middle Silurian) and Lochkovian (early Lower Devonian), a major evolutionary change in the activities of the apical meristem took place. The derivation of leaf primordia from cells at the side of the apical meristem would have been the first step toward the formation of the microphyllous leaf typifying the earliest Devonian lycopsid, *Drepanophycus* (Schweitzer, 1980). Sporangia would be derived from cells produced adjacent to the apical meristem in the same manner as the leaves in the early lycopsids. The "eusporangiate" form of the sporangia would be a genetically controlled feature carried over from the ancestral stock of cooksonioid plants.

What is the potential for interpreting the ontogeny of the sporangia in the remains of plants thought to represent the early lycopsids? In Recent lycopsids the primordium of a sporangium has three sites in which it may occur: (1) in the adaxial surface of a leaf primordium, (2) in the axil of a leaf primordium, or (3) in the protoderm of the stem immediately above the formation of a leaf primordium. In all of these instances the primordium for the sporangium arises from cells of the protoderm of a leaf or of the stem. The protoderm is a derivative of the apical initials and is produced continuously during the growth and expansion of the axis. The primordia of the leaves and sporangia are initiated secondarily and are very close to the early derivatives of the apical initials. They do not affect the activity of the apical initials except perhaps by the pressures they exert in the physically and perhaps genetically controlled development of the phyllotaxy. In the Recent lycopsids there is no vascular trace nor vestigial remains of procambial tissue entering the base of the sporangium. This characteristic could suggest that sporangia in the ancient lycopsids also were not supplied by vascular tissue. Such appears to be the case thus far among the early fossil lycopsids; none of the fertile material has been shown to have vascular tissue entering the "stalk" of the sporangium. The vein in the leaf remains only within close proximity of the base of the sporangium. *Asteroxylon mackiei* Kidston & Lang, 1920 (Lyon, 1964) is perhaps an exception to this observation. On this point I offer a hypothesis regarding the form and position of the sporangia in *A. mackiei.* I do not doubt the present interpretation so much as I would prefer to see more serial sections in support of the reconstructed model by Joyce Collard prepared for a pamphlet for the Royal Scottish Museum in Edinburgh (Chaloner & MacDonald, 1980). Considering the fact that the sporangia are shown to exceed the length of the leaves, could the sporangium actually be borne adaxially on a leaf, perhaps some distance from the axil of the leaf? The extension of the leaf distally beyond the attachment of the sporangium might be quite short or nearly vestigial, as indicated in the reconstruction by the slight bulge in the distal valve of the sporangium. Location of the apex of a subtending sporophyll, if present, would require serial transverse or longitudinal sections from the point of attachment of the sporangial "stalk" through the full width of the sporangium. Median and near median longitudinal sections parallel to the long axis of the "stalk" would probably be the most instructive. Perhaps, also, well-prepared and closely monitored serial, longitudinal, thin-sections of the abundant and well-preserved remains of *Asteroxylon* will yield answers to the question of the ontogeny of the sporangium. In light of the position and morphology of the sporangium, one might hypothesize that the sporangium was initiated by a single or double row of several cells aligned transversely on the leaf primordium and not from the whole of the apical initials of the apex of a lateral shoot. If the presence and morphology of a sporophyll is demonstrated for *Asteroxylon,* it will probably be similar to that of *Kaulangiophyton.*

Kaulangiophyton acantha Gensel et al., 1969, is a species recently synonymized with *Drepanophycus spinaeformis* Göppert, 1852 (Rayner, 1984). Reexamination of the holotype and paratype specimens of *K. acantha* has resulted in the need to revise our interpretation of the morphology of the leaves and the relationship of the sporangia to the leaves. I demonstrate my reinterpretation of the species in Figure 4A and 4B with tracings of the photographs that were presented by Gensel et al. (1969: 271, figs. 5, 6). In Figure 5, a revised reconstruction of the species is presented. The leaves are 4–5 mm long, at least twice the length originally described. The sporangium was produced on the adaxial surface of the leaf, distally from the axis at a point about one-third the length of the leaf. The sporangia were large and exceeded the apex of the leaf. Most of the apices of the vegetative as well as fertile leaves were lost during the splitting of the matrix, but some remain, closely adpressed to the underside of the sporangium or plunging into the matrix below the point of attachment of the sporangium. As seen in side view, very fine

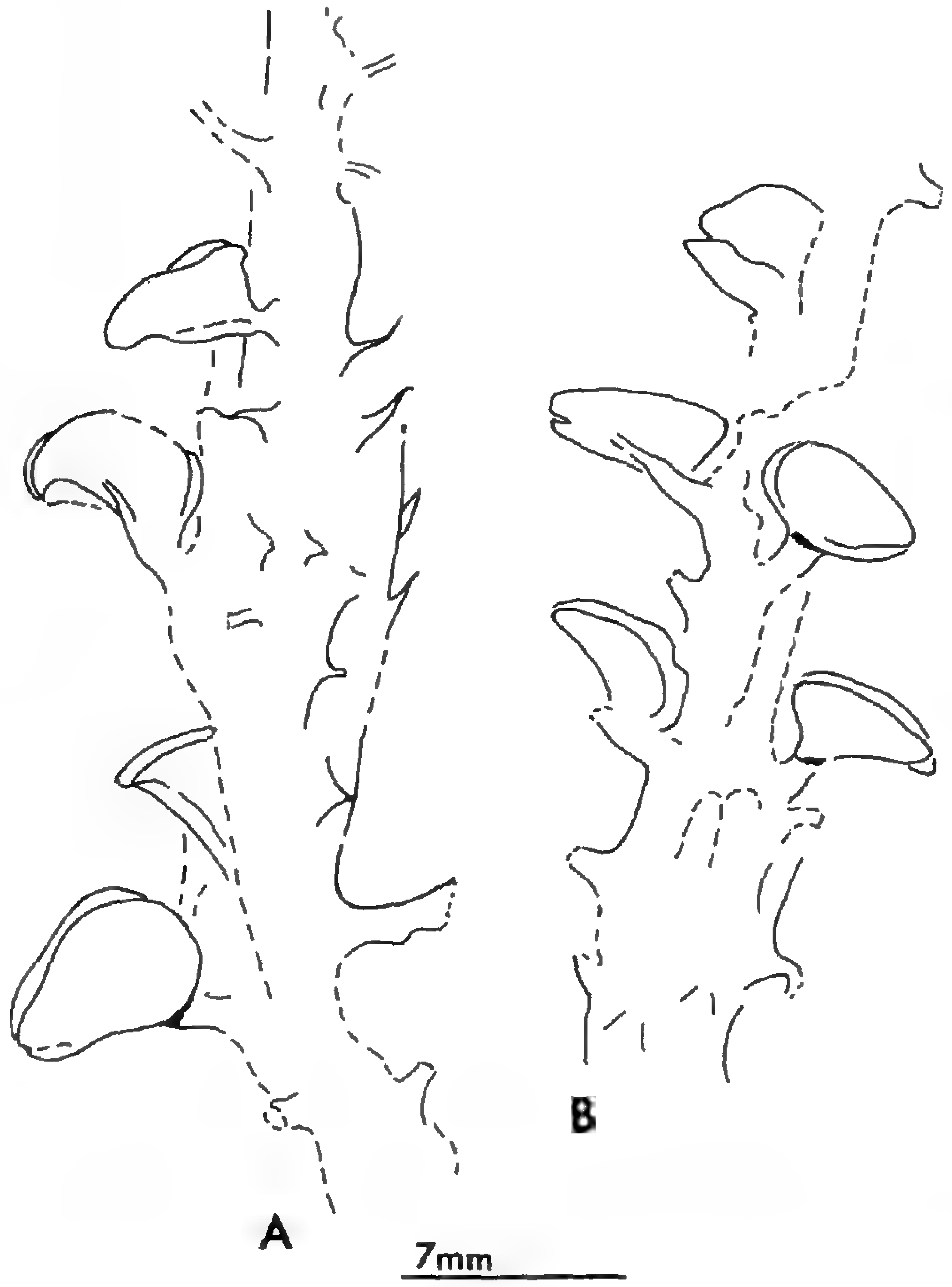

FIGURE 4. A, B. Tracings from photographs of *Kaulangiophyton akantha* Gensel, Kasper & Andrews, 1969.—A. Tracing of figure 5, page 271, Gensel et al. (1969), holotype, to emphasize details of morphology not clearly evident in the original photograph; USNM 43208.—B. Tracing of figure 6, page 271, Gensel et al., paratype, to emphasize details of morphology not clearly evident in the original photograph; USNM 43209.

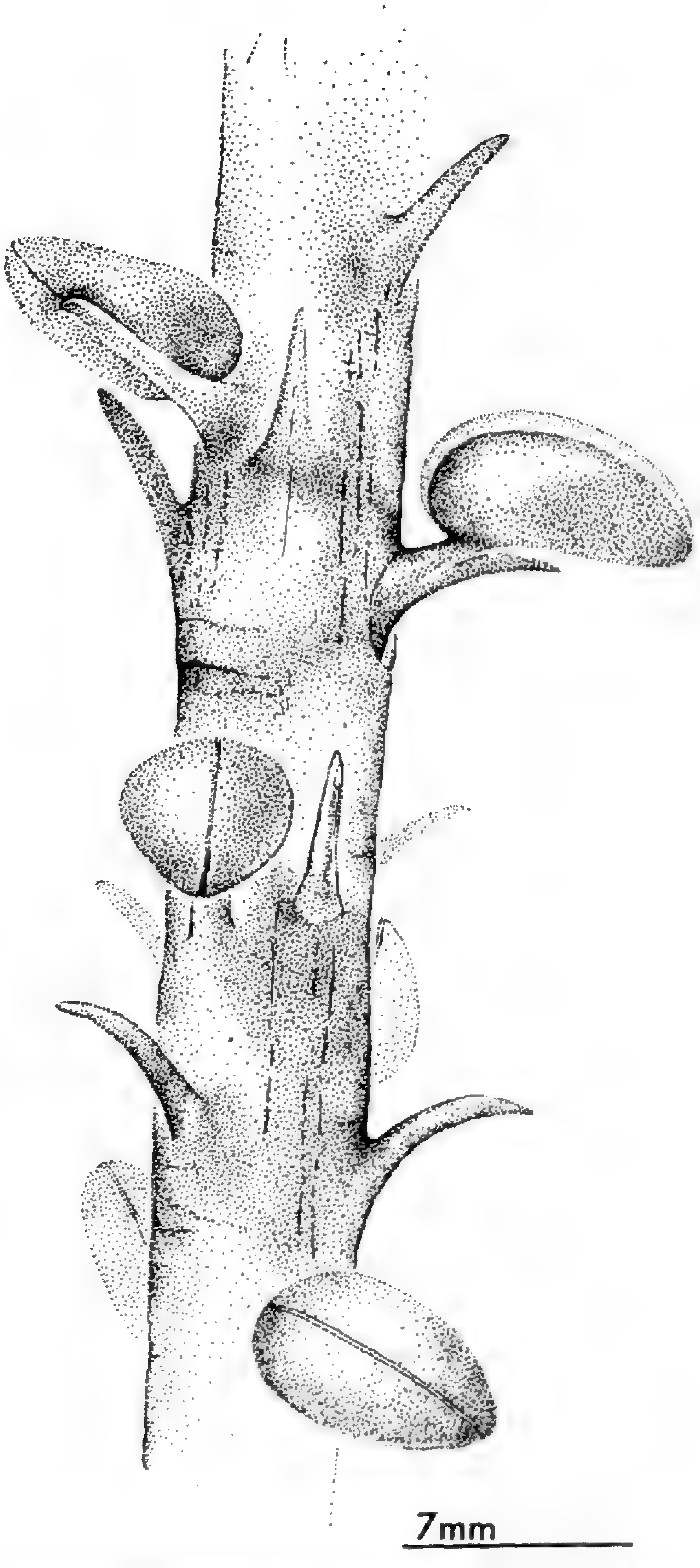

FIGURE 5. Reinterpreted restoration of the fertile zone in the species *Kaulangiophyton akantha* Gensel, Kasper & Andrews, 1969; figure 7, page 272.

lines of carbonized tissue extend outward into the matrix from the broad leaf bases and quite probably represent the vertically compressed body of the leaf. A well-defined line of dehiscence is present and is depicted in the tracings and in the revised reconstruction. The dehiscence is distal, equal, complete, and longitudinal to the axis of the subtending leaf. These findings relate *Kaulangiophyton* to the lycopsids and remove it as a hypothetical link to the zosterophylls. The sporangia were not borne on stalks but were instead borne on the adaxial surface of the leaves.

In *Asteroxylon*, the procambial cells in the body of the leaf (Fig. 6A, B) might have differentiated as xylary elements producing the vein observed in the "stalk" of the sporangium. Reproduction was probably initiated under the genetic and physiologic stimuli of auxin and nutrient accumulations in the stem apex. The evolution of the xylem and formation of the vein in the leaf might have resulted from the pressures exerted for the transport of nutrients required for the development of the sporangium and spores. Transport of sufficient nutrients would have required a more efficient system than that of diffusion from the truncated vein as seen in vegetative leaves (Fig. 6C, D). Even more plausibly, one might suggest that leaves bearing sporangia, thus with two growth centers as opposed to sterile leaves with only one, produced higher levels of auxins causing more complete xylem differentiation regardless of the metabolic requirements of mature tissues on the water transport system.

THE APICAL MERISTEM OF *ASTEROXYLON*

A well-permineralized apical meristem of a Devonian lycopsid has not yet been illustrated to my knowledge. I thus illustrate here a median longitudinal section of a well-developed and very well preserved lateral branch of *Asteroxylon mackiei* (Fig. 7A–C). The ground-thin section was prepared by John Hutchison in 1952 from material given to Sergius H. Mamay by John Walton in 1951. The apex is flat and comprises remains of several apical initials (Fig. 7B.2), a region of central mother cells (Fig. 7B.4), zones of the partially delimited cortex (Fig. 7B.6), the regions of the procambium and differentiation of the xylem strand (Fig. 7B.7), a procambial strand leading to a leaf (Fig. 7B.5), leaf traces (Fig. 7B.8), leaf primordia (Fig. 7B.3), and leaves in various stages of growth (Fig. 7B.1). This fossilized apex resembles the morphology and anatomy of a Recent species of *Lycopodium*, *L. reflexum* Lamarck, as illustrated by a camera lucida drawing in Haupt (1953: 219). A paper by Wardlaw (1957) on the organization and reactivity of the shoot apex in vascular plants diagrammatically shows the apex of *Lycopodium* as flat. In the context of these illustrations one can appreciate more fully the significance of the morphology and anatomy of the apex of *Asteroxylon* and feel with more confidence that *Asteroxylon* is a bona fide lycopsid. The apex of a lateral branch on a specimen of *Drepanophycus gaspianus* in the form of a compression (Fig. 7D), suggests that the apical morphology in *Drepanophycus* may be the same as that in *Asteroxylon*.

BARAGWANATHIA: ARGUABLY THE EARLIEST LYCOPSID

The lycopsids maintain the unique record for the longest continuously recognizable lineage of any vascular plant group, perhaps ranging from among the early land vascular plants of Gorstian age (lower Late Silurian) to the present, a period of nearly 424 million years (Table 1). However, the origin of the group is enigmatic and open to interpretation. No fossil has been found with a basic morphological or anatomical organization that could be taken as a precursor to the species *Baragwanathia longifolia*, which is accepted by some paleobotanists, paleontologists, and geologists as the oldest member of the lycopsid lineage (Edwards & Fanning, 1985; Garratt, 1978, 1981; Garratt & Rickards, 1984; Garratt et al., 1984; Richardson & Edwards, 1989; Tims & Chambers, 1984). I personally do not accept the species as the oldest because I remain unconvinced of the age of the earliest stratigraphic occurrence of it in Victoria, Australia. The dating, I feel, is too subjective as it is not based on adequate numbers of well-preserved and (most importantly) unambiguously identified graptolites. Two localities are involved and are interpreted as approximately stratigraphically equivalent by Garratt & Rickards (1984). Their localities are Limestone Road (4) and Ghin Ghin (1), Victoria, Australia. The few specimens of graptolites identified as *Bohemograptus bohemicus bohemicus* (Barrande) from Locality 4 are illustrated by the authors and are used in defining the biostratigraphic age of the sediments. The species *B. bohemicus* is cited as a common, cosmopolitan graptolite not known from strata younger than Ludlow (Late Silurian; see Table 1). The specimen that was formerly identified by Garratt (1978, fig. 5A) as belonging to the *Pristiograptus dubius* (Suess) group is re-illustrated as *B. bohemicus bohemicus* (Barrande). The authors, however, give neither descriptions nor comparisons in support of the identification of the species and subspecies. They mention that one or two specimens in the collections show morphological variations from the species but that those particular specimens do not change the interpretation of the age of the site from Ludlow. If the confidence of identification is to the level of subspecies, it would seem appropriate to furnish a description that would fully justify the taxonomic position of the specimens at hand.

The identification of specimens of graptolites from Locality 1 is accompanied by a comparison to *Monograptus uncinatus* sens. str., a species restricted to the Gorstian (Lower Ludlow or lower Late Silurian). However, the authors (Garratt & Rickards, 1984) are not fully confident in their identification of the specimens and refer to them

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FIGURE 6. A, B, C, D. Anatomy of leaves and veins of *Asteroxylon mackiei* Kidston & Lang, 1920.—A. Slightly oblique, longitudinal section of axis showing at (1) a leaf base with undifferentiated procambium extending downward toward the leaf trace and upward into the leaf, at (2) portions of the central xylem strand, and at (3) the leaf trace.—B. Enlarged view of the median longitudinal section of the leaf, as seen in A, with procambium extending into the center of the leaf.—C. Longitudinal section of leaf base with partially differentiated xylem of the vein (arrow).—D. Enlarged view of the partially differentiated tracheids (arrow) in leaf trace as seen in C. A, B, USNM 446311; C, D, USNM 446312.


1mm
1
2
3
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0.2mm
B
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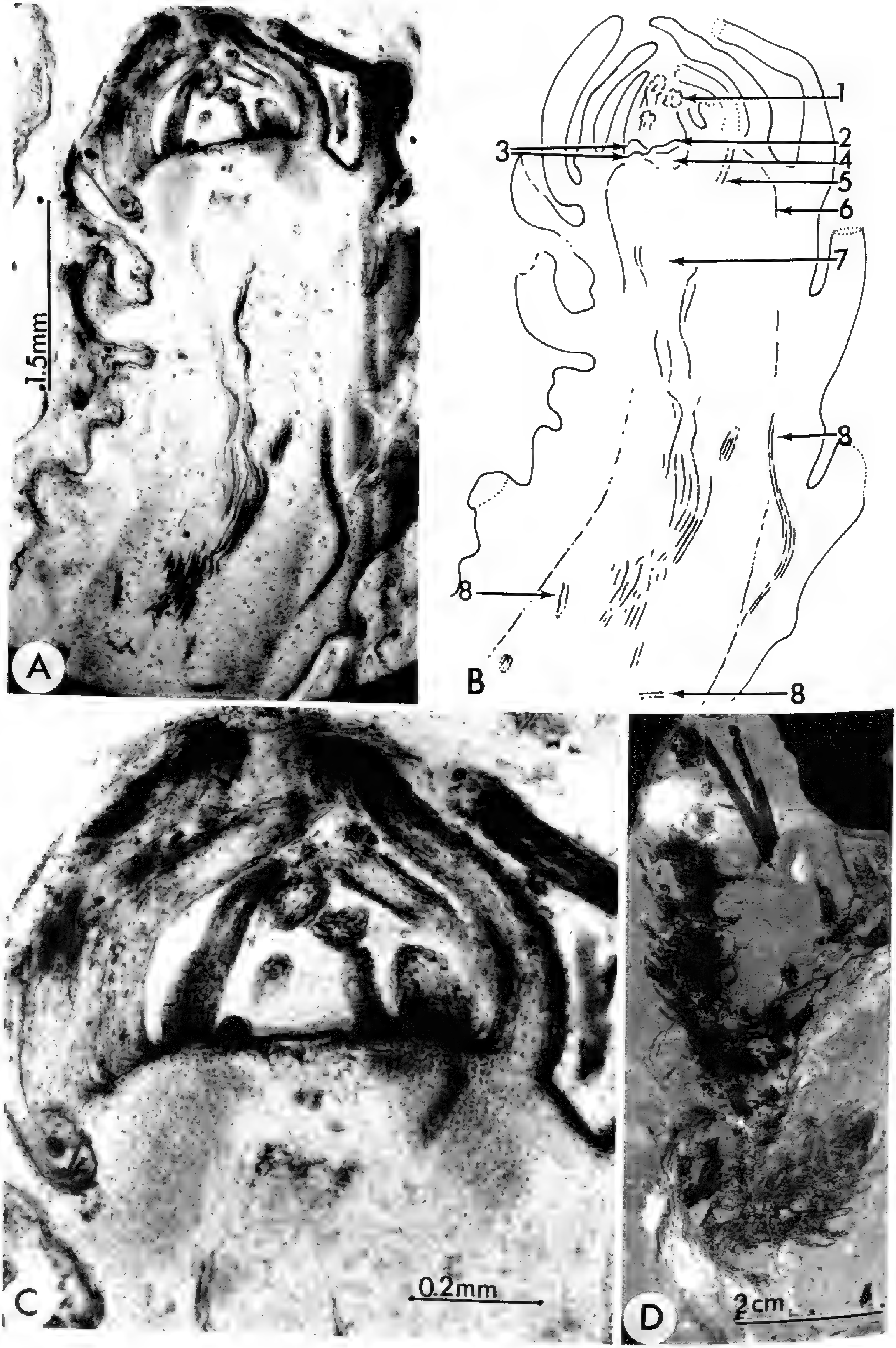
1.5mm
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1
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8
8
B
0.2mm
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2cm
D

as *Monograptus* aff. *uncinatus uncinatus* Tullberg on the grounds that the preservation differs from any described post-Ludlow species and that the specimens are very close to European specimens of *M. uncinatus* sens. str. On the other hand, Jaeger (1978, 1979) claimed that certain morphological characteristics of *M. uncinatus* persist into the Devonian, and the morphology serves as a template for some evolutionary lineages of graptolites in the Devonian. Such an observation suggests that objectivity in the definition of a taxon is prerequisite to defining graptolite biozones (Temple, 1988) and subsequently for defining an age for a stratigraphic occurrence of a potentially significant taxon. If specimens of graptolites are abundant at both localities, as stated by Garratt & Rickards (1984), more effort should be applied to define taxa as support for the determination of the age of the occurrences.

The plant remains found at Garratt and Rickard's Localities 4 and 1 are referred to as the "Lower Plant Assemblage." The *Baragwanathia longifolia* found at Locality 4 is conspecific with fossil remains found in an "Upper Plant Assemblage," the fossil flora described by Lang & Cookson (1935), which is dated as Pragian in age (middle Lower Devonian) (Jaeger, 1966, 1967). The two assemblages are vertically separated by 1,700 m of sediment. If the Lower Plant Assemblage is of Gorstian age (lower Late Silurian) and the age of the Upper Plant Assemblage is Pragian (middle Lower Devonian), then the section of sediments was accumulated over a period of about 24 million years. During that period no significant change occurred in the composition of the floras or assemblages. It seems unusual that such assemblages of plants would remain so static, with no evolutionary changes, for such a long period of time. The occurrences of the remains of the plants indicates that they were dislodged and drifted from their sites of growth on a landmass bordered by marine waters. It is hazardous to attempt to interpret the paleo-latitude or paleo-longitude of their occurrences, if the sites are among any of those accretionary terranes that appear to form a large part of the eastern quarter of the present-day continent of Australia (Condie, 1988, fig. 6.26).

Baragwanathia, as an example of an advanced form of an early land plant, is not the sole basis for our discussion over the differing ages assigned to the two assemblages. The discussion rests more logically on the occurrence and identical representation of three of the four major groups of early land plants in the two assemblages, i.e., Rhyniophytina (*Salopella*), Zosterophyllophytina (zosterophyll species), and Lycophytina (*Baragwanathia*) (Tims, 1980; Tims & Chambers, 1984; Holmes, 1988). The Trimerophytina, the fourth group, is represented only in the Upper Assemblage by *Dawsonites subarcuatus* Tims & Chambers. The three plant groups common to the assemblages are at the same level of evolutionary development, and yet it is proposed that they are separated in time by 24 million years. Fossil evidence for the evolution of a flora of the type comprising the Lower Plant Assemblage is lacking for the period of time between the *Cooksonia* sp. of Late Homerian age in Ireland (Edwards & Feehan, 1980) and the Lower Plant Assemblage here in question. That period of perhaps three million years would have been followed by a stasis in the evolution of the flora for 24 million years. If the two assemblages are treated as similar or identical associations in more nearly synchronous occurrences, then there is fossil evidence for their evolution based on numerous, similar, well-dated associations in widely geographically separated localities (Chaloner, 1970; Chaloner & Sheerin, 1979; Banks, 1980). The levels of evolutionary development of these associations are not based solely on the rhyniophytes but instead are interpreted on the basis of all of the component taxa. The early rhyniophytes (e.g., *Salopella* Edwards & Richardson, 1974) should no longer be considered the basis for deriving lineages of all land plant groups, but instead the possible progenitors of the lineage of the Trimerophytina. A plexus of cooksonioid plants may, on the other hand, represent the basis for the derivation of the lineages of the Zosterophyllophytina and the Lycophytina. In the early land floras (Late

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FIGURE 7. A, B, C. *Asteroxylon mackiei* Kidston & Lang, 1920.—A. Median, longitudinal section of a permineralized, small, lateral axis in which the apical meristem is well preserved.—B. Tracing of the photograph in A with arrows to indicate (1) transverse sections of young leaves, (2) zone of apical initials, (3) leaf primordia, (4) zone of central mother cells, (5) procambium of vein of leaf, (6) zone of differentiation of the zoned cortex, (7) zone of procambium with xylem differentiation, (8) leaf traces.—C. Enlarged view of the apical meristem in which details of cells in the zones noted in B can be more clearly observed.—D. *Drepanophycus gaspianus* (Dawson) Kräusel & Weyland, 1948. Compression fossil of young lateral axis, which if permineralized would perhaps exhibit the same organization of the stem apex as in A–C. A–C, USNM 446313; D, USNM 446314.

Silurian and Earliest Devonian) the lineages were independent, and their evolution proceeded at a rapid rate during the late Lower Devonian, Middle Devonian, and into the Upper Devonian. The northern and southern early land floras, although disjunct as fossil remains in their present distributions, are essentially in synchronization and need not be modified by the advent of interpretations that are insufficiently well founded to be readily accepted.

The Pragian (middle Early Devonian) age of *Baragwanathia longifolia* and its associates (Jaeger, 1966, 1967; Tims & Chambers, 1984; Holmes, 1988), as opposed to Gorstian (Lower Ludlow), seems more realistic in light of the fossil evidence at hand and for the general scheme of evolution of the Kingdom Plantae.

The story of the early lycopsids and their subsequent evolution may begin with a very fine, unique, and perhaps ancient species: *Baragwanathia longifolia* has all of the defining features of a lycopsid, and approximately 25 million years after its putative first appearance in the fossil record it is followed or accompanied by an array of fossil plant remains that are interpretable as lycopsids. Some of these fossils may not belong to the lineage at all, because although they may exhibit morphologies characteristic of the lycopsids, fertile specimens are not available to confirm the identifications. It is beyond the scope of this paper to attempt a revision of all of the species of early lycopsids. Such a revisionary task would require a highly objective re-examination of all of the specimens used to derive a particular species concept. I am attempting, at this time, to relate my own experiences with the problems of defining the species of fossil lycopsids, lycopsidlike plants, and their associates. The lycopsids are common in nearly all deposits of Devonian plant remains. The herbaceous forms reached their maximum diversity in a ca. 29-million-year span of time between middle Early Devonian (Pragian) and early Late Devonian (Frasnian). Where and when the arborescent habit was derived from the large stock of Middle Devonian herbaceous lycopsids remains unclear.

Baragwanathia longifolia can be recognized as a lycopsid (Fig. 8A–D, Fig. 9A–D; see also Lang & Cookson, 1935, plates 29–31), and its morphology is homologous with that of some Recent species (e.g., *Lycopodium mandioccanum* Raddi; Fig. 10A, B). A morphologically comparable species, *B. abitibiensis* Hueber, 1983, occurs only slightly later in late Lower Devonian strata of Emsian age in northern Ontario, Canada. If the earliest date is correct, these occurrences establish a time span of approximately 35 million years during which *Baragwanathia* occupied its niche in the early land floras. The first appearance of *Baragwanathia* in the fossil record de novo, if it is correctly dated, is an enigma. Its extinction is a matter of conjecture, which will be discussed below.

Specimens of *Baragwanathia* bearing sporangia are uncommon. I collected a single specimen at the Nineteen Mile Quarry site in Victoria, Australia, and it is illustrated here in Figure 9A–D. Part and counterpart of the specimen are illustrated along with photographic enlargements of portions of the axis. The mode of preservation of the axis presents problems in interpretation of the morphology and position of the sporangia. A layer of microcrystalline quartz and an unidentified mineral containing barium was formed within the cavity that resulted from the decay of the fleshy, inner tissues of the plant. The minerals formed casts of the leaf bases and at the same time minutely dissected the carbonized remains of the sporangia. The mineralized layer split unevenly, resulting in irregular exposure of the upper and lower surfaces of the axis as it lies along the bedding plane of the matrix. In Figure 9C and 9D an attempt has been made to label the abaxial and adaxial view of the leaf bases and their associated sporangia, which appear to be axial in position. Because of the fragmentation of the sporangia, a line of dehiscence is difficult to recognize and illustrate; however, two examples are noted in the illustrations as slitlike, curved openings along the distal margin of the sporangia. Lang & Cookson (1935) demonstrated the presence of spores in the sporangia observed in their specimens. I have not yet had such good fortune. This information regarding the position and dehiscence of the sporangia is valuable in furthering the recognition of *Baragwanathia* as a lycopsid.

A description of *Baragwanathia longifolia* is here based on an analysis of the holotype and

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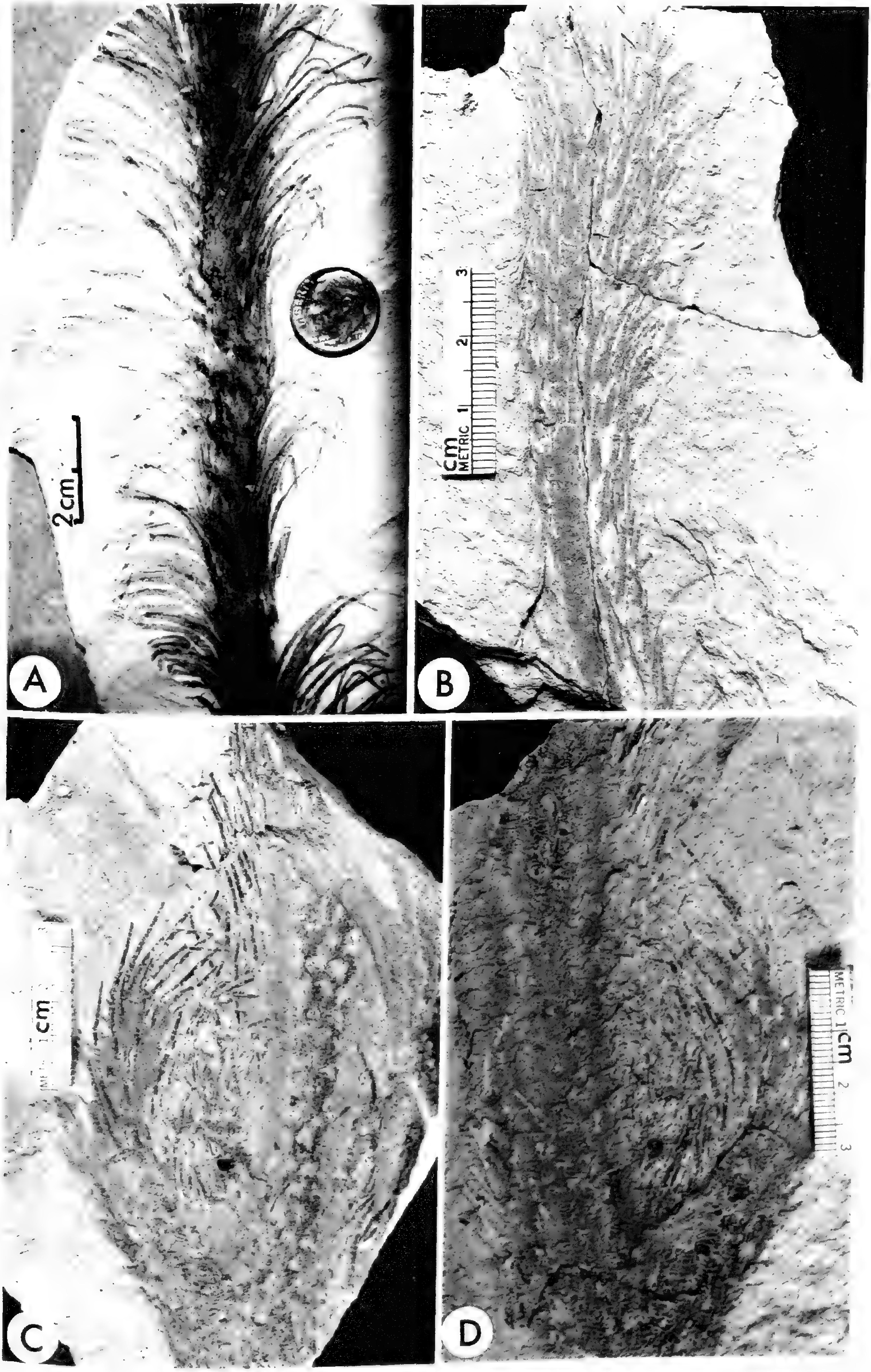
FIGURE 8. A, B, C, D. *Baragwanathia oblongifolia* Lang & Cookson, 1935.—A. Vegetative axis from the Upper Plant Assemblage in the Devonian of Victoria, Australia; USNM 446315.—B. Vegetative axis from the Lower Plant Assemblage in the Silurian of Victoria, Australia; USNM 446316.—C, D. Part and counterpart of "pseudomonopodially" branched axis from the Upper Plant Assemblage in the Devonian of Victoria, Australia; USNM 446317.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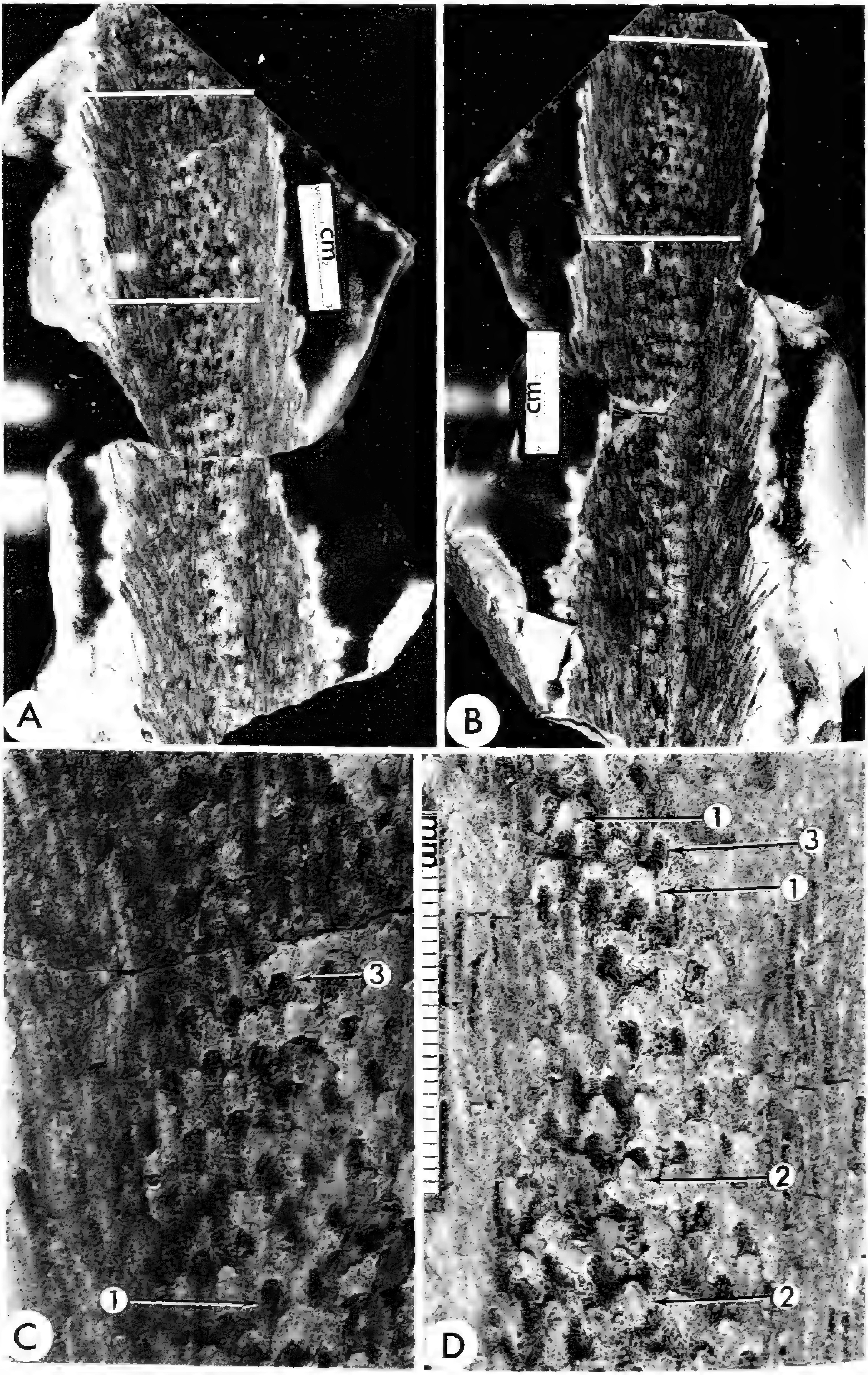
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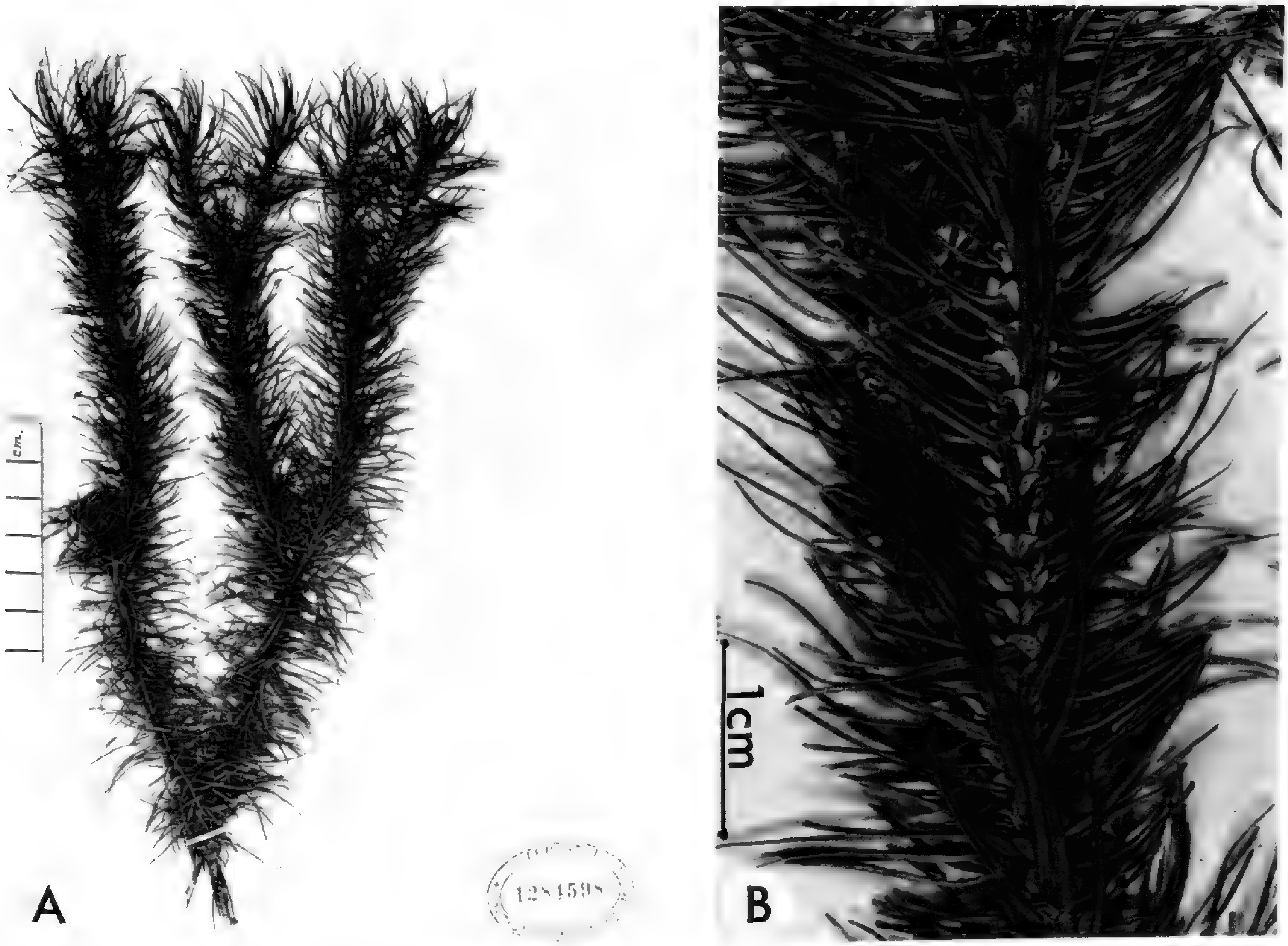

FIGURE 10. A, B. *Lycopodium mandioccanum* Raddi for comparison with *Baragwanathia longifolia.*—A. Specimen illustrating the morphology of the axis and leaves.—B. Enlarged view of the axis showing position and morphology of the sporangia.

paratypes in conjunction with a large suite of specimens housed in the Museum of Victoria in Melbourne, the collections of Jack Douglas, Melbourne, and small collections I obtained at the sites of the Lower Plant Assemblage and the Upper Plant Assemblage in Victoria, Australia. The sequence of details for characterization of the species coincides with that given in the list at the beginning of this paper. *Baragwanathia longifolia* is a vascular plant with stem, true roots (not rhizoids), and leaves; reproduction vegetative and by spores; terrestrial; recumbent; branching dichotomously to pseudomonopodially; fleshy herbaceous; roots adventitious; leaves microphyllous, entire, simple, arranged in helices; sporangia borne in axils of leaves, in fertile regions on the stem, dehiscence by distal slit transverse to the leaf; homosporous; spores trilete; vascular strand protostelic, exarch, lobed; leaf traces ascend upwardly from margins of xylem strand as a single vein. Certain attributes of the species are based on interpretation of the fossils with regard to their occurrence, appearance, and state of preservation. The rarity of fertile specimens as compared with the abundance of vegetative material suggests that vegetative reproduction by fragmentation was a character of the species; this point will be discussed below in connection with other lycopsids. The presence of well-developed roots suggest that the plant was terrestrial, and there is no record of other plants of sufficient size on which it could be an epiphyte. Its recumbent habit is based on interpretation of the morphology of large

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FIGURE 9. *Baragwanathia longifolia* Lang & Cookson, 1935.—A, B. Part and counterpart of fertile portion of axis.—C, D. Enlarged views of areas as marked in A, B and with arrows to define (1) adaxial view of a sporangium with cast of a leaf base behind the sporangium, (2) abaxial view of a sporangium with a cast of a leaf base in front of the sporangium, and (3) partially displaced line of dehiscence along distal margin of sporangium. A, B, USNM 446318.

specimens. That the species was fleshy is discussed in a later section of this paper in connection with other fleshy members of the early lycopsid complex. The roots are adventitious, as they are seen in some specimens to arise directly from the leafy stems. The sporangia are defined as eusporangiate on the basis of extrapolation from the morphology and position of sporangia in Recent representatives of the group. The remaining characters are clearly observable in the suite of specimens available in the collections mentioned above.

DREPANOPHYCUS: ANOTHER EARLY LYCOPSID

From the advanced, early lycopsid *Baragwanathia* we retrogress to the less-advanced, somewhat less-organized genus *Drepanophycus*. At its earliest occurrence, in the Devonian, *Drepanophycus* is reported from the uppermost Lochkovian (Gedinnian) at Vichtbachtal near Röetgen, Germany (Schweitzer, 1980). That occurrence is about 25 million years after the ostensibly first appearance of *Baragwanathia*. The two genera occur together at the latest occurrence of *Baragwanathia* in sediments of Emsian age (Hueber, 1983). *Drepanophycus* is last reported from sediments of Frasnian age by Banks & Grierson (1968) thus indicating that the genus existed for at least 22 million years. The type species of the genus, *D. spinaeformis*, may be characterized as follows: vascular plant with stem, true roots and leaves, reproduction vegetative and by spores; terrestrial; recumbent; branching dichotomously to pseudomonopodial; herbaceous; roots adventitious, branching dichotomously; leaves microphyllous, entire, simple, arranged in helices or randomly; "eusporangiate" sporangium borne on adaxial surface of normal leaf, or on short stalk with or without relationship to a leaf, in alternating fertile and sterile regions on the stem, dehiscence distally, transverse to the leaf or tangentially to the surface of the main axis; spores as yet not described; vascular strand protostelic, maturation exarch, variously lobed, traces to leaves extend upwardly from the ridges of the xylem entering the leaf as a single vein.

Which characteristics in the description of *D. spinaeformis* differ from those given for *Baragwanathia* and those in the broader characterization of the Recent lycopsids? First, the arrangement of the leaves in *Drepanophycus* can be random, which is not a characteristic of *Baragwanathia* but can be found in the Recent lycopsids. Certainly the lack of the character in *Baragwanathia* does not diminish its classification with the lycopsids even though, generally, the presence of helically arranged leaves usually is weighted more heavily in the analysis of the group. *Drepanophycus spinaeformis*, on the other hand, can possess both helically and randomly arranged leaves and can just as well fit into a broader concept of the leaf arrangement typifying the lycopsids. The second differing characteristic, and the one most used to eliminate *Drepanophycus* from the lycopsids, is how and where the sporangia were borne on the plant. I cannot add any evidence to this discussion because I do not have well-preserved specimens of fertile *Drepanophycus*. The reader may consult Grierson & Banks (1963), Banks & Grierson (1968), Fairon-Demaret (1971, 1978), Schweitzer & Giesen (1980), Schweitzer (1980, 1983) and Rayner (1984) for additional descriptions and discussions. A report on collections from the region of Gaspé Bay, Quebec, and northern New Brunswick, Canada, was given at the annual meeting of the American Institute of Biological Sciences by Kasper (1977). The illustrations used in conjunction with the oral report indicated the presence of valuable material for the description and clarification of details centering on fertile *Drepanophycus* from the Devonian of North America. Some of the sporangia seemed to be borne on the adaxial surfaces of leaves, but the careful preparation required for elucidating the details has not yet been completed.

As the reader might gather from my review of the sporangia of *Kaulangiophyton* and the speculations regarding the ontogeny of the sporangia in *Asteroxylon*, I am not convinced that the sporangia on *Drepanophycus* are borne on "stalks." I prefer to wait and see what is discovered with the preparations of better preserved specimens that lend themselves to maceration and isolation of the sporophylls for examination in three dimensions. The sporangia are of such large size, and as in *Kaulangiophyton*, they may exceed the length of the leaf and may mask its apex. Some of the drawings of the sporophylls of *Drepanophycus spinaeformis* by Kräusel & Weyland (1935) may be interpreted in that way and may serve as the basis for making closer observations of nearly prepared material. At the same time, there has been little attention given to the mode of dehiscence in *Drepanophycus*. In his description of specimens of *Drepanophycus* (*Protolycopodites*) *devonicus* (Weyland & Berendt), Schweitzer (1980) mentioned the presence of thickening along the upper margin of the sporangium, which he attributes to originating probably from the line of dehiscence. The detail is illustrated in the reconstruction of the sporangium, but is not clearly defined in the reconstruction of the whole plant. The same is true of his reconstruction of the whole plant of *D. spinaeformis* (Schweitzer, 1980).

The line of dehiscence and its position on the sporangium among the early lycopsids offers little or no support for interpreting the phylogeny of the group. There are only two positions of the line of dehiscence known for the early lycopsids. The dehiscence of the sporangium distally and longitudinally to the axis of the leaf is, for example, characteristic of *Drepanophycus*, *Protolepidodendron* Kräusel & Weyland, 1932, *Colpodexylon*, *Leclercqia* Banks et al., 1972, and the later appearances in the Carboniferous of the arboreous and arborescent lepidodendralean lycopsids and the ancestral stock of the Recent Isoetales. Dehiscence of the sporangium distally and transverse to the axis of the leaf is characteristic of *Baragwanathia*, *Asteroxylon* (probably) and most of the Recent members of the Lycopodiales.

The morphology of the xylem strands of the above examples reveals that lobed protosteles are characteristic of *Drepanophycus*, *Colpodexylon*, *Baragwanathia*, and *Asteroxylon*, while solid, coronate protosteles are characteristic of *Protolepidodendron* Stur, 1882, *Leclercqia*, and the Carboniferous lepidodendralean lycopsids. Only in the characteristics of the xylem do I feel that some element of a phylogeny might possibly be derived. I have held this opinion and expressed it orally at the Tenth International Botanical Congress in Edinburgh (Hueber, 1964) after the publication of the details of the anatomy of *Protolepidodendron gilboense* Grierson & Banks, 1963, and before the publication of the details of the anatomy of *Drepanophycus gaspianus* (Grierson & Hueber, 1967). The lobed protostele of the early lycopsids may well be reflected in the variously lobed and dissected protosteles that characterize most of the Recent Lycopsida, whereas the solid, coronate protostele seems to have been the basic form on which the arboreous and arborescent, lepidodendralean lycopsids expanded and then declined, leaving the Isoetales as the only Recent derivative to retain this particular trait.

MORPHOLOGY OF THE LEAVES OF EARLY LYCOPSIDS

The morphology of the leaves of the early lycopsids shows an even greater disparity among the genera. No clear phylogenetic signal can be derived from them. There are simple leaves in *Drepanophycus*, *Baragwanathia*, *Asteroxylon*, *Lycopodites oosensis* Kräusel & Weyland, 1937, and the Carboniferous lepidodendralean lycopsids. *Protolepidodendron* has bifurcate leaves. *Colpodexylon* has trifurcate leaves. *Leclercqia* has quinquefurcate leaves. There also are sagittate-entire leaves as in *Haskinsia colophylla* Grierson & Banks, 1983; hastate-entire leaves as in *H. sagittata* Edwards & Benedetto, 1985; deltoid-serrate leaves as in *Archaeosigillaria vanuxemii* (Göppert) Kidston, 1901 (Fairon-Demaret & Banks, 1978) and *Artschaliphyton unicum* Senkewich, 1971 (not seen; publication date pers. comm. H. P. Banks, species = *Gilboaphyton goldringiae* Arnold, 1937; Kräusel & Weyland, 1949; Senkewich, 1956); and linear-serrate leaves as in *Barsostrobus famennensis* Fairon-Demaret, 1977. Presented here in Figure 11A–R are illustrations of these various leaves. The information that these illustrations supply is of taxonomic value, though that is all that can be said with confidence.

Bonamo et al. (1988) pointed out the value of leaf morphology in the identification of genera in which the morphology of the surfaces of the stems otherwise appear identical. This observation is particularly true in the genera they discuss: *Leclercqia*, *Protolepidodendron*, and *Haskinsia*.

EARLY LYCOPSIDS: ANATOMY OF EXTINCTION

The species among the early lycopsids *Baragwanathia*, *Drepanophycus*, and *Asteroxylon* apparently were fleshy or at least did not have the hypodermal layers of thickened, fiberlike cells evident in the other contemporaneous lycopsids. The trabeculate, aerenchymalike tissue that appeared to form the major part of the cortex in *Asteroxylon* may be the model for the other "fleshy" genera. In most specimens of *Baragwanathia* and especially in *Drepanophycus*, all that remains in the compression fossils of the axes is the cuticle of the stem and leaves, the xylem strand, and the leaf traces. The xylem strand in compressions generally is about one-eighth to one-tenth the diameter of the stem. Such a strand could hardly have given much support to the axis. Observations (Kidston, 1893; Halle, 1916; Kräusel & Weyland, 1935; Rayner, 1984) have led to the interpretation that the axes and leaves were parenchymatous. The axes probably had either thick zones of cortical parenchyma or a combination of such parenchyma and aerenchymalike tissue comparable to that mentioned earlier as typical in the stems of *Asteroxylon*. Turgor pressure within the tissues of the stem could have maintained the ability of the stems to stand erect above the substrate. I do not interpret these stems as those of halophytes, as was expressed by Kräusel & Weyland (1935), nor did

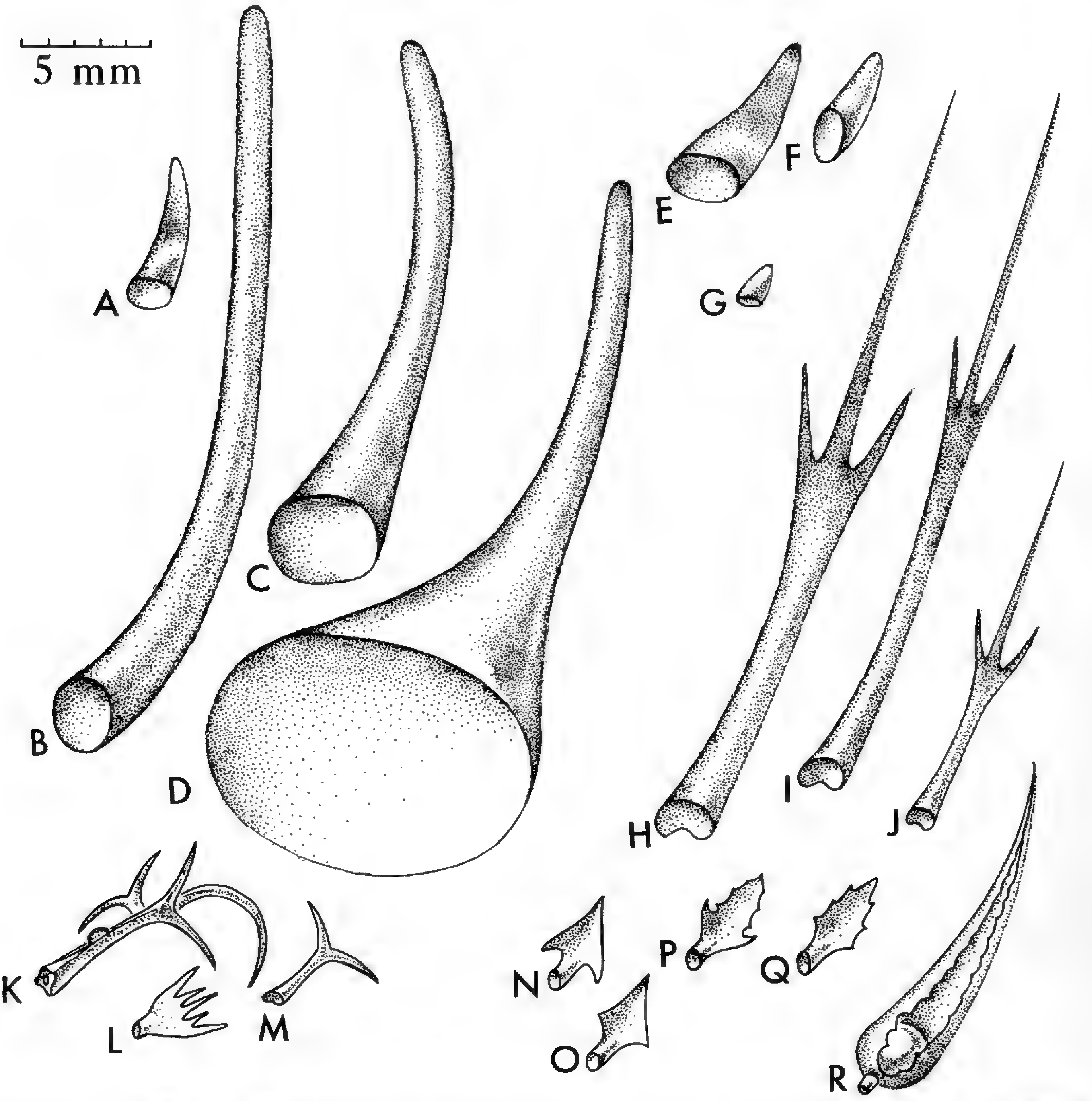


FIGURE 11. Generalized restorations of the morphology of the leaves of early lycopsids.—A. *Asteroxylon mackiei* Kidston, 1901.—B. *Baragwanathia longifolia* Lang & Cookson, 1935.—C. *Baragwanathia abitibiensis* Hueber, 1983.—D. *Drepanophycus spinaeformis* Göppert, 1852 (large form).—E. *Drepanophycus gaspianus* (Dawson) Kräusel & Weyland, 1948.—F. *Drepanophycus spinaeformis* (Dawson) Kräusel & Weyland, 1948 (small form).—G. *Lycopodites oosensis* Kräusel & Weyland, 1935.—H. *Colpodexylon trifurcatum* Banks, 1944.—I. *Colpodexylon deatsii* Banks, 1944.—J. *Colpodexylon cachiriense* Edwards & Benedetto, 1985.—K. *Leclercqia complexa* Banks, Bonamo & Grierson, 1972.—L. *Leclercqia complexa* as identified by Kasper & Forbes, 1979.—M. *Protolepidodendron scharyanum* Stur, 1882.—N. *Haskinsia colophylla* Grierson & Banks, 1983.—O. *Haskinsia sagittata* Edwards & Benedetto, 1985.—P. *Archaeosigillaria vanuxemii* (Göppert) Kidston, 1901.—Q. *Artschalophyton unicum* Senkewich, 1971.—R. *Barsostrobus famennensis* Fairon-Demaret, 1977.

Halle (1916) interpret them in this manner. There is no evidence of association of the remains of the plants with the remains of marine or brackish water animals. The occurrences of *Drepanophycus* in Gaspé, Quebec and northern New Brunswick, Canada are in continentally derived freshwater sediments, and in many instances the plants occur in situ on or in mudstones suggesting that they preferred particularly wet sites. We have come full circle in an interpretation that the fleshy lycopsids required turgor pressure within the axis to remain erect and therefore required an abundance of water as would have been available on mud flats or moist flood plains of rivers or lakes. It might be suggested also that the requirements for the successful development of the gametophytes of these early lycopsids were as highly specific as we see in the Recent lycopsids.

The extinction of the large (and very fleshy) early lycopsids may have been directly connected with the relatively unstable habitats to which they had become adapted. Their growth was nearly completely vegetative with an attendant highly reduced reproduction by spores. Destructive floods would either partially or completely disrupt and carry away the colonies from their substrate or completely bury and obliterate the colonies under sediment. The few spores and even fewer gametophytes may have been the only, tenuous means by which new colonies could be reestablished under favorable growth conditions. With the continual breakup and disruption of the habitats of these early lycopsids and the concomitant changes in the availability of adequate water for their survival, it was likely that their numbers diminished rapidly, and any additional, major change of climate would have been the final factor in their extinction.

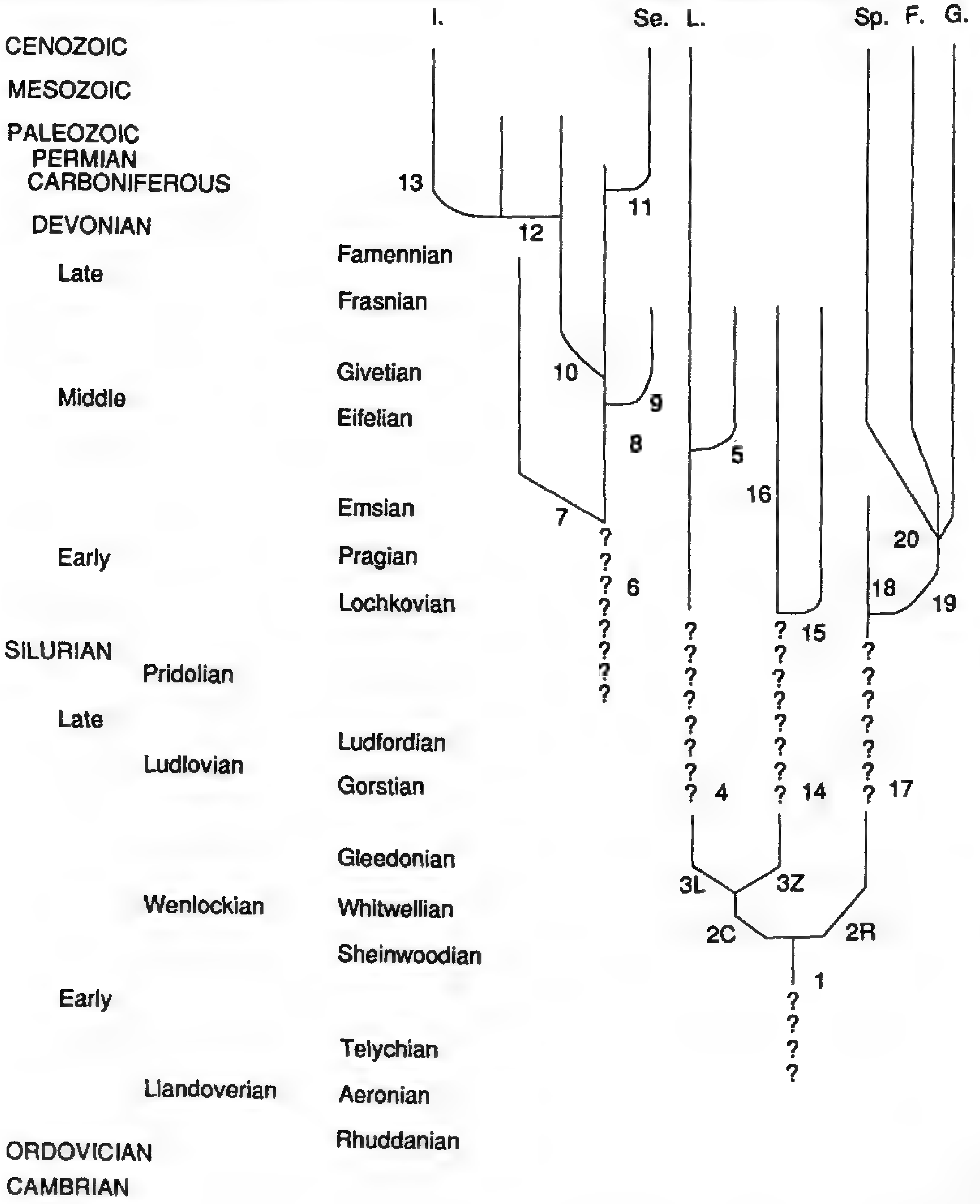
This scenario of extinction can be witnessed in a segment of the history of *Drepanophycus* in the extensive section of the Emsian into ?Early Eifelian sediments exposed around Gaspé Bay, Quebec, Canada (York River, Battery Point, and Malbaie Formations; McGregor, 1967). Along the north shore of the Bay, colony after colony of *Drepanophycus* is found buried in situ by coarse sediments of sufficient thickness to kill the colony. Interestingly, one finds in the coarser sediments fragments of *Drepanophycus* that had been brought from sites further upstream in the ancient river system. As one progresses upward in the section, the frequency of the genus diminishes. There are red beds of sediment indicating either drying of the surface of the delta or of the land mass from which the sediments were being derived. The genus is not found in the Malbaie Formation that comprises numerous redbeds and a spore flora indicating a displacement of the earlier flora represented in the preceding formations (McGregor, 1967).

EARLY LYCOPSIDS: THE LINEAGES

We may suggest that the continuation of the herbaceous line of the lycopsids was a plant like *Colpodexylon*, with its lobed xylem strand and the structural strengthening of its axis with the addition of a hypodermal layer comprising thick-walled, fiberlike cells. This strengthened hypodermal layer perhaps appeared with the first occurrence of *Leclercqia*, if appropriately identified, in the Early Devonian of Maine (Kasper & Forbes, 1979). Later occurrences of the genus are in Middle and early Late Devonian such as those of the type species and that in Queensland, Australia (Fairon-Demaret, 1974). The thickened hypodermal layer is prominent in compressions as well as in permineralizations of the axes. The stems were probably considerably strengthened by the tissue, and the characteristic of the thickened hypodermis was carried through the Devonian and into the Carboniferous among the arboreous and arborescent lycopsids as well as into many species of Recent herbaceous lycopsids.

There is no evidence for a gradual advent of the arborescent habit among the early lycopsids. Instead, the arborescent forms appear de novo with the discovery of *Lepidosigillaria whitei* Kräusel & Weyland, 1949. It was found in marine black shales of early Late Devonian age (Frasnian) near Naples, New York, and became known as the "Naples Tree." The length of the trunk was not given, but it may have been as much as 10 m and was unbranched. The generic name was chosen to indicate that the trunk exhibited the form and arrangement of leaf cushions characteristic of the genera *Lepidodendron* and *Sigillaria* of Carboniferous age. Grierson & Banks (1963) thought that many of the lycopsid axes found in the marine black shales at many sites around New York State might represent the branches of the genus. J. D. Grierson (pers. comm. 1978) held the idea that the trunks identified as *Eospermatopteris textilis* (Dawson) Goldring, 1924, might be those of *Lepidosigillaria* from which all surface tissues had been eroded. Only the thickened strands of hypodermal tissue remained and in turn produced the pattern one sees on the trunks of *Eospermatopteris*. Fisher (1962–1963), in his reconstruction of some of the genera of plants found in the Devonian of New York State, implied that he had the same opinion about the synonymy of *Lepidosigillaria* and *Eospermatopteris*, but he did not express it explicitly in writing. For a description and synonymy of *Lepidosigillaria* see Grierson & Banks (1963) and for photographs and full description see White (1907). I will only mention some other arboreous and/or arborescent genera and not give a description of each. All are Late Devonian in age (Frasnian and Famennian). *Leptophloeum rhombicum* Dawson, 1862, and *L. australe* (McCoy) Walton, 1926, require additional study, the former is probably arboreous, the latter is arborescent on the basis of the size of fragments of stems and trunks. *Cyclostigma kiltorkense* Haughton, 1859–1860, is also deemed to be arborescent on the basis of the size of specimens recovered from Late Devonian sediments in Kiltorcan, Ireland. One last example is *Phytokneme rhodona* (Andrews et al., 1971), which could be interpreted as arboreous or as a branch of an arborescent form; it is from the Late Devonian (Famennian) of Adair County, Kentucky.

TABLE 2. A partial summary of the evolution of the Lycophytina and Zosterophyllophytina as well as the hypothetical derivatives from the Rhyniophytina. (1) Plexus of unornamented, dichotomous axes of probable land plants. (2) Differing ontogeny of sporangia; 2C, the terminal globular or reniform cooksonioids; 2R, the terminal fusiform rhyniophytoids. (3) Differing ontogeny of the sporangia; 3L, Lycophytina; 3Z, Zosterophyllophytina (see text). (4) Axes with dissected xylem strand; simple singly veined leaves; sporangia borne in close relationship to leaves; homosporous. (5) Dissected xylem strand; trifid leaves; sporangium borne on adaxial surface of leaf; herbaceous habit; homosporous. (6) Origin of coronate xylem strand and ligule uncertain. (7) Coronate xylem strand; ligulate, five-parted leaf; herbaceous; sporangium borne on adaxial surface of leaf; homosporous. (8) Coronate xylem strand; ligulate, simple leaves; homosporous. (9) Coronate xylem strand; bifid leaves; sporangia borne on adaxial surface of leaves; homosporous. (10) Coronate xylem strand; ligulate; arborescent habit; rhizomorph; simple single-veined leaves; sporangia borne in axils of leaves; homosporous. (11) Dissected xylem strand; ligulate, simple leaves; heterosporous; herbaceous; rhizomorph. (12) Coronate xylem strand; ligulate; arborescent habit; rhizomorph; heterosporous. (13) Coronate xylem strand; ligulate; heterosporous; herbaceous; rhizomorph. (14) Stems smooth or variously ornamented with spines or nonvascularized emergences; sporangia cooksonioid in ontogeny and morphology, depleting whole of meristem; exarch protostele generally bipolar. (15) Terminal or lateral fertile spike, determinate in growth. (16) Fertile axis indeterminate in growth. (17) Axes smooth; branching dichotomous; sporangia terminal and fusiform, depleting the apical meristem during ontogeny. (18) Plants of determinate growth resulting from depletion of all apical meristems in the production of terminal, fusiform sporangia, sporangia apparently indehiscent. (19) Sporangia fusiform, borne terminally on lateral shoots, dehiscent; branching generally pseudomonopodial; some secondary tissues developed. (20) Plexus of plants with anatomically diverse xylem strands and arrangements of lateral vegetative and fertile shoots; basis for interpretation of subsequent evolutionary lines; homospory predominant; heterospory and seed-megaspores appear along with increased secondary growth. No attempt is made here to elucidate the evolution of plants outside of the lycopsids. I. = *Isoetes*; Se. = *Selaginella*; L. = Lycophytina; Sp. = Sphenopsida; P. = Pteropsida; G. = Gymnospermopsida.



We still lack sufficient data to propose or demonstrate any clear evolutionary pathways among the early lycopsids, and there is no evidence for pre-lycopsids (or "pro-lycopsids"), if *Baragwanathia longifolia* is accepted as the oldest representative of the lycopsid lineage. All attributes of that species were realized in the same length of time (Wenlockian–Gorstian) that was required for the zosterophylls to become recognizable in the early floras. The lycopsids were precocious in their production of leaves, which served as improved and more efficient organs for increased photosynthesis. The zosterophylls never seemed to derive the ability to produce anything more than an array of usually randomly arranged trichomes or emergences. The value of these outgrowths may have been for clambering on or around one another, much as one can see today in *Galium*, *Rubus*, or *Rosa*. Of course the outgrowths could also have served as protection against predation by arthropods and other early, terrestrial animals, which were evolving rapidly along with the plants.

My hypothesis as to the relationship of the zosterophylls to the lycopsids, as based on morphology and anatomy of the sporangium, is that they both perhaps had the same origin in a plexus of cooksonioid plants. However, the two groups became separate quite early, sometime between late Early Silurian and early Lower Devonian, perhaps on the basis of differing functions within the apical meristem for the production of sporangia. The zosterophylls utilized the whole of the apical initials in the production of a sporangium or parts of them to produce lateral axes that in turn utilized the whole of their apical initials in the production of sporangia. The lycopsids, on the other hand, utilized protodermal derivatives of the apical initials to produce leaves that were in turn the sites of the production of sporangia. The production of the leaf primordium was immediately followed by the production of the sporangial initials either from protoderm of the leaf or from cauline protoderm cells, which were derived immediately after those of the leaf primordium.

Perhaps all of these hypotheses will direct attention toward further, thorough investigation of the ancient lycopsids, which occur so abundantly and widely in the fossil record. We are fortunate to have a large and increasing number of techniques for preparation, study, and illustration of fossil plant remains, many of which were not available during the early history of paleobotanical study. With the determined use of the new techniques for study of specimens, some (though certainly not all) hypotheses may, in due time, be replaced by supportive evidence for description and interpretation.

In Table 2 a brief and partial summary is presented suggesting the evolution of the Lycophytina and Zosterophyllophytina, as well as the hypothetical derivatives of the Rhyniophytina.

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EXPERIMENTAL CLADISTIC ANALYSIS OF ANATOMICALLY PRESERVED ARBORESCENT LYCOPSIDS FROM THE CARBONIFEROUS OF EURAMERICA: AN ESSAY ON PALEOBOTANICAL PHYLOGENETICS[1]

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ABSTRACT

This evolutionary cladistic analysis of the arborescent (wood-producing) lycopsids, an exclusively fossil group of vascular plants, is confined to the strongest available data: anatomically preserved fossils that have been painstakingly reconstructed into conceptual whole plants. Ten Carboniferous genera are represented by 16 species: four pseudoherbs/"shrubs" and 12 of the arboreous (tree-sized) species that epitomize the Pennsylvanian coal swamps of Euramerica. The 69 vegetative and 46 reproductive characters are described in detail; several key terms are redefined and homologies reassessed. Binary coding was imposed throughout the data matrix, which contained only 5% missing values despite limited X-coding. Lack of an acceptable outgroup necessitated construction of a hypothetical ancestor for character polarization and tree rooting.

Our experimental approach analyzed the full data matrix plus four submatrices (growth habit characters excluded, *Chaloneria* excluded, vegetative characters only, reproductive characters only) and screened topologies of subminimal as well as minimal length. Interpretation focuses on the ten monophyletic genera and marginally favors the topology ((*Paurodendron, Oxroadia*) (*Anabathra* (*Chaloneria* (*Sigillaria* ((*Diaphorodendron, Synchysidendron*) (*Hizemodendron* (*Lepidodendron, Lepidophloios*))))))). Other parsimonious topologies allow dissociation of the *Paurodendron–Oxroadia* clade (probably justified), transposition or unification of *Anabathra* and *Chaloneria*, and addition of *Sigillaria* to the *Diaphorodendron–Synchysidendron* clade. The analysis confined to vegetative characters translocates *Hizemodendron* close to the base of the clade, thus uniting the non-trees as an ostensibly paraphyletic basal group. The analysis confined to reproductive characters more closely resembles the analysis of all characters, but fails to resolve relationships among the four basal, bisporangiate-coned genera, and between *Hizemodendron* and *Lepidodendron*. These observations cast doubt on the value of partial-plant and isolated-organ phylogenies.

Parsimonious use of the increasingly sophisticated and *K*-selected reproductive strategies as the basis of the overall phylogeny inevitably renders homoplastic the partly discordant vegetative architectures (including the tree habit). Consequently, a poorly resolved paraphyletic plexus of four primitive, bisporangiate-coned genera (*Paurodendron, Oxroadia, Anabathra, Chaloneria*) subtends a monophyletic monosporangiate-coned clade of three well-supported, monophyletic families: the Sigillariaceae (*Sigillaria*) are primitive relative to the Diaphorodendraceae (*Diaphorodendron* sens. str., *Synchysidendron*) and the Lepidodendraceae (*Hizemodendron, Lepidodendron* sens. str., *Lepidophloios*), which together are characterized by a single functional megaspore per megasporangium. This apparently progressive evolutionary trend toward seedlike reproduction increased ecological specialization and is consistent with adaptive scenarios.

In contrast with reproductive features, vegetative features such as the determinate growth, centralized rhizomorphic rootstock, and small number of module types that constitute the bauplan (rhizomorph and stem essential, lateral and crown branches optional) apparently predisposed the arborescent lycopsids to nonadaptive saltational evolution. Mutation of genes controlling early development allowed radical changes in growth architecture, and consequent

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epigenetic readjustment and adaptive honing affected many other vegetative characters. The progenetic (heterochronic) origin postulated for the pseudoherb *Hizemodendron* may also apply to *Chaloneria* and the other pseudoherbs (*Paurodendron, Oxroadia*), arguably comprising their value in scoring habit characters for the hypothetical ancestor.

Other limitations of the present data matrix are the large number of genus-level autapomorphies (at least partly reflecting the absence of pre-Pennsylvanian arboreous species), the inclusion of only one bisporangiate-coned tree (*Anabathra*) and of only one putative isoetalean (*Chaloneria*). More primitive OTUs are needed to investigate the origins of profound character states shared by all OTUs in the present study (e.g., secondary thickening, determinate growth, centralized rhizomorph, heterospory), and to confirm the crucial hypotheses of monophyly for the monosporangiate cone and the single functional megaspore. Repeated simplification of growth architecture by progenesis and of megaspore ornamentation by functional redundancy show that evolution did not consistently increase morphological complexity among the arborescent lycopsids. Synapomorphies of highest burden (and therefore lowest homoplasy) tend to represent features of intermediate scale.

We have not identified any significant drawbacks of cladistically analyzing an exclusively extinct set of OTUs. Rather, we recommend further study of some under-researched aspects of phylogeny reconstruction in general: (1) the effect of missing values on tree length calculations and on character state optimization; (2) the minimum acceptable level of empirical support (apomorphic states per OTU); (3) means of recognizing heterochrony in cladograms; and (4) less methodologically constrained phenetic adjuncts to strict cladistic analyses.

Coal-swamp floras from the Pennsylvanian of Euramerica have remained the most intensively investigated and best known of all Paleozoic plant communities throughout the last two centuries of detailed scientific study. Their popularity largely reflects the unusual abundance of spores, adpressed megafossils, and anatomically preserved megafossils in these depositional environments and the economic importance of coal (e.g., Scott, 1987). Studies of permineralized coal-ball floras (e.g., Scott & Rex, 1985) have been especially important in providing detailed information on the morphology and anatomy of the plants that comprised the coal-swamp communities (e.g., Taylor, 1981; Stewart, 1983; Bateman, 1991b; DiMichele et al., 1992). Early workers (e.g., Grand'Eury, 1877; Williamson, 1893; Scott, 1908; Seward, 1910) soon recognized that the majority of the coal-ball floras were of low diversity and dominated (both in terms of body size and biomass) by trees that exhibited clear morphological (and, by inference, phylogenetic) similarities to an extant group of ecologically insignificant, exclusively herbaceous, free-sporing plants, the lycopsids or "clubmosses" (see Appendix 1A for discussion of the nomenclature and systematics of higher taxa).

The fossil tree-lycopsids occur in a severely disarticulated condition, and must be painstakingly reconstructed if they are to be understood as biological entities. Some early speculative *restorations* of these plants were remarkably accurate (e.g., Grand'Eury, 1877). Recently, more rigorous *reconstructions* (DiMichele, 1979a, b, 1980, 1981, 1983, 1985; DiMichele & Phillips, 1985) have been achieved using evidence of organic connection supported by quantified association/dissociation values (e.g., Bateman & Rothwell, 1990) and paralleled by increased knowledge of ontogeny (Walton, 1935; Eggert, 1961; Chaloner & Meyer-Berthaud, 1983; Phillips & DiMichele, 1992) and reproductive biology (e.g., Thomas, 1978, 1981; Phillips, 1979).

Earlier higher classifications of the arborescent lycopsids focused on ostensibly well-known genera such as *Sigillaria, Bothrodendron, Lepidophloios,* and '*Lepidodendron*' sens. lat. and remained fairly stable throughout much of this century (see Chaloner, 1967, for the most detailed account). More recently, these conventional supraspecific classifications have been challenged. Thomas & Brack-Hanes (1984) devised a controversial system of satellite taxa that more accurately reflects the variable and fragmentary nature of the paleobotanical data, albeit at the expense of emphasizing reproductive structures rather than whole plants. Using a contrasting philosophy (but generating an equally controversial result), DiMichele (1979a, b, 1980, 1981, 1983, 1985) revised several arborescent lycopsid genera as part of a program of whole-plant reconstruction, implicitly intended to delimit potentially monophyletic taxa within *Lepidodendron* sens. lat. This revision has been extended by Bateman & DiMichele (1991) and DiMichele & Bateman (1992).

We believe that sufficient credible whole-plant reconstructions of arborescent lycopsids are now available (Figs. 1, 2) to allow explicit phylogenetic analysis, using cladistic methods. To date, cladistic analysis has been applied sparingly to long-extinct (i.e., paleobotanical) species, which have invariably been admixed with their extant putative descendants. Most of these studies focused on seed plants (Hill & Crane, 1982; Crane, 1985a, b; Doyle & Donoghue, 1986a, b, 1987a, b; Donoghue & Doyle,

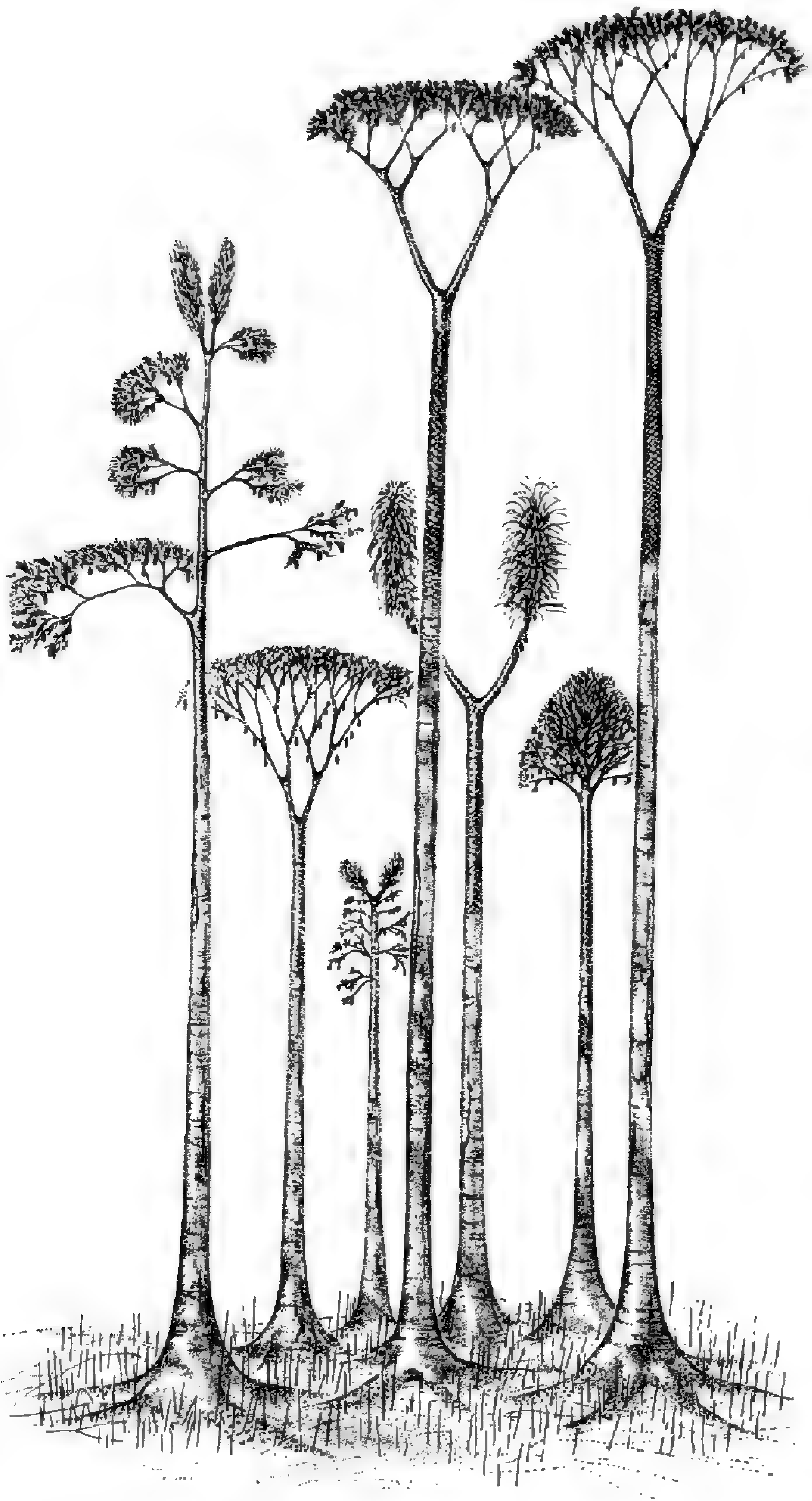

FIGURE 1. Reconstructions of tree lycopsids, listed from left to right: *Diaphorodendron scleroticum* (modified after Wnuk, 1985, fig. 19), *Lepidophloios hallii* (modified after DiMichele & Phillips, 1985, fig. 2), *Anabathra pulcherrima* (redrawn from DiMichele & Phillips, 1985, fig. 2), *Synchysidendron dicentricum* (modified after Wnuk, 1985, fig. 19), *Sigillaria approximata* (modified after Hirmer, 1927, fig. 284, and Stewart, 1983, fig. 11.19). *Diaphorodendron phillipsii, Lepidodendron hickii* (after Wnuk, 1985, fig. 12, and Thomas & Watson, 1976, textual description). All ×0.003.

1989a, b; Donoghue, 1989; see also Hill & Camus, 1986, on marattialean "ferns"). Conceptually, our study owes much to Doyle & Donoghue (1986b) in particular, but differs from all the above studies in focusing on relationships of taxa within a widely accepted order (Class Lycopsida, Order Lepidodendrales) that may lack extant descendants; certainly, all of the genera analyzed are extinct. The lycopsids are of particular phylogenetic interest as a potential sister group of the remainder of the tracheophyte clade (Doyle & Donoghue, 1986b, fig. 1; DiMichele & Skog, 1992).

Our purpose was not merely to unravel the historical relationships of various arborescent lycopsids. We chose to analyze our data within the now well-established framework of evolutionary cladistics (e.g., Wiley, 1981; Farris, 1983; Funk & Brooks, 1990; Wiley et al., 1991) in order to test scenarios concerning patterns and underlying mechanisms of evolution within the group. In particular, we wished to assess preconceived hypotheses concerning the phylogenetic distributions, functional roles, and ecological significance of aspects of growth architecture and reproductive biology.

The structure and content of this paper reflect the philosophical framework outlined by Neff (1986) and elaborated by Bryant (1989). Bryant (1989, fig. 1b) emphasized the creative, deductive nature of a priori character analysis and a posteriori phylogenetic interpretation relative to the purely synthetic, empirical, inductive procedure of tree construction. Our phylogenetic analysis investigates all three of these phases in detail, attempting to exploit the main benefit of cladistics: conceptual and methodological explicitness.

SELECTION AND PARTITIONING OF WHOLE-PLANT SPECIES

In order to qualify for inclusion in this study, plants had to be (1) either members or potential outgroups of the Order Lepidodendrales (lycopsids possessing rhizomorphs, secondary thickening, periderm, ligules, and heterospory: Stewart, 1983), (2) anatomically preserved, and (3) known in sufficient detail that all disarticulated component organs could be reconstructed to form a conceptual whole plant (Chaloner, 1986; Bateman & Rothwell, 1990; Bateman, 1991a); only whole-plant species can be thoroughly characterized. In practice, these three prerequisites confined our study to the Carboniferous of Euramerica (Fig. 3), specifically to two species of *Oxroadia* from Mississippian volcanigenic terrains (Bateman, 1988, 1992) and 15 species of nine genera (Appendix 1C) from Pennsylvanian coal swamps (e.g., Hirmer, 1927; Phillips, 1979; DiMichele & Phillips, 1985). (We have deliberately avoided formal reclassification in this paper, though several recommendations for taxonomic revision are outlined in Appendix 1C. Papers derived from this study segregated *Hizemodendron* from *Lepidodendron* sens. str. (Bateman & DiMichele, 1991) and *Synchysidendron* from *Diaphorodendron*, as well as erecting the new family Diaphorodendraceae (DiMichele & Bateman, 1992). Our use of the generic name *Anabathra* rather than *Paralycopodites* follows Pearson (1986) and is justified in Appendix 1B).

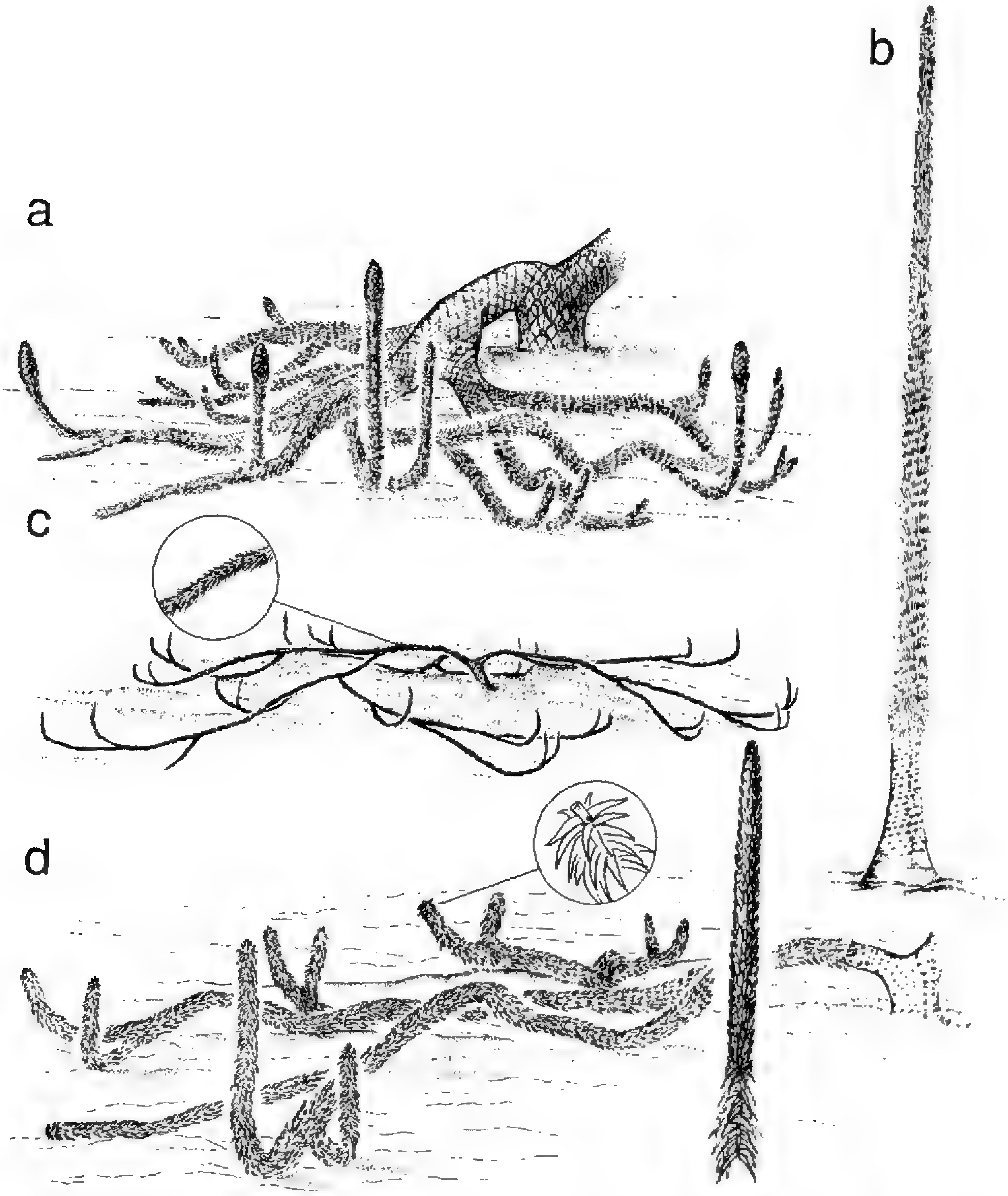

FIGURE 2. Reconstructions of small-bodied lycopsids.—a. *Hizemodendron serratum.*—b. *Chaloneria cormosa* (redrawn from Pigg & Rothwell, 1983a, fig. 1).—c. *Paurodendron fraipontii* (redrawn from Schlanker & Leisman, 1969, fig. 13).—d. *Oxroadia gracilis* (modified after Bateman, 1988, fig. 7.11). Aspects of the *Hizemodendron* reconstruction in particular are speculative, and it is more appropriately described as a restoration (Bateman & DiMichele, 1991). a, b = ×0.03, c, d = ×0.12.

These conceptual whole-plant species of arborescent lycopsid are listed in Table 1, together with the bibliographic sources of much of our data. Each conceptual whole plant encompasses at least nine readily distinguished organs (rootlet, rhizomorph, stem, branch, leaf, megasporophyll, megaspore, microsporophyll, microspore) that are formally named, either individually or in aggregates, as organ-species. Table 2 correlates the more important of the organ-species that have been awarded Linnean binomials. Some organ-species binomials encompass more than one organ; most of the larger-bodied whole-plant species encompass five named organ-species (rootlet/rhizomorph, stem/branch/leaf, strobilus/megasporophyll/microsporophyll, megaspore, microspore) and the smaller-bodied four (rootlet/rhizomorph is not nomenclaturally distinguished from stem/branch/leaf). Other binomials are applied to homologous organs of more than one whole-plant species (i.e., form-species sensu Bateman & Rothwell, 1990: an organ whose morphological expression is indistinguishable in two or more whole-plant species). Confining our study to anatomically preserved material avoided the further complication of correlating the same organs of the same whole-plant species in different preservation states (e.g., Galtier, 1986; Bateman, 1991a).

Evidence for the reconstruction of these organ-species into whole-plant species can be ascribed to three main categories (in order of increasing probability of correct correlation): association/dissociation (co-occurrence in space and time), anatomical similarity, and organic connection (this has traditionally been regarded as proof of successful reconstruction, though Bateman & Rothwell (1990) argued that at best it constitutes only a strong hypothesis). In practice, anatomical similarity is

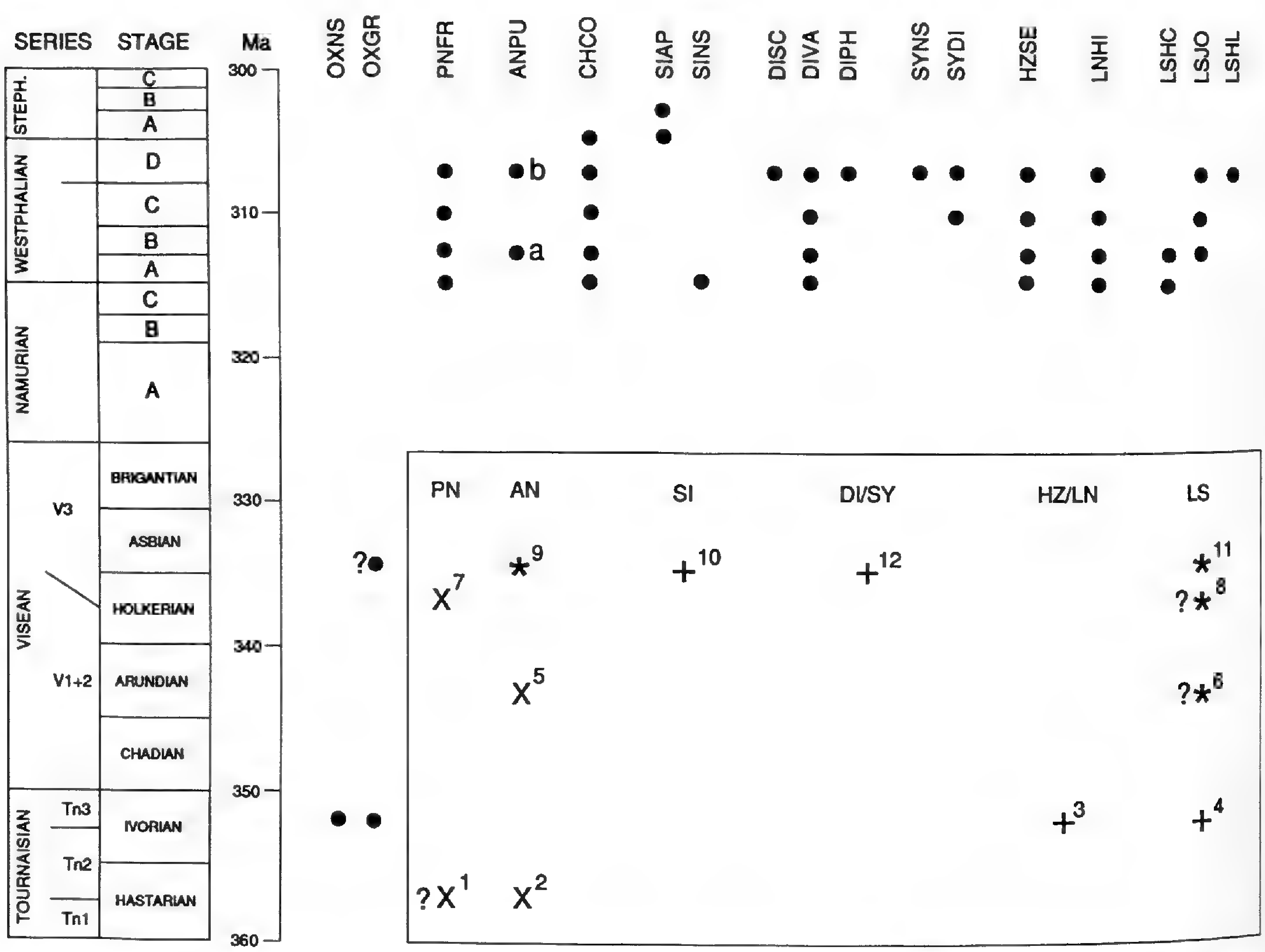

FIGURE 3. Reported time ranges of OTUs (see caption to Table 3 for key to abbreviations). In general, last appearances are more reliable than first appearances. Inset shows first recorded occurrences of the genera (× = vegetative remains only, + = reproductive remains only, * = vegetative and reproductive remains). Superscripts denote bibliographic sources; Montagne Noire, south-central France: Rowe & Galtier, 1989, Bateman, 1992 (1), Meyer-Berthaud, 1984 (2); Burnmouth, northeastern England: Long, 1964 (3), Long, 1968 (4); Glenarbuck, southwestern Scotland: Smith, 1962 (5), Smith, 1962, 1964 (6); Laggan, Arran, southwestern Scotland: Fry, 1954 (7), Walton, 1935, Scott, 1990 (8); Pettycur, southeastern Scotland: Williamson, 1872, 1893, Scott, 1900, 1920, Gordon, 1910, Jongmans, 1930, DiMichele, 1980, Pearson, 1986 (9), Benson, 1908 (10), Scott, 1901, Gordon, 1908 (11); Kingswood, southeastern Scotland: Scott et al., 1986 (12) (see also Scott et al., 1984). Time scale follows Leeder (1988). [a] *Flemingites schopfii* cone. [b] *F. diversus* cone.

usually employed in conjunction with association/dissociation, and both are used as an adjunct to organic connection, especially when attempts to reconstruct whole plants by organic connection are only partially successful. In the case of our tree-lycopsids, organic connection is particularly difficult to demonstrate between reproductive organs and vegetative axes. It is easier to achieve correlations between different organs within these two main categories; for example, by extracting in situ megaspores and microspores from cones (e.g., Thomas, 1987; Willard, 1989a, b). Additional information acquired since our analyses were performed suggests a closer relationship between *Lepidophloios johnsonii* and *L. hallii*. Otherwise, the least conclusive reconstructions in our analysis are *Hizemodendron serratum*, where doubts surround its habit and tentatively correlated microsporangiate cone (cf. Baxter, 1965; Leisman & Rivers, 1974; Bateman & DiMichele, 1991), and *Sigillaria* "sp. nov.," which is strictly a Westphalian A composite from more than one locality.

It should be emphasized that the inevitable disarticulation of their constituent individual organisms into organ-aggregates or single organs renders the reconstructed whole-plant species both conceptual and typological. Each species is conceptual in the sense that it is a summation of several probabilities of correlation of pairs of organs rather than an integral, demonstrable fact. It is typological in the sense that intraspecific variation can only be documented among different specimens of the same organ; complete data sets cannot be compiled for specific individuals, in contrast with morphometric studies of extant plants (e.g., Bateman & Denholm, 1989a, b). This prevents objective de-

TABLE 1. List of OTUs (1–16) with selected synonyms and bibliographic sources. *Oxroadia* sp. nov. (2a) was not used as an OTU as it did not differ from *O. gracilis* (2) in the qualitative characters scored.

Number	Taxon
1	*Paurodendron fraipontii* (Leclercq) Fry (syn. *Botryopteris fraipontii, Selaginella fraipontii*) Fry (1954); Phillips & Leisman (1966); Schlanker & Leisman (1969); Rothwell & Erwin (1985)
2	*Oxroadia gracilis* Alvin Alvin (1965, 1966); Long (1964, 1971, 1986); Bateman (1988, 1992)
2a	*Oxroadia* sp. nov. Bateman (1988, 1992)
3	*Anabathra pulcherrima* Witham (syn. *Paralycopodites brevifolius, Lepidodendron brevifolium* pro parte) Felix (1954); Brack (1970); Morey & Morey (1977); DiMichele (1980)
4	*Chaloneria cormosa* (Newberry) Pigg & Rothwell (syn. *Polysporia mirabilis*) DiMichele et al. (1979); Pigg & Rothwell (1979, 1983a, b, 1985)
5	*Sigillaria approximata* Fontaine & White Schopf (1941); Delevoryas (1957); Eggert (1972)
6	*Sigillaria* sp. nov. Brongniart (1836); Benson (1918); Lemoigne (1961)
7	*Synchysidendron* sp. nov. DiMichele (1979b, 1981); DiMichele & Bateman (1992)
8	*Synchysidendron dicentricum* (Felix) DiMichele & Bateman (syn. *Lepidodendron dicentricum, Diaphorodendron dicentricum*) Arnold (1960); DiMichele (1979b, 1981, 1985); DiMichele & Bateman (1992)
9	*Diaphorodendron phillipsii* DiMichele (syn. *Lepidodendron phillipsii*) DiMichele (1981, 1985)
10	*Diaphorodendron vasculare* (Binney) DiMichele (syn. *Lepidodendron vasculare*) Carruthers (1869); Hovelacque (1892); Seward (1910); DiMichele (1981, 1985)
11	*Diaphorodendron scleroticum* (Pannell) DiMichele (syn. *Lepidodendron scleroticum*) Pannell (1942); DiMichele (1981, 1985)
12	*Hizemodendron serratum* (Felix) Bateman & DiMichele (syn. *Lepidodendron serratum*) Felix (1952); Baxter (1965); Leisman & Rivers (1974); DiMichele (1981, 1983); Bateman & DiMichele (1991)
13	*Lepidodendron hickii* Watson (syn. *L. aculeatum* pro parte, *L. obovatum* pro parte) Scott (1906); Seward (1906); Watson (1907); DiMichele (1983); Willard (1989a)
14	*Lepidophloios harcourtii* (Witham) DiMichele (syn. *Lepidodendron harcourtii*) Bertrand (1891); Seward (1899); Zalessky (1912); Koopmans (1928); Calder (1934)
15	*Lepidophloios johnsonii* (Arnold) DiMichele Arnold (1940); DiMichele (1979a); Winston (1988)
16	*Lepidophloios hallii* (Evers) DiMichele Evers (1951); Felix (1952); Andrews & Murdy (1958); Brotzman & Schabiliov (1972); DiMichele (1979a)

limitation of individual organisms into species using morphological discontinuities and hinders attempts to distinguish genetic (and thereby taxonomically and phylogenetically useful) contributions to phenotype from those caused by ontogeny and ecophenotypy (e.g., Bateman & Denholm, 1989c). Ironically, this inability to resolve variation at the whole-organism level can be considered advantageous in a cladistic analysis. In most cases, less information is discarded when a paleobotanical spe-

TABLE 2. Correlations of organ-species that constitute the whole-plant OTUs listed in Table 1. Asterisked whole-plant species lack recognized autapomorphies (see caption to Table 3 for explanation of abbreviations).

OTU	Rhizomorph	Vegetative axes	Cones
PNFR	←	*Paurodendron fraipontii*	→ *Selaginellites crassicinctus* (⚥)
OXGR*	←	*Oxroadia gracilis*	→
OXNS*	←	*Oxroadia* sp. nov.	→
ANPU	*Stigmaria ficoides*	*Anabathra pulcherrima*	*Flemingites diversus/schopfii* (⚥)
CHCO	←	*Chaloneria cormosa*	→
SIAP	*Stigmaria* sp. nov.	*Sigillaria approximata*	*Mazocarpon oedipternum* (♀+♂)
SINS*	*Stigmaria* sp. nov.	*Sigillaria* sp. nov.	*Mazocarpon schorense/cashii* (♀+♂)
SYNS	*Stigmaria ficoides*	*Synchysidendron* sp. nov.	*Achlamydocarpon varius* (♀+♂)
SYDI	*Stigmaria ficoides*	*Synchysidendron dicentricum*	*Achlamydocarpon varius* (♀+♂)
DIPH	*Stigmaria ficoides*	*Diaphorodendron phillipsii*	*Achlamydocarpon varius* (♀+♂)
DIVA*	*Stigmaria ficoides*	*Diaphorodendron vasculare*	*Achlamydocarpon varius* (♀+♂)
DISC	*Stigmaria ficoides*	*Diaphorodendron scleroticum*	*Achlamydocarpon varius* (♀+♂)
HZSE*	←	*Hizemodendron serratum*	*Achlamydocarpon* sp. nov. (♀) *Lepidostrobus minor* (♂)
LNHI	*Stigmaria ficoides*	*Lepidodendron hickii*	*Achlamydocarpon takhtajanii* (♀) *Lepidostrobus* cf. *oldhamius* (♂)
LSHC*	*Stigmaria ficoides*	*Lepidophloios harcourtii*	*Lepidocarpon lomaxi* (♀) *Lepidostrobus oldhamius* (♂)
LSJO*	*Stigmaria ficoides*	*Lepidophloios johnsonii*	*Lepidocarpon lomaxi* (♀) *Lepidostrobus oldhamius* (♂)
LSHL	*Stigmaria ficoides*	*Lepidophloios hallii*	*Lepidocarpon lomaxi* (♀) *Lepidostrobus oldhamius* (♂)

cies is reduced to a single unvarying (and thus, by definition, typological) data set (the normal procedure prior to cladistic analysis) than in comparable studies of extant species. Also, the paleobotanist is effectively constrained to conceptual morphospecies and is therefore spared the trauma experienced by neobotanists when selecting an appropriate species concept (cf. de Queiroz & Donoghue, 1988, 1990; Nelson, 1989; Wheeler & Nixon, 1990; Nixon & Wheeler, 1990). Although we wished primarily to investigate generic relationships, our use of species (of whatever kind) as basic operational taxonomic units (OTUs) created fewer difficulties when typologically eliminating intra-OTU variation than the more common approach of selecting sets of OTUs from higher (and often variable) levels in the taxonomic hierarchy (cf. Doyle & Donoghue, 1986b).

SELECTION, PARTITIONING, AND POLARIZATION OF CHARACTERS

The provisional selection of whole-plant species preceded the partitioning of the conceptual organisms into characters and, subsequently, of the characters into putatively homologous character states. Our chosen characters are listed below; they are identified by numbers prefixed by the letter C.

Partitioning a representative, conceptual organism of a species into morphological characters is based on the assumption that each character represents a discrete, recognizable, and homologous feature. This is the most subjective and ultimately most influential phase of any cladistic analysis; it is especially unfortunate that the only sources of evidence to support assertions of homology are circumstantial; consequently, such assertions cannot be conclusively verified (e.g., De Beer, 1971; Riedl, 1979; Patterson, 1982; Kaplan, 1984; Roth, 1984, 1988, 1991; Tomlinson et al., 1984; Neff, 1986; Ridley, 1986; Bryant, 1989; G. P. Wagner, 1989). Features that do not vary among the chosen OTUs provide no information on their phylogenetic relationships, though such characters are valuable in characterizing the entire ingroup (they may, of course, have a greater level of universality than the ingroup alone). Continuously variable characters can be artificially partitioned into binary or multiple character states (e.g., by gap coding (Archie, 1985) or segment coding (Chappill, 1989)), but we believe that such "soft" characters are more appropriately analyzed by phenetic methods (cf. Bateman, 1990a; Farris, 1990). We therefore excluded continuous (metric) and quasicontinuous (meristic) characters from our data matrix, even though they were the only potential source of unique

TABLE 2. Continued.

Megaspore	Microspore
Triangulatisporites triangulatus	*Cirritriradiates annulatus*
Setispora subpalaeocristata	*Auroraspora* cf. *asperella* 'A'
Setispora pannosa	*Auroraspora* cf. *asperella* 'B'
Lagenicula rugosa	*Lycospora orbicula*
Valvisisporites auritus	*Endosporites ornatus*
Tuberculatisporites reinschii	*Crassispora kosankei*
Tuberculatisporites mamillarius	*Crassispora* sp. nov.
Cystosporites varius	*Granasporites medius*
Cystosporites varius	*Granasporites medius*
Cystosporites varius	*Granasporites medius*
Cystosporites varius	*Granasporites medius*
Cystosporites varius	*Granasporites medius*
Cystosporites giganteus	*Lycospora* cf. *pusilla*
Cystosporites giganteus	*Lycospora pusilla*
Cystosporites giganteus	*Lycospora pellucida*
Cystosporites giganteus	*Lycospora* sp. nov.
Cystosporites giganteus	*Lycospora granulata*

(and thereby distinguishing) characters for eight of the 17 species initially selected for study (Table 2).

We opted for a uniformly bistate data matrix, on the grounds that bistate characters are more readily analyzed algorithmically and the distributions of character states on the resulting trees are more easily interpreted. This decision had three potentially deleterious consequences:

First, the hierarchy of organs that constitute the plants introduced a degree of character duplication; we often found it necessary to include a character scoring an organ present or absent (e.g., the rhizomorph: C8) before partitioning additional characters (C9–C13) to describe its detailed morphology in those OTUs that possess that structure. This is to be expected, given the strongly hierarchical nature of morphological and anatomical homologies (Riedl, 1979; Fortey & Jefferies, 1982; Wimsatt & Schank, 1988; Roth, 1991). We adopted a similarly relaxed attitude to the inclusion of potentially coupled characters "correlated for developmental-genetic reasons" (Doyle & Donoghue, 1986b: 338); indeed, we hoped that our analysis would reveal such character correlations, which are by no means intuitively obvious a priori.

Second, even more complicated hierarchies of related characters, such as stelar (C14–C19) and periderm (C39–C43) anatomy, occur in complexes. In such cases, a broad concept of character can be selected, allowing coding in multistate rather than bistate format. Such multistate characters tend to be especially difficult to polarize satisfactorily and may have to be input unordered. If they are to be ordered, several methods are available for coding and polarizing such characters (e.g., O'Grady & Deets, 1987). The preferred options are additive binary coding (Brooks, 1984) or nonredundant linear coding (O'Grady & Deets, 1987; O'Grady et al., 1989). Both operate via a hypothetical tree representing transitions between the polarized multiple states of the character in question. By reducing the character states to a set of bistate subsets, additive binary coding labels every node of the character tree and thus generates a large number of narrowly defined operational characters. Nonredundant linear coding avoids this proliferation of characters, but at the expense of retaining characters in a multistate format and arbitrarily designating within the tree a major axis that forms the basis for coding the remaining branches (minor axes). Once mixed with other (typically mostly bistate) characters, multistate characters complicate the generation and subsequent interpretation of cladograms (e.g., Gensel, 1992). We therefore preferred the more primitive but also more intuitive additive binary system, despite the risk of eliminating a priori some ambiguities in the data.

Third, polarization of spore ornamentation characters was rendered especially problematic. They tend to be evolutionarily displacive rather than additive; there appears to be a developmental constraint on the range of features exhibited by the exine of any one species, so that a new type of ornamentation supplants rather than supplements the previous type. We spurned the option of scoring these characters as unordered multistate in order to maintain a uniformly polarized binary matrix. Thus, we treated each type of spore ornamentation as a separate character and assumed a hypothetical plesiomorphic spore lacking all features.

Polarization also presented a more general problem. All three OTUs (*Oxroadia gracilis–Oxroadia* sp. nov., *Paurodendron fraipontii, Chaloneria cormosa*) originally screened as potential outgroups (Maddison et al., 1984) exhibited some character states that we were reluctant to regard as plesiomorphic. In *Oxroadia* and *Paurodendron,* we initially believed that such characters were few and almost confined to spore ornamentation. However, *Chaloneria* proved too derived to root the tree successfully. Consequently, we constructed a hypothetical ancestor possessing putatively plesiomorphic states for all characters; it largely reflected character states shared by *Oxroadia* and *Paurodendron,* though for a few problematic characters we elected to screen more distantly related lycopsids for presumed plesiomorphic states.

As in all cladistic analyses, our recognition of alternative character states as *plesiomorphic* and *apomorphic* preceded tree-building. We restrict these terms to character states and use *primitive* and *derived* to describe the relative positions of OTUs on the resulting trees.

Many of the characters considered for inclusion were rejected on the grounds that they were known for less than two-thirds of the OTUs. The most important examples are the detailed histology of the rhizomorph and rootlets (which are well known for the form-species *Stigmaria ficoides* but not for the different types of this rhizomorph correlated with specific whole-plant species), of the leaves (well-documented only for *Oxroadia*: Bateman, 1988), and of the gametophyte (described for few cone-species; e.g., Galtier, 1964, 1970; Brack, 1970; Phillips, 1979; Stubblefield & Rothwell, 1981; Pigg & Rothwell, 1983b), and ultrastructure of spore walls (e.g., T. Taylor, 1973; W. Taylor, 1990).

One hundred fifteen bistate characters were eventually accepted: 69 are vegetative (C1–C4, C8–C72) and 46 are reproductive (C5–C7, C73–C115). The large number of characters reflects the stringent selection criterion of detailed knowledge that was applied to potential OTUs; inclusion of poorly known OTUs would have increased the proportion of missing values in some characters sufficiently to warrant exclusion of those characters from the data matrix.

THE CHARACTERS

Characters are apportioned into 11 categories: the overall habit of the organism (A) and ten constituent organs (B–K). For each category, lists of characters and character states are preceded by discussions of relevant homologies and descriptive terms.

A. Habit (7 characters)

We perceived habit as an overall property of an organism, expressed as a specific bauplan. We describe the group of habits colloquially known as trees (C1) as "arboreous," and use "arborescent" strictly to describe the ability to generate secondary tissues (C29). Thus, all 16 OTUs are considered arborescent, but only 12 are truly arboreous. We reject the frequently used term "secondary wood," because wood is by definition secondary. Only mature woody plants greater than 2 m in overall height are termed trees; *Chaloneria* does not qualify as a tree on this criterion, despite possessing wood (albeit poorly developed) and an elongate, unbranched, upright stem (Pigg & Rothwell, 1983a, b). Recumbent OTUs generating limited amounts of wood are termed pseudoherbs (Bateman, 1988, 1992; DiMichele & Bateman, 1989; Bateman & DiMichele, 1991).

In lepidodendraleans, the main aspects of habit are stem length (C2), frequency of lateral and terminal branching (C3–C4, C6), and the position on the bauplan of reproductive structures (C5–C7). Various combinations of these character states generate several distinct architectures (Figs. 1, 2). Four of these characters (C3–C4, C6–C7) reflect the mode and timing of branching during ontogeny. Lepidodendralean stems branched isotomously (or near-isotomously) only during the final stages of growth (Walton, 1935; Andrews & Murdy, 1958; Eggert, 1961; Wnuk, 1985); terminal branching is profuse in most OTUs, but infrequent in *Anabathra, Sigillaria,* and *Diaphorodendron,* and absent in *Chaloneria* (C3). Strongly anisotomous apical divisions during stem growth result in lateral branches that were deciduous (C4) in all OTUs except *Diaphorodendron scleroticum,* where thick bark and wood suggest retention (DiMichele, 1981). The anisotomies terminate in cones (C6), either individually on short peduncles (*Sigillaria*) or collectively on large, repeatedly dichotomous peduncle systems (C7; *Anabathra* and *Diaphorodendron*). In all other OTUs, anisotomous cone-bearing branches were borne only on the terminal, isotomously branched, determinate crown. We regard cauline peduncles and cone-bearing lateral branches as homologous (DiMichele & Bateman, 1989). *Chaloneria* lacked cones (C5), instead bearing sporophylls directly on fertile zones of the unbranched stem (Pigg & Rothwell, 1983a, b). Consequently, it is scored as missing for C6 and C7.

Polarity decisions for several of the habit characters were taken with considerable reservations (especially C1, C2 and C7). Also, in retrospect, the addition of a character representing equality of "crown" branching among the pseudoherbs would have distinguished *Oxroadia* (dominantly isotomous) from *Paurodendron* and *Hizemodendron* (both dominantly anisotomous).

1. Nonarboreous (0); arboreous (1).
2. Stem short (relative to any branches), plant recumbent (0); stem tall, plant upright (1).
3. Dichotomy of trunk apex frequent (0); infrequent or absent (1).
4. Persistent lateral branches absent (0); present (1).
5. Cone present (0); cone absent (1).
6. Lateral branches and/or cone peduncles borne on dichotomous crown (0); excurrent trunk (1).
7. Number of cones on lateral branches one (0); more than one (1).

B. *Rootstock* (6 characters)

Until recently, the stigmarian rhizomorph (C8) was regarded as arguably the most reliable ubiquitous character state defining the Lepidodendrales (e.g., Phillips & DiMichele, 1992). Rothwell (1984) and Rothwell & Erwin (1985) suggested that the stigmarian rhizomorph is a shoot system modified for rooting; we recognize that it is a shootlike developmental system, but prefer to regard it as a unique organ reflecting limited developmental options within the arborescent lycopsid bauplan. The rhizomorph is radially symmetrical (C9), undergoes repeated isotomous apical dichotomy (C10), is woody (C11), and emits in helical rhizotaxy rigid absorbent rootlets (C12), each containing a single monarch vascular strand. Rothwell & Pryor (1990, 1991) concluded that the tracheary elements of such rhizomorphs are derived largely from the equivalent of a primary thickening meristem. Such branched rhizomorphs were considered radically different from other unbranched rootstocks, whether radial, as in *Paurodendron* (Rothwell & Erwin, 1985), or bilateral, as in *Protostigmaria-Lepidodendropsis* (Jennings, 1975; Jennings et al., 1983), *Chaloneria* (Pigg & Rothwell, 1983a; Pigg & Taylor, 1985), and *Isoetes* (Karrfalt & Eggert, 1977 et seq.; Karrfalt, 1984). However, other studies of rhizomorphs have rendered less profound the distinctions between radial and bilateral symmetry (Karrfalt, 1981, 1984; G. W. Rothwell, pers. comm. 1989) and branched and unbranched vasculature (Bateman, 1988). In our analysis, bilateral symmetry (C9) is retained as a character state; it is scored as an autapomorphy of *Chaloneria* and thus does not affect tree topologies. Scoring the rhizomorph of *Oxroadia* as branched is an oversimplification; it is extremely compact, so that the cortex branches shallowly and less frequently than the vascular system (Long, 1986; Bateman, 1988).

Stigmarian axes exhibit a suite of anatomical character states that, with sufficient study, can be shown to parallel those of correlated stem genera. Given the current paucity of such studies, we used only one such character: the ovoid rootlet gaps (C13) found in *Chaloneria* (Pigg & Rothwell, 1983a) and *Sigillaria approximata* (Eggert, 1972).

8. Rhizomorph absent (0); present (1).
9. Rhizomorph symmetry radial (0); bilateral (1).
10. Rhizomorph branched (0); unbranched (1).
11. Secondary xylem in rhizomorph absent (0); present (1).
12. Rootlets absent (0); present (1).
13. Rootlet gap in wood fusiform (0); ovoid (1).

C. *Stele* (18 characters)

The morphology and histology of lepidodendralean vascular systems, described in detail by previous authors, are valuable for distinguishing both genera and species (Fig. 4a). Unfortunately, much less attention has been paid to determining homologies and polarizing these complex characters. We recognize six distinct forms of stelar medullation (C14–C19). All genera but *Diaphorodendron* and *Synchysidendron* are regarded as primitively protostelic (C14). The protosteles of *Anabathra, Chaloneria, Sigillaria, Hizemodendron, Lepidodendron,* and *Lepidophloios* are medullated (C15). The core of the stele consists of unlignified cells whose dimensions are typical of tracheids, suggesting that they are procambial de-

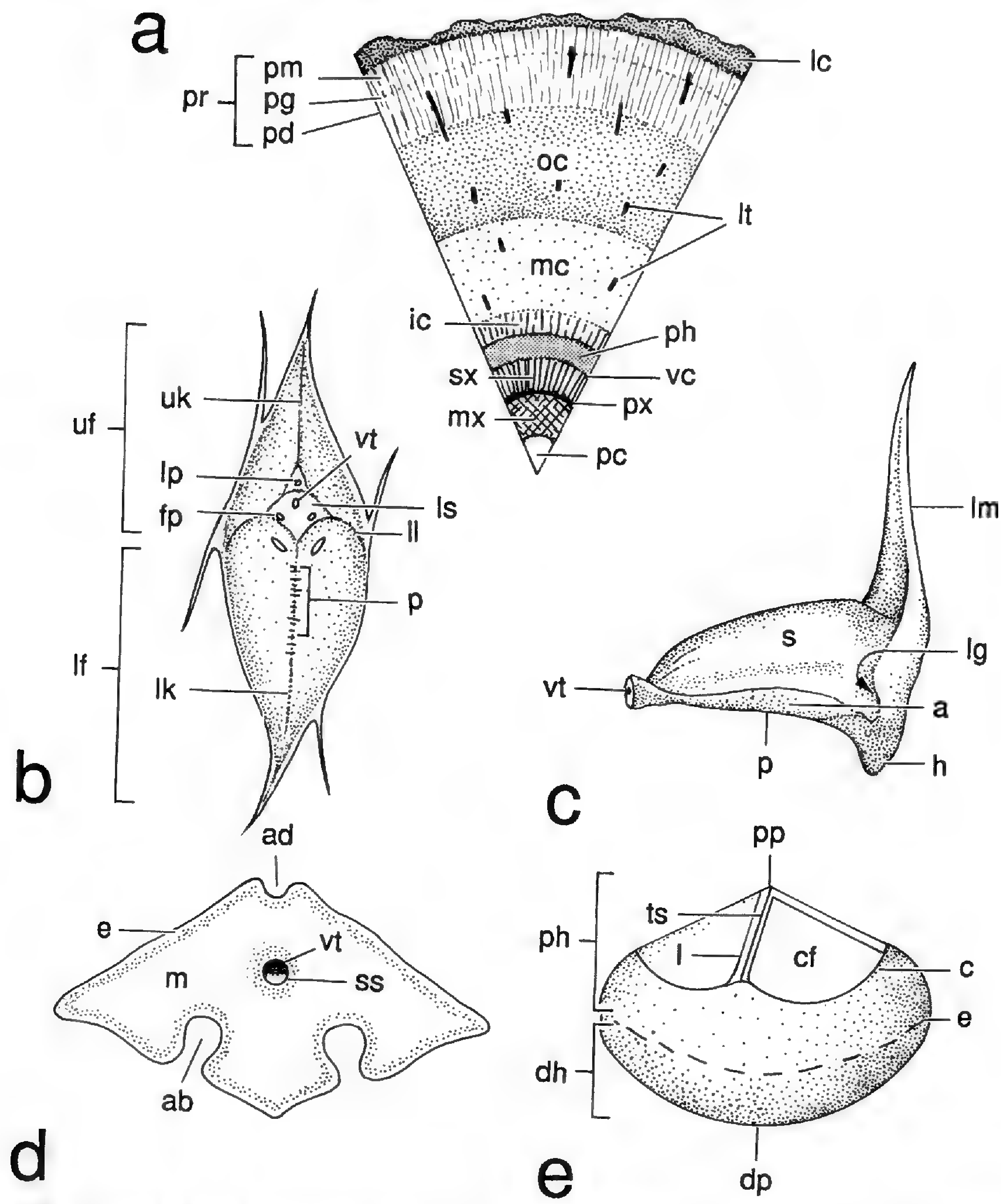

FIGURE 4. Morphological and anatomical terminology for arborescent lycopsids.—a. Axial anatomy (redrawn from fig. 9.44 of Gifford & Foster, 1989: pc = parenchymatous core, px = protoxylem, mx = metaxylem, sx = secondary xylem, vc = vascular cambium, ph = phloem (primary), ic = inner cortex, mc = middle cortex, oc = outer cortex, pr = periderm, pd = phelloderm, pg = phellogen, pm = phellem, lt = leaf traces, lc = leaf cushions).—b. External morphology of leaf base following leaf loss (modified after fig. 11.3B of Stewart, 1983: ls = leaf scar, vt = vascular trace, fp = foliar parichnos, lp = ligule pit, uf = upper field, uk = upper keel, lf = lower field, lk = lower keel, p = plications).—c. External morphology of sporophyll (modified after fig. 11.16C of Stewart, 1983, and fig. 2A of Phillips, 1979: p = pedicel, a = alations, h = heel, lm = lamina, lg = ligule, s = sporangium, vt = vascular trace).—d. Leaf anatomy in proximal transverse section (modified after fig. 11.9E of Stewart, 1983, and fig. 1A of Reed, 1941: vt = vascular trace, ss = sclerenchymatous sheath, m = mesophyll, e = epidermis, ab = lateral abaxial grooves, ad = median adaxial groove).—e. External morphology of spore (pp = proximal pole, dp = distal pole, ph = proximal hemisphere, dh = distal hemisphere, e = equator, ts = triradiate (trilete) suture, l = laesura, c = curvatura, cf = contact face).

rivatives that remained parenchymatous (Walton, 1935; DiMichele, 1979a, b). In *Lepidodendron* and two of the three *Lepidophloios* species, randomly oriented filamentous cells apparently infilled a central cavity (C16; DiMichele, 1979a). In *Diaphorodendron* and *Synchysidendron*, central parenchyma cells are distinctly smaller than those of associated tracheids, suggesting that these genera had a true pith sensu Beck et al. (1982). The two *Synchysidendron* species share the synapomorphy of a solidly parenchymatous pith (C17), and each possesses a histological autapomorphy: secretory cells in *Synchysidendron* sp. nov., and secondarily thickened cells in *S. dicentricum*.

Deep parenchymatous invaginations in *S. dicentricum* and *Synchysidendron* sp. nov. (C20) are not considered homologous with the shallower invaginations of *Chaloneria* (C21); in the *Synchysidendron* species, the parenchymatous wedges are raylike, many cells wide and high, and are often confluent with the pith parenchyma (DiMichele, 1980, 1981). In contrast, the invaginations of *Chaloneria* are smaller and do not reach the central parenchymatous area of the stele (DiMichele et al., 1979; Pigg & Rothwell, 1983a).

Protoxylem configuration and leaf trace emission comprise an integrally linked complex of characters (C22–C28; Fig. 4). Protoxylem is exarch in all OTUs and, with the exception of *Oxroadia* and *Paurodendron*, forms a continuous sheath enclosing the metaxylem (C22). Concentrations of protoxylem observed in transverse sections of axes of many genera are often described individually as "poles" or "points" and collectively as a "corona." This two-dimensional terminology is misleading; protoxylem actually occurs as more-or-less longitudinal strands that are raised to form ridges in "coronate" genera (Bateman, 1988). These protoxylem strands are longitudinal and linear in *Oxroadia, Paurodendron,* and *Lepidodendron,* but reputedly anastomose in *Lepidophloios* (C28; Bertrand, 1891).

We have coined new terms for four distinct modes of leaf trace emission (C23–C25; Fig. 5). Leaf traces departing from a longitudinal protoxylem ridge are termed *evaginate.* Those of *Oxroadia* and *Paurodendron* are emitted from a single uninterrupted ridge and are termed *evaginate-direct* (Fig. 5a). Those of *Lepidophloios* originate within a protoxylem ridge at the point where it bifurcates and are termed *evaginate-internal* (C25; Fig. 5d). Most of the genera lack discernable protoxylem ridges and are said to emit *superficial* leaf traces (C23; Fig. 5b). In *Chaloneria,* the trace originates from a submarginal position in the stele and is associated with shallow parenchymatous invaginations (C24, Fig. 5c; DiMichele et al., 1979; Pigg & Rothwell, 1983a). We used X-coding (Doyle & Donoghue, 1986b) to permit evolution of evaginate-internal and invaginate states directly from

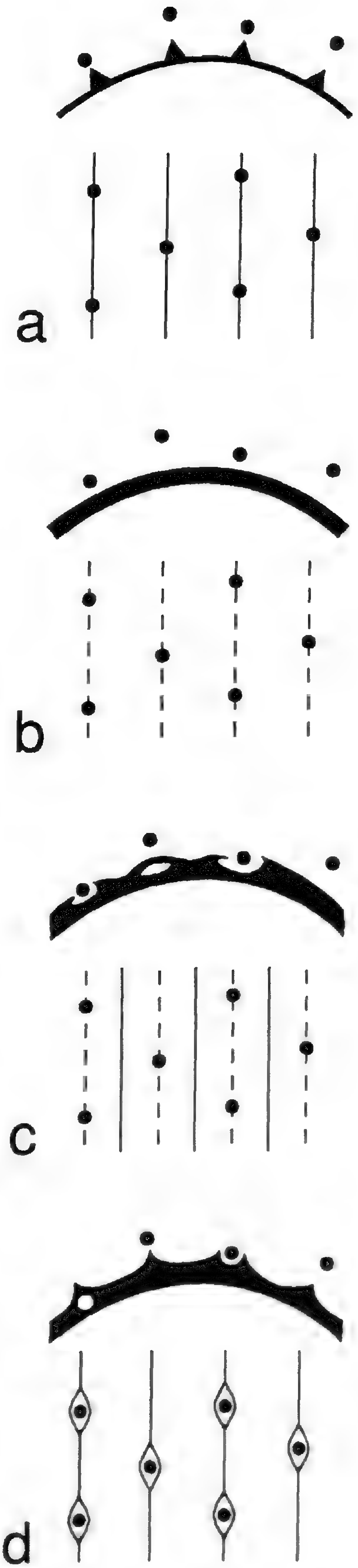

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FIGURE 5. Protoxylem morphology and modes of leaf trace emission. Transverse section above, longitudinal projection of surface of xylem bundle below. Protoxylem in black, spots = leaf traces, solid lines = ridges, dashed lines = leaf trace orthostiches where these do not coincide with ridges.—a. Evaginate direct: *Paurodendron* and *Oxroadia.*—b. Superficial: *Anabathra, Hizemodendron,* and *Lepidodendron.*—c. Invaginate: *Chaloneria.*—d. Evaginate internal: *Lepidophloios.*

the plesiomorphic evaginate-direct state (thus bypassing the superficial state), but to inhibit improbable evolutionary routes that treat the evaginate-internal and invaginate states as intermediate.

The stele morphology and leaf trace emission of *Sigillaria* are especially difficult to interpret. The undulatory outer margin of the continuous primary xylem sheath represents tangential variation in the amount of primary xylem produced; protoxylem thickness is greatest on the flanks of the undulations. In contrast with other genera possessing discernable protoxylem ridges, sigillarian leaf traces appear to originate from the intervening troughs, leading to suggestions that each trace may be derived from both of the adjacent protoxylem ridges (e.g., Lemoigne, 1961). However, we were unable to confirm their putative bipolar origin and therefore scored *Sigillaria* leaf traces as superficial. The alternative option of recognizing *Sigillaria* traces as bipolar would generate an additional genus-level autapomorphy.

Secondary xylem occurs in the stem and at least the more proximal crown branches (if present) of all OTUs (C29), but extends into the lateral branches (C30) only in *Diaphorodendron vasculare* and *D. scleroticum*. Most OTUs possess homogeneous rays composed of small-diameter cells, though heterocellular rays characterize *Synchysidendron*. Consistent nonpreservation prevented characterization of the phloem.

14–19. Solid protostele (000000); medullated protostele (010000); medullated protostele with filamentous core (011000); siphonostele with mixed pith (100000); siphonostele with solidly parenchymous pith including secretory cells (100110); siphonostele with solidly parenchymous pith including cells with secondary wall thickenings (100101).
20. Deep parenchymatous invaginations or radial partings absent (0); present (1).
21. Shallow parenchymatous invaginations absent (0); present (1).
22. Exarch protoxylem sheath discontinuous (0); continuous (1).
23–25. Leaf trace origin evaginate, direct (000); superficial (100); invaginate (X10); evaginate, internal (X01).
26. Longitudinal ridges of protoxylem strands discernable (0); indiscernable (1).
27. Leaf trace originates from one protoxylem strand (0); two protoxylem strands (1).
28. Anastomoses of protoxylem strands absent (0); present (1).
29. Secondary xylem in trunk absent (0); present (1).
30. Secondary xylem in lateral branches and/or peduncles absent (0); present (1).
31. Rays homogeneous (0); heterogeneous (1).

D. Cortex (5 characters)

All OTUs possess a three-zoned cortex (C32; Fig. 4a). It consists of a narrow inner cylinder of compact, barrel-shaped parenchyma cells, a thick middle cylinder of even thinner-walled, more-or-less isodiametric parenchyma cells that often decay to leave a cavity, and a broader outer zone of thicker walled cells that are longitudinally elongate (especially in the central portion of the cylinder of tissue) and often grade into sclerenchyma (particularly in the smallest diameter cells, close to the epidermis). This peripheral sclerenchyma is especially well developed in *Diaphorodendron scleroticum*. Leaf traces passing through the middle cortex are ensheathed with cells characteristic of, and in continuity with, the inner cortex; they are secretory in several OTUs (C33) and adaxially concentrated in *Synchysidendron* sp. nov. (C34). In *Sigillaria* sp. nov., *Synchysidendron*, and *Diaphorodendron*, each leaf trace is surrounded by a broad cylinder of thinner-walled cells when passing through the outer cortex (C35), increasing apparent cellular heterogeneity. No attempt was made to divide variations in the angle of passage of the leaf traces through the cortex into discrete character states. Vertically elongate cavities at the cortex-periderm transition (C36) characterize *D. phillipsii*.

32. Outer cortex two-zoned (0); three-zoned (1).
33. Intracortical leaf-trace sheaths not secretory (0); secretory (1).
34. Intracortical leaf-trace sheaths circumferential (0); adaxial (1).
35. Thin-walled parenchyma surrounding leaf trace in thick-walled outer cortex absent (0); present (1).
36. Cavities at outer cortex-periderm transition absent (0); present (1).

E. Periderm (14 characters)

Periderm occurs in all of the OTUs (C37), though its distribution (and thereby its protective and supportive function) is extremely restricted in the bauplans of *Oxroadia* and *Paurodendron*. Common references to periderm as "secondary cortex" are an anatomical non sequitur; cortex is a region of an axis (between the stele and the epidermis) rather than a specific tissue type. The periderm of most genera cannot be differentiated histologically into phellem and phelloderm. The exceptions are *Diaphorodendron* and *Synchysidendron*, where clear bizonation is strong evidence for a bifacial cambial layer that produced much greater quantities of centripetal phelloderm than centrifugal phellem (C38; DiMichele, 1981). Additional, indirect evidence indicates bifaciality in *Anabathra* (DiMichele, 1980) and *Lepidophloios* (DiMichele, 1979a). Given the determinate growth and early onset of peridermal cambial function that are evident in lepidodendraleans, the cambial layer may have fully differentiated or been active only near the apices of stems and rhizomorph axes. Either phenomenon would inhibit preservation of the cambial layer per se. It is also possible that the centripetal and centrifugal products of cell division are sufficiently similar to prevent recognition of a potentially fully differentiated cambium.

Periderm is the most abundant tissue type produced by arboreous lycopsids and often occurs as abundant disarticulated fragments in coal-ball assemblages (Phillips & DiMichele, 1981; DiMichele et al., 1986). Fortunately, the detailed anatomy and histology of the periderm (C39–C43) allow identification of five groups of OTUs. Primitive genera (*Oxroadia, Paurodendron, Anabathra, Chaloneria*) have a uniform periderm, which is modified to include bands of resinous cells in *Sigillaria* (C40). *Diaphorodendron* and *Synchysidendron* possess bifacial periderm (C41); *Synchysidendron* is distinguished from *Diaphorodendron* by its uniform (C43) rather than banded (C42) phelloderm. *Lepidodendron* and *Lepidophloios* have two- or three-zoned periderm (C39) and are X-coded for resinous cell clusters to suppress improbable evolutionary routes that attain histological modifications via the acquisition of zonation.

Glandular periderm histology (C47) is shared by *Lepidodendron* and two of the three *Lepidophloios* species, and resinous sacs (C48) occur in *Sigillaria, Lepidodendron,* and *Lepidophloios*. The passage of leaf traces and infrafoliar parichnos strands through the periderm also distinguish OTUs. Prominent leaf traces, more-or-less perpendicular to the length of the axis and surrounded by thin-walled parenchyma (C49), are an autapomorphy of *Anabathra*. Similarly, well-developed infrafoliar parichnos strands (C50) characterize *Sigillaria* periderm.

Many lepidodendraleans retained leaf cushions on the stem surface as periderm production expanded axial girth. We recognize three retention mechanisms (C44–C46). The first two are, by definition, mutually exclusive; interareas exhibit either a plastic response and expand (C44; *Sigillaria* and *Synchysidendron*) or a brittle response and fissure (C45; *Diaphorodendron*) (DiMichele, 1981). In contrast, *Lepidodendron hickii* accommodates growth by expansion of cells beneath the cushion (C46; DiMichele, 1983). This character state could have replaced interarea expansions or fissuring, or it could have arisen directly from the plesiomorphic state; it is X-coded to allow any of these options. Evidence for the interarea expansion of *Lepidodendron* is confined to compression fossils (Thomas, 1966).

37. Periderm in stems absent (0); present (1).
38. Phellem and phelloderm not histologically differentiable (0); histologically differentiable (1).
39–43. Cellular composition of periderm uniform (00000); cells form two or three distinct zones (1X000); bands of resinous cell clusters (01000); periderm bifacial, alternating bands of thick- and thin-walled cells in phelloderm (00110); periderm bifacial, phelloderm ± uniform (00101).
44–46. Leaf cushion retention mechanism absent (000); tangential interarea expansion (100); interarea fissuring (010); subcushion cellular expansion (XX1).
47. Periderm nonglandular (0); glandular (1).
48. Periderm nonresinous (0); at least partially resinous (1).
49. Leaf traces in periderm obscure (0); prominent (1).
50. Infrafoliar parichnos strands in periderm absent (0); present (1).

F. Leaf bases (15 characters)

Lepidodendralean leaf base characters are well reviewed by DiMichele (1979a, b, 1981, 1983) for anatomically preserved species and by Thomas (1970b, 1977, 1978) and Thomas & Meyen (1984) for adpressed species.

Lycopsid leaves attenuate bilaterally close to the stem, where they are consequently most readily detached. The area proximal to the constriction persists as a symmetrical structure raised above the surface of the axis and is termed a leaf base; aggregates of leaf bases preserve the phyllotaxy of the axis after leaf loss. In our more primitive OTUs (*Oxroadia, Paurodendron, Anabathra, Chaloneria*), leaf bases are small, ellipsoid in transverse section, widely spaced on the axial surface, and are fully transitional into the leaf lamina (C51). In the more derived OTUs, the leaf base is more elaborate and only a portion emits the leaf; it is then termed a leaf cushion (Fig. 4b). Such cushions typically exhibit a simple angular outline in tangential section: hexagonal in *Sigillaria*, and diamond-shaped in *Diaphorodendron*, *Synchysidendron*, *Hizemodendron*, *Lepidodendron*, and *Lepidophloios* (this character was not coded). Cushions are further elaborated by the development of raised upper (C54) and lower (C55) keels, and by division into upper and lower fields that are usually separated by a lateral line (C58) and are independently plicate (C56–C57). *Sigillaria* is plesiomorphic for all five characters, while *Diaphorodendron* and *Synchysidendron* are apomorphic for all five. *Lepidophloios* only possesses keels. *Hizemodendron* possesses plications but lacks an upper keel, while *Lepidodendron* lacks upper field plications but possesses a lateral line.

The leaf cushion can be regarded as an elaborated leaf base and thus as fundamentally foliar and appendicular in nature. This interpretation is supported by the leaflike structural and positional attributes of leaf cushions; rejection of the foliar nature of leaf cushions would require their recognition as developmentally distinct organs of a kind unknown in other plants. Even the relatively simple cushions of *Sigillaria* are helically arranged, closely packed but discrete, well-defined features. Leaf bases of all the arborescent lycopsids analyzed bear ligules, which are ancestrally foliar in the class (Bonamo et al., 1988). All of these characters are features of appendicular organs produced laterally to the apical meristem through the formation of primordia. In order to be axial rather than foliar, leaf cushions would have to be epidermal/subepidermal elaborations that enlarged below, and concurrently with, leaf primordia as the leaves expanded. There is no evidence in any arborescent lycopsid (with or without cushions) for such an unintuitive developmental mechanism wherein the leaf determines differentiation of the axis. Moreover, stomata occur on leaves and leaf bases, but are absent from axes; they are exclusively foliar.

Together, the above qualitative characters separate all of the cushion-bearing genera studied here, though morphometric quantification is necessary to separate species within each genus (Thomas, 1970b; DiMichele, 1983; Chaloner & Meyer-Berthaud, 1983; DiMichele et al., 1984; Wnuk, 1985). Although we have deliberately excluded metric characters from our analysis, to avoid arbitrary division of such characters into states, we made an exception for the length : width ratio of the leaf cushions (C52–C53). Since the early nineteenth century, the plesiomorphic condition of greater leaf cushion length than width has been crucial for delimiting *Lepidodendron* sens. lat. (DiMichele, 1983). Despite early knowledge that awarding primacy to this character resulted in the lumping of morphologically and anatomically dissimilar species (e.g., Scott, 1908; Seward, 1910), only recently has *Lepidodendron* sens. lat. been disaggregated into the morphologically distinct segregates *Anabathra* (DiMichele, 1980), *Diaphorodendron* sens. str. (DiMichele, 1983), *Synchysidendron* (DiMichele & Bateman, 1992), *Hizemodendron* (Bateman & DiMichele, 1991), *Lepidodendron* sens. str., and *Lepidophloios* (DiMichele, 1979a, 1983). Horizontally (i.e., tangentially) elongate leaf cushions are, however, a valid generic autapomorphy of *Lepidophloios*, together with radial elongation (C64–C65). Obscure evolutionary relationships of the arched and the perpendicular states of radial elongation among different *Lepidophloios* species necessitated X-coding.

All OTUs possess ligules (C59), and most recess the ligule in the cavity that communicates with the adaxial surface of the leaf base via a deep pit (C60). The plesiomorphic exceptions are *Paurodendron*, where the ligule is fully exposed (Phillips & Leisman, 1966), and *Anabathra*, where it is afforded some protection by the leaf cushions (DiMichele, 1980). Foliar parichnos (C61) occur in all OTUs but *Oxroadia* and *Paurodendron* (Bateman (1988) was unable to substantiate Long's (1986) tentative identification of parichnos in *Oxroadia*). In contrast, infrafoliar parichnos (C62) are confined to *Lepidodendron* (Weiss, 1907; DiMichele, 1983) and *Lepidophloios* (W. A. DiMichele, pers. obs.).

The presence of a leaf cushion (C51) is positively correlated with deciduousness (C63) in all OTUs but *Hizemodendron*, where retention is probably secondary (Bateman & DiMichele, 1991). We deliberately avoid describing leaf loss in lepidodendraleans as abscission (cf. Chaloner & Meyer-Berthaud, 1983). Despite the consistent absence of leaf laminae from axes (including almost all twigs), an abscission layer has not been detected in any OTU at any stage of development. We suggest that lycopsid leaves atrophy and are mechanically removed. This occurred more readily in trees such as *Sigillaria* than in smaller erect plants such as *Chaloneria* and recumbent pseudoherbs such as *Oxroadia*, due to the higher basal stresses imposed by the long microphylls of the arboreous species. Fracture occurs where the lamina constricts to form the leaf base; its position relative to the axis and lamina is more consistent in OTUs possessing leaf cushions, where a sharp structural (and, presumably, physiological) boundary is represented as a leaf scar. The scar is situated within the leaf rather than at the leaf-axis junction. Deciduous lateral branches may also have been shed by this mechanism; according to Jonker (1976), triangular marks below ulodendroid scars indicate that the branches were torn away at their junctions with the stem. However, R. A. Gastaldo (pers. comm. 1990) argued that most specimens lack these features, which may be taphonomic overprints.

51. Leaf is outgrowth of entire leaf base (0); portion of leaf base (1).
52. Length : width ratio of cushions on stems and large branches >1 : 1 (0); <1 : 1 (1).
53. Length : width ratio of cushions on small branches and twigs >1 : 1 (0); <1 : 1 (1).
54. Upper keel absent (0); present (1).
55. Lower keel absent (0); present (1).
56. Upper field nonplicate (0); plicate (1).
57. Lower field nonplicate (0); plicate (1).
58. Lateral line separating upper and lower fields absent (0); present (1).
59–60. Ligule absent (00); superficial or in shallow depression (10); in deep cavity with narrow neck (11).
61. Foliar parichnos absent (0); present (1).
62. Infrafoliar parichnos absent (0); present (1).
63. Consistent basal limit to leaf atrophy absent (0); present (1).
64–65. Leaf cushion not radially elongate (00); elongate, strongly arched (1X); elongate, ± perpendicular to axis (X1).

G. *Leaves* (7 characters)

Leaves are the organs most frequently neglected when attempts are made to reconstruct lepidodendraleans. Admittedly, their deciduousness and consequent absence from the upper axes hinders organ correlation by organic connection, but even more consistent disarticulation has not prevented indirect correlation of cone species with the vegetative axes that bore them. Failure to correlate leaves with their parent plants is unfortunate, as Graham (1935) and Reed (1941) demonstrated the wide range of potentially phylogenetically valuable characters present in isolated lepidodendralean leaves, and Bateman (1988) recorded many characters (including details of the cuticle, epidermis, and stomata) of leaves attached to *Oxroadia* axes. We discarded most of these characters for this analysis, because they would have contained unacceptably large proportions of missing values.

The presence of two vascular strands (C67) is autapomorphic for *Sigillaria*, which also shares V-shaped strands (C68) with *Chaloneria*. Dorsiventrally flattened strands (C69) occur in *Lepidodendron*, *Lepidophloios*, and *Diaphorodendron scleroticum*; ambiguous evolutionary pathways from plesiomorphic terete strands necessitated X-coding. All OTUs whose leaves possess nonterete strands also possess pronounced lateral abaxial grooves (furrows) containing stomata (C70; Fig. 4d); these are supplemented with a median adaxial groove in *Sigillaria* (C71). The vascular strands of most of the more apomorphic OTUs are surrounded by a sclerenchymatous sheath (C72), though this is absent from *Hizemodendron*.

Angle of leaf attachment (C66) refers only to the angle subtended by the basal portion of the mature lamina relative to the distal portion of the axis, thus avoiding the effect of recurvation in OTUs such as *Oxroadia*. This character distinguishes genera with hispid, generally short leaves (*Paurodendron*, *Anabathra*, *Chaloneria*, *Lepidodendron*), but can result from one of several developmental mechanisms and is therefore prone to homoplasy.

66. Angle of leaf attachment relative to axial apex ± horizontal (0); acute (1).
67. Number of vascular strands per leaf one (0); two (1).
68–69. Transverse section of vascular strand terete (00); dorsiventrally flattened (1X); V-shaped (X1).
70. Lateral abaxial grooves absent (0); present at least near base (1).
71. Median adaxial groove absent (0); present at least near base (1).
72. Sheath of sclerenchyma around trace absent (0); present (1).

H. *Cones* (4 characters)

Intensive study of lepidodendralean reproductive structures has generated thorough reviews of both anatomically preserved (Arber, 1914; Balbach, 1967; Brack, 1970; Hanes, 1975; Phillips, 1979; Brack-Hanes & Thomas, 1983; Willard, 1989a) and adpressed (Lesquereux, 1880; Kidston, 1923–1925; Willard, 1989b) organ-species. Reproductive characters played important roles in the delimitation of the genera; not surprisingly, many are genus-level autapomorphies. Moreover, many of the traits are functionally linked and can be used to define reproductive strategies in the same manner that vegetative morphology defines growth habits.

All of the lycopsids included in this analysis are heterosporous (C75). *Oxroadia, Paurodendron,* and *Anabathra* have primitively bisporangiate strobili (C76), with microsporangia concentrated toward the cone apex. The fertile zones of *Chaloneria* (arguably a derived condition) are similarly bisporangiate; all other OTUs bore monosporangiate cones.

Characters 73 and 74 describe the relationships to the parent stem of the lateral cone-bearing axes, whether peduncles or branches (*Chaloneria* is unbranched and was scored as missing for C73). Lateral branches are subtended by stelar gaps (C73) in *Diaphorodendron, Synchysidendron, Lepidodendron,* and *Lepidophloios,* and are medullated (C74) in *Sigillaria, Diaphorodendron, Lepidodendron,* and *Lepidophloios.*

73. Stelar vascular gap associated with departure of peduncle or lateral branch absent (0); present (1).
74. Pith in trace of peduncle or lateral branch absent (0); present (1).
75. Plants homosporous (0); heterosporous (1).
76. Cones/fertile zones bisporangiate (0); monosporangiate (1).

I. Sporophylls and sporangia (15 characters)

Literature review suggests that the terms describing most components of the sporangium-sporophyll complex have become standardized (Fig. 4c). The sporophyll is divided into a proximal portion ("pedicel"), perpendicular to the cone axis, and a distal portion ("distal lamina"), parallel to the cone axis and oriented toward the cone apex. The adaxial surface of the pedicel bears the sporangium and (immediately distal to the sporangium) the ligule. The pedicel is triangular in median transverse section and attenuates abaxially, to a structure that has been termed a keel if sufficiently prominent (Phillips, 1979), and laterally, to structures that have received various names. "Lateral laminae" is used most commonly; alternatives are "lateral extensions" (e.g., Meyen, 1987), "wings" (e.g., Arber, 1914), "flanges" (e.g., Sporne, 1975), and "alations" (e.g., Phillips, 1979). Some authors (e.g., Phillips, 1979) have distinguished the most developed state of this character (long and enrolled) as "integuments," by analogy with the true seeds of "spermatophytes." The apically directed distal lamina is much less three-dimensional and usually appears as a shallow "V" in transverse section. An antapically directed extension from the right-angled junction of the pedicel and distal lamina is termed the heel.

Comparing sporophylls with sterile microphylls, we believe that the pedicel is homologous with the leaf base (including the leaf cushion), and the sporophyll distal lamina is homologous with the leaf lamina. We suggest that the qualifier "distal" should be abandoned for the sporophyll lamina (there is no *proximal* lamina), and that the lateral extensions of the pedicel should be termed alations, irrespective of size and orientations (use of the term "integuments" for extensive enrolled alations misleadingly implies homology with the integuments of true seeds).

Little attention is paid in the literature to angle of pedicel attachment relative to the cone axis (C77), which may be prone to ontogenetic change as an aid to passive spore dispersal (Bateman, 1988). Thus, our identification of *Oxroadia* as autapomorphic for obtuse sporangia is tentative. With this exception, all sporophyll and sporangium characters (C78–C91) are scored as plesiomorphic for the four most primitive OTUs possessing bisporangiate cones (*Oxroadia, Paurodendron, Anabathra, Chaloneria*), which differ quantitatively rather than qualitatively. A good example is the number of megaspores per megasporangium, which also separates species of the same genus (e.g., *Anabathra*: Felix, 1954; Brack, 1970; see also Appendix 1B). It is tempting to distinguish qualitatively between megasporangia containing four spores, derived from one spore mother cell, and those containing more than four spores, derived from more than one spore mother cell. However, each condition characterizes one of the two species of *Oxroadia* (Bateman, 1988), and spore counts are complicated by frequent and apparently random abortions.

Differences among the remaining (monosporangiate) genera focus on megasporangiate cones and reflect their shared transition in the nature of the dispersal unit from isolated megaspores to a megasporangium-sporophyll complex (C81). The apomorphic state of this character encapsulates a broad spectrum of morphologies (elaborated in C80 and C82–C90) that may reflect parallel (i.e., homoplastic) responses to similar selective regimes. In all monosporangiate genera but *Sigillaria,* this evolutionary trend results in reduction to a single functional megaspore (C90) that germinates within the sporangium (C80; Phillips, 1979). Probably as an aid to dispersal and/or protection, these changes are accompanied by lateral expansion of the pedicel to form alations (C82–C84). These are coded as short and horizontal in *Sigillaria, Diaphorodendron,* and *Synchysidendron,* short and erect in *Hizemodendron* and *Lepidodendron,* and long and erect (typically enrolled) in *Lepidophloios.* These characterizations require further revision; the lateral margins of the pedicel can be proportionately longer in *Anabathra* (e.g., fig. 9 of Brack, 1970) and more erect in *Diaphorodendron* and *Synchysidendron* (e.g., pl. 8.4 of Phillips, 1979) than those of *Lepidodendron* (e.g., pl. 5.4 of Phillips, 1979). Moreover, shortness may not be homologous between vertical and horizontal alations; hence, X-coding was used to allow evolution of short, erect alations from either absence of alations or short, horizontal alations, and to suppress evolution of short, horizontal alations from short, vertical alations.

Megasporangia of *Diaphorodendron* and *Synchysidendron* are strongly dorsiventrally flattened (C85–C86) and dehisce proximally (C87–C89), while those of *Hizemodendron, Lepidodendron,* and *Lepidophloios* are strongly bilaterally flattened and dehisce distally. *Sigillaria approximata* undergoes indehiscent fragmentation (C89), presumably an apomorphic character state. We have used X-coding to allow its evolution by one step from any of the three dehiscence mechanisms. *Sigillaria approximata* possesses another autapomorphy, the enclosure of megaspores with parenchyma (C91).

Heterocellular sporangium walls (C79) characterize *Diaphorodendron* and *Synchysidendron.* Only *Lepidodendron* possesses a multiseriate sporangium wall; together with greater sporangium size (a quantitative character and therefore not coded), this distinguishes *Lepidodendron* sporangium-sporophyll complexes from the otherwise identical equivalents of *Hizemodendron.*

77. Angle of sporophyll attachment relative to cone apex ± horizontal (0); obtuse (1).
78. Sporangium wall uniseriate (0); multiseriate (1).
79. Sporangium wall homocellular (0); heterocellular (1).
80. Megaspores shed from sporangium prior to germination (0); megaspores germinate within sporangium (1).
81. Dispersal unit megaspore (0); megasporangium-sporophyll complex (1).

82–84. Alations of megasporophyll pedicel absent (000); short, horizontal (100); short, suberect (X10); long, erect (011).

85–86. Transverse section of megasporangium ± circular (00); strongly bilaterally flattened (10); strongly dorsiventrally flattened (01).

87–89. Megasporangium dehisces longitudinally (000); distally (100); proximally (010); indehiscent fragmentation (XX1).

90. Functional megaspores per megasporangium more than one (0); one (1).
91. Parenchyma enclosing megaspores absent (0); present (1).

J. Megaspores (10 characters)

Figure 4e summarizes terms describing the "geography" of the exteriors of lycopsid spores.

Morphological and ultrastructural studies of lycopsid megaspores preserved in situ in cones have been undertaken since the earliest applications of palynology to biostratigraphic and paleoecological problems (Schopf, 1938; Bocheński, 1939; Brack, 1970; Taylor, 1990; see also Bartram, 1987).

Polarity decisions for laesural (C94–C96) and equatorial (C92–C93) characters were problematic; they are generally poorly developed in distantly related lycopsids, but better developed and more complex in putatively more closely related outgroups (e.g., *Selaginella*: Stanier, 1965; Tryon & Lugardon, 1978; Minaki, 1984) and in the more primitive ingroup members (*Oxroadia, Paurodendron, Chaloneria*) than in the more derived OTUs. Prominent laesural expansions characterize *Oxroadia,* where they are fimbriate and do not extend beyond the curvaturae (C95: Alvin, 1965, 1966; Bateman, 1988), and *Paurodendron,* where they are plicate and extend to the equatorial flange (C96: Guennel, 1952). The laesurae of *Diaphorodendron* and *Synchysidendron* megaspores are gulate (C94); the spongy, trilobate proximal massa is a key taxonomic character. Equatorial expansions provide autapomorphies for *Paurodendron,* in the form of a perisporial plicate flange (C93: Guennel, 1952), and *Chaloneria,* in the form of auriculae (ear-shaped expansions of the exine) opposite laesural rays (C92: Pigg & Rothwell, 1983b).

Most OTUs lack dispersed proximal and distal ornamentation. Contact-face ornamentation is confined to *Oxroadia* (sparse, robust, buttressed spines: C97), *Paurodendron* (reticulate: C98), and *Chaloneria* (rugose: C99). The megaspore of *Sigillaria* sp. nov. could not be scored for this character, but its distal surface clearly bears short spines (C100: Benson, 1918; Pigg, 1983). Large and more complex buttressed spines typify *Oxroadia* megaspores. *Paurodendron* megaspores bear a striking distal reticulum (C101).

92–93. Equatorial ornamentation absent (00); auriculate (10); flanged (01).

94–96. Laesural ornamentation absent (000);

gulate (100); fimbriate (01X); plicate (0X1).

97–99. Contact-face ornamentation absent (000); echinate (100); reticulate (010); rugose (001).

100–101. Distal ornamentation absent (00); echinate (10); reticulate (01).

K. Microspores (14 characters)

Several lycopsid microspores commonly encountered in dispersed miospore assemblages (sensu Chaloner, 1970) have been correlated with source cones, both anatomically preserved (Brack, 1970; Courvoisier & Phillips, 1975; Willard, 1989a) and compressed (Thomas, 1970a, 1987; Willard, 1989b). Classification of lycopsid microspores has focused on equatorial elaboration and general surface ornamentation. The only exception in our list of characters, strongly raised laesurae (C105), occurs in *Chaloneria* and *Lepidophloios harcourtii.*

In *Chaloneria,* separation of the sexine and nexine layers distal to the contact faces has generated a pseudosaccus (C102: Brack & Taylor, 1972). All of the monosporangiate-coned genera exhibit some form of equatorial elaboration (C106–C108). *Anabathra, Hizemodendron, Lepidodendron,* and *Lepidophloios* microspores possess a thickened equatorial band (cingulum: C106); in *Hizemodendron, Lepidodendron,* and some *Lepidophloios* species, this is supplemented with an external membranous flange (zona: C108). *Sigillaria, Diaphorodendron,* and *Synchysidendron* microspores bear a crassitude equatorial thickening (C107) that appears structurally distinct from a cingulum. Cingula of some OTUs are further elaborated; those of *Hizemodendron, Lepidodendron,* and *Lepidophloios harcourtii* are bizonate (C103) and those of *Anabathra* are distally ornamented (C104).

Characterization of microspore general surface morphology is increasingly dependent on the greater resolution of scanning electron microscope (SEM) studies relative to light microscopy (LM). As in the megaspores, ornamentation is described separately for contact faces (C109–C111) and the distal hemisphere (C112–C115), though *Lepidophloios johnsonii* is insufficiently known to be scored. Contact faces of *Hizemodendron, Lepidodendron,* and *Lepidophloios* microspores are granulate (C109; Leisman & Rivers, 1974; Willard, 1989a), those of *Diaphorodendron* and *Synchysidendron* grade into a more foveolate texture (C110; Courvoisier & Phillips, 1975), and those of *Oxroadia* and *Paurodendron* are echinate (C111; Schlanker & Leisman, 1969; Bateman, 1988). Several OTUs lack contact-face ornamentation, but only *Chaloneria* and *Lepidophloios harcourtii* lack distal ornamentation. In *Oxroadia* and *Paurodendron,* the echinate contact faces are paralleled by the distal ornamentation (C115). *Diaphorodendron* and *Synchysidendron* microspores are papillate (C114), those of *Sigillaria* are characterized by a mixture of spines and cones (C113), and those of *Hizemodendron, Lepidodendron,* and *Lepidophloios hallii* bear dense grana (C112).

102. Pseudosaccus absent (0); present (1).

103–104. Equatorial expansion absent (00); unornamented bizonate cingulum complex (10); distally ornamented cingulum complex (01).

105. Laesurae subdued (0); strongly raised (1).

106–108. Equatorial ornamentation absent (000); cingulum complex (100); crassitude (010); zona (001).

109–111. Contact-face ornamentation absent (000); granulate (100); granulo-foveolate (010); echinate (001).

112–115. Distal ornamentation absent (0000); densely granulate (1000); echino-conate (0100); papillate (0010); echinate (0001).

THE DATA MATRIX

After all 115 characters had been scored, two whole-plant species (*Oxroadia gracilis* and *Oxroadia* sp. nov.) possessed identical data sets, demonstrating that they differ in quantitative but not qualitative characters. The duplicate data set provided no useful information and was therefore omitted, reducing the original 17 whole-plant species to 16 OTUs that, in our opinion, represent 10 genera. This gave a ratio of characters : OTUs of 115 : 16 (7.2 : 1).

The resulting 1,840-byte data matrix (Table 3, excluding HYAN) contained 94 missing values that each reflected one of four factors. Two of these factors result from ignorance of whether the OTU possesses the feature or what state the feature exhibits, one from unwillingness to specify the precursor state of the character (the X-coding procedure discussed in detail by Doyle & Donoghue, 1986b: 344–350; see also Appendix 2), and one from absence of the relevant feature, which therefore cannot be scored. The first three categories indicate varying degrees of ignorance concerning the nature of the character and can be replaced by a posteriori optimization, substituting values most parsimonious with the cladogram in question. The fourth type of missing value (coded # in Table 3) is also replaced during optimization, but here the result is merely an operational necessity. It does not generate a potentially biologically meaningful hypothesis; there is no obvious meaning in scoring a character state as present for an OTU that completely lacks the feature in question (for example, in Fig. 6 *Chaloneria* is optimized as possessing peduncle/branch gaps (C73) but actually lacks both types of organ). This situation is more frequent in data matrices that include OTUs of highly divergent morphology, where the probability of obtaining fully compatible sets of homologous features is less. The most gap-ridden (12% missing values) of our data sets is *Chaloneria cormosa*, where 11 of the 14 missing values reflect lack of the coded feature (i.e., absence rather than ignorance). Compared with OTU selection, we were less rigorous when excluding gap-ridden characters from the matrix; the worst examples (C34, C40, C69) possess 31% missing values, most of these X-coded to represent ambiguity of precursor states. Nevertheless, the overall proportion of missing values in our data matrix (5%) compares favorably with those of other studies (e.g., 24% in Table 2 of Doyle & Donoghue, 1986b).

We believe that every cladistic data matrix should routinely carry character:OTU ratios to indicate the average strength of empirical support for nodes and percentage missing values to indicate the completeness of the data matrix, just as the resulting trees now routinely carry consistency indices to summarize levels of homoplasy (Kluge & Farris, 1969; Brooks et al., 1986).

OPTIMIZATION, CHARACTER STATES, AND MISSING VALUES

The distribution of an apomorphic character state among all the OTUs can be assigned to one of three categories:

1. The apomorphic state is confined to a single OTU and is thus an autapomorphy at the least inclusive (species) level in the taxonomic hierarchy. It is important to note that the autapomorphic condition is a relative concept; a synapomorphy (shared derived character) at the species level in our analysis can be an autapomorphy (unshared derived character) at the more inclusive level of genus. Autapomorphies at the least inclusive level analyzed distinguish OTUs, but are phylogenetically uninformative. Consequently, they are omitted from algorithmic analysis to avoid artificially increasing length and decreasing perceived levels of homoplasy by including characters that are, by definition, nonhomoplastic (e.g., Brooks et al., 1986; Kluge, 1989; Sanderson & Donoghue, 1989).

2. The apomorphic state is ubiquitous among the OTUs (including the outgroups if used), thereby justifying their status as a potential clade. Although such character states are conventionally described as "basal synapomorphies" or "invariant characters" (e.g., Sanderson & Donoghue, 1989), we prefer to coin the more parsimonious term "holapomorphy." It could be argued that such character states are merely plesiomorphies, but they cannot be defined as such in the absence of an equivalent apomorphic state. Our definition of the term synapomorphy is also unconventional in implicitly excluding holapomorphic character states. Holapomorphy, like autapomorphy, is a relative concept; addition to the suite of taxa analyzed of an OTU lacking the apomorphic character state transforms a formerly ubiquitous holapomorphy into a nonubiquitous synapomorphy. Holapomorphies also resemble autapomorphies in being phylogenetically uninformative within the confines of a particular data matrix. Hence, like autapomorphies, holapomorphies should be (and in this study were) omitted from tree length calculations.

3. When the apomorphic state occurs in more than one but less than all of the OTUs, it is deemed phylogenetically informative and included in the algorithmic computation of tree length. Most such character states are synapomorphic, although category (3) also encompasses homoplasies (these are generally regarded as refuting the initial hypothesis of homology between the plesiomorphic and apomorphic states: e.g., Wiley, 1981; Funk & Brooks, 1990). The perception of synapomorphies as homoplastic (i.e., as parallelisms and/or reversals) or nonhomoplastic (evolving only once and persisting throughout the derived portion of the clade) is the least stable aspect of cladistic analysis, since these conditions are a property only of the interaction of a specific tree topology with a specific optimization algorithm (see below). Also, character states can be both homoplastic and partially synapomorphic; for example, a particular state may be a meaningful synapomorphy of the OTUs forming clade A+B but be represented as a parallelism in their non-sister OTU D (J. I. Davis, pers. comm. 1990). Surprisingly, the terminologically rich discipline of cladistics does not appear to have generated unique terms to describe the important (albeit ad hoc) distinction between synapomorphies sens. str. (i.e., holapomorphies excluded) that are homoplastic and those that are not; only the latter

TABLE 3. Cladistic data matrix. Operational taxonomic units: Hypothetical ancestor (HYAN), *Paurodendron fraipontii* (PNFR), *Oxroadia gracilis*-sp. nov. (OXGR), *Anabathra* (*Paralycopodites*) *pulcherrima* (ANPU), *Chaloneria cormosa* (CHCO), *Sigillaria approximata* (SIAP), *Sigillaria* sp. nov. (SINS), *Synchysidendron* (*Diaphorodendron*) sp. nov. (SYNS), *Synchysidendron dicentricum* (SYDI), *Diaphorodendron phillipsii* (DIPH), *Diaphorodendron vasculare* (DIVA), *Diaphorodendron scleroticum* (DISC), *Hizemodendron* (*Lepidodendron*) *serratum* (HZSE), *Lepidodendron hickii* (LNHI), *Lepidophloios harcourtii* (LSHC), *Lepidophloios johnsonii* (LSJO), *Lepidophloios hallii* (LSHL). Known values: primitive (0), derived (1); missing values (coded 9 in PAUP; functional states in preferred most parsimonious tree are indicated by subscripts): not known whether OTU possesses relevant feature

	Habit (1–7)							Rootstock (8–13)					
OTU					5					10			
				+	+			@	+		@	@	
HYAN	0	0	0	0	0	0	0	0	0	0	0	0	0
PNFR	0	0	0	0	0	0	0	1	0	1	1	1	$?_0$
OXGR	0	0	0	0	0	0	0	1	0	0	1	1	$?_0$
ANPU	1	1	1	0	0	1	1	1	0	0	1	1	0
CHCO	0	1	1	0	1	$\#_0$	$\#_0$	1	1	1	1	1	1
SIAP	1	1	1	0	0	1	0	1	0	0	1	1	1
SINS	1	1	1	0	0	1	0	1	0	0	1	1	$?_0$
SYNS	1	1	0	0	0	0	0	1	0	0	1	1	0
SYDI	1	1	0	0	0	0	0	1	0	0	1	1	0
DIPH	1	1	1	0	0	1	1	1	0	0	1	1	0
DIVA	1	1	1	0	0	1	1	1	0	0	1	1	0
DISC	1	1	1	1	0	1	1	1	0	0	1	1	0
HZSE	0	0	0	0	0	0	0	1	0	0	1	1	0
LNHI	1	1	0	0	0	0	0	1	0	0	1	1	0
LSHC	1	1	0	0	0	0	0	1	0	0	1	1	0
LSJO	1	1	0	0	0	0	0	1	0	0	1	1	0
LSHL	1	1	0	0	0	0	0	1	0	0	1	1	0

	Cortex (32–36)					Periderm (37–50)						
OTU				35					40			
	@		+		+	@	*		*	*	*	*
HYAN	0	0	0	0	0	0	0	0	0	0	0	0
PNFR	1	0	$?_0$	0	0	1	0	0	0	0	0	0
OXGR	1	0	0	0	0	1	0	0	0	0	0	0
ANPU	1	0	0	0	0	1	0	0	0	0	0	0
CHCO	1	$?_1$	0	0	0	1	0	0	0	0	0	0
SIAP	1	1	0	0	0	1	0	0	1	0	0	0
SINS	1	$?_1$	$?_0$	1	0	1	0	0	1	0	0	0
SYNS	1	1	1	1	0	1	1	0	0	1	0	1
SYDI	1	0	0	1	0	1	1	0	0	1	0	1
DIPH	1	1	$?_0$	1	1	1	1	0	0	1	1	0
DIVA	1	1	0	1	0	1	1	0	0	1	1	0
DISC	1	1	0	1	0	1	1	0	0	1	1	0
HZSE	1	0	0	0	0	$-_1$	$-_0$	$-_0$	$-_0$	$-_0$	$-_0$	0
LNHI	1	0	0	0	0	1	0	1	X_0	0	0	0
LSHC	1	$?_1$	$?_0$	0	0	1	0	1	X_0	0	0	0
LSJO	1	1	$?_0$	0	0	1	0	1	X_0	0	0	0
LSHL	1	1	0	0	0	1	0	1	X_0	0	0	0

reliably characterize an entire monophyletic portion of a clade.

We are also surprised at the paucity of literature concerning optimization, as it proved to be a crucial aspect of our analysis. Optimization is an a posteriori procedure performed using one of a range of algorithms that are designed to apply specific logical precepts to specifying the nature (e.g., reversal vs. parallelism) and location of each character transition on a tree whose topology and length

TABLE 3. Continued.

(–), OTU possesses relevant feature but character state unknown (?), OTU lacks relevant feature (#), precursor state ambiguous (X; X-coded sensu Doyle & Donoghue, 1986b). Functional level of generality of derived character state in preferred most parsimonious tree: + = species level autapomorphy (character state restricted to a single OTU; these provide no information on historical relationships of species or genera), * = genus level autapomorphy (character state restricted to a single genus but occurring in more than one species; these provide no information on historical relationships of genera), @ = holapomorphy (= basal synapomorphy; these provide no information on historical relationships of species or genera).

Stele (14–31)																	
	15					20					25					30	
*			*	+	+	*	+			+	*		*	*	@	*	*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0
0	1	0	0	0	0	0	1	1	X_1	1	0	1	0	0	1	$\#_0$	0
0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0
0	1	0	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0
1	0	0	1	1	0	1	0	1	1	0	0	1	0	0	1	0	1
1	0	0	1	0	1	1	0	1	1	0	0	1	0	0	1	0	1
1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0
1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0
1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0
0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	$?_1$	0	0
0	1	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
0	1	0	0	0	0	0	0	1	X_1	0	1	0	0	1	1	0	0
0	1	1	0	0	0	0	0	1	X_1	0	1	0	0	1	1	0	0
0	1	1	0	0	0	0	0	1	X_1	0	1	0	0	1	1	0	0

Periderm (cont'd.)							Leaf bases (51–65)									
	45					50					55					60
	*	+			+	*		*							@	
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	1	0
0	0	0	0	0	0	0	0	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	1	1
0	0	0	0	0	1	0	0	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	1	0
0	0	0	0	0	0	0	0	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	$\#_0$	1	1
1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	1	1
1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	1	1
1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1
1	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1
0	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1
0	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1
0	1	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1
0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	1	1
X_0	X_0	1	1	1	0	0	1	0	1	1	1	0	1	1	1	1
0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	1	1
0	0	0	1	1	0	0	1	1	1	1	1	0	0	0	1	1
0	0	0	0	1	0	0	1	1	1	1	1	0	0	0	1	1

have already been fixed. In theory, optimization cannot alter the length of a tree (though see below for a critical reappraisal of this conventional wisdom).

Rooting the tree using the hypothetical ancestor had the advantage of maximizing the number of optimization algorithms that could legitimately be applied (Swofford, 1985: 3.10). We tested all five optimization algorithms available in PAUP 2.4: ACCTRAN maximizes reversals, as in practice does

TABLE 3. Continued.

OTU	Leaf bases (cont'd.)					Leaves (66–72)						
					65					70		
				*	+		*				*	
HYAN	0	0	0	0	0	0	0	0	0	0	0	0
PNFR	0	0	0	0	0	1	0	0	0	0	0	0
OXGR	0	0	0	0	0	0	0	0	0	0	0	0
ANPU	1	0	0	0	0	1	0	0	0	0	0	0
CHCO	1	0	0	0	0	1	0	X_0	1	1	0	0
SIAP	1	0	1	0	0	0	1	X_0	1	1	1	1
SINS	1	0	1	0	0	0	1	X_0	1	1	1	1
SYNS	1	0	1	0	0	0	0	0	0	0	0	1
SYDI	1	0	1	0	0	0	0	0	0	0	0	1
DIPH	1	0	1	0	0	0	0	0	0	0	0	$?_1$
DIVA	1	0	1	0	0	0	0	0	0	0	0	1
DISC	1	0	1	0	0	0	0	1	X_0	1	0	1
HZSE	1	0	0	0	0	1	0	0	0	0	0	0
LNHI	1	1	1	0	0	0	0	1	X_0	1	0	1
LSHC	1	$?_1$	1	1	X_0	0	0	1	X_0	1	0	$?_1$
LSJO	1	$?_1$	1	1	X_0	0	0	1	X_0	1	0	1
LSHL	1	1	1	X_1	1	0	0	1	X_0	1	0	1

OTU	Megaspores (92–101)									
				95					100	
	+	+	*	+	+	+	+	+		+
HYAN	0	0	0	0	0	0	0	0	0	0
PNFR	0	1	0	X_0	1	0	1	0	0	1
OXGR	0	0	0	1	X_0	1	0	0	1	0
ANPU	0	0	0	0	0	0	0	1	0	0
CHCO	1	0	0	0	0	0	0	0	0	0
SIAP	0	0	0	0	0	0	0	0	0	0
SINS	0	0	0	0	0	$?_0$	$?_0$	$?_0$	1	0
SYNS	0	0	1	0	0	0	0	0	0	0
SYDI	0	0	1	0	0	0	0	0	0	0
DIPH	0	0	1	0	0	0	0	0	0	0
DIVA	0	0	1	0	0	0	0	0	0	0
DISC	0	0	1	0	0	0	0	0	0	0
HZSE	0	0	0	0	0	0	0	0	0	0
LNHI	0	0	0	0	0	0	0	0	0	0
LSHC	0	0	0	0	0	0	0	0	0	0
LSJO	0	0	0	0	0	0	0	0	0	0
LSHL	0	0	0	0	0	0	0	0	0	0

FARRIS; in contrast, DELTRAN maximizes parallelisms. MINF concentrates character state transitions toward the terminal branches, MINRES concentrates all possible transitions toward the root, then concentrates the remainder toward the terminal branches. For our preferred most parsimonious tree (PMPT), FARRIS yielded similar (though not identical) results to ACCTRAN, and MINRES yielded similar results to DELTRAN and, to a lesser degree, MINF. We preferred MINRES and MINF, as they minimized perceived homoplasy in the lower (genus-level and above) branches that were of greatest interest to us; they also tended to yield the greatest number of intuitively satisfactory selections when (1) choosing between reversals and parallelisms, and (2) substituting 0 or 1 for missing values of specific characters (see below). Reservations expressed by Swofford (1985: 3.9–3.10)

TABLE 3. Continued.

Cones (73–76)				Sporophylls & Sporangia (77–91)														
		75					80					85					90	
		@		+	+	*					*		*		*	+		+
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
$\#_1$	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
$?_1$	1	1	1	0	0	0	0	1	1	0	0	0	0	X_0	X_0	1	0	1
$?_1$	1	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
1	0	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0
1	0	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0
1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0
1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0
1	1	1	1	0	0	1	1	1	1	0	0	0	1	0	1	0	1	0
0	0	1	1	0	0	0	1	1	X_0	1	0	1	0	1	0	0	1	0
1	1	1	1	0	1	0	1	1	X_0	1	0	1	0	1	0	0	1	0
1	1	1	1	0	0	0	1	1	0	1	1	1	0	1	0	0	1	0
1	1	1	1	0	0	0	1	1	0	1	1	1	0	1	0	0	1	0
1	1	1	1	0	0	0	1	1	0	1	1	1	0	1	0	0	1	0

Microspores (102–115)													
			105					110					115
+		+				+		*			*	*	
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	1	0	0	1	0	0	1	0	0	0	1
0	0	0	0	0	0	0	0	0	1	0	0	0	1
0	0	1	0	1	0	0	0	0	0	1	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	1	0	0	0	0	0	1	0	0
0	0	0	0	0	1	0	0	0	0	0	1	0	0
0	0	0	0	0	1	0	0	1	0	0	0	1	0
0	0	0	0	0	1	0	0	1	0	0	0	1	0
0	0	0	0	0	1	0	0	1	0	0	0	1	0
0	0	0	0	0	1	0	0	1	0	0	0	1	0
0	0	0	0	0	1	0	0	1	0	0	0	1	0
0	1	0	0	1	0	0	1	0	0	1	0	0	0
0	1	0	0	1	0	0	1	0	0	1	0	0	0
0	1	0	1	1	0	0	0	0	0	0	0	0	0
0	$?_1$	0	0	1	0	0	$?_1$	$?_0$	$?_0$	$?_1$	$?_0$	$?_0$	$?_0$
0	0	0	0	1	0	0	1	0	0	1	0	0	0

concerning MINRES encouraged our consistent use of MINF.

During optimization, each missing value (coded 9 in the PAUP data matrix) is replaced with 0 or 1 in accordance with (1) the topology of the tree and (2) the intended effect on patterns of character state transformation of the chosen optimization algorithm (this is an a priori opportunity to modify evolutionary interpretations). The substitutions that result are different for every tree of every analysis; for example, those presented as subscripts to missing values in our data matrix (Table 3) refer only to the preferred MPT of analysis A following application of the MINF optimization algorithm. Replacement of missing values is achieved parsimoniously in accordance with the topology of the tree, so that further homoplasy will not be introduced. Hence, we presume that this procedure artificially reduces levels of homoplasy relative to those that would have been determined from the same matrix if complete (i.e., gap-free).

Doyle & Donoghue (1986b: 352) imposed dual origin (parallelism) where a structure was simplified, and an origin and a loss (reversal) where a structure became more complex, on the assumption that "it is easier to reduce or lose a complex structure than to elaborate one from a simple structure." We did not consider this generalization sufficiently reliable to warrant a posteriori modification of our algorithmically optimized character state distributions, though we did emphasize complex, apparently conservative characters in subsequent evolutionary interpretations.

According to Bateman (in prep.), when all OTUs are scored as possessing either the plesiomorphic or apomorphic state for a character, the assignment of that character to one of these three ostensibly exclusively categories (autapomorphy, holapomorphy, synapomorphy sens. str.) is *definitive*; its condition is fixed for that data matrix. However, this principle does not apply if the character column contains at least one missing value (9), when the results of optimization determine the status of the character as informative or uninformative. For example, in our data matrix, a character scored as fifteen 1s and one 9 (e.g., C29) will be holapomorphic if the 9 is replaced a posteriori with a 1, but synapomorphic if the 9 is replaced with a 0 (in practice, this will occur only if the OTU scored 9 is placed at the base of the cladogram). Similarly, a character scored as fourteen 0s, one 1, and one 9 (e.g., C94, C98) will be autapomorphic if the 9 is replaced with a 0 but nonautapomorphic if the 9 is replaced with a 1. Hence, there is a need for the concepts of *transient* autapomorphy, *transient* holapomorphy, and *transient* synapomorphy, to accommodate characters that contain missing values. These concepts are relative, even within a single data matrix; they characterize only a single combination of a specific topology and a specific optimization algorithm. In our novel terminology, definitive and transient autapomorphies together constitute *operational* autapomorphies (likewise for holapomorphies and synapomorphies).

In contrast with definitive autapomorphies and holapomorphies, transient autapomorphies and holapomorphies cannot be screened out of an analysis a priori. Consequently, they contribute to tree length as calculated during cladistic analysis; they introduce spurious extra steps in an unpredictable manner, often generating alternative trees that are incorrectly considered of equal length by the parsimony algorithm. For example, a data matrix generates two topologies, A and B, both X steps in length. A posteriori screening for transient autapomorphies/holapomorphies reveals four in topology A and two in topology B. A is then preferred over B as its true length is X − 4, relative to X − 2 in topology B. Unfortunately, topology C, perceived by the algorithm as X + 1 steps long but containing six transient autapomorphies/holapomorphies, has a true length of X − 5 steps and is actually the most parsimonious tree. Thus, the true lengths of trees generated from a data matrix containing missing values can only be calculated a posteriori. Algorithmically determined tree lengths are unreliable, and trees other than those that are ostensibly the most parsimonious must also be screened individually via apomorphy lists for spurious additional steps. The alternative option of omitting all *potential* transient autapomorphies and holapomorphies a priori (appendix 1 of Sanderson & Donoghue, 1989) deleteriously discards potential synapomorphies merely because their frequencies among the OTUs approach zero or unity.

PARSIMONY ANALYSIS

Cladograms were generated from the data matrix using Version 2.4 of PAUP (Swofford, 1985), which employs unrestricted parsimony via the Wagner method (Kluge & Farris, 1969; Farris, 1970; Felsenstein, 1982; Swofford & Maddison, 1987; Wiley et al., 1991). Some of the computational difficulties encountered by us and discussed below have been at least partially surmounted by more recent software (see Appendix 2). Despite the long run-times incurred on our IBM-PS2/#80, the branch-and-bound option (a modification of the algorithm devised by Hendy & Penny, 1982) was used routinely to obtain the definitive shortest trees.

Once character scoring had been finalized, five different configurations of the data matrix were analyzed:

A. All 16 OTUs and all 115 characters included. This basic analysis provided a yardstick by which to measure the remaining analyses.

B. All OTUs included, "habit" characters (C1–C7) excluded. We wished to reassess the phylogeny without these characters for two reasons. First, they describe the most generalized aspects of plant morphology and are thus most prone to epigenesis. Second, we wished to map the distribution of lycopsid bauplans onto a phylogeny constructed independently of such characters (see also Bateman & DiMichele, 1991; Phillips & DiMichele, 1992).

C. All characters included, but *Chaloneria cormosa* excluded. Survey of tree topologies from analyses A and B demonstrated that *Chaloneria* is the most unstable OTU; it is supported by the least robust node, characterized only by homoplastic and autapomorphic characters, and possesses more autapomorphies (six) than any other OTU (Fig. 6). This most awkward OTU was omitted in order to determine how the topologies of the more parsimonious trees would be altered and whether homoplasy would decrease significantly.

D. All OTUs included, analysis restricted to vegetative characters (C1–C4, C8–C72).

E. All OTUs included, analysis restricted to reproductive characters (C5–C7, C73–C115). Analyses D and E were performed to determine the relative contributions of vegetative and reproductive characters to the whole-plant phylogeny (cf. Bateman & DiMichele, 1991), and to assess the likely accuracy of phylogenies based on the partial plants that constitute most paleobotanical "species." Data matrices for organ-species phylogenies are much easier to construct than those for whole-plant phylogenies, given the difficulty of correlating vegetative and reproductive organs.

After some experimentation, we developed an analytical routine that was applied to each of our main groups of analyses (A–D above; analysis E generated more equally most parsimonious trees than PAUP 2.4 can store). In each case, an initial run used the BANDB command to find all equally most parsimonious topologies by branch-and-bound, and the combination of the OPT=MINF optimization algorithm and APOLIST print command to identify the putative location and direction of each character state transition. Having thus determined the length of the shortest tree(s) (L_{min}), we then reanalyzed the data matrix by replacing the BANDB command with BB = 'X', where 'X' was one step longer than the shortest tree (i.e., L_{min+1}). This second run found and saved trees of lengths L_{min} and L_{min+1}; in order to determine the number of topologies of length L_{min+1}, the total number of topologies found at BB = L_{min} was subtracted from the total number of topologies found at BB = L_{min+1}. This procedure was repeated up to lengths of about L_{min+4} (depending on the particular submatrix under scrutiny). Tree number increases more-or-less exponentially with increase in length; the maximum capacity of PAUP 2.4 to store trees (N = 100) is soon exceeded, so that it becomes untenable to routinely scrutinize topologies much longer than L_{min}.

We found such scrutiny desirable for two reasons. First, we wished to know how many genus-level topologies occurred at each length, as opposed to species-(OTU-)level topologies routinely detected by the tree-building algorithm. Second, we wished to use lists of apomorphies following optimization to assess each tree for transient holapomorphies and autapomorphies, so that they could be subtracted to obtain its true length (determined entirely by synapomorphies sens. str.). In practice, this time-consuming screening procedure was not applied to trees longer than L_{min+1} (a new algorithm is required for this purpose), rendering optimization and the retention of apomorphy lists redundant from L_{min+2} onward (analyses A, B, D) or L_{min+3} onward (analysis C).

Having surveyed all optimally (L_{min}) and suboptimally ($L_{min+\leq 3}$) parsimonious trees, we focused on particular trees of interest, including all most parsimonious trees (MPT, i.e., tree of length L_{min}). These were reprinted with APOLIST (a list of node by node character state transitions) and CHGLIST (a list of character by character state transitions) for full interpretation (e.g., Figs. 6, 7). Topologies of potential interest longer than those routinely surveyed (i.e., longer than ca. L_{min+4}; Fig. 7) were specified using the TOPOLOGY command in "user tree" mode (Swofford, 1985: 2.20–2.22).

In summary, our cladistic analyses were experimental sensu Doyle & Donoghue (1986b). The basic philosophy of this approach was well summarized by Johnson (1982) and Bryant (1989: 218): "Parsimony determines the *order* by which viable hypotheses should be tested; one *starts* with the simplest" (our italics). Alternative hypotheses are then considered in order of increasing complexity until a self-imposed threshold is reached. In contrast, nonexperimental cladistic studies both start *and finish* with the simplest.

SPECIES-LEVEL RELATIONSHIPS

Although this experimental cladistic study was aimed primarily at elucidating genus-level relationships, we chose to perform our analyses at the species level. This decision partly reflected a subsidiary interest in species-level relationships, but was taken primarily because species-level OTUs provide a test of the presumed monophyly of genera. Genera can then be re-delimited if necessary. The following discussion is based primarily on analysis A, but also applies to analyses B–D (analysis E produced an untenably large number of equally most parsimonious trees).

Only four of the ten genera in the data matrix are represented by more than one OTU (Table 1): *Sigillaria* (two species), *Diaphorodendron* (three species), *Synchysidendron* (two species), and *Lepidophloios* (three species, but see Appendix 1D).

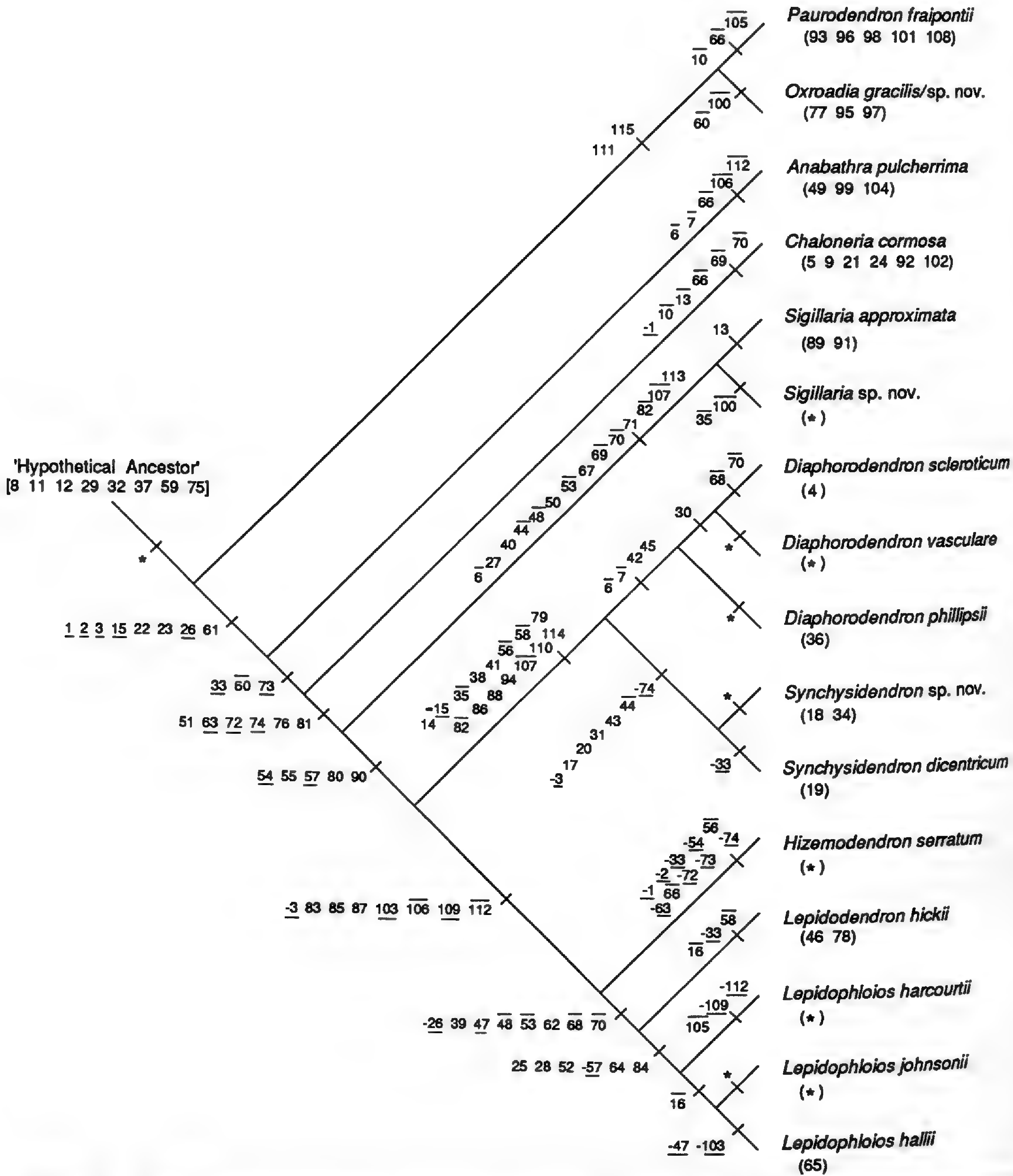

FIGURE 6. Preferred most parsimonious cladogram for analysis A (all OTUs and all characters). Holapomorphies are placed in square brackets below the hypothetical ancestor, and autapomorphies are placed in parentheses below OTUs; all character state transitions on terminal branches are therefore homoplastic. Characters that experience reversal are underlined (with a minus sign where a reversal occurs), parallelisms are overlined. Asterisks indicate absence of character state transitions at specific nodes.

Each of these four genera proved very robust (i.e., dismantling each genus in any way resulted in much longer trees), but relationships of the species within at least two of the genera are less clear (the two species of *Sigillaria* and *Synchysidendron* respectively do not allow multiple topologies).

The three-taxon problem presented by *Diaphorodendron phillipsii*, *D. vasculare*, and *D. scleroticum* is very poorly resolved (Fig. 6), resting entirely on the nonhomoplastic synapomorphy of secondary xylem in lateral branches (C30) that unites *D. scleroticum* and *D. vasculare* (Fig. 8d). Treating C30 as a synapomorphy of the clade and as a secondary loss in *D. phillipsii* (a tenable hypothesis more consistent with stratigraphic evidence; Fig. 3) costs only one extra step and col-

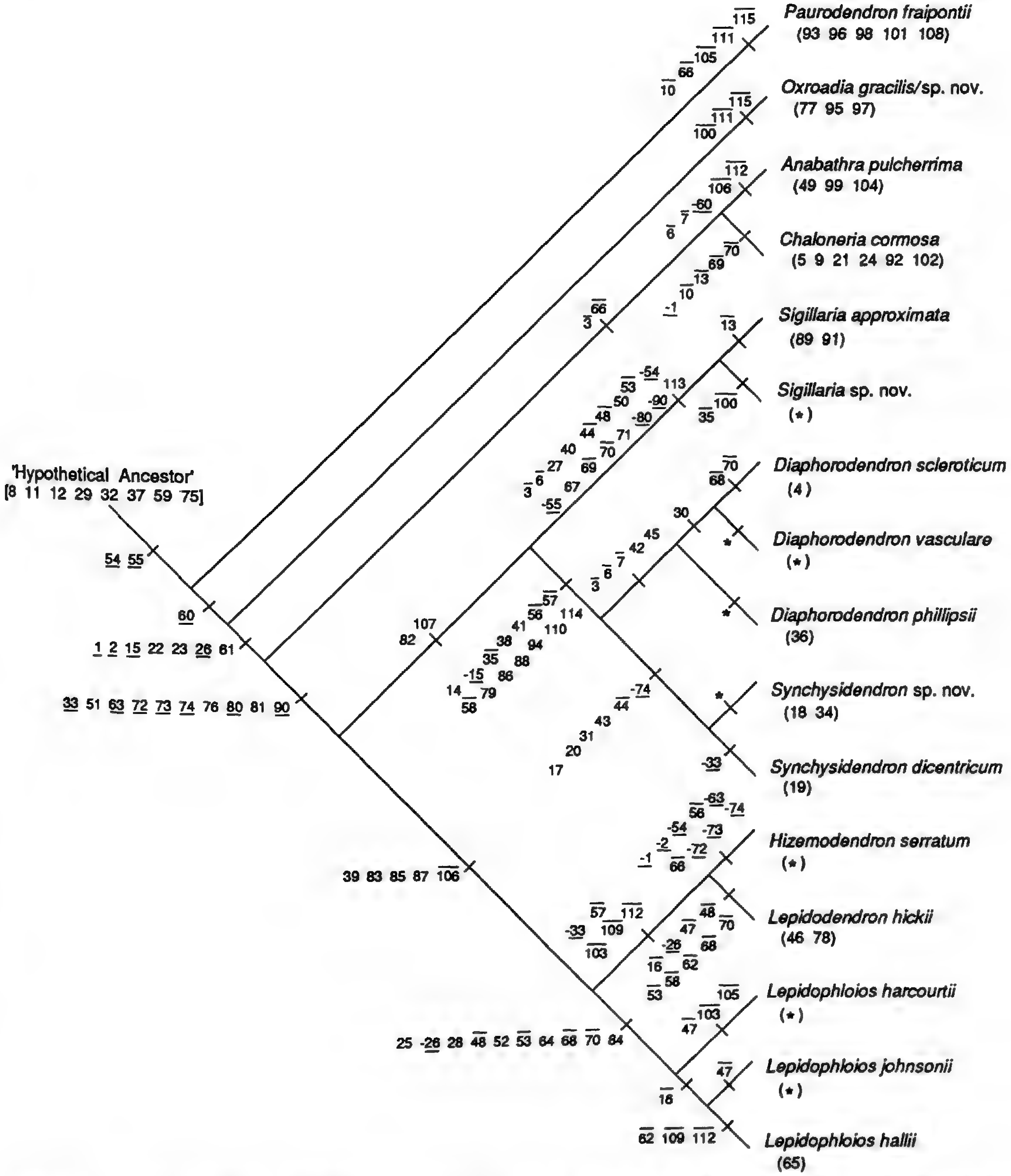

FIGURE 7. Fully annotated cladogram for analysis A showing alternative generic topologies of potential interest. It differs from Figure 6 in that (1) *Paurodendron* is a sister group of *Oxroadia* (cost = two steps), (2) *Anabathra* and *Chaloneria* form a clade (cost = nil), (3) *Sigillaria* and *Diaphorodendron* form a clade (cost = one step), and (4) *Hizemodendron* and *Lepidodendron* sens. str. form a clade (cost = five steps). Character notation follows Figure 6.

lapses the relationship into an uninformative trichotomy (Fig. 8e). This polychotomy was a persistent cause of trivially multiple topologies in our analyses (see Appendix 2).

The phylogenetic relationship of the three putative *Lepidophloios* species is obscured by extensive homoplasy that is compounded by ambiguities caused by missing values for some characters. *Lepidophloios hallii* and *L. harcourtii* are subtended only by homoplasies, while *L. johnsonii* is not subtended by any characters (it even lacks qualitative autapomorphies; Fig. 6). We obtained three equally most parsimonious solutions to this three-taxon problem (Fig. 8a–c). The first (Fig. 8a) links *L. johnsonii* and *L. hallii* by the homoplastic synapomorphy of a filamentous core to the protostele

(C16). The second (Fig. 8b) links *L. johnsonii* and *L. harcourtii* by the homoplastic synapomorphy of a glandular periderm (C47) and by the ostensibly nonhomoplastic synapomorphy of arched leaf cushions (C64). Unfortunately, this character is scored as missing for *L. hallii* as a result of X-coding (Table 3) and can therefore be treated as either apomorphic or plesiomorphic during optimization. As a result of inconsistent replacement during optimization, the apomorphic state is depicted as characterizing all three *Lepidophloios* species in Figure 8a but only two species in Figure 8b. The third topology (Fig. 8c) treats C16 as a loss in *L. harcourtii* and C64 as present in all three species, which consequently collapse to a trichotomy.

Given that all three solutions are equally most parsimonious, every topology that differed in the positions of OTUs other than *Lepidophloios* species was repeated three times by the tree-building algorithm to accommodate the multiple solutions to the *Lepidophloios* problem (hence our division by three of the algorithmically determined numbers of species-level topologies to yield the smaller, more meaningful values listed in Table 4). The arrangement of *Lepidophloios* species shown in Figure 8a best fits their reported sequence of relative appearance in the fossil record (Fig. 3); on the basis of this weak evidence, it was preferred when selecting the trees shown in Figures 6 and 7.

EXPERIMENTAL CLADISTICS: A SURVEY OF GENUS-LEVEL TOPOLOGIES

In all analyses, *Synchysidendron* and *Diaphorodendron* sens. str. consistently remained united as a monophyletic group and are not distinguished in Figures 9 and 10. Also, the following discussion occasionally refers to *Synchysidendron* as derived relative to *Diaphorodendron* and *Lepidophloios* as derived relative to *Lepidodendron*. As these pairs of genera are sister groups (Fig. 6), these assertions of derivation are subjectively imposed by us, based on comparison of the number and inferred evolutionary significance of the character state transitions supporting each genus.

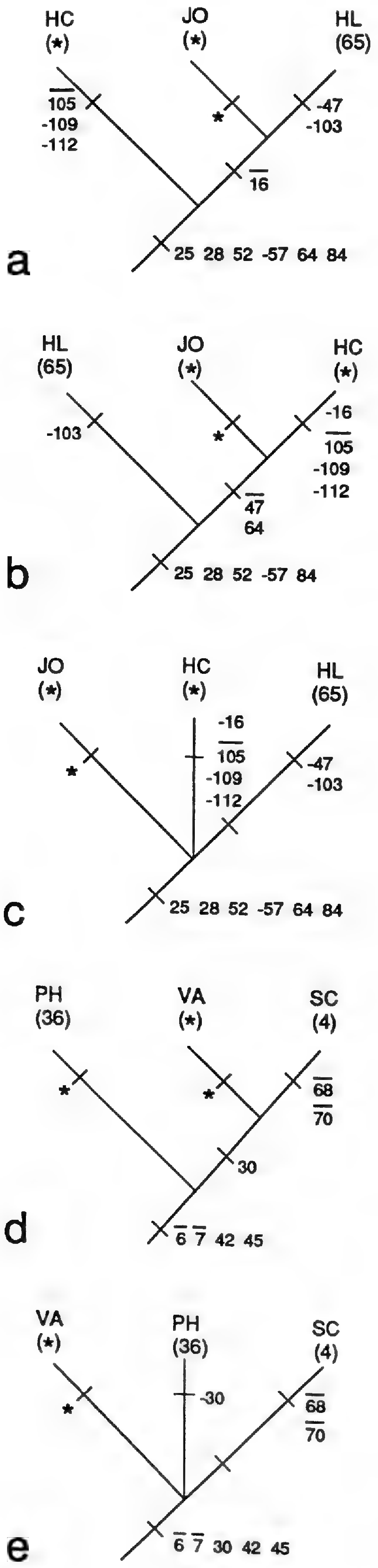

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FIGURE 8. Poorly resolved relationships between species of the same genus (see caption to Table 3 for key to abbreviations). a–c show three equally parsimonious (12-step) solutions to the three taxon problem presented by the *Lepidophloios* species. d and e show two solutions to the three taxon problem presented by the *Diaphorodendron* species (d = 7 steps, e = 8 steps). Notation largely follows Figure 6, though lines below character numbers emphasizing reversals are omitted.

TABLE 4. Comparison of cladistic parameters for five permutations (A–E) of the data matrix in Table 3. A = all taxa and all characters included; B = all taxa included, habit characters (C1–C7) omitted; C = *Chaloneria cormosa* omitted, all characters included (the total number of characters declines from 115 to 109 due to the elimination of *Chaloneria*'s six autapomorphies; also one former synapomorphy becomes an autapomorphy of *Paurodendron*); D = vegetative characters (C1–C4, C8–C72) only; E = reproductive characters (C5–C7, C73–C115) only. For numbers of trees, the initial figure is the number of species-level topologies of that length, the figure in parentheses is the number of genus-level topologies of that length, and the figure in square brackets is the cumulative total of genus-level tree topologies (ND = not determined). Figures for topologies longer than L_{min+1} may be inaccurate, as it was not feasible to screen by eye large numbers of trees for transient holapomorphies and transient autapomorphies (see "Optimization, character states, and missing values"). Strictly, each species-level value should be multiplied by three to reflect three equally parsimonious solutions to the relationships of the three species of *Lepidophloios* (this triangular relationship became unreliable in all analyses at L_{min+4}). The figure for analysis E remains greatly inflated by repeated dichotomies. Note that *Hizemodendron serratum* was treated as a new genus distinct from *Lepidodendron* sens. str. when calculating the genus-level values. Segregating *Synchysidendron* from *Diaphorodendron* sens. str. did not affect calculation of tree numbers, as the two genera consistently behaved as a monophyletic group.

Parameter		Analysis				
		A	B	C	D	E
Number of OTUs (excluding HYAN)		16	16	15	16	16
Total number of characters		115	108	109	69	46
Number of operational holapomorphies		8	8	8	7	1
Number of operational species-level autapomorphies		27	25	22	11	16
Number of informative characters remaining (synapomorphies sens. str.)		80	75	79	51	29
Minimum length (L_{min}; steps)		128	115	121	77	43
Consistency index at L_{min}		0.625	0.652	0.653	0.662	0.674
Number of trees of minimum and near-minimum length	L_{min}	3 (3) [3]	2 (2) [2]	1 (1) [1]	2 (2) [2]	270 (ND) [ND]
	L_{min+1}	14 (11) [11]	9 (7) [7]	3 (2) [2]	13 (11) [11]	—
	L_{min+2}	31 (19) [22]	28 (18) [18]	5 (4) [5]	44 (ND) [ND]	—
	L_{min+3}	62 (ND) [ND]	70 (ND) [ND]	14 (10) [11]	129 (ND) [ND]	—
	L_{min+4}	134 (ND) [ND]	133 (ND) [ND]	32 (ND) [ND]	—	—
	L_{min+5}	—	—	51 (ND) [ND]	—	—

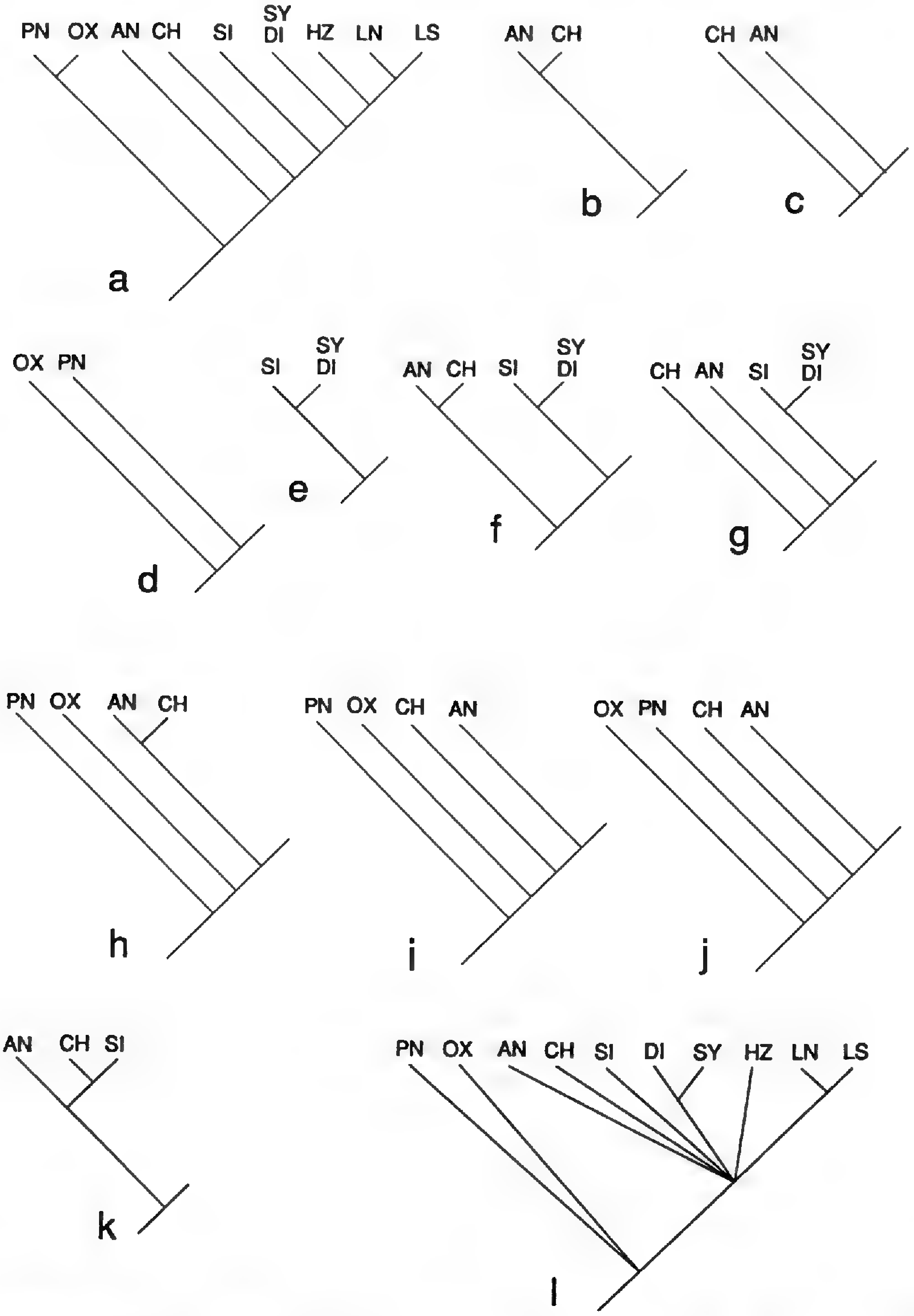

FIGURE 9. Generic topologies of analysis A at L_{min} (a–c) and L_{min+1} (d–k) (see caption to Table 3 for key to abbreviations). For analysis B (habit characters omitted), a and b occur at L_{min} and c–f, h at L_{min+1} (the relationship between *Chaloneria* and *Anabathra* became unresolved in c). For analysis C (*Chaloneria* omitted), only single generic topologies occur at L_{min} (that seen in a–c less *Chaloneria*) and at L_{min+1} (that seen in e–g). l is a strict consensus tree for analysis A at L_{min+2}, analysis B at L_{min+2}, and analysis C at L_{min+3} (less *Chaloneria*). *Synchysidendron* and *Diaphorodendron* are not distinguished in Figures a–g as they consistently behave as sister groups. All character information is omitted.

Analysis A (all OTUs and all characters included). Analysis A yielded three equally most parsimonious trees (MPTs; Fig. 9a–c) that unite *Oxroadia* and *Paurodendron* as a basal clade. The preferred most parsimonious tree (PMPT) depicts the remaining genera as a perfectly nested sequence of increasingly apomorphic OTUs (Figs. 6, 9a). The three MPTs differ in the position of *Chaloneria*, which occurs immediately above *Anabathra* in the preferred MPT (Fig. 9a), immediately below *Anabathra* in the second MPT (Fig. 9c), and is united with *Anabathra* to form a monophyletic clade in the third MPT (Fig. 9b).

Decreasing the level of parsimony by adding one step (L_{min+1}) yields another eight generic topologies (Fig. 9d–k). Three of these unite *Sigillaria* with *Diaphorodendron–Synchysidendron* (Fig. 9e–g), otherwise repeating the three possible relationships between *Chaloneria* and *Anabathra* seen in Figure 9a–c. Four others dissociate the *Oxroadia–Paurodendron* clade, so that each arises directly from the major axis (Fig. 9d, h–j); three of these (Fig.

9h–j) also involve changes in the relative positions of *Anabathra* and *Chaloneria.* It is then equally parsimonious to have *Oxroadia* (Fig. 9d, j) or *Paurodendron* (Fig. 9h, i) as the basal OTU of the tree. The eighth topology unites *Sigillaria* and *Chaloneria,* linking both to *Anabathra* to form a substantially different topology (Fig. 9k).

At $L_{\min+2}$, some topologies unite *Chaloneria* and *Sigillaria,* others allow the exchange of *Hizemodendron* and *Sigillaria* across *Diaphorodendron–Synchysidendron* (cf. Fig. 9a). The putative *Sigillaria–Diaphorodendron–Synchysidendron* clade can be placed above *Hizemodendron.* Alternatively, placing *Chaloneria* immediately below *Anabathra* allows the *Sigillaria–Diaphorodendron–Synchysidendron* clade to be situated between or immediately below these genera. Together, the five genera can form a sister clade to *Hizemodendron–Lepidodendron–Lepidophloios,* either with *Chaloneria–Anabathra* and *Sigillaria–Diaphorodendron–Synchysidendron* as sister groups or as a nested clade ((((*Diaphorodendron–Synchysidendron*) *Sigillaria*) *Anabathra*) *Chaloneria*).

Analysis B (all OTUs, "habit" characters C1–C7 omitted). The two MPTs of analysis B are identical to two of the three MPTs of analysis A (Fig. 9a, b). Five additional topologies occur at $L_{\min+1}$; one fails to resolve the relationship between *Chaloneria* and *Anabathra* (dashed line on Fig. 9c), two unite *Sigillaria* and *Diaphorodendron–Synchysidendron* (Fig. 9e, f), and two allow dissociation of the *Oxroadia–Paurodendron* clade (Fig. 9d, h). At $L_{\min+2}$, *Chaloneria* can be united with *Sigillaria, Hizemodendron* and *Sigillaria* can be transposed across *Diaphorodendron–Synchysidendron,* and the putative *Diaphorodendron–Synchysidendron–Sigillaria* clade shown in Figure 9e can be placed above *Hizemodendron* or below *Anabathra* and *Chaloneria.* All topologies found in analysis B at $L_{\min+2}$ were also found in analysis A at $L_{\min+2}$.

Analysis C (Chaloneria omitted, all characters included). The only MPT from analysis C merely deletes *Chaloneria* from the preferred MPT of analysis A (Fig. 9a). Increasing the number of steps allow a *Sigillaria–Diaphorodendron–Synchysidendron* clade, either below ($L_{\min+1}$) or above ($L_{\min+2}$) *Hizemodendron,* and disaggregation of the *Oxroadia–Paurodendron* clade ($L_{\min+2}$). The range of topologies substantially increases at $L_{\min+3}$. Once again, *Sigillaria* and *Hizemodendron* can be exchanged across *Diaphorodendron–Synchysidendron.* A putative *Sigillaria–Diaphorodendron–Synchysidendron* clade can be placed low in the tree, between *Oxroadia–Paurodendron* and *Anabathra,* or it can be appended to *Anabathra* to yield a more innovative topology.

A strict consensus tree (Nelson, 1979, 1983) at $L_{\min+2}$ (analyses A, B) or $L_{\min+3}$ (analysis C), has only four nodes (Fig. 9l); only *Oxroadia* and *Paurodendron* (at the base of the tree), *Diaphorodendron* and *Synchysidendron,* and *Lepidodendron* and *Lepidophloios* (at the apex) are consistently conjoined and/or juxtaposed.

Analysis D (all OTUs, vegetative characters only). The preferred MPT for analysis D (Figs. 10a, 11) is pectinate (each genus is connected directly to the major axis) and differs substantially from the preferred MPT of analyses A–C (see also Bateman & DiMichele, 1991). *Lepidodendron* and *Lepidophloios* remain linked at the top of the tree, but two pairs of adjacent branches are transposed (*Sigillaria* and *Diaphorodendron–Synchysidendron, Anabathra* and *Chaloneria*). The *Oxroadia–Paurodendron* clade is split into its constituent genera, each of which forms an equally parsimonious sister group to the rest of the ingroup (Fig. 10a, b). *Hizemodendron* is sister group to the most derived genera *Lepidodendron* and *Lepidophloios* in the preferred MPT of analysis A (Fig. 9a), but is derived relative only to *Oxroadia* and *Paurodendron* in the preferred MPT of analysis D.

All of the variation among the eight additional generic topologies at $L_{\min+1}$ occurs below *Diaphorodendron–Synchysidendron* in the tree, indicating that the more apomorphic portion of the tree is the most robust. An unresolved trichotomy replaces the *Oxroadia–Paurodendron* clade (Fig. 10c). The remaining topologies place *Anabathra* below *Chaloneria* (Fig. 10d–f) or unite *Anabathra* and *Chaloneria* as a separate clade (Fig. 10g–j). *Hizemodendron* is the least stable genus; it can occur below (Fig. 10a–e, g, i) or above (Fig. 10f, h, j) *Anabathra* and *Chaloneria.* In the most radical topology, *Hizemodendron* is the sister group of *Anabathra* and *Chaloneria,* together forming a separate clade (Fig. 10k).

Analysis E (all OTUs, reproductive characters only). In contrast with the other analyses, it was not possible using PAUP 2.4 to store and thereby screen all 810 MPTs for analysis E (270 trees, if the equally most parsimonious solutions to the *Lepidophloios* species relationships are ignored). Available evidence suggests that the number of MPTs was grossly exaggerated by repeated polychotomies and conceals a much smaller number of substantially different topologies. A representative and fully annotated MPT is shown in Figure 12a.

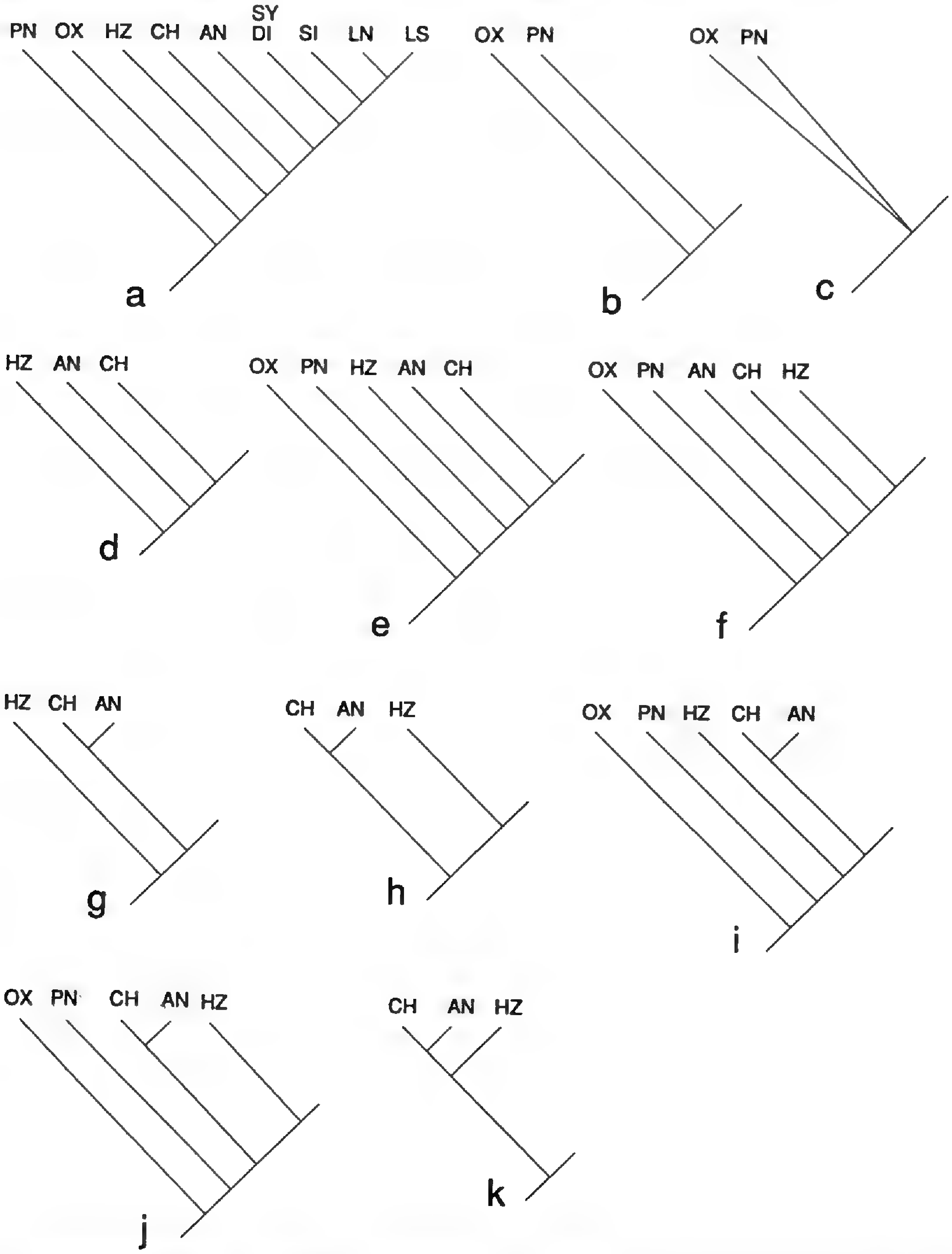

FIGURE 10. Generic topologies of analysis D (vegetative characters only) at L_{min} (a, b) and L_{min+1} (c–k). (See caption to Table 3 for key to abbreviations.) Only those portions of trees that differ from the preferred most parsimonious tree (a) are shown, and all character information is omitted.

Unlike analyses A–D, the relationship between the four most primitive OTUs is unresolved, as are the relationships between (1) the three species of *Diaphorodendron* sens. str., and (2) *Hizemodendron* and *Lepidodendron*. The most radical innovation is the depiction of *Lepidophloios* as polyphyletic; the relatively primitive *L. harcourtii* is separated from *L. johnsonii* and *L. hallii* by *Lepidodendron* and *Hizemodendron*. Restoring *Lepidophloios* to monophyly costs one additional step (Fig. 12b).

Methodological conclusions. For any cladistic matrix, progressive one-step increases in length relative to the MPT result in a rapid increase in the number of topologies obtained (Table 4). The gradient of this increase provides an estimate (albeit crude and dependent on matrix size) of the relative resolution of different data matrices; more confidence can be placed on a most parsimonious tree from a matrix that yields few alternative trees of optimal or near-optimal length (more rigorous, statistical methods are now available for determining confidence limits of specific topologies; e.g., Felsenstein, 1985; Archie, 1989b; Sanderson, 1989).

For our data, the complete data matrix (analysis A) provides a yardstick by which to measure the relative resolution of analyses based on selectively reduced permutations of the matrix presented in Table 3 (i.e., analyses B–E). Omitting the five synapomorphic habit characters (analysis B) yield-

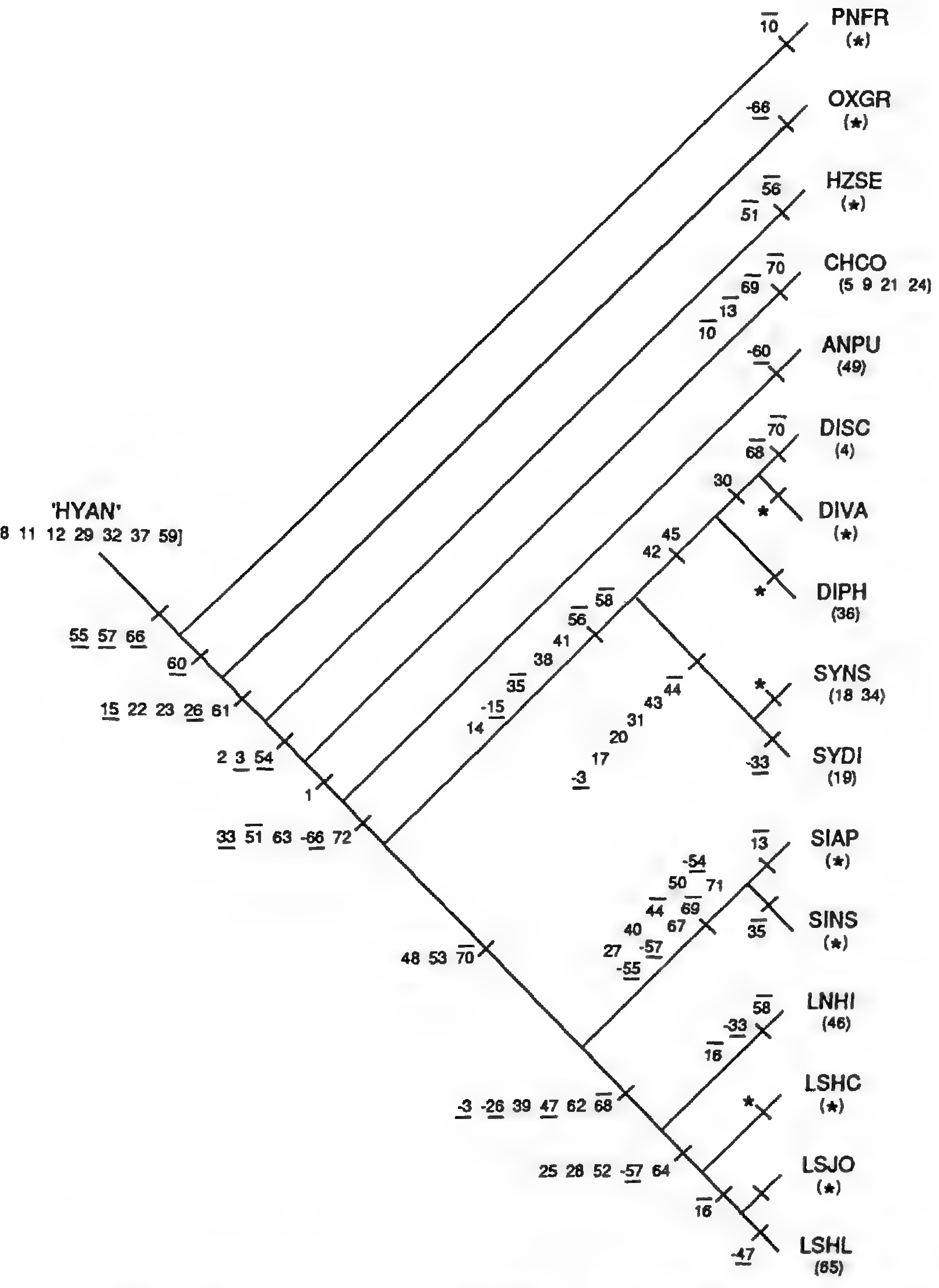

FIGURE 11. Preferred most parsimonious cladogram for analysis D (vegetative characters only). Character notation follows Figure 6, OTU notation follows Table 3.

ed fewer topologies of length L_{min}–L_{min+1} and slightly increased the consistency index (Table 4). Omitting *Chaloneria*, the least stable OTU (analysis C), increased the consistency index by a similar amount to that of analysis B and generated an even more highly resolved set of trees that included only one most parsimonious topology (Fig. 9a).

Substantially reducing the size of the data matrix analyzed by including only vegetative characters (analysis D) or only reproductive characters (analysis E) also increased consistency index values relative to those of analysis A. However, in contrast with analyses B and C, analyses D and E yielded less resolved sets of topologies (Table 4). Analysis D provided acceptable results (Fig. 10), but analysis E yielded 270 equally most parsimonious trees, all containing at least one polychotomy. Thus, it is tempting to argue that vegetative characters are more phylogenetically informative (i.e., less homoplastic) than reproductive characters, but levels of homoplasy are very similar in the MPTs of the vegetative and the reproductive submatrices (consistency index values = 0.66 and 0.67 respectively; Table 4). Rather, the crucial difference apparently lies in the different sizes of the submatrices, which are reflected in different values for the average number of synapomorphic character states per OTU: 3.2 in analysis D and 1.8 in analysis E. For the preferred MPT of our complete matrix, the number of steps per synapomorphy (1.6) and

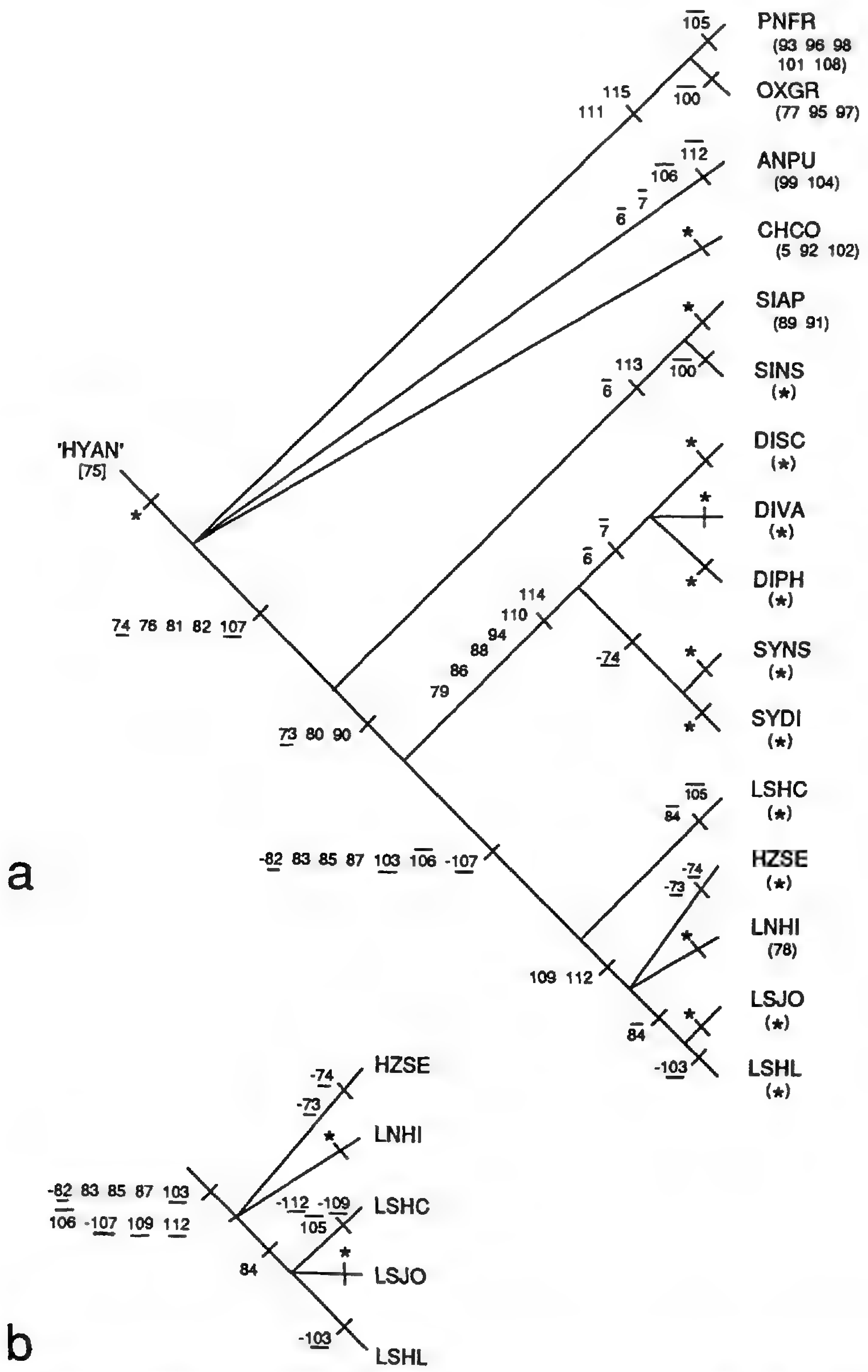

FIGURE 12. a. Preferred most parsimonious cladogram for analysis E (reproductive characters only). Character notation follows Figure 6, OTU notation follows Table 3.—b. Terminal portion of an alternative topology at L_{min+1}.

the resulting consistency index (0.63) are average relative to those of other cladistic data matrices containing similar numbers of OTUs (the main variable influencing consistency index values: cf. figs. 2a and 3 of Archie, 1989a; fig. 1b of Sanderson & Donoghue, 1989). Thus, we suggest that for a data matrix of average homoplasy (as here), there is a threshold of minimum empirical support (2–3 synapomorphies per OTU) below which well-resolved sets of fully dichotomous trees cannot be expected (see also Felsenstein, 1985; Guyer & Slowinski, 1991).

EMPIRICAL SUPPORT FOR ALTERNATIVE HYPOTHESES OF GENERIC RELATIONSHIPS

The relative merits of the topologies described above are best assessed by examining the optimized distributions of character state transitions across the trees and subjectively estimating the probabilities of alternative evolutionary scenarios for particular suites of characters. To this end, many of the near-optimally parsimonious pairings of genera obtained during the topological survey of analysis A are summarized in a single fully annotated tree

(Fig. 7), to enable comparison with the preferred most parsimonious tree (Fig. 6).

Oxroadia and Paurodendron. Oxroadia and *Paurodendron* share only two synapomorphies (Fig. 6). Both are nonhomoplastic and describe echinate distal and proximal surfaces of microspore exines (C111, C115). Disaggregating this clade induces parallelism in these characters, at the cost of one step (Fig. 7). Given that echinate microspore exines could be regarded as a single character, the status of these two genera as a monophyletic group may be even less well supported than parsimony suggests. A phylogenetic study focusing specifically on these and other similarly primitive genera is required to resolve this ambiguity.

Anabathra and Chaloneria. Topologies treating this group as paraphyletic (Fig. 6) or as a monophyletic clade (Fig. 7) are equally parsimonious, differing only in the distributions of a few homoplasies. When united, the genera possess only two synapomorphies: weakly branched or unbranched trunk apex (C3) and acutely angled leaf attachment (C66). Both characters are parallelisms: trunks with little or no branching are depicted as homoplastic, also occurring in *Sigillaria* and *Diaphorodendron.* Angle of leaf attachment, a character prone to ontogenetically related variation and ecophenotypic modification, is represented as a parallel trait in *Paurodendron* and *Hizemodendron.* Thus, evidence for an *Anabathra–Chaloneria* clade is weak.

Uniting *Anabathra* and *Chaloneria* affects optimized character state transitions elsewhere in the tree. In Figure 6, unbranched trunk apex (C3) is perceived as reversed in *Synchysidendron* and in the *Hizemodendron–Lepidodendron–Lepidophloios* clade, but in Figure 7 this character state is depicted as a parallel acquisition in *Anabathra–Chaloneria, Diaphorodendron,* and *Sigillaria.* The absence of a ligule cavity (C60) in *Anabathra* is a plesiomorphy in Figure 6 but a reversal in Figure 7. Missing values for C33 (secretory intracortical leaf sheaths) and C73 (branch gap associated with peduncle) in *Chaloneria* allow these characters to be optimized as apomorphic in Figure 6 (despite the absence of a cone in *Chaloneria*) but plesiomorphic in Figure 7.

Anabathra, Chaloneria, and Sigillaria. In analysis A, these genera formed a clade at $L_{\min+1}$ (Fig. 9k). *Chaloneria* and *Sigillaria* are united by two nonhomoplastic character states, fusiform rootlet gaps (C13) and V-shaped leaf traces (C69), and by the homoplasy of abaxial grooves in the leaf (C70). The apparent synapomorphy for C69 may be false if the V-shaped leaf trace of *Sigillaria* reflects origination from two protoxylem strands, and the abaxial grooves may be developmentally related to leaf trace morphology. *Anabathra* is united with *Chaloneria* and *Sigillaria* on the basis of two homoplasies reflecting habit: the trunk possesses an apex that shows little if any branching (C3) and bears lateral branches and/or cones (C6; a character that could not be coded for the branchless and coneless *Chaloneria*). Both states also characterize *Diaphorodendron* (Fig. 6).

Diaphorodendron and Synchysidendron. The distinction between the segregate *Synchysidendron* (*S. dicentricum* and *Synchysidendron* sp. nov.) and the three species of *Diaphorodendron* sens. str. is well supported (Fig. 6), the former by seven synapomorphies (four nonhomoplastic) and the latter by four synapomorphies (two nonhomoplastic). These characters, which represent habit sens. lat. (C3, C6–C7, C74), leaf base retention (C44–C45), stele histology (C17, C20, C31), and periderm histology (C42–C43), reflect two substantially different growth habits (see Evolutionary Patterns). Nesting *Synchysidendron* within *Diaphorodendron* requires a minimum of four extra steps in analyses A, C, and D, and three extra steps when habit characters C1–C7 are omitted (analysis B). Placing the genera on separate terminal branches is even less parsimonious. Although there is little doubt that *Diaphorodendron* sens. lat. (i.e., sensu DiMichele, 1985) is monophyletic, we believe that the differences between the two monophyletic groups of species that it contains are sufficiently profound to warrant segregation of the new genus, *Synchysidendron* (Appendix 1C).

Sigillaria and Diaphorodendron–Synchysidendron. Sigillaria and *Diaphorodendron–Synchysidendron* are empirically the best supported of all the clades under scrutiny; *Sigillaria* is supported by 14 characters (six nonhomoplastic), and *Diaphorodendron–Synchysidendron* by 15 characters (nine nonhomoplastic). Uniting *Sigillaria* with *Diaphorodendron–Synchysidendron* adds only one step and transforms two reproductive character states from parallelisms into nonhomoplastic synapomorphies: short, horizontal alations on the megasporophyll pedicel (C82), and crassitude microspore laesurae (C107). Balancing these gains, homoplasy is induced by losses in three character states: the presence of a lower keel on the leaf cushion (C55), germination of megaspores within the sporangium (C80), and reduction of viable megaspores to one per sporangium (C90, a logical functional correlate of C80). Although Figure 7 portrays these character state transitions as reversals in *Sigillaria*, they are more likely to represent parallel acquisitions in *Diaphorodendron–Synchysidendron* and in the more derived *Hizemodendron–Lepidodendron–Lepidophloios* clade (loss of these traits in *Sigillaria* would probably confer a severe competitive disadvantage). As all five of the above characters are considered potentially homoplastic, the possible monophyly of *Sigillaria–Diaphorodendron–Synchysidendron* remains equivocal.

Differential optimization alters perceptions of evolutionary patterns of three other characters in Figure 7. The first is stem apical branching (C3, already discussed under *Chaloneria–Anabathra*), and the remaining two describe leaf cushion morphology. In Figure 6, the plicate lower field (C57) evolves below *Diaphorodendron–Synchysidendron* and is subsequently lost in *Lepidophloios*, whereas in Figure 7 it is represented as a parallel acquisition in *Diaphorodendron–Synchysidendron, Hizemodendron*, and *Lepidodendron*. Similarly, in Figure 6, the upper keel evolves below *Diaphorodendron–Synchysidendron* and is lost in *Hizemodendron*, whereas in Figure 7 it evolves below the *Oxroadia–Paurodendron* clade (despite the absence of leaf cushions in these highly plesiomorphic genera) and is independently lost in *Sigillaria* and *Hizemodendron*. For both characters, the optimizations in Figure 6 are more intuitive.

Hizemodendron and Lepidodendron. As depicted in Figure 6, the branches immediately subtending *Hizemodendron* and *Lepidodendron* share only one character state transition: the loss of secretory intracortical leaf-trace sheaths (C33). The other four characters that support the *Hizemodendron–Lepidodendron* clade in Figure 7 are all parallelisms. Three describe microspore equatorial (C103) and contact face (C109, C112) ornamentation and are homoplastic among *Lepidophloios* species. Their frequencies and distributions differ between topologies, due to inconsistent optimization of missing values. These characters are more appropriately treated as reversals within *Lepidophloios* (Fig. 6) than as parallelisms in *Lepidophloios* and *Hizemodendron–Lepidodendron* (Fig. 7). In Figure 6, the fourth character state, plication of the lower field of the leaf cushion (C57), originates below *Diaphorodendron–Synchysidendron* and is reversed in *Lepidophloios*. In Figure 7, this character state originates twice, in *Diaphorodendron–Synchysidendron* and in *Hizemodendron* (a less probable scenario). Missing values allow demotion of infrafoliar parichnos from a nonhomoplastic synapomorphy of *Lepidodendron* and all *Lepidophloios* species (Fig. 6) to a parallelism of *Lepidodendron* and *Lepidophloios hallii* only (Fig. 7). Similarly, a missing value in *Hizemodendron* for multizoned periderm (C39) allows the genus to be plesiomorphic for this character in Figure 6 but apomorphic in Figure 7.

However, the most deleterious consequence of uniting *Hizemodendron* and *Lepidodendron* is the generation between *Lepidodendron* and *Lepidophloios* of five vegetative parallelisms: discernable protoxylem ridges on the stele (C26), resinous periderm (C48), tangentially elongate leaf cushions on twigs (C53), and a leaf with a dorsiventrally flattened vascular strand (C68) and lateral abaxial grooves (C70). The overall cost to parsimony (five steps) appears sufficient to reject the hypothesis of monophyly. Nevertheless, treating these hypothesized character state transitions as reversals in *Hizemodendron* suggests a heterochronic evolutionary mechanism that could allow monophyly (see Evolutionary Patterns).

Lepidodendron sens. lat. Prior to the studies of DiMichele (1985), Bateman & DiMichele (1991), and DiMichele & Bateman (1992), '*Lepidodendron*' sens. lat. encompassed four of the anatomically preserved genera analyzed by us: *Lepidodendron* sens. str., *Hizemodendron, Diaphorodendron*, and *Synchysidendron*. Forcing these four genera into a single clade representing the traditional concept of *Lepidodendron* (not illustrated) cost nine additional steps and revealed only one synapomorphy uniting the clade: a plicate lower field to the leaf cushion, which is reversed in *Lepidophloios* in the preferred MPT (Fig. 6). In contrast, five nonhomoplastic synapomorphies in Figure 6 are rendered homoplastic: short, erect megasporophyll alations (C83) and bilaterally flattened (C85), distally dehiscent (C87) megasporangia are lost in *Diaphorodendron–Synchysidendron*, and zoned periderm (C39) and infrafoliar parichnos (C62) become parallelisms in *Lepidodendron* and some *Lepidophloios* species as a result of ambiguous missing values in the latter. Moreover, homoplasy is increased in other characters already depicted as homoplastic in Figure 6. We conclude that '*Lepidodendron*' sens. lat. is clearly a paraphyletic group.

MULTIVARIATE ANALYSIS

In order to examine patterns of morphological variation free from the rigid constraints imposed by cladistic nested hierarchies, we subjected the cladistic data matrix (Table 3) to multivariate analysis. A value of zero or unity was substituted a priori for each missing value according to optimized distributions of character state transitions in the preferred most parsimonious cladogram (Table 3 subscripts, Fig. 6). The resulting uniformly binary matrix allowed generation of a symmetrical matrix comparing OTUs without a priori standardization, simply using the number of character state conflicts (i.e., 0 vs. 1) as a direct measure of dissimilarity between pairs of OTUs. The dissimilarity values were used to construct an unrooted minimum spanning tree (Gower & Ross, 1969); links in the tree represent specific sets of character state transitions, thus contradicting frequent assertions that phenetic trees inevitably lack such information. Also, principal coordinates (Gower, 1966) were calculated from the data matrix via Manhattan distances, using unpublished software written by J. Alroy. Holapomorphies (which are invariant) were excluded (as in cladistic analysis), but autapomorphies contributed to both the unrooted tree and the ordination.

Links between genera on the minimum spanning tree (Fig. 13a) represent at least 10 character conflicts, those within genera represent no more than five. The 21 conflicts between *Hizemodendron* and *Lepidodendron*, and 14 conflicts between *Synchysidendron* and *Diaphorodendron*, emphasize the need to segregate these new genera (Appendix 1C).

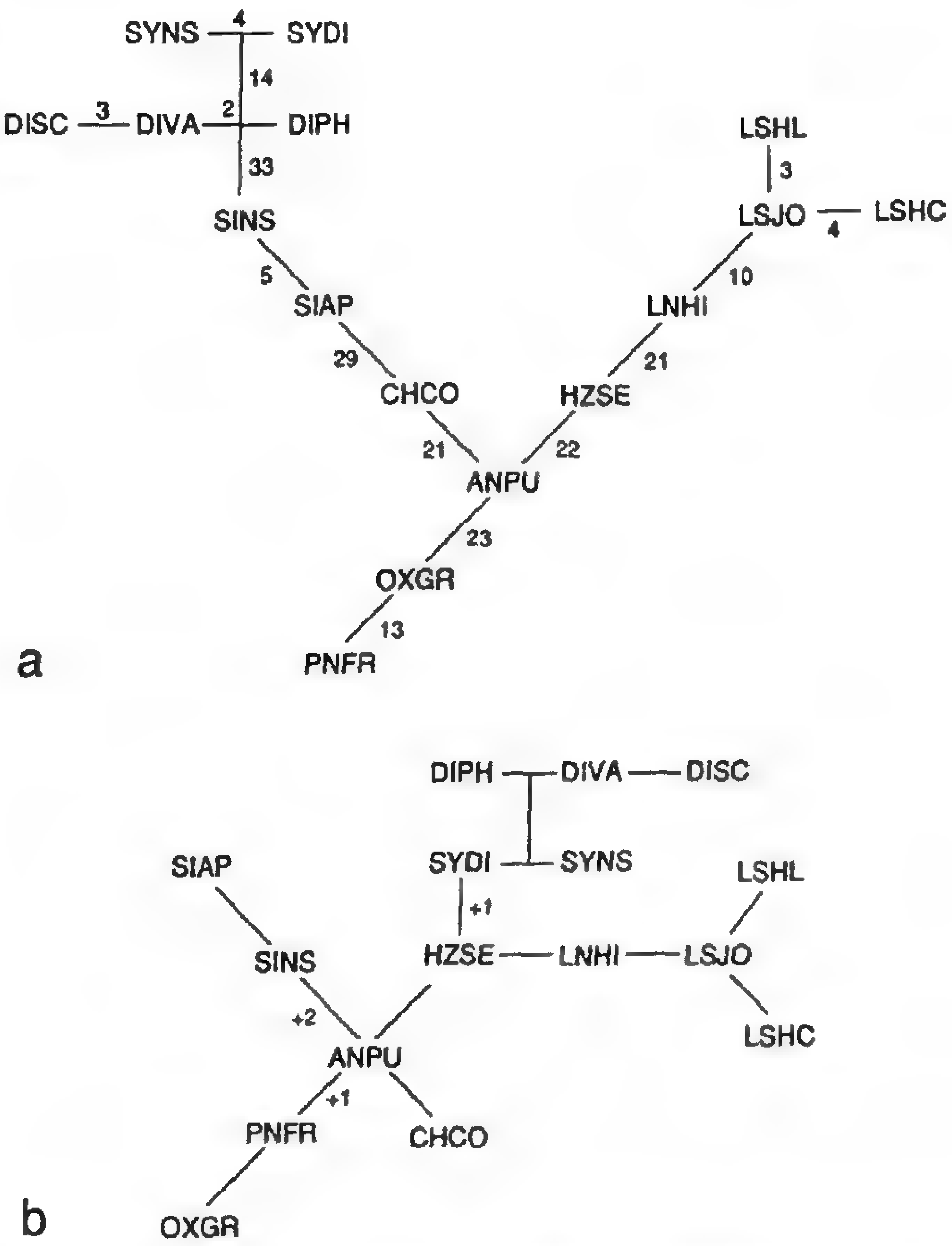

FIGURE 13. a. Minimum spanning tree (unrooted phenetic tree) as based on cladistic data matrix (Table 3, q.v. for key to OTUs). Links represent numbers of character state conflicts.—b. Alternative links that are almost maximally parsimonious; additional steps relative to a are marked.

The minimum spanning tree resembles the preferred most parsimonious cladogram (Fig. 6) in depicting a progression from *Paurodendron* and *Oxroadia* through *Anabathra*, *Hizemodendron*, and *Lepidodendron* to *Lepidophloios* (though *L. johnsonii* is shown as ancestral to the two remaining species). However, *Anabathra* is also depicted as the ancestor of a second lineage, consisting of *Chaloneria*, *Sigillaria*, *Diaphorodendron*, and *Synchysidendron*, that is not represented among the range of cladograms shown in Figure 9. This second lineage is held together by the weakest links in the tree (*Chaloneria–Sigillaria* = 29 conflicts, *Sigillaria–Diaphorodendron* = 33 conflicts) and consequently can be dissociated at the cost of very few additional steps (Fig. 13b), demonstrating that these genera are the most problematic in both the cladistically and phenetically generated phylogenies. Attaching *Sigillaria* directly to *Anabathra*, rather than via *Chaloneria*, creates an intuitively more credible evolutionary hypothesis at the expense of two steps. *Diaphorodendron* and *Synchysidendron* can be attached to *Hizemodendron* at the cost of only one step, but this results in the putatively more derived *Synchysidendron* giving rise to the more primitive *Diaphorodendron*. *Paurodendron* can replace *Oxroadia* as the closer relative of *Anabathra* at the cost of one step.

In summary, the phenetic trees serve primarily to emphasize the potentially pivotal role of *Anabathra* as the most primitive arboreous lycopsid analyzed.

The first three principal coordinates (Fig. 14) account for an unusually large proportion (91%) of the total variance. The first coordinate separates *Diaphorodendron–Synchysidendron* from the other genera, the second coordinate separates *Lepidodendron–Lepidophloios* from the bisporangiate-coned group of *Paurodendron–Oxroadia–Anabathra–Chaloneria* (with *Hizemodendron* intermediate), and the appreciably weaker third coordinate separates *Sigillaria* (and, to a lesser extent, *Chaloneria*) from the remainder. The resulting tetrahedral arrangement of four clusters (excluding *Hizemodendron*), separated by broad morphological discontinuities, underlines the distinctiveness of the three groups of monosporangiate-coned trees (*Sigillaria*, *Diaphorodendron–Synchysidendron*, *Lepidodendron–Lepidophloios*) and the consequent difficulties of resolving their phyloge-

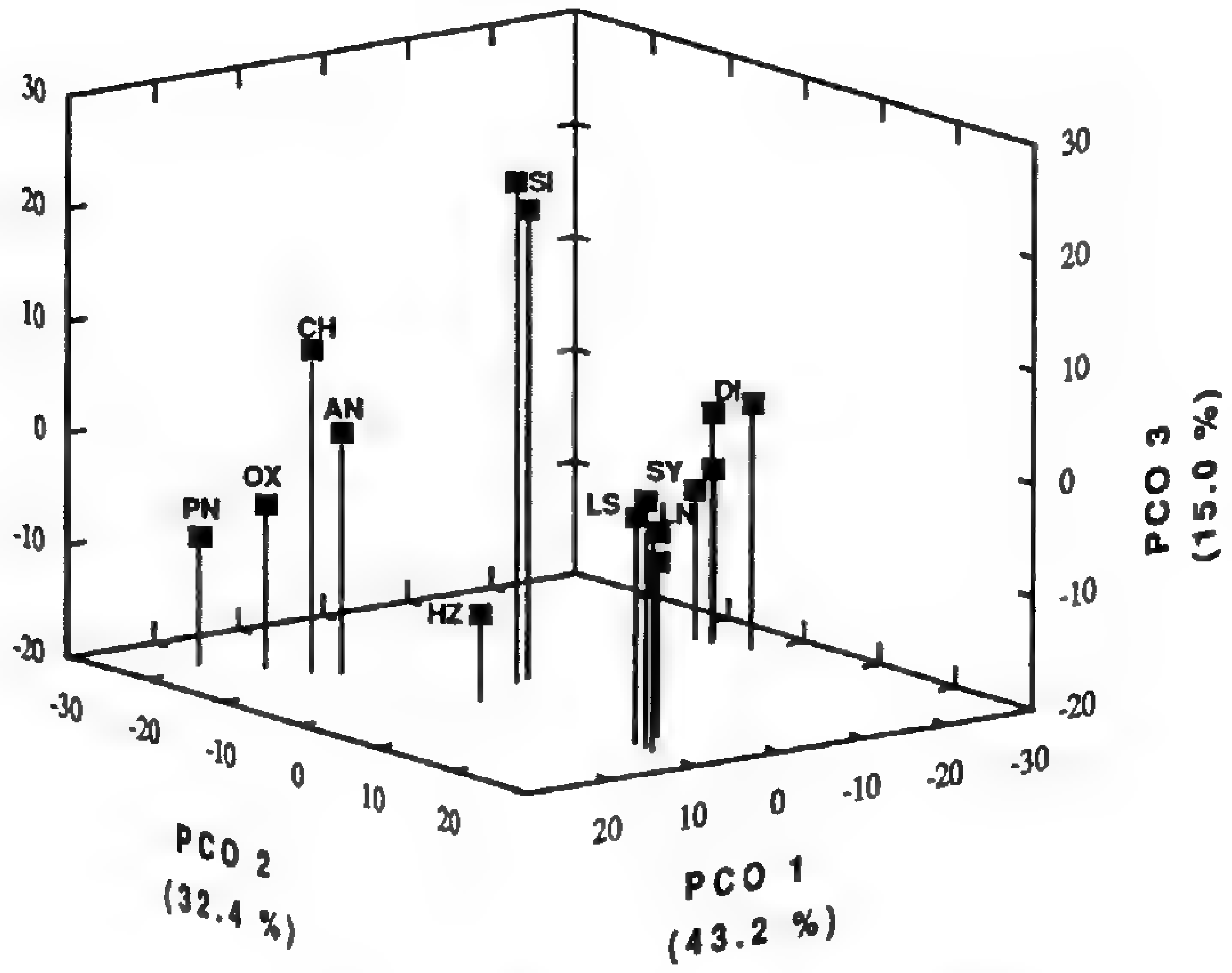

FIGURE 14. Principal coordinates ordination of the OTUs, based on Table 3 (q.v. for OTUs). Only genera are labeled. Two *Diaphorodendron* species are indistinguishable on the first three coordinates.

netic relationships relative to each other and to *Anabathra*, their most likely sister group.

EVOLUTIONARY PATTERNS AND PROCESSES

Overall trends. Much of the variation among arborescent lycopsids can be resolved into a vegetative trend, reflecting in particular morphological and anatomical expression of different growth architectures, and a reproductive trend, representing increasingly sophisticated reproductive strategies. The phylogenetic analyses show that the two trends are not entirely concordant; the preferred MPTs using vegetative characters only (analysis D; Fig. 11) and reproductive characters only (analysis E; Fig. 12) have substantially different topologies. The following discussion of these trends emphasizes characters for which we developed strong (often a priori) hypotheses of high burden and pays particular attention to the relative temporal order of appearance of apomorphic states of different characters (e.g., Donoghue, 1989).

Many (possibly all) of the MPTs of analysis E (reproductive characters only) distinguish the four bisporangiate-coned genera (*Paurodendron*, *Oxroadia*, *Anabathra*, *Chaloneria*) from the five relatively derived genera that possess a suite of characters reflecting the developmental partitioning of mega- and microsporangia into monosporangiate cones (Fig. 12). In contrast, the preferred MPT of analysis D (vegetative characters only) distinguishes four primitive pseudoherbs/shrubs (*Paurodendron*, *Oxroadia*, *Hizemodendron*, *Chaloneria*) from five derived arboreous genera (the derived clade is supported by the tree habit *only*; Fig. 11) and depicts *Sigillaria* as derived relative to *Diaphorodendron–Synchysidendron*. The genera whose positions differ most between the reproductive and vegetative cladograms are the bisporangiate-coned tree *Anabathra*, which is reproductively plesiomorphic and vegetatively apomorphic, and the monosporangiate-coned pseudoherb *Hizemodendron*, which is reproductively apomorphic and vegetatively plesiomorphic (see also Bateman & DiMichele, 1991).

Thus, monosporangiate cones (Fig. 12) and the tree habit (Fig. 11) cannot both be nonhomoplastic, though a full analysis using vegetative and reproductive characters together could have yielded a compromise solution involving homoplasy in both suites of characters. In fact, although its topology differs in detail from those of analyses D and E, the preferred MPT for analysis A (all characters and OTUs; Fig. 6) more closely resembles the exclusively reproductive cladogram (Fig. 12) than the exclusively vegetative cladogram (Fig. 11); in particular, the monosporangiate-coned clade is retained at the expense of depicting the tree habit as homoplastic.

The two subsections that follow discuss in greater detail the reproductive and vegetative trends, focusing on the functional morphology and adaptive (or nonadaptive) significance of specific character states, before returning to the evolutionary implications (and limitations) of the preferred whole-organism cladogram.

Reproductive morphology. Reproductive characters proved to be of little value in elucidating phylogenetic relationships within the plesiomorphic group of bisporangiate-coned OTUs, which differ primarily in autapomorphic spore character states (Fig. 12). Careful revision of bisporangiate cones is desirable, to search for potential synapomorphies less inclusive than the entire group. It is particularly important to understand the ontogeny and reproductive biology of the bisporangiate cones in order to determine how they could have given rise to monosporangiate-coned descendants. All bisporangiate cones have apically concentrated microsporangia and basally concentrated megasporangia irrespective of presumed geotropic orientation, suggesting a shared developmental control of sporogenesis.

In contrast, the functional morphology of reproductive characters within the monosporangiate-coned portion of the lepidodendralean clade has prompted much discussion (e.g., Thomas, 1978; Phillips, 1979; DiMichele & Phillips, 1985; Phillips & DiMichele, 1992; see Appendix 1D for the taxonomic implications). In Figures 6 and 12, the appearance of monosporangiate cones (immediately below *Sigillaria*) is accompanied by lateral expansion of the sporophyll pedicel to form alations and by the functionally important transition in basic dispersal unit from isolated megaspores to the megasporophyll-megasporangium complex. All three character states persist without reversal throughout the derived clade, indicating strong functional linkage that may be evolutionarily tied to elaboration of the leaf bases.

Current evidence suggests that the leaf lamina and leaf base are derived from the same primordium; the leaf cushion, an elaborated leaf base, is also fundamentally foliar. Furthermore, we believe that the sporophyll lamina is homologous with the leaf lamina, and that the sporangium-bearing pedicel is homologous with the leaf base, including an elaborated cushion if present. The strongest evidence supporting these homologies is provided by the ligule (e.g., Phillips, 1979; Bateman, 1988), which occurs adaxially on (*Paurodendron*) or within (all other OTUs) the bases of leaves (Fig. 4b) but on sporophylls occurs close to the distal end of the pedicel, between the sporangium and the more-or-less perpendicular junction of the pedicel and lamina (Fig. 4d). Regarding the attachment of the ligule as a homologous point implies that the pedicel is indeed homologous with the leaf base. Both the leaf base (and thereby cushion) and lamina originate from the same primordium, as do the sporophyll pedicel and lamina. Leaf and sporophyll both bear a ligule and both are fundamentally appendicular in origin. Moreover, there is a strong positive correlation between the complexity of the pedicel-sporangium unit and that of the leaf base; definable leaf cushions appear at the same node of the cladogram as monosporangiate cones, and both structures progressively increase in complexity through the remainder of the clade, culminating in the large, elaborate leaf cushions and equally large, seedlike megasporophyll of *Lepidophloios* (e.g., Reed, 1941; Phillips, 1979). Thus, the evolution of the leaf cushion may have been developmentally linked to that of the sporophyll (T. L. Phillips, pers. comm. 1989). It is not clear whether elaboration of the leaf prompted modification of the sporophyll, or whether increase in size of the appendicular primordial meristems allowed simultaneous expansion and elaboration of both leaf bases and sporophyll pedicels.

Whatever its driving mechanism, the transition from bisporangiate to monosporangiate cones (immediately below *Sigillaria* on Figs. 6 and 12) represents a crucial release from developmental constraints (cf. Endress, 1987, on angiosperms). In particular, it allowed spatially independent development of the mega- and microsporophylls, thereby permitting modifications of the megasporophyll-megasporangium units that could have impaired the function of microsporophyll units if similarly modified (a likely consequence in bisporangiate cones, where mega- and microsporophylls form a developmental continuum). Thus, free megaspores were superseded as the basic dispersal unit by the megasporophyll-megasporangium complex.

The remaining reproductive modifications that delimit increasingly exclusive portions of the monosporangiate-coned clade can be envisioned as a progressive evolutionary trend toward *K*-selection (sensu Pianka, 1970). Megaspores decrease in number and increase in size, and the pedicellate tissues surrounding the megasporangium become adapted for increasingly specialized modes of microspore/microgametophyte capture and diaspore dispersal (e.g., Phillips, 1979). However, arguments that the most derived product of this evolutionary trend, *Lepidophloios–Lepidocarpon*, possesses true seeds (Zhang et al., 1986) are phylogenetically unhelpful; the megasporophylls are clearly analogs rather than homologs of gymnosperm ovules.

Reduction in megaspore number to one per sporangium, and concomitant germination of megaspores within the sporangium, distinguish the remainder of the monosporangiate-coned clade from *Sigillaria* (Figs. 6, 12). The dichotomy immediately above *Sigillaria* results in two clades well supported by reproductive characters: *Diaphorodendron–Synchysidendron* (proximally dehiscent, dorsiventrally flattened, heterocellular megasporangium containing gulate megaspores; granulate-foveolate *Granasporites* microspores), and *Hizemodendron–Lepidodendron–Lepidophloios* (distally dehiscent, cylindrical sporangium subtended by suberect alations; cingulate *Lycospora* microspores). Enveloping, integumentlike alations delimit *Lepidophloios* (Fig. 6; in the analysis of reproductive characters only (Fig. 12a), this single character is insufficient to override differences in microspore ornamentation between *Lepidophloios* species, resulting in depiction of the genus as polyphyletic; inducing monophyly in *Lepidophloios* costs one extra step (Fig. 12b)). Interestingly, the vegetatively well-differentiated species of *Diaphorodendron* and *Synchysidendron* (Fig. 11) are effectively uniform in reproductive characters (the medullated stele attributed to *Diaphorodendron* (C74) strictly applies to the cone-bearing lateral branches rather than the cones per se; Appendix 1D).

Distinguishing between monoecious and dioecious strategies is especially valuable in interpreting the phylogeny and the functional morphology of extant plants (e.g., Bawa, 1980; Givnish, 1980, 1982; Donoghue, 1989). Unfortunately, the almost inevitable disarticulation of cones from vegetative axes undermines attempts to identify the reproductive strategies adopted by members of the monosporangiate-coned lycopsid clade. Were individual plants monoecious or dioecious? If monoecious (as seems more likely), did megasporangiate and microsporangiate cones mature synchronously or sequentially? Or were arborescent lycopsids capable of even more complex strategies, such as gynodioecy?

Overall, spore morphology proved less phylogenetically informative than cone morphology. Many of the spore character states are species-level autapomorphies, and the remainder exhibit significantly greater homoplasy than cone characters (in Fig. 6, the proportion of holapomorphies plus autapomorphies and consistency index for cone and sporophyll characters are 26% and 0.78 respectively, contrasting with values of 42% and 0.64 for mega- and microspore characters). In retrospect, some cases of mistaken homology are clearly evident among spore characters. For example, the distal spines (C100) of *Oxroadia* and *Sigillaria* sp. nov. megaspores differ in detail; those of the former are long and buttressed, those of the latter are short and almost papillate. Also, polarization of spore characters was especially problematic, as character states (especially those representing ornamentation) tend to replace each other in entirety rather than accumulating as sequential elaborations of form (i.e., they are displacive rather than additive). Consequently, patterns of increasing complexity cannot be expected. Indeed, many spore character states (including the more elaborate forms of ornamentation) are confined to the primitive, bisporangiate OTUs. Reduction to a single functional megaspore resulted in the loss of all types of dispersed ornamentation (Table 3), suggesting that they were redundant once megaspores had ceased to be the basic units of dispersal.

Relatively little attention has been paid to the functional morphology of lycopsid spores. Prominent equatorial (*Paurodendron, Chaloneria*) and laesural (*Paurodendron, Oxroadia, Diaphorodendron, Synchysidendron*) megaspore ornamentation has been invoked as an aid to flotation and thereby dispersal. Phillips (1979) argued that openings in the massa of *Diaphorodendron* and *Synchysidendron* megaspores trapped microspores to facilitate fertilization, and a similar function was attributed to the anastomosing fimbriate laesural ornamentation of *Oxroadia* megaspores by Bateman (1988). The pseudosaccus of *Chaloneria* microspores and cingulum of *Hizemodendron, Lepidodendron,* and *Lepidophloios* microspores probably acted as buoyancy aids.

Vegetative morphology. Vegetative characters uniting the arborescent lycopsids are those associated with the production of rhizomorphs and wood, together with ligules and exarch xylem maturation (inferred centrifugal maturation in stigmarian rhizomorphs (Frankenberg & Eggert, 1969) is suspect (Phillips & DiMichele, 1992)). Beginning at the root of the preferred MPT and passing along its major axis (Fig. 6), the node above *Paurodendron–Oxroadia* is characterized by the appearance of the tree habit (habit is discussed more fully in subsequent subsections) and by modifications to vascular tissue that probably reflect greatly increased body size: medullation of the stele, continuous protoxylem sheath, loss of protoxylem ridges (together causing superficial leaf trace emission: Fig. 5b), and the advent of foliar parichnos in the leaf bases, now much more distant from the axial vasculature following acquisition of the arboreous habit. Beyond *Anabathra,* the ligule pit is ubiquitous, though it also occurs in the ostensibly primitive genus *Oxroadia.*

Beyond *Chaloneria,* the evolution of discrete leaf cushions provided a consistent basal limit to leaf atrophy. Many of the characters that support nodes higher in the cladogram represent elaborations of leaf cushion morphology, notably in cushion complexity below *Diaphorodendron–Synchysidendron,* and in overall shape below *Lepidodendron–Lepidophloios.* In contrast, cushion and leaf-trace simplification is evident in *Hizemodendron.* The analysis of vegetative characters only (Fig. 11) places *Hizemodendron* much lower in the tree, eliminating the many character losses shown in Figure 6 but depicting the leaf cushion per se as iterative in (a) *Hizemodendron* and (b) all of the arboreous genera, shown clustered above *Chaloneria* in Figure 11 (also, arbitrary optimization of missing values representing the absence of coded structures led to the nonsensical apparent evolution of specific leaf cushion features below *Paurodendron,* prior to the evolution of the cushions themselves). Further modifications of cushion shape, together with the appearance of infrafoliar parichnos and a return to longitudinal protoxylem ridges, characterize the highly derived *Lepidodendron–Lepidophloios* clade (Fig. 6).

Stelar characters, together with peridermal features, play important roles in the more derived portion of the arborescent lycopsid clade, particularly in delimiting the three main cushion-bearing clades: *Sigillaria*, *Diaphorodendron–Synchysidendron*, and *Hizemodendron–Lepidodendron–Lepidophloios*. The solid protosteles of *Oxroadia* and *Paurodendron* give way to medullation by parenchymatous vitalization in the remaining genera. In most of these, the central portion of the stele consists of parenchyma cells that have lengths and diameters similar to those of the innermost metaxylem tracheids; these appear to be procambial cells that remained unlignified and thus metabolically active throughout the life of the plant. In the largest axes of *Lepidodendron* and *Lepidophloios* (less *L. harcourtii*), the stelar core consists of filamentous cells that probably proliferated into a central void. In contrast with the other lycopsid genera but in parallel with ferns, the *Diaphorodendron–Synchysidendron* clade evolved a true siphonostele. Pith parenchyma cells are much shorter and narrower than the adjacent metaxylem tracheids, suggesting different developmental origins for these tissues. *Diaphorodendron* has a mixed pith of parenchyma and tracheids, with parenchyma increasing in relative abundance toward the centers of larger axes. *Synchysidendron* has a pith region sharply delineated from the tracheary cells, and wood with heterogeneous rays and deep parenchymatous invaginations.

Most characters of the stelar margin constitute genus-level autapomorphies, notably the distinctly different modes of leaf trace emission observed in *Chaloneria*, *Sigillaria*, and *Lepidophloios* (Fig. 5). Of greater interest is the apparent switch from distinct longitudinal protoxylem ridges (yielding "coronate" cross sections) to no discernible ridges immediately above the primitive *Paurodendron–Oxroadia* clade, followed by a return to similar (but not identical) coronate morphology in the most derived *Lepidodendron–Lepidophloios* clade; the protoxylem ridges are further modified in *Lepidophloios*, where they anastomose (Fig. 6). Derivation of *Hizemodendron* from *Lepidodendron* (contra Fig. 12; see Heterochrony) would imply loss of protoxylem ridges. We suggest that the loss of ridges does not reflect complete absence of discrete protoxylem strands, even though the strands are no longer discernible.

Cortical characters of the arborescent lycopsids are surprisingly conservative compared with the other axial tissues. The persistent inner cortex may have provided a barrier of live cells along the outer margin of the phloem, protecting this delicate tissue from exposure to the central void created by the presumed in vivo disintegration of the thin-walled parenchyma of the middle cortex. The medullated steles of *Diaphorodendron* and *Synchysidendron* emit leaf traces that are sheathed by parenchyma when passing through the outer cortex, a character state also found in *Sigillaria* sp. nov. Leaf traces are secretory in most of the arboreous species analyzed.

Periderm is arguably the most unusual and developmentally intriguing vegetative tissue in arborescent lycopsids. As with stelar morphology, the *Diaphorodendron–Synchysidendron* clade is distinct from the other cushion-bearing arboreous genera. Bifaciality in the former group is evident in the clear histological distinction between the thin phellem and much thicker phelloderm. The relatively homogeneous periderm of the latter group may conceal cryptic cambial bifaciality (for example, this may be manifested in the peridermal trizonation of *Lepidodendron–Lepidophloios*), especially if the phellem is very weakly developed or the phellem and phelloderm are histologically identical. Details of periderm histology tend to be homoplastic or species-level autapomorphies, and therefore of limited phylogenetic value. In the analysis of vegetative characters only (Fig. 11), promotion of *Sigillaria* to sister group of the *Lepidodendron–Lepidophloios* clade united the three genera that possess resinous periderm. However, the other two characters supporting this node (cushions on twigs wider than long, leaves with lateral abaxial grooves) are almost certainly miscoded as homologs shared by *Sigillaria* and *Lepidodendron–Lepidophloios*.

Periderm, the main support tissue of the arboreous lycopsids, reached thicknesses of at least 20 cm in some species (DiMichele, 1979a, b, 1981; Phillips & DiMichele, 1981). This considerable increase in trunk girth over that of the primary tissues is difficult to reconcile with the persistence of primary leaf cushions, which probably remained photosynthetic after leaf loss; they are covered in stomata (Thomas, 1970b, 1977; DiMichele, 1979a, b), and both leaf traces and parichnos connections with leaf cushions were maintained through the periderm (Delevoryas, 1957; DiMichele, 1980). Several specialized mechanisms for accommodating girth increase evolved: tangential interarea expansion in *Sigillaria* and *Synchysidendron*, interarea fissuring in *Diaphorodendron*, and subcushion cellular expansion in *Lepidodendron* (DiMichele, 1981, 1983). In arboreous genera with well-developed crowns (*Synchysidendron*, *Lepidodendron*, *Lepidophloios*), periderm thickness diminished through the branching systems and the cortex was probably a major support tissue.

Given the determinate growth of arborescent lycopsids (Andrews & Murdy, 1958; Eggert, 1961), most of the periderm probably formed and differentiated near the stem apex, during (though probably continuing after) differentiation of the primary cortex, leaf cushions, and traces. This coordinated development is indicated by the persistence of the vascular linkages between the stele and leaf cushions through the periderm, and the occurrence of arboreous genera lacking specialized cushion-retention mechanisms (*Anabathra, Lepidophloios*). This mode of growth implies a stem apex analogous to the primary thickening meristem of some monocotyledonous angiosperms, an assertion previously made for stigmarian apices (Rothwell & Pryor, 1990, 1991). Unfortunately, there have been few discoveries of anatomically preserved stigmarian apices (Rothwell, 1984; Rothwell & Pryor, 1991) and none of stem apices, despite detailed and prolonged studies of coal balls. Their rarity may be at least partly explained by preferential decay of the apex, as observed in *Oxroadia* branches (Bateman, 1988). Rapid trunk elongation is suspected in the arboreous species (Phillips & DiMichele, 1992).

The most significant transitions in leaf base characters are the evolution of leaf cushions immediately below *Sigillaria* and their elaboration immediately above, involving the advent of upper and lower keels and lower field plications. The upper keel was subsequently lost in *Hizemodendron*, as were the lower field plications in *Lepidophloios*. Moreover, iteration is evident in several cushion characters: upper field plication in *Diaphorodendron–Synchysidendron* and *Hizemodendron*, the lateral line in *Diaphorodendron–Synchysidendron* and *Lepidodendron*, and the undoubtedly nonhomologous broader-than-long leaf cushions on the twigs of *Sigillaria* and *Lepidophloios*. Such convergences extend beyond the coded characters; for example, the similarity between *Synchysidendron* and *Lepidodendron* leaf cushions is reflected even in patterns of shape change from large to small branches. Also, cushions of both genera are protuberant and therefore have deep ligule pits. Only the infrafoliar parichnos of *Lepidodendron* allow distinction of its axial surface from that of *Synchysidendron*. Thus, many of the characters detailing leaf cushion morphology that have figured so prominently in previous classifications of Paleozoic lycopsids are shown to be homoplastic.

We regard the leaf cushions of derived genera as elaborated leaf bases of their more primitive antecedents such as *Anabathra*, which lacks a clear lamina-cushion distinction. Several features of the leaf base, notably the position of the ligule, suggest development from a leaf primordium. If so, the so-called "abscission" of leaves, which leaves a scar immediately external to the ligule pit aperture, occurred within the leaf rather than at the leaf-axis junction. Moreover, there is no evidence of a discrete abscission layer. Thus, we suspect that leaf laminae merely withered and sheared off at the physically weakest point, where the leaf constricts and is perforated by the ligule pit and, in the more derived genera, by the foliar parichnos.

Acute leaf posture is strongly homoplastic, characterizing unrelated genera with relatively short, broad laminae (*Paurodendron, Anabathra, Chaloneria, Hizemodendron*). The derived arboreous genera (above *Chaloneria*) all possess leaves with sclerenchymatous sheaths, which presumably supported the long, narrow laminae. Interestingly, the sheaths were lost in the short-leaved pseudoherb *Hizemodendron* (Fig. 6). Expansion and invagination of traces may also have aided structural support; dorsiventrally flattened traces characterize the *Lepidodendron–Lepidophloios* clade and *Diaphorodendron scleroticum*, V-shaped traces occur in *Chaloneria* and *Sigillaria*. Such vascular elaboration is invariably manifested externally as lateral abaxial grooves. The V-shaped trace of *Sigillaria* is an inevitable consequence of the vascularization of each leaf by two adjacent protoxylem strands of the parent axis and results in a median abaxial groove in addition to the lateral grooves. Postmortem accentuation of the grooves may have occurred (cf. Rex, 1986).

Arborescent lycopsids as integrated homeostatic organisms. Analogizing arborescent lycopsids with woody seed plants or tree ferns is unsatisfactory when considered in detail; in particular, periderm rather than wood constitutes the main physical support system, and the primary function of branches is reproduction rather than light capture (DiMichele & Phillips, 1985; Phillips & DiMichele, 1992). Perhaps the most profound character distinguishing the arborescent lycopsids is their determinate growth (Walton, 1935; Andrews & Murdy, 1958; Eggert, 1961), which allows analogy with the ontogeny of vertebrates and legitimate use of the terms body and bauplan (Bateman & DiMichele, 1991).

The body of each arborescent lycopsid is composed of at least two of four major determinate structural units (modules): rhizomorph, stem (defined as the length of the axis from the point of root-shoot divergence to the first isotomy of the apical meristem), crown branches (resulting from isotomy of the apical meristem), and lateral branches/cauline peduncles (resulting from strong anisotomy of the apical meristem) (DiMichele & Bateman, 1989; Bateman & DiMichele, 1991). Rhizomorph and stem are ubiquitous modules, though both occur in a severely reduced form in some OTUs. Lateral branches/cauline peduncles and crown branches are each rare or absent from some OTUs, thus defining three basic bauplans: (1) neither type of branch present, (2) crown branching frequent, lateral branching generates peduncles only, and (3) crown branching infrequent, lateral branching dominant. Variations in the sizes and secondary tissue contents of all four modules, and in the frequency of dichotomy of lateral and crown branches, generate a range of growth habits (e.g., Hallé & Oldeman, 1970; Hallé et al., 1978; White, 1979; Tomlinson, 1982, 1983). We suspect that growth of the arborescent lycopsids in general, and arboreous taxa in particular, was largely deterministic (genetically induced), offering much less potential than angiosperms for opportunistic modification of growth architecture by environmental influences or chance factors (e.g., Tomlinson, 1982). Consequently, the conceptual architectural model was unusually faithfully reproduced in the actual habit (Bateman & DiMichele, 1991).

The three basic bauplans outlined above broadly correspond to three of the growth models reviewed by Hallé et al. (1978); two can be subdivided using growth habit.

Bauplan (1) corresponds to Corner's architectural model. In our analysis, this exclusively monoaxial growth is confined to *Chaloneria*, though several penecontemporaneous lycopsids apparently possessed the same habit; these include *Spencerites* (Leisman & Stidd, 1967), *Sporangiostrobus* (Wagner & Spinner, 1976; R. H. Wagner, 1989), *Porostrobus* (Leary & Mickle, 1989), and the as yet unnamed, almost fully articulated compression from the Upper Devonian Cleveland Shale of Ohio (Chitaley, 1982, 1988; S. Chitaley & K. B. Pigg, in prep.). *Chaloneria* is the only OTU in our analysis that consists only of the two ubiquitous modules, a rhizomorph and an unbranched stem (Pigg & Rothwell, 1983a). We have classified its repeated zones of cauline sporophylls as lateral rather than terminal fructifications, as their production did not necessarily result in cessation of stem growth. The wood cylinder is narrow and the stem erect but much shorter than those of the truly arboreous OTUs (cf. Fig. 2b with Fig. 2a–g). The low wood content and lack of branches and cones in *Chaloneria* demonstrate highly economical construction, implying rapid growth. Distributional evidence suggests that *Chaloneria* was an ecological dominant in marshlike associations (DiMichele et al., 1979).

Bauplan (2), which corresponds to Schoute's architectural model, is the most widespread among the OTUs. Stems divide acrotonously (distally) by equal division of the apical meristem, yielding modular (determinate), orthotropic (three-dimensional) branches. The bauplan encompasses two distinct subgroups categorized by the arboreous and pseudoherbaceous habits respectively.

The first subgroup includes the classic arboreous genera *Lepidodendron* and *Lepidophloios*, together with *Synchysidendron* (Fig. 1). Throughout much of their life history, these trees consist of a rhizomorph and telegraph polelike stem capped by a massive primary body, undergoing frequent dichotomous branching to form a determinate crown only during the final phase of growth and subsequent monocarpic reproduction (DiMichele & Phillips, 1985). The cones were borne on stout peduncles that we regard as the homologs of more elaborate lateral branches found in bauplan (3); although evolutionarily significant, the peduncles do not *define* the architecture of bauplan (2) trees. These trees were cheaply constructed. Secondary thickening ceased well before termination of growth; the resulting poor development of wood in both the crowns and the trunks meant that they relied primarily on periderm for structural support (DiMichele, 1979a, b, 1983; Wnuk, 1985). This probably allowed channeling of more photosynthate into reproduction. Rapid generation times and an opportunistic life strategy were postulated for the subgroup by DiMichele & Phillips (1985).

The second subgroup, consisting of *Paurodendron, Oxroadia*, and *Hizemodendron*, is delimited by the pseudoherbaceous growth habit (Bateman, 1988, 1989, 1992; Bateman & DiMichele, 1991). These genera possess the same modules as *Lepidodendron* and *Lepidophloios*, but differ in the relative sizes and shapes of the modules (Fig. 2a, c, d). Also, overall body size of mature individuals is one to two orders of magnitude less than those of comparable arboreous species (cf. Fig. 1 with Fig. 2). In particular, the ubiquitous modules of rhizomorph and stem are greatly reduced (most drastically in *Paurodendron*) relative to the crown, which develops much earlier in the life histories of these genera. Their minimal stems result in a recumbent growth habit (Baxter, 1965; Schlanker & Leisman, 1969; Bateman, 1988), though developmental constraints preclude adaptations typical of truly prostrate growth (Bateman & DiMichele, 1991). Nonetheless, these plants superficially resemble the basally branched architectural model of Tomlinson (Hallé et al., 1978). Restriction of wood to the rhizomorph and highly reduced stem defines the pseudoherbaceous habit sensu Bateman (1988). Rapid determinate growth and a strongly *r*-selected life strategy are inferred for these species, though whether their reproduction was extended, or monocarpic upon cessation of growth, remains equivocal (Bateman, 1988; Bateman & DiMichele, 1991).

Bauplan (3) also encompasses two subgroups. It characterizes *Anabathra, Diaphorodendron* sens. str., and *Sigillaria,* as well as the reconstructed adpression *Bothrodendron punctatum* (Wnuk, 1989). All share Stone's architectural model and the arboreous growth habit. Stone's model resembles Schoute's model in many parameters but exhibits clear differentiation between stem and lateral branches, which were produced throughout much of the life of the individual. Although a degree of dorsiventral flattening has been inferred for the lateral branches (Wnuk, 1985), their stable morphology and spiral phyllotaxy suggest persistent orthotropy sens. lat. rather than a transition to plagiotropy (cf. Hallé et al., 1978, table 7). Deviation from Stone's model occurs during the final phase of determinate growth, occasional isotomous divisions (Hirmer, 1927; DiMichele & Phillips, 1985; Wnuk, 1985), presumably heralding exhaustion of the apical meristem. However, the effect of such divisions is much less profound in bauplan (3) than in bauplan (2). Our assignment of *Sigillaria* to Stone's model, which contradicts Hallé et al.'s (1978, fig. 71) assertion that the genus conforms to Schoute's model, reflects our view that the stout cauline peduncles of *Sigillaria* (and the bauplan (2) genera) are homologous with entire lateral cone-bearing branches of *Anabathra* and *Diaphorodendron*; thus, by definition, *Sigillaria* possesses lateral branches, though we distinguish it as a separate architectural subgroup.

This group of polycarpic plants possessed excurrent trunks and deciduous lateral branches. Wide cylinders of wood and periderm occur in the trunks of all the members of the group; they extend into the lateral branches of *D. scleroticum*, suggesting greater persistence (DiMichele, 1980, 1981, 1985). Growth and reproduction were both prolonged and sustained, conferring greater tolerance to extrinsic stress and allowing these species to occupy suitable habitats for considerable periods (DiMichele & Phillips, 1985; DiMichele et al., 1987). Relatively sporadic reproduction and apomixis (presumably facultative) have been reported in *Sigillaria approximata* (Schopf, 1941; Phillips, 1979; DiMichele & Phillips, 1985).

DiMichele & Phillips (1985) argued that growth architecture and mode of reproduction largely determine the ecological niches of specific arboreous lycopsids, a hypothesis that can be broadened to encompass nonarboreous arborescent species (Bateman, 1988; Bateman & DiMichele, 1991). Bateman & DiMichele (1991) further suggested that transitions in many of the characters describing more detailed aspects of vegetative morphology reflect evolutionary changes in growth architecture. If so, it is especially important to assess the frequency and polarity of architectural changes during the history of the arborescent lycopsids.

Our character analysis (Table 3) focused on specific homologous structures, whereas the five growth habits outlined above are polythetic summaries of several individual character states, some apomorphic and some plesiomorphic (C1–C7). For example, the arboreous habit corresponds with the apomorphic state of C1, the pseudoherbaceous habit with the plesiomorphic state of C2, and the pedunculate habit with the plesiomorphic state of C7; Schoute's model with the apomorphic state of C3, Stone's model with the apomorphic state of C6, and Corner's model with the apomorphic state of C5. Despite their heterogeneity and partial dependence on the cladistic characters, there is considerable interpretative value in mapping the distributions of the growth habits across the preferred MPTs. The procedure is not wholly tautologous, as the preferred MPT for analysis B (habit characters omitted) is identical to that for the complete analysis (A; Fig. 9a), suggesting that habit characters had little direct effect on the topology of the latter.

Two of the five growth habits (Corner's model in *Chaloneria*, pedunculate Stone's model in *Sigillaria*) are autapomorphic at the generic level, preventing assessment of their phylogenetic significance. The preferred MPT for analysis A (Fig. 6) requires homoplasy in at least two of the remaining three growth habits (pseudoherbaceous Schoute, arboreous Schoute, laterally branched Stone). It is equally parsimonious to assume a pseudoherbaceous or arboreous hypothetical ancestor. In the first case, pseudoherbaceousness is replaced by arboreousness immediately below *Anabathra,* with a reversal to pseudoherbaceousness in *Hizemodendron.* The transition to Stone's model also occurs immediately below *Anabathra,* with resumption of Schoute's model in *Diaphorodendron* and the *Hizemodendron–Lepidodendron–Lepidophloios* clade. The only sister groups that unequivocally possess the same habit are *Paurodendron* and *Oxroadia* at the base of the cladogram and *Lepidodendron* and *Lepidophloios* at the apex. Moreover, there is no clear evolutionary trend through the clade; Schoute's model characterizes both the most primitive and most derived genera.

We expected analysis D, based only on vegetative characters, to provide a less homoplastic distribution of the major vegetative architectures. The most profound difference is the unification of the pseudoherbs (all attributed to Schoute's model) as a basal paraphyletic group, thus depicting *Hizemodendron* as much more primitive than it appears in the full analysis (cf. Fig. 11 with Fig. 6). The topology for Figure 11, unlike that for Figure 6, requires recognition of the pseudoherbaceous habit as plesiomorphic. Although *Anabathra* is promoted to sister group of *Diaphorodendron–Synchysidendron,* a transition from Schoute's to Stone's model immediately above the pseudoherbs, followed by independent re-acquisition of Schoute's model in the derived *Synchysidendron* and *Lepidodendron–Lepidophloios* clades, remains the most parsimonious distribution of major architectures.

Heterochrony. The strongly iterative occurrence of the tree habit among the arborescent lycopsids is mirrored in extant tree ferns and seed plants (Hallé & Oldeman, 1970; Hallé et al., 1978; White, 1979; Funk, 1982; Tomlinson, 1983). We believe that radical changes in growth architecture are more readily achieved instantaneously, by mutation of genes involved in the production of the morphogens that control early development (D-genes of Arthur, 1984, 1988), than gradually, by selectively driven adaptation. The resulting morphological change would appear instantaneous on a geological time-scale. In this case, we believe that such saltational events were expressed as heterochrony sens. lat.: a change in the timing of the appearance of a trait between ancestor and descendant (e.g., Gould, 1977; Alberch et al., 1979; Fink, 1982; McNamara, 1982; Rothwell, 1987; DiMichele & Bateman, 1989; Bateman & DiMichele, 1991). Many other correlated morphological and anatomical changes probably occurred immediately, as a result of epigenetic changes within the new bauplan and habit, or subsequently, as a result of adaptive honing by natural selection (Arthur, 1984; Bateman & DiMichele, 1991). This scenario predicts that such macromutants very rarely generated evolutionary lineages, requiring a competition-free niche to allow establishment of the new population prior to adaptive honing (Valentine, 1980; Arthur, 1984, 1988; DiMichele et al., 1987). Hence, heterochronic anomalies must arise frequently to overcome their almost inevitable failure.

Bateman & DiMichele (1991) argued that *Hizemodendron* became pseudoherbaceous by heterochronic reduction from an arboreous ancestor. Precocious division of the primary apical meristem minimized the length of the stem and prompted many subsequent character changes to accommodate the new growth habit. Reduction in size and change in shape of the stem of *Hizemodendron* imply progenesis, a form of paedomorphosis (retention of ancestral characters in the descendant adult).

In this paper, we are concerned less with the details of the postulated mechanism of vegetative reduction than its potential consequences for phylogenetic reconstruction. The preferred MPT for all characters (Fig. 6) depicts *Hizemodendron serratum* as primitive relative to its former congener, *Lepidodendron hickii*; together, the two genera constitute a paraphyletic sister group of *Lepidophloios.* The preferred MPT for reproductive characters only (Fig. 12) shows an unresolved trichotomy, thus allowing monophyly of *Hizemodendron* and *Lepidodendron.* In contrast, the preferred MPT for vegetative characters only (Fig. 11) depicts a very distant relationship between these two genera.

Although the phylogeny based on the greatest number of characters (Fig. 6) has the highest overall probability of accuracy, it may be misleading in this case. If *H. serratum* evolved by progenesis directly from *L. hickii* (admittedly an improbable event, but a useful working hypothesis) and thereby lost all autapomorphies of *L. hickii* (*H. serratum* and *L. hickii* have no exclusive synapomorphies; Table 3), *H. serratum* would be depicted as primitive sister group of *L. hickii.* Losses of character states that the ancestor (*L. hickii*) shared with its former sister group (*Diaphorodendron–Synchysidendron*) are often depicted as reversals on the branch of the descendant (*H. serratum*) (this is only guaranteed if ACCTRAN optimization is used), whereas losses of character states not present in *Diaphorodendron–Synchysidendron* are not recognized as character transitions at all; it is more parsimonious to assume that the ancestor of *Hizemodendron* never possessed them. Thus, heterochrony in general and progenesis in particular can undermine phylogenetic reconstruction, and monophyly of *Hizemodendron* and *Lepidodendron* remains a viable hypothesis.

Bateman (1988, 1992) and Bateman & DiMichele (1991) postulated a similar progenetic origin for the other two pseudoherbs, *Oxroadia* and *Paurodendron.* They are shown as the most primitive OTUs in all analyses (cf. Figs. 6, 11, 12), though they form a polychotomy with the remaining bisporangiate-coned genera (*Chaloneria* and *Anabathra*) in Figure 12. As in the case of *Hizemodendron*, their primitiveness relative to OTUs with similar reproductive morphology is determined by vegetative characters. *Anabathra* is the only bisporangiate-coned tree included in our analysis and therefore provides the only potential arboreous ancestor for *Oxroadia* and *Paurodendron*. However, the three OTUs differ in many spore characters, and the unbranched rhizomorph and superficial ligules of *Paurodendron* label the genus as relatively primitive or relatively derived, depending upon near-arbitrary polarization decisions. Other bisporangiate-coned trees, once reconstructed, will provide more credible ancestors.

A heterochronic origin for *Oxroadia* and *Paurodendron* would weaken our analysis, as an a priori assumption of their primitiveness was used to polarize most of the characters (i.e., they were used as partial outgroups). Inclusion in the data matrix of even more primitive OTUs may support our original assumption that *Paurodendron* and *Oxroadia* are sister groups to the remainder of the arborescent lycopsid clade. Our concern is largely driven by our opinion that the first arborescent lycopsid would have generated secondary tissues throughout its bauplan (the most simple developmental transition from inability to generate secondary tissues), and that restriction of wood to certain modules reflects subsequent developmental modifications. Moreover, determinate growth and a centralized rhizomorphic rootstock are characters shared by all the OTUs, suggesting that they have exceptionally high burden (i.e., they play pivotal roles in the development and function of the organism and influence other dependent characters: Riedl, 1979; Fortey & Jefferies, 1982; Donoghue, 1989). These high-burden characters represent serious ontogenetic constraints to a truly prostrate growth habit (Bateman & DiMichele, 1991), and the bauplan appears much better adapted to upright growth. Increase in body size to arboreous proportions may have occurred subsequently rather than concomitantly with acquisition of wood.

Although *Chaloneria* is not a pseudoherb and is erect, the cladograms for all characters (Fig. 6) and vegetative characters only (Fig. 11) show that its unbranched, bilaterally symmetrical rhizome, unbranched stem, and cauline sporophylls (all autapomorphies in our analysis) are derived. This conclusion is tempered by the possibility that *Chaloneria* is not a genuine member of the ingroup, which would explain its numerous autapomorphies and its role as the greatest cause of topological instability in each analysis (Figs. 9, 10). The only well-supported conclusion from our study is that *Chaloneria* is more primitive than the most primitive member of the clade delimited by reduction to a single functional megaspore per megasporangium (i.e., than *Diaphorodendron–Synchysidendron*).

The phylogenetic position of *Chaloneria* is especially significant because it is the oldest reconstructed genus currently assigned to the Isoetales (Pigg & Rothwell, 1983a; Rothwell & Erwin, 1984). A sister-group relationship with a widely recognized lepidodendralean genus such as *Sigillaria* (e.g., Fig. 9k) would imply paraphyly of the Lepidodendrales and support Meyen's (1987: 70–81) decision to synonymize the Lepidodendrales into the Isoetales. Further resolution of these problems requires a broader cladistic analysis that includes other bona fide isoetaleans (including *Isoetes*), potential arboreous ancestors (e.g., *Lepidodendropsis–Protostigmaria*: Jennings, 1975; Jennings et al., 1983), and ostensibly more primitive OTUs (e.g., *Selaginella*) (see Bateman, 1992).

Outgroups and ancestors. Thus, we return to the fundamental questions that prompted this study. What character states delimit the Lepidodendrales? Is the group monophyletic? If so, what is the most appropriate outgroup? The chosen answer to this question leads to an even more loaded question: What is the most probable ancestor of the ingroup? It also largely determines perception of the phylogenetic relationships among the ingroup members.

We believe that the greatest weakness of our analysis is the narrow temporal and ecological range represented by our OTUs; most of the species are restricted to at most the ca. 10 Ma of the Westphalian (Fig. 3) and to the coal swamps of Euramerica. However, the main phylogenetic groups within the Lepidodendrales (or at least species possessing many of their diagnostic character states; whole-plant reconstructions have not yet been achieved for pre-Westphalian arboreous lycopsids) can be traced back at least another 20 Ma, to the Asbian. Moreover, reproductive organs consistent with the most apomorphic genus, *Lepidophloios*, have been recovered from Ivorian strata, a further 15 Ma older (Fig. 3, inset; Long, 1968). This implies that all of the sister groups of this genus had diverged by the Ivorian; unfortunately, only one of our OTUs (*Oxroadia gracilis–Oxroadia* sp. nov.) was reconstructed from such early assemblages. As yet incompletely reconstructed arboreous lycopsids (not necessarily bona fide lepidodendraleans) were widespread and at least locally ecologically dominant by the latest Devonian (e.g., Scheckler, 1986a, b; DiMichele et al., 1992).

Thus, the combination of the stratigraphic record and our phylogeny suggests that the three main groups of monosporangiate-coned genera recognized in our cladistic analysis (*Sigillaria, Diaphorodendron–Synchysidendron, Hizemodendron–Lepidodendron–Lepidophloios*) diverged at least 35 Ma prior to the Westphalian coal-swamp lagerstätten that provided most of our OTUs. This would explain why these groups show similarly large degrees of divergence from their putative bisporangiate-coned ancestor(s) (Fig. 14) and are supported by many character-state transitions (Fig. 6). Alternatively, the saltational evolutionary scenario erected for major vegetative changes may be extended to encompass reproductive innovations, eliminating the need for intermediate taxa during the early radiation of the group.

Current evidence suggests that our morphologically divergent OTUs together exhibit most of the character states possessed by the arborescent lycopsids as a whole, including other Pennsylvanian species and their Mississippian and Devonian antecedents. However, the paucity of genera in our analysis, and the fact that most represent only the final period of the history of the group, implies that we have sampled only a restricted range of the *combinations* of character states that existed. This would explain the large number of character states that occur as genus-level autapomorphies in our cladogram (Fig. 6), leaving few character states to support the consequently weak links that constitute the main axis of the cladogram and determine perceived genus-level relationships. Inclusion of older OTUs, dating back to the main radiation of the group, would probably alleviate this problem by transforming genus-level autapomorphies into genus-level synapomorphies. In an alternative less gradualistic scenario, the large number of genus-level autapomorphies may reflect evolutionary dynamics, particularly the simultaneous origin of blocks of characters linked by pleiotropic or epigenetic factors (e.g., Levinton, 1988). This mode of evolution may be difficult to resolve cladistically for a variety of methodological reasons (these will be discussed in a future paper; see also Lemen & Freeman, 1989).

Older OTUs are also needed to determine convincingly whether the Lepidodendrales are monophyletic and in particular to provide more satisfactory outgroups. However, before these questions can be addressed, the character states that supposedly delimit the Lepidodendrales should be reviewed. Four are most commonly cited: the possession of rootlet-bearing rhizomorphs, secondary tissues (wood and periderm), ligules, and heterospory (Chaloner, 1967; Stewart, 1983). These structures provided the holapomorphies that unite all the OTUs included in our analysis (Fig. 6), but most (possibly all) have a greater level of universality. For example, a wide range of enigmatic latest Devonian and earliest Mississippian lycopsids possessed wood (Meyer-Berthaud, 1981, 1984; Scheckler, 1986a, b; Matten, 1989; Roy & Matten, 1989). Rhizomorph-like, rootstocks, ligules, and heterospory all characterize homophyllous *Selaginella*, the type genus of the Selaginellales (e.g., Bierhorst, 1971; Bold et al., 1980). Moreover, *Paurodendron* (and therefore, by implication, its sister genus *Oxroadia*) was assigned by Schlanker & Leisman (1969) to *Selaginella*, and it is widely accepted as a member of the Selaginellales (e.g., Taylor, 1981; Stewart, 1983; Meyen, 1987). On these criteria, the Lepidodendrales could be circumscribed to include both *Paurodendron* and homophyllous *Selaginella*.

Moving progressively up the clade, the next OTU encountered is the most primitive tree, *Anabathra*. Regarding this OTU as the most primitive lepidodendralean would allow delimitation of the order using the arboreous habit and associated modifications of stelar anatomy, together with foliar parichnos. Unfortunately, many of these character states are homoplastic as a result of loss during the hypothesized progenetic evolution of pseudoherbs from trees: *Hizemodendron* from a *Lepidodendron*-like ancestor, and possibly *Oxroadia* and/or *Paurodendron* from *Anabathra*-like ancestor(s). Although phylogenetically valuable, these character states are not ubiquitous within the clade. Many workers would argue that the clade is delimited primarily by possession of a stigmarian rhizomorph. However, we were unable to identify any profound characters that distinguish the stigmarian rhizomorph of *Anabathra* from the supposedly nonstigmarian rhizomorph of *Oxroadia*, which is much smaller and more compact but otherwise very similar. Also, this clade contains *Chaloneria*, another nonarboreous OTU. *Chaloneria* possesses several autapomorphies, notably an unbranched stem lacking cones and a bilaterally symmetrical rhizomorph, that suggest affinities with the extant genus *Isoetes*. If Pigg & Rothwell (1983a) correctly ascribed *Chaloneria* to the Isoetales, and if the genus is correctly positioned in our phylogeny (which is by no means certain; Fig. 9), inclusion of *Anabathra* in the Lepidodendrales and continued recognition of the Isoetales would render the former order paraphyletic (Appendix 1A).

Perhaps the most cohesive clade includes *Sigillaria* as its most primitive genus. It is delimited by the nonhomoplastic synapomorphies of leaf cushions and monosporangiate cones that generate megasporangium-megasporophyll disseminules. We are confident of the monophyly of the three main groups of OTUs that constitute the clade (*Sigillaria, Diaphorodendron–Synchysidendron, Hizemodendron–Lepidodendron–Lepidophloios*), and our parsimony analysis strongly supports monophyly of the clade as a whole (nevertheless, we note that such an adaptively valuable suite of character states could reflect parallel responses in two or more lineages to similar selective regimes, thus confounding parsimony: cf. Coddington, 1988). Given that our assumption of homology among the three lineages in monosporangiate cones and the megasporangium-megasporophyll complex as disseminule is the crux of the preferred MPT (Fig. 6), these characters merit even more careful scrutiny. For now, we refer to this clade, more narrowly defined than most perceptions of the Lepidodendrales, as the "Segregationists" (referring to the segregation of megasporangia and microsporangia in different cones). Members of the less inclusive clade that excludes *Sigillaria* and is delimited primarily by reduction to a single functional megaspore that germinates within the sporangium are the "Isolationists."

CONCLUSIONS

Empirical observations. We are confident that each of the 10 genera analyzed by us is monophyletic. This conclusion is not especially profound, as six of the genera are here represented by only one species and thus not cladistically testable (Fig. 8). The analysis prompted segregation of two new genera: *Hizemodendron* from *Lepidodendron* (Bateman & DiMichele, 1991), and *Synchysidendron* from *Diaphorodendron* (DiMichele & Bateman, 1992). However, these decisions were taken primarily on the grounds of differences in several characters (many directly or indirectly reflecting different growth architectures) rather than as attempts to disaggregate para- or polyphyletic groups. *Diaphorodendron–Synchysidendron* is undoubtedly monophyletic; *Hizemodendron–Lepidodendron* is depicted in Figure 6 as paraphyletic but, as we have argued, may nonetheless be monophyletic. Derived (monosporangiate-coned) genera constitute three distinct monophyletic clades that are most appropriately regarded as families: Sigillariaceae (*Sigillaria*), Diaphorodendraceae (*Diaphorodendron–Synchysidendron*), and Lepidodendraceae (*Lepidophloios–Lepidodendron–Hizemodendron*). Each family is supported by several character state transitions (Fig. 6).

Evidence for the postulated monophyly of the monosporangiate-coned clade, and for the primitiveness of the Sigillariaceae relative to the Diaphorodendraceae and Lepidodendraceae, is more equivocal. This largely reflects our inability to make confident statements concerning phylogenetic relationships among the four primitive, bisporangiate-coned genera. They form a highly heterogeneous, paraphyletic (or possibly polyphyletic) plexus of disparate morphologies that share a free-sporing mode of reproduction. *Oxroadia* and *Paurodendron* differ in many characters and are united in Figure 6 by arguably only one synapomorphy; we doubt their apparent monophyletic status. Only *Anabathra* is a tree; the pseudoherbs *Oxroadia* and *Paurodendron* and possibly even the shrub-sized phallos *Chaloneria* are potential progenetic descendants of trees broadly similar to, but probably distinct from, *Anabathra*.

Determining the origin(s) of the monosporangiate-coned clade will require inclusion of pre-Pennsylvanian monosporangiate-coned species and a broader selection of bisporangiate-coned trees; several potential candidates, all requiring further reconstruction before they can be used with confidence in cladistic analyses, are listed in Table 5. Determining the origin(s) of the arboreous lycopsids, and of putatively progenetic bisporangiate-coned genera such as *Oxroadia* and *Paurodendron*, also necessitates inclusion of more distantly related nonarborescent lycopsids (e.g., *Selaginella* sens. lat., *Leclercqia*) to reassess character state polarities. Given these observations, we envisage eventual redelimitation, or possibly amalgamation, of three widely recognized lycopsid orders (Appendix 1A; see also Bateman, 1992).

Absence from the present analysis of nonarborescent species and of any credible ancestor of the most primitive arboreous genus (*Anabathra*) together prevent determination of whether arborescence (secondary thickening) and arboreousness (large body and upright growth) evolved simultaneously or sequentially. Other especially important and potentially linked innovations that possess a higher level of universality than our ingroup are determinate growth and the centralized rhizomorphic rootstock. In general, the most significant evolutionary advances within the bisporangiate-coned plexus appear to have involved vegetative rather than reproductive organs, indicating that

TABLE 5. Selected genera that are potentially phylogenetically informative but are currently insufficiently known to provide satisfactory cladistic data sets (listed in order of appearance in the stratigraphic record). We note that '*Lepidodendron*' *calamopsoides* is not closely related to *Lepidodendron* sens. str. (R. M. Bateman, unpublished obs.) and that *Bothrodendron* sens. lat. is probably a polyphyletic aggregate of several disparate species (Scott, 1920; Thomas & Meyen, 1984). See also reviews by Chaloner (1967), Meyer-Berthaud (1981, 1984), and Matten (1989).

Lepidosigillaria whitei Kräusel & Weyland
  White (1907); Arnold (1947); Grierson & Banks (1963)
    [Late Givetian-Early Famennian: New York State]
Protolepidodendropsis spp. Gothan & Zimmermann
  Høeg (1942); Schweitzer (1965)
    [Famennian: Euramerica]
Trabicaulis spp. Meyer-Berthaud
  Meyer-Berthaud (1981, 1984); Roy & Matten (1989)
    [Famennian-Early Tournaisian: south-central France; New York State]
Cyclostigma kiltorkense Haughton
  Johnson (1913); Chaloner (1967, 1968, 1984); Chaloner & Meyer-Berthaud (1983)
    [Strunian: southwestern Ireland]
Landeyrodendron spp. Meyer-Berthaud
  Meyer-Berthaud (1981, 1984)
    [Early Tournaisian: south-central France]
Lepidodendropsis spp. Lutz–*Protostigmaria eggertiana* Jennings
  Lutz (1933); Iurina & Lemoigne (1975); Jennings (1975); Jennings et al. (1983)
    [Tournaisian: Euramerica]
Valmeyerodendron triangularifolium Jennings
  Jennings (1972)
    [?Tournaisian: Illinois]
Bothrodendron spp. Lindley & Hutton
  Scott (1908); Weiss (1908); Calder (1933b); Stubblefield & Rothwell (1981); Wnuk (1989)
    [Tournaisian-Westphalian: Euramerica]
'*Lepidodendron*' (?*Anabathra*) *calamopsoides* Long
  Long (1964, 1971, 1986); Scott & Galtier (1988)
    [Late Tournaisian: northern Britain]
Levicaulis arranensis Beck
  Beck (1958); Pant & Walton (1961)
    [Mid-Visean: southwestern Scotland]
'*Lepidodendron*' (?*Phytokneme*) *brownii* Unger
  Chodat (1911); Calder (1933a); Meyer-Berthaud (1981)
    [Visean: southern Scotland]

they are economic adaptations (sensu Eldredge, 1989) employed continuously in competition for resources. The cladograms imply that the well-documented sequence of reproductive innovations in the monosporangiate-coned clade, which ultimately led to seed analogs in *Lepidophloios* (e.g., Phillips, 1979), occurred later, though they may have been developmentally linked to additional vegetative modifications (this hypothesis requires further study). Interestingly, the equally well-documented, climatically driven end-Westphalian extinctions of specific elements of the coal-swamp floras (Phillips et al., 1977, 1985; Phillips & Peppers, 1984) most seriously affected the most derived portion of the arborescent lycopsid clade, eliminating the "Isolationist" families Diaphorodendraceae and Lepidodendraceae (Fig. 3). Such extinctions of major monophyletic groups are uncommon (Smith & Patterson, 1988) and require a causal rather than a purely stochastic explanation.

These analyses provide useful (if circumstantial) evidence for the relative burden of particular types of character, in the guise of amounts of homoplasy. Interestingly, this partly reflects the physical scale (dimensions) of the feature represented by the character relative to that of the plant body. Characters of largest scale (notably overall growth habit) and smallest scale (e.g., various details of cellular histology and spore ornamentation) are generally more homoplastic than those of intermediate scale, such as stelar and associated trace morphology, the basic structure of leaf bases and sporophylls, and the nature of the dispersal unit. As a broad generalization, large- and small-scale features delimit species and genera, intermediate scale features delimit families or still higher taxa.

The results of our study will not encourage proponents of organ phylogenies. Merely bisecting our data matrix into submatrices representing vegetative (Fig. 11) and reproductive (Fig. 12) organs generated substantially different preferred MPTs that were clearly inferior to the preferred MPT of the full matrix (Fig. 6). The analysis of reproductive organs could not satisfactorily resolve the relationships among the four most primitive and three most derived genera. The analysis of vegetative organs misplaced *Hizemodendron* as unduly primitive and *Sigillaria* as unduly derived and could only distinguish *Synchysidendron* from *Diaphorodendron* using cone axis characters that mirror those of ultimate vegetative axes. Nonetheless, the arboreous members of the three most derived families (Sigillariaceae, Diaphorodendraceae, Lepidodendraceae) persist as clades in the analyses of both submatrices. This shows that the families as currently known can be approximately delimited using either vegetative or reproductive characters alone, even if their relationships cannot be determined accurately.

Our results are even less encouraging for classifications based on even more reduced suites of characters. We have identified homoplasy in many supposedly diagnostic character states, including some of the leaf-base details that are traditionally used to classify adpressed lycopsid axes. On the basis of these observations, we support in principle the hierarchical system of well-known core taxa and less well-known satellite taxa proposed for the Lycopsida by Thomas & Brack-Hanes (1984), but are convinced that reconstructed, anatomically preserved whole plants provide better core taxa than the reproductive organs favored by Thomas & Brack-Hanes. Certainly, whole-plant reconstructions are essential prerequisites for convincing phylogenetic and ecomorphic interpretations.

Methodological observations. We do not regard phylogenetic reconstruction as an isolated, objective procedure divorced from hypotheses of evolutionary mechanisms; rather, it is positive feedback between the two sets of paradigms that leads to greater understanding. The evolutionary history of the arborescent lycopsids is not a simple story of progressively increasing complexity expressed throughout the bauplan. In particular, high-burden characters such as determinate growth and a centralized rhizomorphic rootstock, together with the small number of module types that constitute the bauplan, predisposed the plants to profound heterochronic changes in body size and body plan; we believe that these were manifested as geologically instantaneous events resulting from changes in developmental regulation. This saltational evolutionary scenario has considerable predictive value, particularly if considered in tandem with advances in understanding of the ontogeny, functional morphology and physiology of these remarkable organisms (e.g., Phillips & DiMichele, 1992). Moreover, saltational scenarios can be falsified (or at least highly modified) by cladograms, if the predicted positively correlated suite of character state transitions is dissociated (e.g., by the interpolation of additional OTUs onto the internode in question: R. M. Bateman, in prep.).

We have been unable to discern any substantive differences between reconstructing the morphological phylogenies of extinct and extant species (cf. Stein, 1987; Gauthier et al., 1988; Donoghue et al., 1989; Boy, 1990). The inevitable typological nature of conceptual whole-plant fossils is not detrimental in the essentially typological realm of cladistics. Our 16 OTUs undoubtedly represent a highly rarified sample of all the arboreous lycopsid species that ever existed. This contributed to several problems, notably the broad morphological discontinuities separating some clades (Fig. 14) and the absence of satisfactory outgroups. However, cladistic analyses based exclusively on extant species are even more selective; unique character combinations found only in the fossil record, especially during the initial radiation of a major clade, are deliberately excluded. Similarly, opportunities to use stratigraphic-temporal evidence to assist polarization and characters, and (more importantly) to select among alternative topologies generated from the same data matrix, are squandered. The question of excluding fossils does not arise in the case of the monosporangiate-coned lycopsid clade, which apparently lacks extant descendants. Despite the serious problems posed by incomplete preservation in the fossil record, we were able to score a large number of characters representing all organs of our OTUs and generated a large data matrix containing only a small proportion of missing values. Although technically feasible, inclusion of less well-known, partially reconstructed OTUs should be postponed pending further investigation of the effects of missing values on tree-length calculation and character state optimization.

This study indicates that well-understood fossils are as valuable for phylogenetic studies as any extant organisms and do not require any special methodological concessions. We note that profound gaps in the fossil record caused by nonpreservation are matched by equally profound gaps in extant floras, namely those resulting from extinction of their precursors. Access to the time dimension, and thereby to character states (and combinations of character states) no longer in existence, justifies a pivotal role for paleontological data in phylogenetic reconstruction.

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Appendix 1. Nomenclatural and Taxonomic Notes

A. Higher taxa. Bateman (1990b) recommended the supra-ordinal classification of Knoll & Rothwell (1981) and ordinal classification of Stewart (1983); together, these classifications imply monophyly of the Division Tracheophyta and Class Lycopsida, but present a provisional, egalitarian (grade) arrangement of six orders within the Lycopsida (Drepanophycales, Protolepidodendrales, Lycopodiales, Selaginellales, Lepidodendrales, Isoetales). Acquisition of further phylogenetic information will require re-delimitation of these orders and their rearrangement into a more hierarchical classification (Bateman, 1990b, 1992; Hueber, 1992). Colloquial (informal) names are consistently rooted in their formal counterparts; thus, "lycopsid" is used for the Class Lycopsida and "lepidodendralean" for the Order Lepidodendrales (Bateman, 1990b).

At present, the Lycopsida are perceived as being delimited by exarch protostele, scalariform metaxylem with Williamson fimbrils, vascularized "microphylls," and foliar/axillary eusporangia (e.g., Stewart, 1983). With the possible exception of stigmarian rhizomorphs, none of the characters traditionally used to delimit the Lepidodendrales (secondary thickening, periderm, ligules, heterospory) is confined to the order. The present analysis shows that the Lepidodendrales as currently delimited may not be monophyletic, and even if monophyletic may not be the most meaningful clade to use as the basis of an ordinal level classification (see also Matten, 1989). Together with the Isoetales and Selaginellales, the Lepidodendrales require redelimitation or amalgamation.

B. Anabathra versus Paralycopodites. We accept Pearson's (1986) arguments that *Paralycopodites brevifolius* (Williamson) DiMichele (formerly '*Lepidodendron*' *brevifolium* Williamson) is identical to, and a junior synonym of, *Anabathra pulcherrima* Witham (cf. Witham, 1833; Williamson, 1872). We also recognize that the adpression genus *Ulodendron* Lindley & Hutton (1831) both resembles and nomenclaturally pre-dates *Anabathra*, but suspect that *Ulodendron* is considerably more inclusive (i.e., more broadly delimited) than *Anabathra*.

Unfortunately, *A. pulcherrima* is a form-species (sensu Bateman & Rothwell, 1990), having been correlated with several cone-species of the plesiomorphic bisporangiate genus *Flemingites* (DiMichele, 1980; Pearson, 1986). The type material of *A. pulcherrima*, from the Late Tournaisian of Allanbank, southeastern Scotland, co-occurred with *Lagenicula horrida* megaspores (these were incorrectly referred to *L. subpilosa* by Pearson, 1986: K. M. Bartram, pers. comm. 1987; H. L. Pearson, pers. comm. 1987), which have been found in *Flemingites gracilis* cones (Chaloner, 1953; Brack-Hanes & Thomas, 1983). Elsewhere, *A. pulcherrima* co-occurs with *F. scottii* at the Late Visean locality of Pettycur, southeastern Scotland (e.g., Williamson, 1872; Jongmans, 1930; DiMichele, 1980; Scott et al., 1984; Pearson, 1986), and with either *F. diversus* or *F. schopfii* at many Westphalian coal-ball localities in Euramerica (DiMichele, 1980). The differences between these cone-species are subtle and not readily resolved cladistically. In particular, our scoring of *A. pulcherrima* focused on Pennsylvanian rather than Mississippian assemblages; *F. diversus* (Westphalian D: Felix, 1954) and *F. schopfii* (Westphalian B: Brack, 1970) differ primarily in the mean number of megaspores per megasporangium and thus were not differentiated in our data matrix (Table 3, Fig. 3).

We anticipate taxonomic revision of vegetative and reproductive organs of *Anabathra* as increased knowledge (particularly of Mississippian forms) allows further whole-plant reconstructions; for example, '*Lepidodendron*' *calamopsoides* Long (1964), which co-occurs with stigmarian rootstocks, *Flemingites*-like strobili and *Lagenicula crassiaculeata* megaspores (Scott & Meyer-Berthaud, 1985; Scott & Galtier, 1988; Scott, 1990), may be a species of *Anabathra* (cf. Table 2). Such plants will form the basis of a new arborescent lycopsid family, the Anabathraceae.

C. Erection of new genera and species. We have deliberately avoided formal reclassification of the 17 whole-plant species included in our study. Thus, the three new species (one each of *Oxroadia*, *Sigillaria*, and *Synchysidendron*) remain unnamed (but see Bateman, 1992; DiMichele & Bateman, 1992).

However, the results of this study encouraged us to restrict further the range of variation encompassed by *Lepidodendron* sens. str., a process that was begun by DiMichele (1981, 1983, 1985) when clarifying the delimiting parameters of *Lepidodendron*, *Lepidophloios*, and *Diaphorodendron* sens. lat. In order to transform

Lepidodendron from an apparently paraphyletic (Fig. 6) to a monophyletic entity, we retained only the anatomically preserved equivalent (*L. hickii*) of the type species (*L. aculeatum*) and erected '*Lepidodendron*' *serratum* as the type species of a new genus, *Hizemodendron* (Bateman & DiMichele, 1991). The two genera share similar reproductive organs, but differ in many vegetative characters; at least most of these differences may reflect the imposition of radically different growth habits on a shared bauplan.

Although our study strongly supports monophyly for *Diaphorodendron* sens. lat. (i.e., sensu DiMichele, 1985; see Fig. 6), the precedent of generic distinction of species sharing similar reproductive organs but exhibiting major differences in growth habit and ontogeny requires the recognition of the two most apomorphic species, '*D.*' *dicentricum* and '*Diaphorodendron*' sp. nov., as a new genus of arboreous lycopsid, *Synchysidendron*. In contrast with the more plesiomorphic *Diaphorodendron* (epitomized by the type species, *D. vasculare*), *S. dicentricum* and *Synchysidendron* sp. nov. lack lateral branches and were probably monocarpic (DiMichele, 1981, 1985; Bateman & DiMichele, 1991; DiMichele & Bateman, 1992), thus possessing the same bauplan, growth habit, and reproductive strategy as *Lepidodendron* sens. str. (Fig. 1).

D. Revision of the cone-genera. As currently delimited, cone form-genera serve as shorthand for co-occurring complexes of character states. A few cone-genera are assignable to single stem-genera (Table 2), notably *Mazocarpon* to *Sigillaria* (e.g., Schopf, 1941; Feng & Rothwell, 1989) and *Lepidocarpon* to *Lepidophloios* (DiMichele, 1983). The microsporangiate genus *Lepidostrobus* characterizes *Hizemodendron, Lepidodendron,* and *Lepidophloios*; cone-species of each of these stem-genera can only be distinguished by continuous quantitative characters and microspore morphology (e.g., Willard, 1989a). In contrast, *Achlamydocarpon* is a greatly inflated form-genus (e.g., Leisman & Phillips, 1979) encompassing three main morphological groups: (1) megasporangiate *A. takhtajanii*-type, (2) megasporangiate *A. varius*-type, and (3) microsporangiate *A. varius*-type (Table 2). Groups (2) and (3) are restricted to *Diaphorodendron–Synchysidendron*; cones of all three *Diaphorodendron* species and both *Synchysidendron* species can only be distinguished by the medullated steles of the latter, despite major differences in growth architecture and vegetative anatomy between the two genera (DiMichele, 1981). Group (1) cones characterize *Hizemodendron* and *Lepidodendron* (DiMichele, 1983; Bateman & DiMichele, 1991). We believe that megasporangiate *A. takhtajanii* and *A. varius* are sufficiently distinct to merit generic distinction (the latter would require a new organ-genus). Assignment of megasporangiate and microsporangiate *A. varius* to different cone-genera would be more consistent with the systematic treatment of *Hizemodendron, Lepidodendron,* and *Lepidophloios* cones in Table 2, though Phillips (1979: 256, 259) presented several arguments against this option.

APPENDIX 2. ANALYTICAL ADVANCES

Given the appropriate microcomputers and software, more elegant solutions are now available to some of the difficulties that we encountered when performing these analyses in 1989. For example, the problem of storage of only superficially different topologies, resulting from polychotomies, has been solved in Version 3.0 of PAUP (Swofford, 1991). There is much to commend an analytical approach that entails initial parsimony analysis in PAUP 3.0, subsequent comparison of MPTs with those generated by using Hennig86 Version 1.6 (Farris, 1989), and printing of interesting topologies and character state distributions using MacClade Version 3.0 (Maddison & Maddison, 1991). Estimation of degrees of support for particular nodes using bootstrapping (Efron, 1982; Felsenstein, 1985; Sanderson, 1989) is gaining in popularity, though there is no statistical substitute for detailed examination of suboptimal-length topologies.

COMPARATIVE ECOLOGY AND LIFE-HISTORY BIOLOGY OF ARBORESCENT LYCOPSIDS IN LATE CARBONIFEROUS SWAMPS OF EURAMERICA[1]

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ABSTRACT

The comparative ecologies of *Diaphorodendron, Lepidodendron, Lepidophloios, Paralycopodites* (= *Anabathra*), and *Sigillaria* in Late Carboniferous coal swamps serve as a context for assessing life cycles and exploring possible structure-function relations. The distinctive aspects of the "lycopsid tree habit" in lepidodendrids are emphasized as part of the arborescent reproductive architecture of relatively short-lived (10–15 years) plants. These include: determinate apical growth of the aerial shoot system and the anchoring stigmarian system, which have marked homologies; limited amount of secondary xylem, lack of secondary phloem, and periderm as the major support tissue; differentiated gas-diffusion system associated with appendages, including lacunae and parichnos; abscission of appendages and lateral branches; retention of leaf cushions; and close relationships between mode and timing of branching, to cone-bearing and heterosporous reproductive biologies. Vegetative structure-functions explored include the possibility that lacunae and parichnos were involved in internal mediation of gas diffusion as opposed to aeration functions. The possibility exists that parts of the stigmarian system were involved in CO_2 acquisition from substrates; some may have been photosynthetic. These functions are considered in the context of the light sharing and diffuse photosynthesis evident in the pole architecture. The combination of such possibilities is related, in part, to the xeromorphic characteristics of the arborescent habit, raising the question about a modified kind of C_3 photosynthesis such as CAM (Crassulacean Acid Metabolism). Stigmarian lycopsids dominated tropical Westphalian coal swamps as an array of genera with relative distributional abundances reflecting habitat partitioning according to edaphic conditions, including temporal disturbance patterns. Species appear to exhibit different levels of tolerance to disturbances and range from colonizers to site occupiers. *Paralycopodites,* with prolific, free sporing, bisporangiate cones, was most abundant in frequently disturbed, partially exposed, peat- to mineral-rich habitats (ecotonal). Monosporangiate *Lepidophloios* and *Lepidodendron* were associated typically with deeper, standing-water habitats, and, in association with terminal branching, monocarpically produced specialized monosporic megasporangium-sporophyll units, termed aquacarps. *Diaphorodendron* species were monosporangiate with aquacarps and range from a typically persistent, low level reproductive output on deciduous lateral branches, to monocarpy (*D. dicentricum*) with terminal branching. *Sigillaria* was less closely associated with peat swamps, as a sporadic occupant associated with major disturbances, such as flood/dry down cycles. Whorls of monosporangiate cones were produced intermittently, perhaps in seasonally wet-dry conditions, with megaspore-sporangial dispersal units derived from cone fragmentation. In North America *Sigillaria* was the principal lepidodendrid survivor of the swamp extinctions near the Middle-Upper Pennsylvania boundary. The ecological roles of stigmarian lycopsids in Westphalian coal swamps are distinctive as an array of heterosporous reproductive architectures that were collectively dominant. Plants were characteristically much taller than other trees, yet did not shade out lower vegetation. They also were a major stabilizing influence on substrates with their extensive, baffling and anchoring systems in the high disturbance and abiotically stressed environments of peat swamps. The environmental circumstances of the first major coal age appear to have selected against long-lived or slow-growing trees in most coal swamps. Lepidodendrids constituted the most important of the arborescent genera both because of their unusual array of reproductive biology in such large structural and yet short-lived growth habits, as well as many physiological attributes that are only partially known or conjectured.

Trees referred to as lepidodendrids or stigmarian lycopsids encompass lycopsid zeniths in size, structural complexity, and heterosporous diversification as well as ecological dominance in Late Carboniferous tropical swamps. Lepidodendrid trees were so different anatomically, functionally, and ecologically from arborescent forms of other non-lycopod lineages as to merit distinction of a "lycopsid tree habit." The principal lepidodendrid genera of the Late Carboniferous coal swamps, known from anatomical preservation, include *Diaphorodendron, Lepidodendron, Lepidophloios, Paralycopodites*

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(= *Anabathra*), and *Sigillaria*. Anatomical and developmental studies drawn from these genera provide a composite picture of the lycopsid tree habit that emphasizes some of the differences from conventional trees.

Lepidodendrids were apically determinate in both the aerial shoot system (Andrews & Murdy, 1958; Eggert, 1961; Lemoigne, 1966; Chaloner & Meyer-Berthaud, 1983) and apparently also in the anchoring stigmarian system (Frankenberg & Eggert, 1969); the anatomical transition from stem to rhizomorph occurred in the unbranched base of the trunk. Marked homologies between stem and rhizomorph systems, both in axial organization and in appendage anatomy and arrangement, indicate that the stigmarian rhizomorph was, in part, functionally but not morphologically a "root system." Its anchorage and support of the pole-type trunk was provided by dichotomous branchings and the extensive appendages they bore. There were no root caps or root hairs. The apex of the growing stigmarian axes tapered abruptly to a rimlike apical groove associated with appendage origins; this was terminated with a protective plug of apparently parenchymatous tissue (Rothwell, 1984). The cylindrical appendages were largely air filled, apparently buoyant, with a large external surface to biomass ratio. They radiated for lengths of 0.5 m or more; some are known to have been once dichotomous in the sigillarian stigmarias (Lemoigne, 1963).

The aerial shoot system exhibited structural support mainly by nonwoody tissues, especially periderm, formed beneath the leaf cushions or bases in larger stem parts. The relatively modest amount of secondary xylem in the trunk was high in conductance (Cichan, 1986). Both aerial and stigmarian systems had wood and periderm, but neither had secondary phloem (Eggert, 1972; Eggert & Kanemoto, 1977). In the *Lepidodendron* and *Lepidophloios*-type trees with dichotomous terminal branching, the primary body showed progressive diminution of all tissue zones in the branching system. There were progressively fewer and smaller leaf cushions and lamina, and finally maturation of apices. Secondary tissues diminished upward from the trunk base with periderm extending further up than wood. For trees with divided lateral branches (*Paralycopodites*, most *Diaphorodendron* species) the same determinate changes occurred in the lateral branches, and presumably in the main trunks. Genera that ultimately terminated their pole architecture with at most a fork or two (*Paralycopodites, Sigillaria*) also are thought to have had primary body diminution with apical dichotomy.

Pole branching was coordinated apparently with reproduction (DiMichele & Phillips, 1985). Lateral branches were either ramified, bearing multiple cones, or pedunculate with a terminal cone. Terminal "crown type" branching was simply an expanded scaffolding for cone production and dispersal. Deciduous lateral or terminal branching represented minimal interference with light penetration and wind dispersal. In short, the lepidodendrids represent arborescent reproductive architecture with determinate growth and fairly short life spans (Stewart, 1983: 104; DiMichele & Phillips, 1985) despite their large statures.

Lepidodendrids were indeed tree sized with a pole design; however, their morphology suggests a short life span, perhaps up to 10–15 years as a conservatively high estimate. Their developmental design indicates a different way to be a big pole tree, rapidly and temporarily. Some were also small trees, especially in the coal swamps. Most reconstructions show lepidodendrids in late to terminal reproductive or "death" stages. As unconventional as these trees were structurally, and, by inferences, functionally, we have good reason to query what else is known or likely about their biology, their earlier history, and the origin of genera. In turn, what do these aspects suggest about the wetland environments where they dominated?

Lepidodendrids were confined to the tropical wetlands of the late Paleozoic, apparently associated with soft substrates (peat as well as mostly inorganic). Such habitats are accordingly referred to as coal (peat-forming) or clastic (inorganic substrates) swamps. There were additional lacustrine and fluvial environments associated with the better-drained parts of the wet lowlands. Because the habitats of lepidodendrids were also depositional environments, there is an unparalleled fossil record of compressions, casts/molds (see Gastaldo, 1986), permineralized anatomy, and spore floras. Recognition and interpretation of this record is particularly enhanced by the unusually distinctive structures of tree-sized lepidodendrids.

Stigmarian lycopsids represented in our study were the principal genera of the Westphalian (mid-Late Carboniferous) coal swamps. The five genera coexisted in Westphalian (mid-Pennsylvanian) coal swamps for about nine million years (Hess & Lippolt, 1986) in an area from Europe to mid-continental United States. Additional occurrences in clastic deposits provide a means of tracking their broader geologic distribution, despite taxonomic limitations of cross-preservational comparison (see Gastaldo, 1987).

One of the most important perspectives to emerge from lepidodendrid ecology is that the biological differences among genera seem to reflect habitat partitioning according to edaphic conditions, including temporal disturbance patterns. Lepidodendrid life cycles apparently constrained the plants to relatively short-term occupation of variously disturbed or certain temporarily stable wetland habitats. The lycopsid tree habit clearly reflects elevation of reproductive organs, permitting dispersal from a high point. This was very important in the face of repeated expansions and contractions of habitable environments, including the necessity of recolonization from scattered refugia. Lepidodendrids had no known means of vegetative propagation. Consequently, the life cycles provide perspectives on ecological resource partitioning, gradient distributions, repetitive occupation of sites, or patterns of replacement by another lepidodendrid ("succession"). The unusual life cycles contributed to the collective dominance of swamps by lycopsids. The heterogeneity of swamp environments, as well as geologic changes in environments, also can be inferred from the mix or combination, and relative abundances of lepidodendrid genera (DiMichele et al., 1985).

The principal lepidodendrid genera of the Westphalian coal swamps had very long geologic ranges, some extending for more than 100 million years. All have anatomically known occurrences in the very early Carboniferous. The lepidodendrid radiation occurred in the earliest Carboniferous, and perhaps latest Devonian (Scheckler, 1986), and it is likely that the development of the stigmarian system constituted the major adaptive breakthrough. *Paralycopodites* is known from the Tournaisian (Meyer-Berthaud, 1981) and *Lepidodendron, Lepidophloios, Diaphorodendron,* and *Sigillaria* were present during the Visean (Long, 1968; Scott et al., 1984). There are several reported, older occurrences of *Lepidodendron*-like plants. Lepidodendrids subsequently attained pantropical distribution as wetlands underwent a net expansion and, as a group, reached their zeniths in Euramerican coal swamps by the onset of the Westphalian. With the exception of *Sigillaria,* these genera became extinct in coal and clastic swamps in North America, rather abruptly, near the Middle-Upper Pennsylvanian boundary (Winslow, 1959; Phillips et al., 1974; Kosanke & Cecil, 1989). A drastic decline occurred in Europe also near the Westphalian–Stephanian boundary with several genera surviving in the Stephanian of the Donets Basin of Ukraine, Massif Central of France, and Spain (see Phillips et al., 1985; Wagner, 1989). The Westphalian-Stephanian transition and ensuing Permian distribution of lepidodendrids in the Cathaysian paleofloristic province is quite different from that of Euramerica (Li & Yao, 1982; Wang, 1985). Some of the same genera continued as major components of Cathaysian coal swamps to the end of the Paleozoic (Tian & Zhang, 1980; Tian & Guo, 1987).

PERSPECTIVES AND BASES FOR INTERPRETATION

The most important aspect of our inquiry into structure-function relationships is relationship between the peculiar morphology of the lepidodendrids and their physiology and how this best relates to their ecology and reproductive biology. It is known that lycopsids probably represent an evolutionary lineage distinct from other vascular plants. The many distinctive aspects of morphology often are interpreted, however, based on the structure-function relationships of other vascular plants, especially seed plants. In retrospect, most of us have followed such analogies. Lepidodendrids are so quaintly familiar to paleobotanists that such exceptional morphological features as the stigmarias are reduced to "root system" status without asking what these shootlike systems might be doing that is of importance to lepidodendrids, or to our understanding of other rhizomorphic lycopsids. Similarly, we have relegated structures with seed-like morphology (*Lepidocarpon, Achlamydocarpon*) to the status of almost seeds, extrapolated even to the pollination syndrome (Thomas, 1981). In short, our comparative morphological treatments of the lepidodendrids have been too strongly influenced by seed-plant morphology with analogy to its implications of function.

Also misleading have been evolutionary scenarios wherein lepidodendrids are the starting point for a reductional series from arboreal to herbaceous rhizomorphic (centrally "rooted") forms. Quite to the contrary, we believe that the arborescent lycopsids represent an extreme specialization which evolved from diminutive predecessors whose near relatives survive to the present day. In short, the "reduction series" of classic literature treats the true ancestors as the descendants. This places exceptional importance on the study of the surviving members of the isoetalean line. These may provide insights into the lepidodendrids and their relatives, which dominated the swamps *and* marshlands of the tropical Carboniferous, and a diversity of environments from wetlands to more xeric habitats of other paleofloristic areas and geologic times (Meyen, 1982, 1987).

The success of rhizomorphic lycopsids in such harsh environments takes on special importance in light of their distinctive morphology and probably unique physiology. Why were rhizomorphic lycopsids so successful in conspicuous contrast to other plant types that also had basic laminate and arborescent characteristics by the late Devonian–earliest Carboniferous? As a consequence of their distinctiveness, lycopsids provide an "outgroup" by which we can assess the constraints form and physiology place on ecology. Despite our own reservations about multiple speculations of form-function relationships, the intent is to utilize lepidodendrids as a model system that has high resolution because of anatomical preservation, size of structures, dominance of vegetation, and long geologic ranges and broad paleogeographic distribution. The rhizomorphic lycopsids are acknowledged to have been generally xeromorphic despite the seemingly contrary ecological associations with wetlands and xeric habitats—both harsh extremes. These extremes in the environments of the late Paleozoic, and even the Triassic, mark capabilities of lycopsids that were not mediated just by differences in reproductive biology, but by particular physiological capabilities.

Available Data

Most data and results drawn upon in this study are derived from anatomically preserved plant assemblages in coal-ball deposits. Coal balls are concretions, principally of carbonate permineralization, entombing peat stages of coal swamps. The greatest abundances of coal balls occur in the Westphalian (middle Upper Carboniferous) of Europe and the United States (Phillips, 1980). More than 60 coals are represented and localities number in the hundreds. These extend from the lowermost Westphalian A to near the top of the Westphalian D, stratigraphically including part of the Lower Pennsylvanian and the entire Middle Pennsylvanian in the United States. At least 10 coals are represented by occurrences in the Upper Pennsylvanian, from the Illinois Basin to the Appalachians. There are significant permineralized deposits also in the Stephanian of France (Galtier & Phillips, 1985).

There is more anatomically based information on the swamp plants of the Late Carboniferous tropics than for any other comparable interval in the geologic record because of the occurrences of coal balls. This continues to improve resolution of the systematic, ecological, and evolutionary understanding of lepidodendrids and their relatives based, in part, on anatomy, development, and reproductive biology. While the relevant sources are too extensive to cite comprehensively, key publications are given here for major reviews or compilations, revised systematics, developmental studies, and the vegetational data and analyses, with other citations accompanying the pertinent text.

The lepidodendrids are reviewed by Chaloner & Boureau (1967) and Thomas (1978). Reproductive biology of some lepidodendrids has been summarized by Phillips (1979) and DiMichele & Phillips (1985). Extensive reviews of general ecological studies are found in Scott (1977) and Collinson & Scott (1987).

SYSTEMATICS AND DEVELOPMENT

Revisions in the systematics of coal-swamp taxa have resulted in the delineation of *Paralycopodites* (= *Anabathra*) as an arborescent lycopsid (DiMichele, 1980; Pearson, 1986) corresponding to *Lepidodendron brevifolium* in the older literature (see Williamson, 1893). *Diaphorodendron*, the "coal-swamp *Lepidodendron*," has been segregated (DiMichele, 1985) from true *Lepidodendron* (DiMichele, 1983) with additional revision and description of a new species (DiMichele, 1979b, 1981). The megasporangiate and microsporangiate cones of *Diaphorodendron*, known as *Achlamydocarpon varius*, were described in detail by Leisman & Phillips (1979). *Lepidophloios* has been revised (DiMichele, 1979a), including major systematic changes for the fructifications (Balbach, 1965, 1967). The principal *Sigillaria* studies include those by Schopf (1941) on *Mazocarpon* cones, by Delevoryas (1957) on stems, and by Eggert (1972) on stigmaria from the same American deposits. The principal work on European sigillarias is that of Lemoigne (1960). Additional species of *Mazocarpon* have been described from the Appalachians by Pigg (1983) and by Feng & Rothwell (1989). A detailed updated account of *Stigmaria ficoides* is given by Frankenberg & Eggert (1969). The phylogeny of the lepidodendrids is reviewed by Bateman et al. (1992).

While the above and other studies include many developmental aspects of the lepidodendrids, the seminal papers on aspects of arborescent growth include those by Walton (1935), Andrews & Murdy (1958), and Eggert (1961), with excellent summaries by Delevoryas (1964) and Stewart (1983).

Stigmarian biology has received a special emphasis as the result of the studies of Frankenberg & Eggert (1969), Eggert (1972), Paolillo (1982), Jennings et al. (1983), Rothwell (1984), and Rothwell & Erwin (1985).

VEGETATIONAL ANALYSES

Vegetational analyses of Late Carboniferous peat swamps are based on quantified identification of tissues, taxa, and preservational states (fusain). Sampling methods are described by Phillips et al. (1977); modifications of this sampling method have been described by Raymond (1988), Pryor (1988), and Feng (1989). These studies provide an outline of vegetational changes in the Westphalian and Stephanian that are paralleled by more extensive sampling in spore floras of the coals (see Peppers, 1984; Phillips & Peppers, 1984).

Summaries of vegetational data in relation to palynology are given in Phillips & Peppers (1984) and Phillips et al. (1985) with specific site or coal studies appearing in Phillips & DiMichele (1981), DiMichele & Phillips (1985, 1988), Eggert & Phillips (1982), Eggert et al. (1983), Willard (1985, in press), and Winston (1988). The techniques of analyses are found in Phillips & DiMichele (1981), DiMichele et al. (1986), and Raymond (1988).

The Lycopsid Tree Habit

Lycopsids are so different evolutionarily from other vascular plants that even the concept of the "lycopsid tree habit" tends to be misleading because the primary frame of reference for "trees" tends to be non-lycopsids. The lycopsid tree habit has become epitomized by lepidodendrids or "stigmarian trees," which include the largest known lycopsids. However, it is well to emphasize that basic pole architecture was shared by a wide size range of lycopsids from robust "herbs," such as *Chaloneria*, to terminally, determinately branched *Lepidodendron* "trees." The general distinctions of relative pole sizes and even branching do not consistently or meaningfully separate "trees" from robust "herbs" or stigmarian lycopsids from other arborescent forms.

PRIMARY THICKENING

The large primary body and the early addition of secondary xylem necessitate a large primary meristem, a feature also reflected in the large appendages of both axial systems (Andrews & Murdy, 1958; Eggert, 1961; Rothwell, 1984). Such a large apex may have been supplemented by some kind of primary thickening meristem, particularly important in the establishment growth phase. The common diamond design of most leaf bases may have permitted structural accommodations of growth vectors generated by combinations of vertical and transverse expansion during primary thickening. While distinctions are recognized herein between primary and secondary thickening meristems, it seems quite possible that the relationships between them were not so clearcut. This may be a matter of shift to more localized meristematic activity and eventually a lack of thickening meristem activity.

XYLARY SYSTEM

The protostele in the shoot–stigmarian transition region is minute, composed of only a few tracheids. Primary xylary expansion in both directions led to progressively larger diametered "siphonosteles" (or medullate protosteles) corresponding to an increase in the entire primary body size. The protostelic transition region is quite long, encompassing both the trunk and the basal stigmarian axis, including the region where appendage traces first occur.

At some indeterminate distance from the transition zone within the dichotomously forked part of the stigmaria axis, the stelar structure significantly changed. The stigmarian primary xylem apparently expanded into essentially a spiral array of appendage traces, indicated by perimedullary protoxylem groups, closely associated with a mostly hollow parenchymatous pith. There is continuity of the parenchyma with each xylary trace across the secondary xylem. The radial xylary maturation has been described as centrifugal because of associated tracheids thought to be endarch metaxylem. However, it is not possible to distinguish objectively between secondary xylem tracheids and those of the primary appendage trace. Considering the centripetal maturation of stem xylem, it is likely that maturation of stigmarian protoxylem was also centripetal; if so, the perimedullary pith sleeve represents a nontracheidal frame in which the procambial strands, differentiated as appendage traces, were the only stelar xylem. Given the sparse vascular construction of this modified "siphonostele" of the primary xylem or appendage-trace network, conduction requires a continuity of xylem afforded only by the concomitant development of secondary xylem. It is presumed that secondary xylem was rapidly added in the stem at the same time.

The diameter expansion (forking stages) of the stigmarian primary body may have been more rapid and perhaps less costly to achieve than that of the aerial pole. Each of the four main stigmarian axes were produced apparently almost simultaneously by a pair of successive dichotomies. The pith cavity of most *Stigmaria ficoides* axes has long been considered a taphonomic artifact, but the best preservation available (Williamson, 1887; Frankenberg & Eggert, 1969) argues that there was only a perimedullary pith rim surrounding a hollow central cavity (except at each end). This pith rim had clear continuity with the parenchyma accompanying each xylary trace across the wood. Two aspects of aeration seem important in this regard. First, there was an air cavity in the center of the *Stigmaria ficoides* axes, and secondly, parenchymatous connections extend from perimedullary pith rim not only across the wood but to the base of each appendage where a transverse septum (diffuser) separates the appendage lacuna from the axis. The parenchyma associated with the xylary trace in the wood has been termed a primary medullary ray by Williamson (1871), and a lateral appendage gap and largely secondary ray by Frankenberg & Eggert (1969). The key point here is that these lenticular shaped lacunae, as seen in tangential wood sections, are completely lined with parenchyma, at least 4–5 cells thick, and apparently frame slightly larger-sized cells that are more subject to degradation. The lacuna is slightly wider toward the outer periphery of the wood. In many cases it has been assumed that lack of preservation accounts for the lacunae and that the "ray" or "lateral appendage gaps" were fully filled by parenchyma. This seems likely; however, like the large cells of the middle cortical tissues of the appendages, observed basally in some cases, these may degrade early. The lacunae associated with the appendage xylary traces and surrounded by parenchyma are likely key parts of the aeration system.

The addition of the secondary xylem to the primary body likely occurred very near the apex in both pole and stigmarian axes. This seems reasonable, given the necessity to conduct water to the developing aerial shoot, which otherwise would have a protostelic bottleneck in the transition region. If secondary xylem were added rapidly at a growth level where primary tissues were still radially expanding, radial expansion of both systems in concert may have facilitated incorporation of the traces in the secondary xylem without disrupting them. The continuity of appendage trace systems was maintained during the addition of periderm tissues as well. In stigmaria, the secondary xylem may have provided the functional link between otherwise isolated traces, as well as providing a structural frame for the incorporated aeration passages. In young forked *Lepidophloios* sporophytes just emergent from the megasporangium, secondary xylem has been observed in both axial systems in what should constitute part of the transition zone (Phillips, 1979).

PHLOEM AND LONG-DISTANCE TRANSLOCATION

Given the developing suite of conducting and support tissues, it is natural to wonder about the long-distance photosynthate translocation system of a tree-sized plant that had no recognizable equivalent of secondary phloem (Arnold, 1960; Lemoigne, 1966; Eggert & Kanemoto, 1977). In lepidodendrid stems (*Diaphorodendron*) the primary phloem occurs as a discontinuous ring of strands separated by regions of parenchyma that accompany departing leaf traces (Eggert & Kanemoto, 1977). A discontinuous ring of primary phloem also occurs in the *Stigmaria ficoides* system where the interruptions in the ring mark locations where lateral appendage traces pass outward (Eggert, 1972).

The primary phloem "bottleneck" in the transition region, in particular, poses the problem of how food from the aerial pole reached the stigmarian system, especially as lepidodendrids became larger. Primary phloem bands were displaced outward, presumably by basal secondary xylem development, and never augmented. Another way to look at the anatomy is that the bands of primary phloem constitute all that were formed. This supposed constraint in long-distance translocation draws general attention to a broader problem: how could lepidodendrids attain such large sizes, even as short-lived plants, if they had limited capabilities to translocate photosynthate between aerial and subterranean systems, as well as within the shoot?

It is suggested that lepidodendrids relied on somewhat different functional uses of pole and stigmarian systems. These may be described generally as diffuse photosynthesis with limited translocation and with tissue growth and maintenance derived from local sites of photosynthesis. This may have occurred independently in both axial systems and was possibly critical in their respective developments. The next topics explore ideas about this in order to frame the constraints broadly; then we attempt to assess the early establishment of growth stages. In assessing these, it is well to keep in mind that lepidodendrids did not develop into large long-lived trees with progressively enlarging crowns, trunks, and anchorage systems. They had arborescent architectures, but were determinate in all respects.

SECONDARY THICKENING—PERIDERM

The principal secondary structural support of lepidodendrids was the periderm, added in such a way as to retain external tissue integrity for a prolonged growth interval. The circumferential position of the periderm constitutes the maximum support with the least allocation of resources. Also, as Cichan (1986) pointed out, the shift of prime support function to the periderm and other nonvascular tissue circumvented the trade-off between support and conduction roles and permitted more modest development of wood specialized for high conductance. Both pole and stigmarian axes developed a bifacial phellogen with the bulk of the periderm formed toward the inside. In stigmaria, secondary cortex was extensive but less radially aligned and more parenchymatous than in the stems. In *Stigmaria ficoides* (*Lepidodendron, Lepidophloios*) there was apparently a continuous meristematic region near the outer edge of the cortex; in sigillarian stigmaria the meristematic zones consisted of concentric rings in the outer cortex (Eggert, 1972). In both cases the accompanying cell division of derivatives was extensive and varied. It should be emphasized that the exact nature of this periderm is uncertain, but it was likely composed of persistently living cells, potentially meristematic, and might have been photosynthetic if exposed to light (Frankenberg & Eggert, 1969).

Secondary thickening in the pole stages resulted in more discretely patterned tissues than in stigmaria, derived from a circumferential meristematic zone beneath the leaf cushions or bases (Kisch, 1913). In some of the studied lepidodendrids (e.g., *Diaphorodendron*), the bifacial meristematic activity resulted in a sharp distinction between the inner and outer periderm. Whereas the inner periderm is usually more abundant and transitional to primary cortical parenchyma, the outer is characteristically dense and somewhat woodlike in cross section and became quite thick in some trees. The outer is the principal support tissue, and judging from its preservation under different circumstances, it was extremely decay resistant, probably quite rigid, and relatively impervious when externally exposed. In other taxa (e.g., *Lepidophloios, Lepidodendron, Paralycopodites*, and *Sigillaria*) a clear distinction between inner and outer periderm is lacking, the entire tissue is of the decay-resistant, dense, "woody" type. In general, the periderm tissues appear to have been living and could have been so for most of the plant's life. However, circumferential expansion of the periderm required special mechanisms to retain the external leaf cushions and associated tissues.

The leaf cushion or base of typical diamond outline is also a good structural support design (commonly used in reinforcing mesh for concrete). In lepidodendrids it imposes constraints to stem expansion. As far as we know, leaf cushions had very limited capacity to expand in basal width or height after maturation. Cells beneath lepidodendron-type leaf cushions could divide and accommodate some girth enlargement; in some species intercushion proliferation resulted in separation bands, which interestingly enough, exhibit cuticle and stomata like the leaf cushions (Thomas, 1970). In others, there were simply splits formed between leaf cushions (e.g., *D. scleroticum*). In the *Lepidophloios* leaf-cushion design, with the wide dimension being transverse to the stem, there was little means for such expansion without compromising the leaf-cushion cover. In *Lepidophloios* the primary body seems to have been relatively large. The crown branches had little periderm, which may have permitted leaf cushion retention and photosynthetic input, during the time and in the locus of cone formation.

With circumferential expansion, leaf cushions typically became obliterated or were sloughed off in older, lower trunk portions in most large plants. Some of these observations may be questioned because dead trees may have stood for some time with accompanying loss of cushions before entering depositional environments. However, some trunks as much as a meter in diameter were found buried in situ with leaf cushions still intact at the base. In some cases, the cushions on these stems appear to have "faded" through stretching and weathering, supporting patterns of subcushion expansion seen in petrifactions. The persistence of prominent leaf cushions on stems over 0.5 m in diameter is problematic and an explanation for this is lacking.

The key difference in the addition of periderm in lepidodendrids, compared to dicot trees, is that most of the living tissues were formed to the *inside*; the outermost, which were the principal support elements in some taxa, were not actually externally exposed until leaf cushions or bases were sloughed off. The most common concern in speaking about periderm or bark in lycopsids is that such terms tend to convey seed-plant equivalences. The periderm tissues are quite different from traditional bark. The chemical composition of the walls of the tissues is not known (see Logan & Thomas, 1987). The activity of the periderm-producing meristem in the pole apparently continued longer than secondary xylem formation and eventually extended further up, as well as out into some branches. Secondary xylem was probably fully formed for a given level of the plant early, compared to extended cortical cambial activity. At least one species of *Diaphorodendron* exhibits wood and thick periderm development out into some branches (DiMichele, 1981).

"LIGHT SHARING" AND DIFFUSE PHOTOSYNTHESIS

POLE HABIT

Among the most unusual ecological aspects of lepidodendrid architecture in tropical swamps are the "light sharing" consequences of determinate growth in relation to the lycopsid tree habit. A corollary of this architecture is limited light capture because of the pole design. Needless to say, in comparison to tropical angiosperms it is anomalous for the largest and dominant forest trees to be "light sharing" as opposed to preempting such resources and shading the understories. This is perhaps understandable in the context of intense tropical sunlight and suggested physiological functions mentioned later. In the case of lepidodendrids, this light sharing needs to be assessed, first from the perspective of its implications for lepidodendrid physiology and the peculiar morphological structure of the plants, and second its impact on community structure.

Lepidodendrid trees are commonly pictured as determinately branched with "crown"-like tops, as in the terminal reproductive phase of *Lepidophloios* or *Lepidodendron*. As did the pole habit that constituted most of the plant's life span, these final stages permitted high light penetration. Those genera with lateral branches typically dropped them (deciduous), reflective of the determinate growth of laterals. Such branches were usually not maintained as sources of photosynthesis after local cessation of cone production. Considering that sizes and numbers of leaf cushions and leaves in the lateral and terminal branch systems diminish acropetally (Chaloner & Meyer-Berthaud, 1983), concern about photosynthetic capacity was expressed early in the recognition of determinate growth (Andrews & Murdy, 1958). However, with the progressive loss of the larger, more basal leaf laminae, the leaf cushions were in a position to receive sunlight and continue photosynthesis, even on the mature trunk. Evidence of cuticle and stomata is consistent with continuation of photosynthesis by leaf cushions after leaf abscission (Thomas, 1977). Leaf cushions also contained parichnos (Weiss, 1907).

High levels of light penetrance through crowns, and through stands of trees, may have been crucial to the success of plants with a limited capacity to translocate photosynthates, as well as dissipate heat with evapotranspiration. Photosynthesis was by necessity a dispersed function in the pole-development phase. Small amounts of phloem placed limits on long-distance source to sink translocation. Yet, cortical cambia evidently continued to function beneath the leaf cushions in lower parts of the plants for some time, suggesting that leaf cushions were a likely local source of photosynthate. Even more intriguing is the implication of limited phloem for massive, in some cases monocarpic, cone production on determinate, terminal branches. The largest of all cones among lower vascular plants were produced on short lateral branches borne within the crown in plants such as *Lepidophloios*. The extremely large distal laminae of the sporophylls, especially of the *Lepidocarpon* type, may have been a major photosynthetic source contributing to cone development and to the massive megaspore reserves (DiMichele & Phillips, 1985). The lepidodendrids produced the largest endosporic megagametophytes among lower vascular plants.

In the above circumstances, high light penetrance permitted by the pole architecture, and the reduced sizes of crown leaves, would allow an appreciable level of photosynthetic capacity in the lower portions of the trees. Loss of leaf laminae and lateral branches would have further minimized obstacles to light penetration allowing sunlight to reach the forest floor and permitting establishment of the propagules of lepidodendrids or other plants. As a consequence, lycopsids were likely not climax species, except where abiotic conditions selected strongly against other kinds of plants. It is likely that many lepidodendrids were seral, and required high-light levels for germination and growth.

STIGMARIAN SYSTEM

The high light penetrance permitted by the pole architecture of lepidodendrid trees is particularly important for interpretation of the functions of the stigmarian system. The stigmarian system represents a special problem for food supply, in that sustained growth of the two axial systems simply exacerbates the puzzle of the lack of a recognizable long-distance, photosynthate translocation mechanism. The primary phloem connection in the transition zone is miniscule and secondary phloem is lacking. The appendages of the main stigmarian

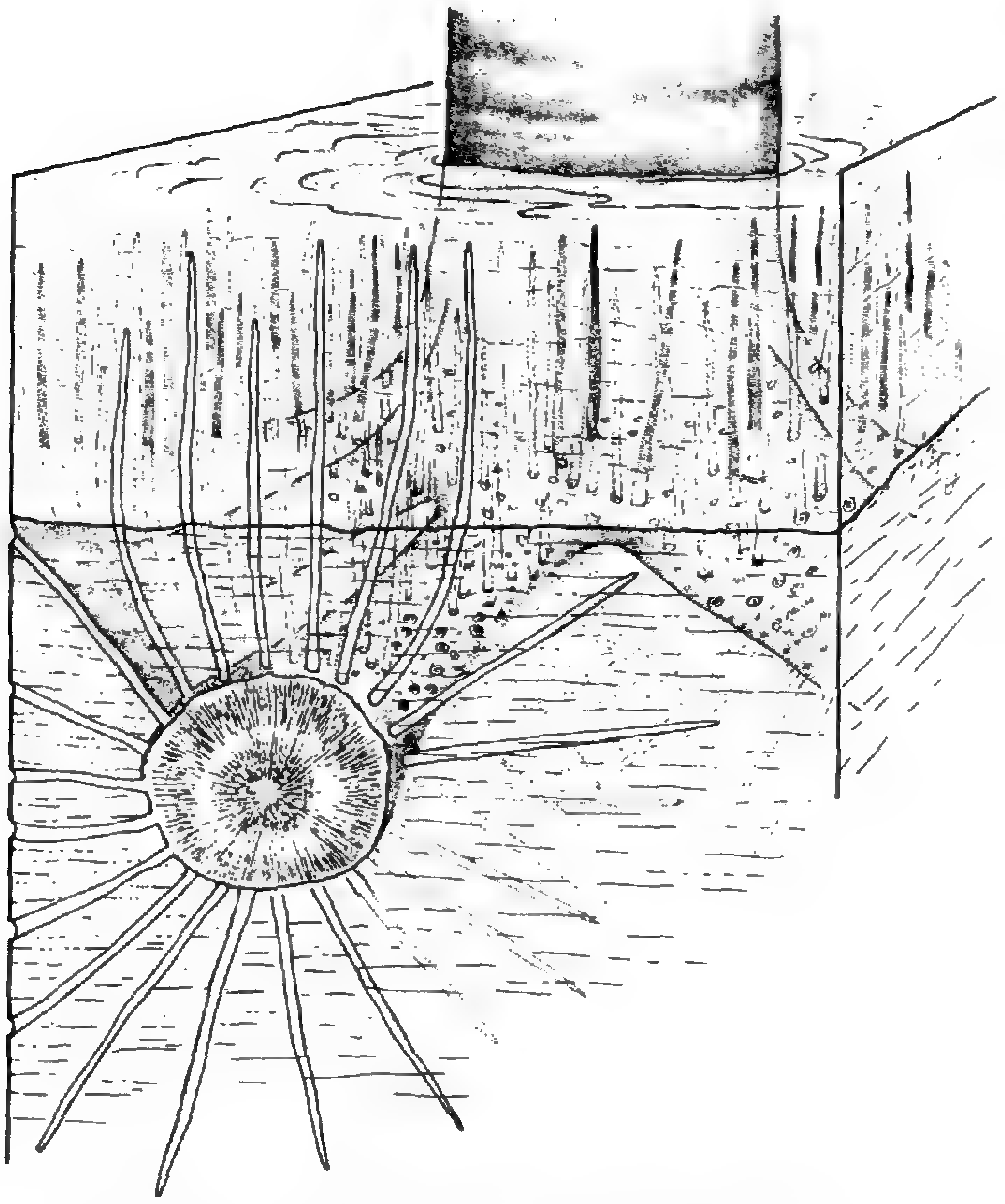

FIGURE 1. Reconstruction of the transition zone between trunk and stigmarian rhizomorph in a lepidodendrid tree. Shallow burial of the dichotomously branched rhizomorph axis and flooding of the swamp surface permit exposure of the stigmarian appendages to light in the water column. The "star-burst" pattern of appendages surrounding the rhizomorph axis can be observed in clastic sediments, where substrates were homogeneous in consistency. Studies of coal balls suggest a less regular pattern in peats, which have a heterogeneous fabric.

axes were helically dispersed and radiated in all directions. Attached to each of the four multiply dichotomized main axes, appendages penetrated and trapped sediment providing shallow anchorage and nutrient supply, along with water conduction. In addition, appendages provided the pathway for diffusion of gases throughout the stigmarian system and into the basal trunk; the aerial system had its own aeration system. Many of the stigmarian appendages were directed upward from the main axis and would have entered the water column after penetrating the substrate surface (Fig. 1). In depths of up to 0.5 m or somewhat more, the appendages could have been buoyant and floated to near the water surface. We do not suggest that they were emergent pneumatophores in *Stigmaria ficoides*. Their structural constraints do not seem to have permitted that. In such a water-bathed environment, gas exchange or a higher oxygen content was likely, though probably quite varied according to circumstances.

Several possibilities exist regarding gas exchange, photosynthesis, and the uncertainties about food supply in the stigmarian system. If the near surface appendages were capable of photosynthesis and light penetration of the water surface were adequate, the stigmarian systems may have been self-reliant, producing their own photosynthate. In this case, the paucity of phloem between the photosynthetic shoot and stigmarian axes would not limit stigmarian growth. One especially critical environmental aspect is that light penetration of the water was adequate. The organic matter in such circumstances could have limited that severely. While there is no anatomical support for the stigmarian appendages being, in part, photosynthetic, this line of reasoning is worth pursuing to some of its theoretical and logical ends.

PARICHNOS AND LACUNAE: INTERNAL DIFFUSION VERSUS EXTERNAL GAS EXCHANGE

PHOTOSYNTHETIC IMPLICATIONS

Aerial shoot-system morphology provides more clues to the internal diffusion of O_2/CO_2 in lepidodendrids than does even the stigmarian system. However, there are some analogies between well-differentiated air exchange passages recognizable in each. Appendicular structures have parichnos or lacunae closely associated with but clearly separated from the vascular strands by parenchymatous tissues in leaf bases, lamina (including sporophylls), and stigmarian appendages.

Whereas the structure and distribution of parichnos differ among the lepidodendrid genera, all have a pair that are present in *primary* tissues of the leaf base and extend, in most genera, into the lamina. The most distinctly traceable, as a pair, are in sporophyll leaves of *Lepidocarpon* from the pedicel to near the tip of the distal lamina. The distinctive cellular construction in the sporophyll lamina is identical to that in the leaf cushion. In the vegetative leaves, such as those of *Lepidophloios*, only a single parichnos or "lacuna" passage occurs abaxial to the vein (Graham, 1935).

Were it not for the presence of both parichnos and stomata in both leaf base (cushion) and lamina, external gas exchange would appear to be the obvious function of the parichnos. For photosynthetic leaves and leaf cushions with stomata, the parichnos would appear to be an internal system of gas exchange associated with photosynthesis, corresponding more to recycling of CO_2 and O_2 than to external diffusion balances, which were presumably mediated by functional stomata on photosynthetic surfaces. This would be particularly true in genera such as *Paralycopodites* or *Diaphorodendron*, where the parichnos system was entirely internal prior to leaf loss. The loss of laminae from most lepidodendrid leaf cushions is accepted as an abscission process, paralleling that of stigmarian appendages. However, if abscission in lycopsids were even roughly comparable to that of other vascular plants, the parichnos may have been obstructed at the abscission point in the leaf cushion and would not have functioned in external gas exchange, as analogized with lenticels. Two divergences from this *Diaphorodendron-Paralycopodites* parichnos pattern are evident. The first, represented by *Lepidodendron* and *Lepidophloios*, characteristically exhibited a lower pair of infrafoliar parichnos on the leaf cushion connected to the main parichnos system; this pair is hidden in *Lepidophloios* by cushion imbrication and has been identified (by us) only recently from anatomically preserved specimens. It is reasonable to assume that these external parichnos functioned in diffusion. The second is found in *Sigillaria*, which has the most prominent parichnos among the lepidodendrids. A pair flank the vascular strand and extend inward from the leaf cushion through thick periderm to form a single fusiform mass of highly distinctive, dense, almost resinous tissues. It is not really possible to distinguish sharply among parichnos that may have been aerating systems for deep-seated tissues, such as in *Sigillaria*, for functional exchange or venting as in *Lepidodendron*, or only internal recycling as suspected in *Diaphorodendron*. We can only raise the possibilities of differences, especially for the coal-swamp centered genera.

It is likely that some lepidodendrids may have been primeval photosynthetic giants in coal swamps. With limited water transport capacity, general xeromorphy and a variety of anatomical features that suggest CO_2 conservation, they may have utilized physiological attributes that resembled CAM (Crassulacean Acid Metabolism) plants in their aerial shoot systems. If this were the case, it follows that their stigmarian systems were also CAM-like if photosynthetic. Barring the potential role of stigmarian systems as being partially photosynthetic, it seems likely that they could have been major systems of CO_2 acquisition.

If stigmarian appendicular tissues could photosynthesize, CO_2 may have been obtained both from the organic-rich swamp water and from respiration. The concentrations of CO_2 could have been extremely high, minimizing photorespiration. In a sense, the possible design is most similar to a "submerged version" of a CAM plant that has no stomates to open at night and a surplus CO_2 supply. This may fit with the peculiar lacunar design of the stigmarian appendages where the inner wall surface is about the same as the outer with the excentric vascular strand loosely connected with the outer cortex. Those stigmarian appendages that may have been photosynthetic would have been both major sources of food and aeration for the submerged system, while others provided anchorage and nutrients, functions dependent on the microenvironment in which they developed; these were expendable appendages of limited duration permitting the axis system to meet changing environmental circumstances. If stigmarian appendages utilized only a part of the high CO_2 concentration in photosynthesis, the water conduit would have been a means of moving dissolved CO_2 to aerial portions. This could have enhanced the photosynthetic capacity of the shoot with the parichnos perhaps mediating O_2–CO_2 physiological balance. While emphasis here is on the possibility of photosynthesis in the stigmarian system, the collective arguments for internal recycling of CO_2/O_2 in the pole system follow the same line of reasoning for a CAM-like physiology.

The high light penetration permitted by lepidodendrids is consistent with, but not necessarily demanding of, such interpretations. However, in a lepidodendrid dominated tropical-swamp forest with pole-tree canopies, light intensity would have been high enough to support floating or submerged vascular aquatics very near the surface. As far as we know, there were no such plants. Even in the shallow reaches, accessible to other trees and herbs, there may have been relatively little shading. There could have been an enormous mass of buoyant stigmarian appendages in many water surface areas. In fact, if you pursue the strategies of lepidodendrids in the coal swamps, it is the "light permissiveness," allowing light to reach their own trunks and branches, their reproductive offspring on the surface of the water or exposed peat, and perhaps their stigmarian appendages, that constitutes the ultimate anomaly in tree design.

The estimated biomass of stigmarian structure preserved in peat deposits are taphonomically biased by what happens after burial. However, of the stigmarian biomass preserved in coal balls, 75–90% of it is appendicular as opposed to axial. Only in a few "root peats" with repeated "rerooting" of stigmarian systems do the percentages drop to the 60% level. With that much biomass allocated to appendages, it is reasonable to suggest that perhaps such appendages were more than conventional "rooting" organs.

It is well beyond our scope to try to carry our ideas about CO_2 uptake and CAM in lepidodendrids to the living *Isoetes* (= *Stylites*). However, the discovery of CAM in *Isoetes* (Keeley, 1981, 1982; Keeley et al., 1984) and further studies of the process in these plants (Boston, 1986; Boston et al., 1987a, b; Raven et al., 1988; Sandquist & Keeley, 1990, and references therein) should not be divorced from potential implications for both small and large rhizomorphic lycopsids of the geologic past. That stigmarian lycopsids suggest physiological attributes comparable to extant *Isoetes* is mostly a matter of their large size, excellent preservational integrity, and our ability to resolve their ecologies broadly. Perhaps the most pertinent speculation about the late Paleozoic rhizomorphic lycopsids would be, "What if they were CAM plants?" We should not bias relevant comparisons to just the smaller ones (Raven et al., 1988), nor continue to hold to the great reductional series (Thomas, 1985) with its implications about aquatic morphologies. This may aid in viewing *Isoetes* (*Stylites*) as a model system for how some lycopsids (vascular plants) invaded seasonally dry terrestrial environments (Keeley et al., 1985) as well as tropical swamps.

The evolutionary generalization we suggest about the open canopy of the lepidodendrids is that they probably radiated under such conditions, perhaps in the virtual absence of non-lycopsids and utilized diffuse photosynthetic distribution systems to permit their growth in height, while allowing sunlight to reach the full range of their organ systems. With their short-term strategies for reproduction this reemphasizes their "giant herb" status. This brings in a recurrent question about why lepidodendrids were so tall compared to their contemporary tree types in the tropical swamps. While actual sizes differed greatly between coal and clastic swamp lepidodendrids, and even among coal swamps with time and circumstances, they were consistently the tallest by far.

Early Stage Development

The early development of the lepidodendrid plant must have involved even closer coordination of stem and rhizomorph development than that projected for later stages. Briefly, the early stage may be considered as a temporally coordinated development, in which the pole and stigmarian shoots share resources during establishment growth. In order for expansion of the primary bodies in both systems, and increase in appendicular sizes and functions, there has to be a closer coordination of shared food supply than presumed in later stages. This mode of development is dependent upon some of the possibilities put forth about stigmarian photosynthetic potential. It depends, in part, on precocious branching of the stigmarian axis and attainment of a large primary body without a central pith or even a legitimate siphonostele.

If there is a "lepidodendrid" logic of developmental sequencing, it suggests that the pole trunk must be adequately stabilized, even if not necessarily well anchored, before achieving a massive apical plume of large leaves. In order to provide the mix of a stable platform and a large, perhaps domed or cone-shaped pole stage with a primary thickening meristem, one axial system has to develop somewhat ahead of the other. If both were photosynthetic, it is reasonable that it should be the stigmarian system (Fig. 2), with its early appendicular development and axial branching in the least demanding allocation strategy—the sparse "stele" of only appendage traces and a mostly hollow pith, that permits a rapid increase in circumference for appendage display. Also, stigmarias are more cheaply constructed than pole stages and lack the evapotranspiration limitations. The earliest formed appendages of stigmaria come from the transition region and may not have been indicative of the larger ones later produced. Nonetheless, the basalmost leaf cushions of the pole phase, while not necessarily indicative of the first leaves formed, give evidence of an enormous expansion capability reflective of a large apical meristem, primary thickening, and perhaps expansion processes that go beyond these.

If stigmarian systems developed more extensively than stems in the "early stages" of tree establishment, then there is a stronger case for the photosynthetic potential of some stigmarian appendages. This supposes that the primary phloem translocation worked well, at least for a while, to supply the pole stage development. As development of the two organ systems ensued, the separate photosynthetic capabilities and the high light penetrance permitted by the pole design would become increasingly important. If a stigmarian system radiated outward before the pole stage expansion, there would be less self-shading. Considering the eventual primary-body expansion of the pole stage, it seems probable that the stigmarian system precociously assumed a prime photosynthetic, anchorage, nutrient, and water supply role in the critical establishment phase. If any or most of this proves to be the case, it is no wonder that stigmarian systems were the adaptive breakthrough of the mosaic lepidodendrid conquests of tropical swamps.

On a less speculative note, the relatively long-term growth and extensively ramified stigmarian

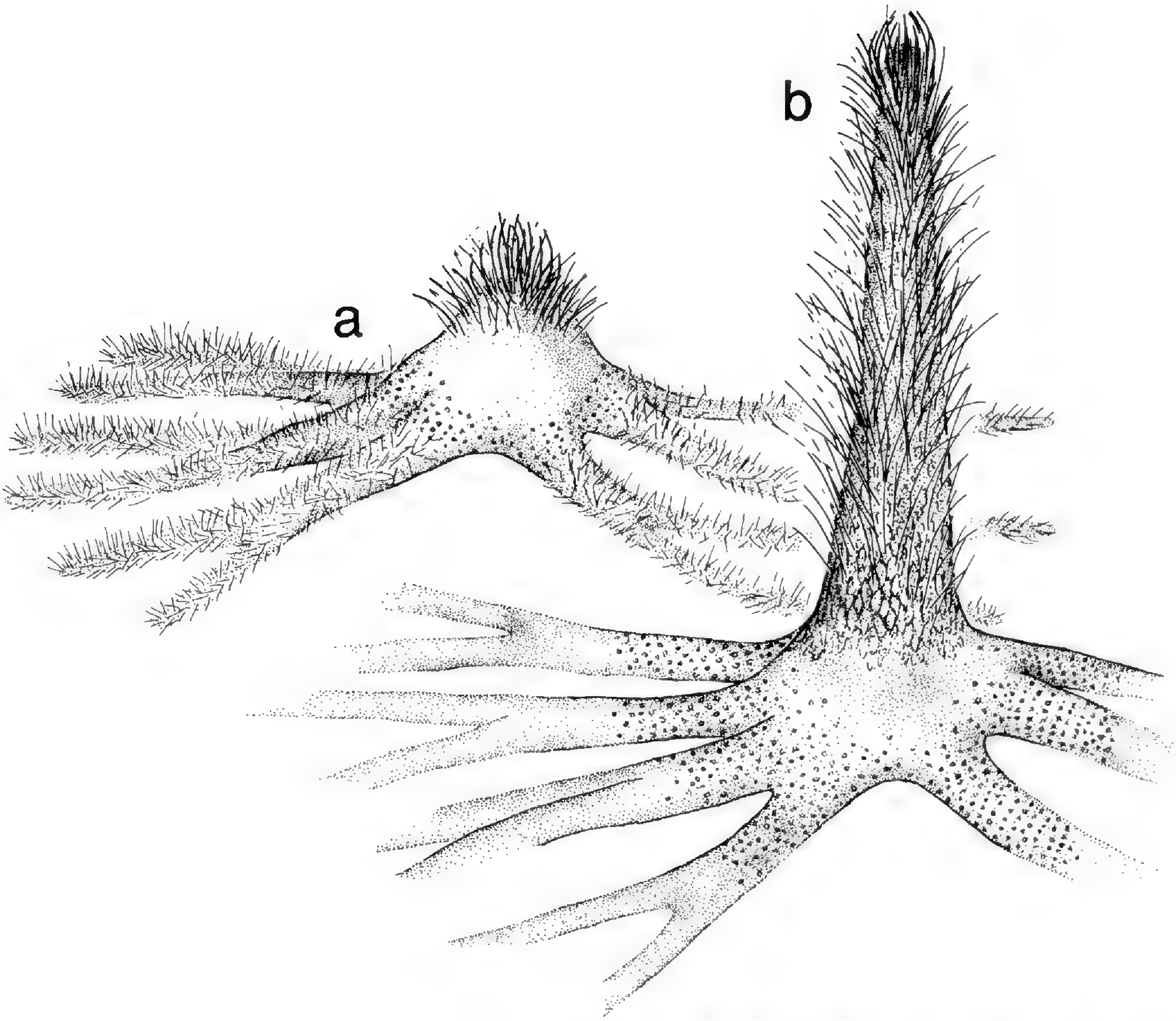

FIGURE 2. Hypothetical early growth stages of a lepidodendrid tree. Each reconstruction represents a successive stage, a, and b. In this hypothetical sequence, the stigmarian system is elaborated more rapidly than the trunk, made possible by an independent photosynthetic capacity. Early stages are rosettelike; once the stigmarian system is sufficiently elaborated to provide a stable base of support and supply of nutrients, trunk elongation occurs rapidly.

system was essential to the support and sustained or massed reproductive capacities of the lepidodendrids whether stigmarias were photosynthetic or not. The capacity to ramify and extensively permeate the substrates of soft sediment and water was crucial to longer lived and larger arborescent reproductive strategies; this is the critical distinction between lepidodendrids and the lepidodendropsids (*Lepidodendropsis*) and other isoetaleans that inhabited wetlands with them during the Early and/or Late Carboniferous.

PRINCIPAL GENERA

TAXONOMY AND COMPARATIVE MORPHOLOGY

Comparative morphological studies of the principal lepidodendrids in Late Carboniferous peat-swamp assemblages indicate very distinctive morphological groups corresponding to the currently recognized genera (Bateman et al., 1992). The known assemblages of each genus exhibit markedly different megasporangium-sporophyll units (Phillips, 1979), which largely frame the accepted generic limits at present. In part, the megasporangiate morphology of genera seems so stereotyped in basic structure that it is not useful currently below the generic level for taxonomic delimitation, except in *Sigillaria* and perhaps *Paralycopodites*.

The microsporangia and especially the microspores provide sharp distinctions among *Sigillaria*, *Diaphorodendron*, and the three *Lycospora*-bearing genera (Courvoisier & Phillips, 1975; Willard, 1989a). Taxonomic distinctions among some of the *Lycospora* microspores correlate, in large part, with the different genera (*Paralycopodites*, *Lepidodendron*, *Lepidophloios*) and, in turn, permit separation of *Lepidophloios harcourtii* from *L. hallii* (Willard, 1989a, b).

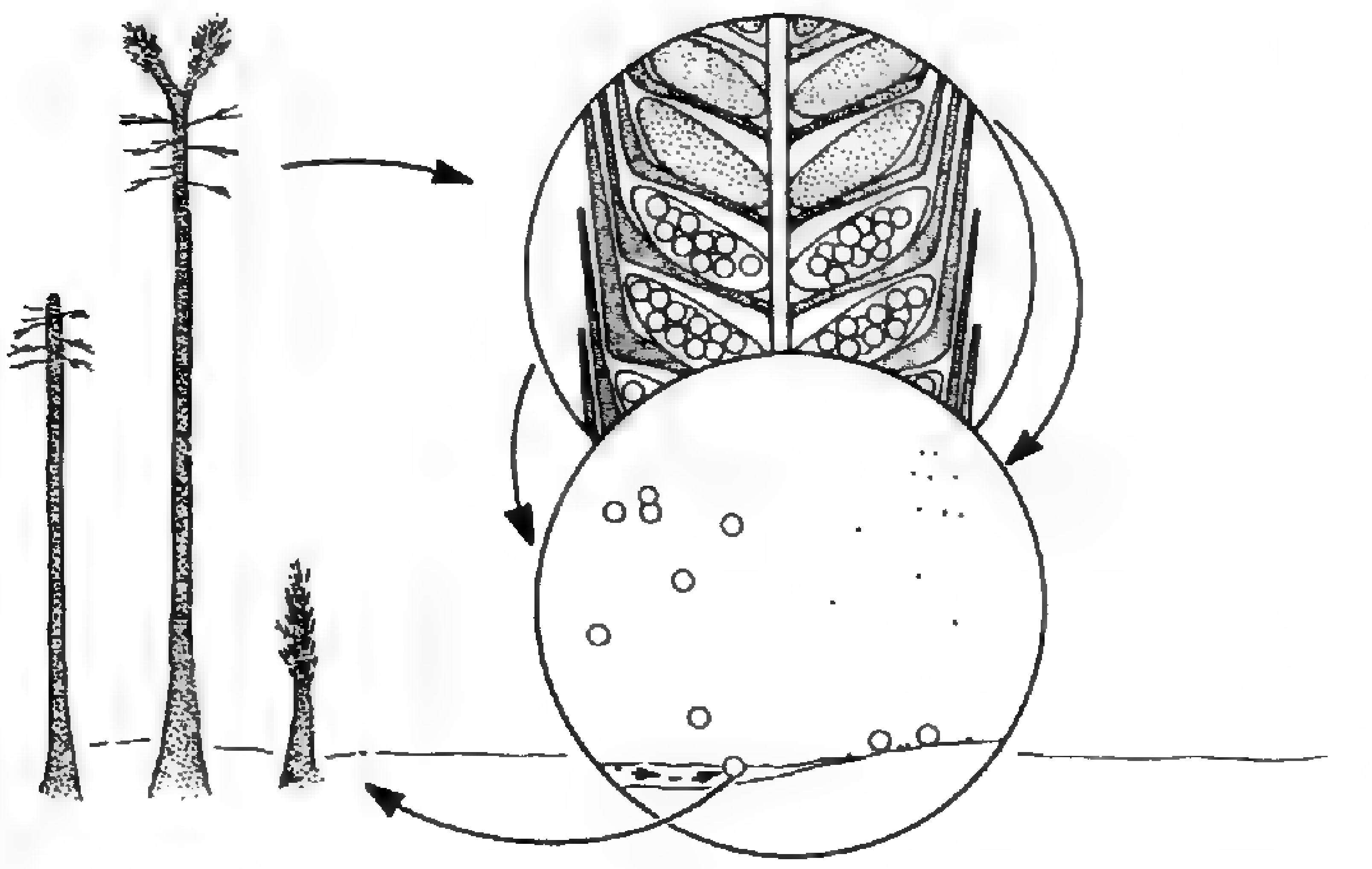

FIGURE 3. Inferred life history of *Paralycopodites* (= *Anabathra*) species. This was the only one of the lepidodendrid trees to produce a bisporangiate cone (*Flemingites*), freely releasing megaspores and microspores. Cones were produced on deciduous lateral branches. Plants appear ultimately to have been determinate, suggested by a limited number of apoxogenetic apical dichotomies.

Whereas each of the five lepidodendrid genera are now recognized to be quite distinctive anatomically, there is a paucity or lack of known vegetative characteristics to separate coal-swamp species within *Paralycopodites* and within *Lepidodendron*. Sigillarias are too poorly known in coal swamps to apply rigorous vegetative comparisons; however, the sigillarian stigmarian system certainly is the most distinctive of the lepidodendrid genera. By contrast, *Diaphorodendron* species, as very abundant lepidodendrids in peat swamps, are now separable only by vegetative morphology (DiMichele, 1979b, 1981, 1985).

Paralycopodites (= *Anabathra*)

Three species of *Paralycopodites* can be recognized in the Carboniferous, based on reproductive organs. One species producing a *Flemingites scottii* cone is known from the Lower Carboniferous of western Europe (Meyer-Berthaud, 1981). In Pennsylvanian peat swamps of the United States, two species have been recognized, one producing *F. schopfii* in the Westphalian C (Brack, 1970), and one with *F. diversus* in the Westphalian D (Felix, 1954). The vegetative organs of these species are indistinguishable; the leaves have enlarged bases but lack distinctions of a leaf cushion and lamina. All those species described produce *Lycospora orbicula* microspores (Willard, pers. comm.).

Paralycopodites abundances are highest in ecotonal habitats marking the transition from peat to clastic substrates. In peat profiles, *Paralycopodites*-rich zones often occur adjacent to clastic partings or in parts of the coal seam enriched with mineral matter (DiMichele & Phillips, 1985, 1988; Willard, 1989a). Similar patterns are suggested by spore data (Calder, in press; Eble & Grady, in press). Medullosan pteridosperms often are part of this assemblage in the Westphalian D. *Paralycopodites* appears to have been a colonist, preferring open, disturbed, but nutrient-enriched parts of peat swamps, probably not subjected to long-term flooding. Little is known of these kinds of plants from purely clastic deposits. The genus *Ulodendron* (sensu Thomas, 1967) may be the closest counterpart. A lepidodendrid that appears to occupy a comparable habitat in some clastic swamps is *Bothrodendron* (sensu Wnuk, 1989).

Paralycopodites trees bore opposite rows of small, deciduous, lateral branch systems on the trunk. At the ends of the lateral branches cones were produced in abundance. Trunks ultimately dichotomized, but apparently only in the later phases of determinate growth. Habit reconstructions can be found in Hirmer (1927, for *Ulodendron majus*) and in DiMichele & Phillips (1985). These reconstructions emphasize that the fundamental function of the lateral branch systems was cone display; as with monocarpic forms, branching formed a scaffold on which cone production occurred.

The reproductive biology of *Paralycopodites* in combination with its habit appear to have been the keys to its ecological success (Fig. 3). Cones were bisporangiate; microsporangia occurred in the apical part of cones, megasporangia in the basal portion. Multiple megaspores were produced within each megasporangium and were freely released into the environment. The prolific production of cones by *Paralycopodites* in the frequently disturbed ecotonal habits commonly resulted in the abundance of cones and cone fragments, many still containing spores, associated with their vegetative litter. Exceptionally well preserved endosporic gametophytes have been documented in phenomenal detail (Brack, 1970; Brack-Hanes, 1978; Brack-Hanes & Vaughan, 1978).

The nearly continuous production of cone-bearing branches, the overall large allocation to cones, and the assured presence of both male and female gametophytes provided by bisporangiate cones of *Paralycopodites* are consistent with its role as a colonizing, pioneer species. Continuous saturation of the local habitat with megaspores and microspores and the potential for some widespread water dispersal, even for cone fragments, during occasional floods, may have circumvented unpredictability of local conditions. This could have introduced some plants into a wide variety of settings, some favorable for establishment. In this sense, *Paralycopodites* may have escaped the constraints of heterospory, which imposes an absolute need for separate male and female gametophytes to be present within a narrow spectrum of wet environmental conditions if sporophytes are to be produced; this is not the optimal life history for a colonizing species. However, modification of sporophytic architecture, so that megaspores and microspores were produced nearly continuously over an extended life span, permitted it to sustain prolific reproductive functions in a role not generally accessible to free-sporing bisporangiate plants of shorter life spans.

Sigillaria

Sigillaria is a diverse genus, comprising at least two subgenera. Nearly all of the species have been described from clastic environments, including a number of structurally preserved forms (Lemoigne, 1960). In peat-forming swamps, *Sigillaria* occurs throughout the Pennsylvanian, although no swamp-centered evolutionary lineages can be identified. Based on cone morphologies, sizes of plants inferred from the dimensions of preserved organs, and anatomies of the swamp species, it appears that sigillarians sporadically entered, became established, and then disappeared from peat swamps. They were generally a minor, but detectable part of most Westphalian and Stephanian swamp habitats. Relatively higher abundances occur in the late Westphalian A to early B and in the Stephanian. Sigillarias produced separate microsporangiate and megasporangiate cones; both were basically free sporing but with a complex megasporangiate dispersal pattern. Cones are assigned to *Mazocarpon* if preserved anatomically (see Benson, 1918; Phillips, 1979). Microspores belong to the dispersed spore genus *Crassispora*.

The sigillarians appear to encompass a range of ecological conditions that suggest drier habitats or lower water tables associated with wetlands. Although it is not possible to give specifics for such a large group, the hallmark of their ecology appears to be a preference for the more marginal wetland settings with entry into peat swamps following floods and dry downs. Their common occurrence in channel lag sandstones suggests growth of some species along stream margins. Others may have been part of wet levee communities (Gastaldo, 1987), or occupied freshwater, nutrient-enriched parts of swamps, close to channels, and perhaps intermittently in flowing water (DiMichele & Nelson, 1989). In peat swamps of the Westphalian, *Sigillaria* abundance was usually associated with abundant ground cover, medullosans, and sometimes species of *Diaphorodendron*; *Sigillaria* is less commonly associated with indicators of long periods of standing, possibly stagnant water (e.g., Phillips & DiMichele, 1981; Willard, 1990).

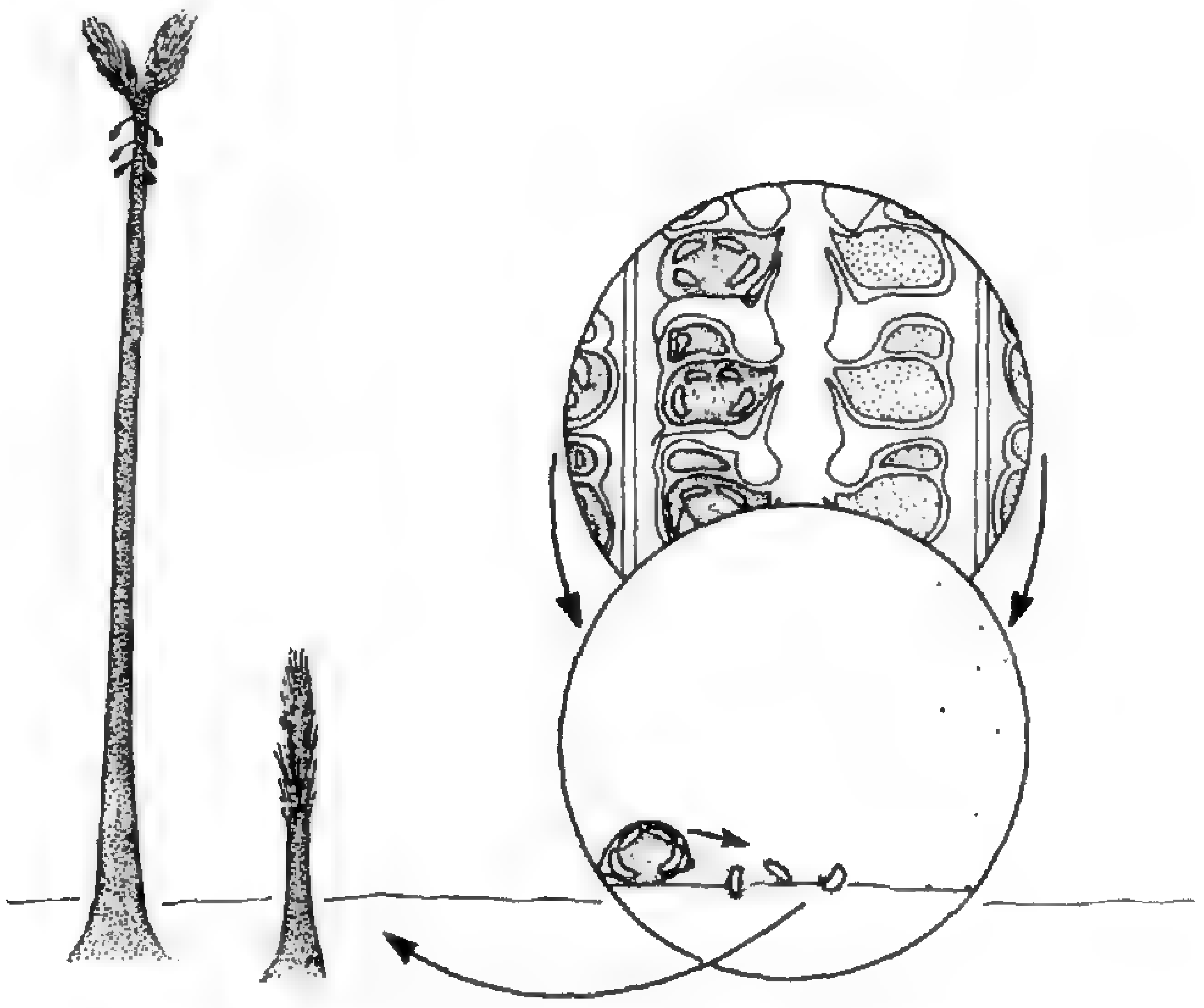

FIGURE 4. Inferred life history of *Sigillaria ichthyolepis* (= *S. approximata*), from the Late Pennsylvanian. All *Sigillaria* produced separate megasporangiate and microsporangiate cones assignable to *Mazocarpon; S. ichthyolepis* produced *M. oedipternum*. Megaspores of *M. oedipternum* had a thick subarchesporial pad covering the proximal face. We suggest in this reconstruction that this pad may have obviated sperm access to eggs, fostering apomixis as the link between sporophyte and gametophyte.

Several aspects of sigillarian architecture may provide some additional insights on their biology (Fig. 4). The trunks apparently were sparsely branched terminally at maturity, and some may not have branched at all except during cone-bearing phases (e.g., Hirmer, 1927). In coal-ball deposits it is most common to find accumulation of bark sheets or fragments of large stems without ever encountering twigs or smaller axes that could suggest a crown. These peats often show evidence of considerable exposure and decay. Stigmarian systems were smaller and more compact than those found in other lepidodendrids, and it is strongly suspected that they were the most distinctive, both in branching architecture and function. Lemoigne (1960) suggested that some branching of sigillarian stigmarias may have penetrated the substrate deeply. This would have strongly anchored these plants and could have tapped lower water tables and perhaps more aerated groundwater; in other lycopods the stigmarian systems were buried shallowly and formed a broader platform at the base of the tree. The small sigillarian stigmarian appendages contain a connective, a band of tissue linking the vascular strand to the outer cortex; small size and the connective also provide greater structural strength than is found in the balloonlike appendages of the other lepidodendrids.

Reproductively, cones apparently were produced intermittently and were borne by peduncles directly on the trunk in whorls. This suggests, in context of their habitats and habit, that they were tolerant of fluctuation in the relative wetness of the environments and perhaps responded to drier and wetter episodes to reproduce. Because sigillarians were basically free-sporing, this intermittent reproduction entailed the risk of mistiming spore release unless the local environments were wet, at least soon after dispersal.

The largest known sigillarias in peat swamps are from the Stephanian, a size feature shared with tree ferns, calamites, and medullosan seed ferns. Several sigillarian species were present, based on cone morphology (Schopf, 1941; Pigg, 1983; Feng & Rothwell, 1989). Our reconstruction (Fig. 4) is of *Sigillaria approximata* and *Mazocarpon oedipternum.* The megasporangiate cones are the best known among the sigillarias, with the megaspores embedded in a subarchesporial pad of parenchyma, apparently a generic characteristic. Benson (1918) and Schopf (1941) suggested that the cones were deciduous and the contents were dispersed by sequential cone, sporangial, megasporesporangial fragment units. These units could have been disaggregated after or during dispersal by mechanical means, or germination may have occurred locally where the cones originally fell. The presence of megagametophytes and possibly embryos in *M. oedipternum* (Schopf, 1941) led us (DiMichele & Phillips, 1985) to suggest apomictic origin of the embryos. It is not the presence of putative embryos alone that leads to this suggestion, but rather the adherence of archesporial parenchyma to the proximal surface of the megaspore, obviating access of sperm to the eggs. Details of sigillarian reproductive organs are discussed in papers by Phillips (1979), Pigg (1983), and Feng & Rothwell (1989). Sigillarian cone and megaspore morphology suggest evolutionary changes in mode of dispersal during the Pennsylvanian. Earlier megaspore types had barblike (apiculate) or similar appendages. The Late Pennsylvanian ones lack these and had adherent tissue protection.

Sigillaria may have made some ecologically significant, evolutionary modifications in timing of reproduction and dispersal mechanisms as a response to environmental variability. Morphological differences among cones provide evidence of changing circumstances within the Late Carboniferous peat swamps (Benson, 1918; Schopf, 1941; Pigg, 1983). Considering evidence of frequent disturbances in peat-swamp environments, including fluctuations in water tables, sigillarias may have tracked the most extreme dry-wet seasonal fluctuations or comparable changes in water tables caused by other factors. Morphological features of some megaspores may have been as important for prevention of desiccation, or for protection in flood transport (as proposed for *Porostrobus,* Leary & Mickle, 1989).

Diaphorodendron

Diaphorodendron species comprise two life-history groups, one polycarpic, the other monocarpic (DiMichele, 1979b, 1981). Three polycarpic species have been identified in Pennsylvanian-age coal swamps, but the similarity in morphology of many of these forms probably masks greater species diversity. *Diaphorodendron vasculare* occurs throughout the Westphalian except for the uppermost Westphalian D. It probably represents a species complex. *Diaphorodendron phillipsii* occurs in the Westphalian C–D, and *D. scleroticum* is known only from the Westphalian D. The monocarpic forms have been subsumed in a single species, *D. dicentricum,* which probably represents a group of related species. All species in this genus appear to have identical reproductive structures (Fig. 5). Cones are assigned to *Achlamydocarpon varius* (Leisman & Phillips, 1976). Megasporangiate cones had one functional megaspore (*Cystosporites varius*) per sporangium. Microspores are described now as *Granasporites medius* (Ravn et al., 1986) and were frequently dispersed as tetrads.

The *Diaphorodendron* species, individually and collectively, are the most difficult of the arborescent lycopsids for which to deduce ecological strategies because they have such broad ecological amplitudes. They occur in markedly different kinds of assemblages within peat swamps, as dominant to minor elements. Furthermore, both polycarpic and monocarpic forms occur in clastic as well as peat-forming habitats, an overlap that apparently extends to the species level (e.g., Wnuk, 1985). This is the only aquacarpic genus thus far recognized that appears to have undergone marked evolutionary change within the Westphalian. Much as the recognition of *Diaphorodendron* as a genus distinct from *Lepidodendron* was long delayed (DiMichele, 1985), so has there been delay in the separation of species ecologically. All species of *Diaphorodendron* appear to have the very same reproductive morphologies. This is in contrast to *Sigillaria* where there were differences in megasporangiate and megaspore reproductive morphology and in vegetative, and presumably physiological, strategies. Polycarpic species of *Diapho-*

rodendron appear to have favored areas of infrequent, irregular disturbance. Monocarpic forms appear to have been colonizers of disturbed areas, but apparently lived for quite a long time on these sites, attaining large size (Wnuk, 1985).

Diaphorodendron vasculare is characteristic of the ancestral condition in this genus. Its distributional history indicates a broad ecological amplitude. Trees produced deciduous lateral branches on an otherwise unbranched columnar trunk. Reproductive allocation appears to have been low at any given time. Even in coals where *D. vasculare* is the only lycopsid tree, reproductive organs are not encountered frequently, and relative abundances of *Granasporites* in spore-pollen samples greatly underestimate the biomass of the parent plants (Peppers, in Eggert & Phillips, 1982). The lateral branches contain little wood or bark, were of quite limited sizes, and served largely to support the cone array. The extended, low-level reproductive output may have positioned these plants to recover rapidly from severe but unpredictable (irregular) disturbances. They are rarely fusinized and occur in some assemblages in association with marine invertebrates, so disturbances such as wind throw, storm surges of marine waters into peat swamps, or other causes may have been more important than fire.

Diaphorodendron scleroticum is built along the same plan as *D. vasculare*, except the amount of wood and bark is greater throughout the tree, extending even into the lateral branch systems (DiMichele, 1981). This suggests a longer life span than *D. vasculare* and retention of lateral branch systems, perhaps approximating the habit reconstructed by Walton (see Thomas, 1978). In this species the lateral branches may have formed a diffuse crown, the main function of which was light capture. Wnuk's (1985) discovery of whole trees indicates that lateral branches were distributed sparsely along the main trunk. As with *D. vasculare*, reproductive allocation in *D. scleroticum* appears to have been relatively low at any one time. Community ecological studies of several late Westphalian D coals (Phillips & DiMichele, 1981; DiMichele & Phillips, 1988; Willard, 1990) suggest great variation in the taxonomic and structural composition of assemblages associated with *D. scleroticum*. It is conceivable that these plants opted for tolerance of all but the most severe disturbances, leading to variable but taxonomically diverse, associated vegetation. This species of *Diaphorodendron*, more than any other lepidodendrid, somewhat approaches the status of a "conventional" (dicot) tree, with sustained structural support and maintenance of a crown. It is noteworthy that *D. scleroticum* is presently known only in the Westphalian D.

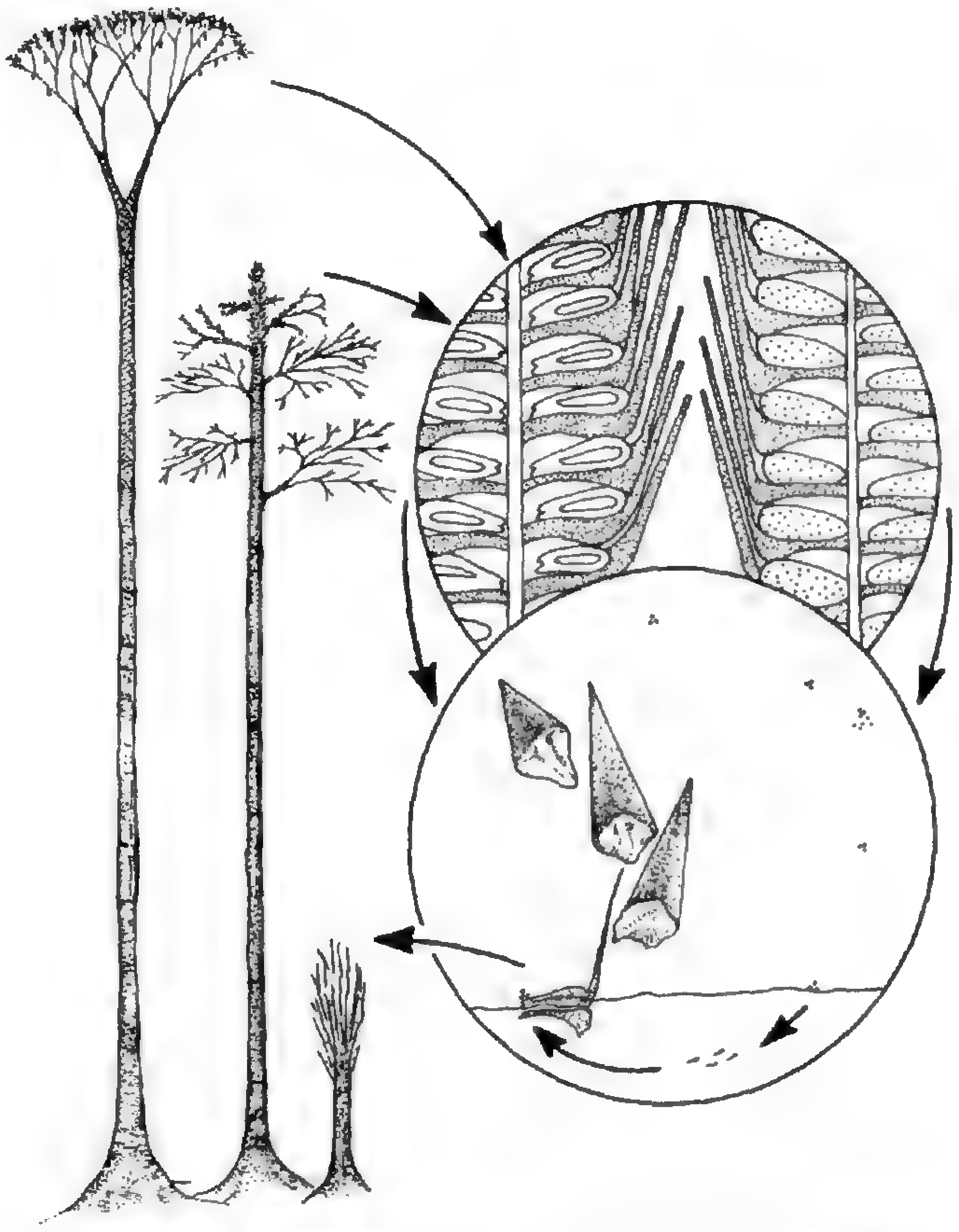

FIGURE 5. Inferred life history of the two major *Diaphorodendron* lineages, here represented by *D. dicentricum* (large tree to left, outside, with terminal crown) and *D. scleroticum* (center tree with crown of laterally borne branches). Innermost tree is a juvenile. Despite extensive differences in growth form and vegetative anatomy and morphology between these lineages, and even within some of the lineages, all species have indistinguishable reproductive morphology. Reproduction is characterized by separate megasporangiate and microsporangiate cones. The megasporangiate cones fragmented into aquacarp units composed of a sporangium with single functional megaspore and associated sporophyll tissues. Fertilization probably was aquatic.

The monocarpic *Diaphorodendron dicentricum* was also a large tree, nearly 30 m in height in clastic swamps (Wnuk, 1985). Structurally, the tree was cheaply constructed, with thin-walled cells in the periderm and broad bands of parenchymatous tissue in the wood (DiMichele, 1979b). The trunk was unbranched until the terminal phases of growth when a scaffold of branches was produced. Cones were borne on small side branches, derived from highly anisotomous apical divisions. Short-term, and perhaps lifetime, allocation to reproduction appears to have been much higher than in other *Diaphorodendron* species; very abundant *Achlamydocarpon varius* microsporangiate cones and megasporangium-sporophyll units typically occur in association with vegetative litter. The species can be found rarely as a codominant of intraseam assemblages (coupled with *Lepidophloios* near the end of the Westphalian D) and occurs widely at less than 10% biomass in assemblages from other late Westphalian D coals (DiMichele & Phillips, 1985). In these, its highest abundances occur in taxonomically and structurally diverse assemblages with a rich assortment of vines and ground cover (DiMichele & Phillips, 1988). We have suggested (DiMichele & Phillips, 1985) an invasive strategy for this tree, which is consistent with monocarpic habit and highly dispersed distribution. The cheaper construction and widespread but low density occurrence suggest *D. dicentricum* as a potential counterpart to *Lepidophloios* in longer-term monocarpic reproductive cycles. That is, *D. dicentricum* may be an ecological counterpart in longer-term life cycles for monocarpic lepidodendrids. The larger relative tree sizes and greater diversity-abundance patterns in some Westphalian D peat-swamp vegetation suggest temporal changes in disturbance frequencies.

The dispersal units of *Diaphorodendron* are apparently more stereotyped morphologically than those for any other genus of the five lepidodendrids, indicating that the sexual life cycle is extremely specialized in both microspore and megaspore dispersal and the linkage of these functions to morphology (Fig. 5). The tolerances of these linkages have been suggested by the distinctive morphology of a massa that was probably hydrophilic (Taylor & Brack-Hanes, 1976), an interlocking of microspores with the massa, and by the common dispersal of microspore tetrads. Leisman & Phillips (1979) noted that channels in the massa are about 65 μm in diameter, a dimension that would have allowed docking and entrapment of the microspores. It is interesting to note that the proximal faces of both the microspores, in persistent tetrads, and the functional megaspore with a massa were protected.

The dispersal units in *Diaphorodendron* morphologically fall between the relatively unspecialized free-sporing habit of *Paralycopodites* and the complex aquacarps of *Lepidophloios* (Phillips, 1979). *Achylamydocarpon varius* cones (Leisman & Phillips, 1979) may have been borne upright rather than pendent on the parent trees. Although monosporangiate, nothing is known about distribution of microsporangiate or megasporangiate cones among or within trees. That such widely differing life histories of the species are associated with the same set of morphological reproductive features suggests that evolution in the timing of reproduction, the tolerances of disturbance, and allocation to costly bark and wood, all features of the sporophyte, were species-determining elements in *Diaphorodendron* ecological strategies.

Lepidodendron

Lepidodendron (sensu DiMichele, 1983) was the clastic-swamp counterpart to *Lepidophloios.* Many species have been described, primarily from the compression-impression record; many of these are *Diaphorodendron* or other as yet nonsegregated genera that may be distinct from *Lepidodendron* sens. str. in anatomy and reproductive biology. Nonetheless, *Lepidodendron* does appear to have been far more diverse and abundant in mineral substrate wetlands than in peat swamps. Two well-circumscribed species are known from peat-forming environments: the arborescent *Lepidodendron hickii,* which appears to be the anatomical counterpart to the compression *L. aculeatum,* and the scrambling ground cover plants *L. serratum* (Felix, 1952; Baxter, 1965), which Bateman & DiMichele (1991) have segregated as a new genus. Both occur throughout the Westphalian. At least one other form, similar to *L. mannabachense* (Thomas, 1970), occurs in late Westphalian D coals. *Lepidodendron* persisted into the Stephanian in western European clastic swamps (e.g., Lorenzo, 1979) and may have lasted until the end of the Permian in both clastic and peat swamps of China (see Chaloner & Boureau, 1967). The megasporangiate cones of *L. hickii* from peat swamps are assigned to *Achlamydocarpon takhtajanii* (= *A. belgicum*) (Snigirevskaya, 1964; Balbach, 1966; Schumacker-Lambry, 1966); microsporangiate cones are of the *Lepidostrobus* type and produced *Lycospora pusilla* microspores (Willard, 1989a).

Species of *Lepidodendron,* with the important exception of *L. serratum,* were monocarpic. Most arborescent growth occurred as an unbranched, columnar stem. Growth terminated with a determinate "crown" of dichotomous branches (Thomas & Watson, 1976). Cones were borne laterally in the crown on strongly anisotomous branches. The *Achlamydocarpon takhtajanii* megasporangium-sporophyll units are similar morphologically to *Lepidocarpon* in general shape, site of megasporangial opening, and morphology of the megaspore (Phillips, 1979). They are about one-half the size of *Lepidocarpon* and lack the lateral alations or integuments that enclose the *Lepidophloios* megasporangium. *Lepidodendron* aquacarps appear to have been suited for aquatic fertilization and dispersal (Phillips, 1979).

These aspects of reproductive biology suggest growth in environments with standing water and sufficient environmental stability for completion of a monocarpic life cycle. However, *Lepidodendron hickii* appears to have been less tolerant of the low nutrient conditions of flooded peat swamps than *Lepidophloios*. Its observed dominance in peat swamps has thus far been limited to some Appalachian coals. Its occurrences almost never coincide with those of *Lepidophloios* in peat swamps (see Phillips & DiMichele, 1981; Gastaldo, 1987). There are exceptions, most notably in the vicinity of paleochannels and split coal. In clastic environments *Lepidodendron* is often a dominant in low diversity assemblages, frequently as preserved in organic-rich shales. In many instances it is a dominant in coal roof-shale assemblages, where it may represent a final swamp forest formed during drowning associated with rising water tables and clastic influx. Evidence of cohorts of trees in flooded, near channel backswamps, rich in clastic material (e.g., DiMichele & DeMaris, 1987), is consistent both with requirements for higher nutrients than offered by peat swamps, with dispersal in aquatic media, and with monocarpic habit.

Lepidodendron shares with *Lepidophloios* several anatomical traits that suggest tolerance of flooding. Large, highly lacunate stigmarian appendages suggest the ability to withstand long periods of flooding. The thick, yellowish resinous appearing bark is highly decay resistent. This decay resistance is associated with little root penetration of littered bark fragments. Where it occurs in peat-swamp floras, *Lepidodendron*-rich peats are poorly preserved, suggesting aerobic decay and high levels of activity by microorganisms.

The parallels between *Lepidodendron* and *Lepidophloios* are striking. Morphological similarities, most of which are highly derived, suggest close phylogenetic relationships. Ecological similarities suggest early partitioning or segregation of these lineages into very similar kinds of swamp habitats, but differing in basic mineral nutrient availability or the temporal-physical aspects of the environment associated with peat versus clastic accumulation. *Lepidodendron* appears to have been more diverse at the species and subhabitat level than *Lepidophloios*. The large number of species of *Lepidodendron*, as in *Sigillaria*, suggests more opportunities for speciation on a basic morphological theme in clastic environments than in peat swamps.

Lepidophloios

There are three known species of *Lepidophloios* in Pennsylvanian-age coal swamps: *L. harcourtii*, *L. hallii*, and *L. johnsonii* (Arnold, 1940; DiMichele, 1979a). *Lepidophloios harcourtii* has been identified in the megafossil record from the Westphalian A–C; its microspore, *Lycospora pellucida*, occurs throughout the Westphalian. Megafossils of *Lepidophloios hallii* have been found in coals of the Westphalian C–D; its microspore, *Lycospora granulata*, occurs throughout the Westphalian and into the Stephanian of Europe. *Lepidophloios "johnsonii"* was recognized by Winston (1988) from the late Westphalian D equivalent in the Illinois Basin. It could be conspecific with *L. johnsonii* (DiMichele, 1979a) from the Lower Pennsylvanian of Colorado, extending its known range, or be more closely related to *L. harcourtii*. This remains unresolved but no microspores have been correlated with *L. "johnsonii"* (Willard, 1989a) and *Lycospora pellucida* from *Lepidophloios harcourtii* does occur in the Westphalian D.

Lepidophloios abundance was centered in peat-forming environments. All species show the similar basic habitat preferences in their highest distributional abundances. They appear to have been more tolerant of longer periods of standing water than any other peat-swamp trees. Such tolerance is suggested by the frequent occurrences of high-dominance, low-diversity assemblages with little ground cover and few free-sporing components (Phillips & DiMichele, 1981; DiMichele & Phillips, 1988). The stigmarian systems of these plants were robust, with large appendages and substantial air cavities in both appendages and main axes. This is also consistent with their thick, highly decay-resistant bark, which is yellowish in color and may have been resinous and impervious to water. Such bark is often found relatively unaltered in peat litter and is almost never penetrated by roots in otherwise highly decayed peats. It appears that their range of tolerance permitted growth in some habitats from which other species were largely excluded and this is where they dominated. However, *Lepidophloios* species probably were not confined exclusively to such high-stress habitats. The plants also occurred more widely within peat swamps often in highly mixed assemblages, although these may represent the taphonomic effects of time averaging and a subsequent lack of temporal separation of successive forest stands.

One of the most striking aspects of the *Lepidophloios* life history (Fig. 6) is apparent monocarpy (DiMichele & Phillips, 1985). Two types of branching appear to have been confined to the final stages of growth. Isotomous dichotomies formed a crown scaffold in which cones were produced. The cones were borne laterally, terminating peduncles that were the product of strongly anisotomous

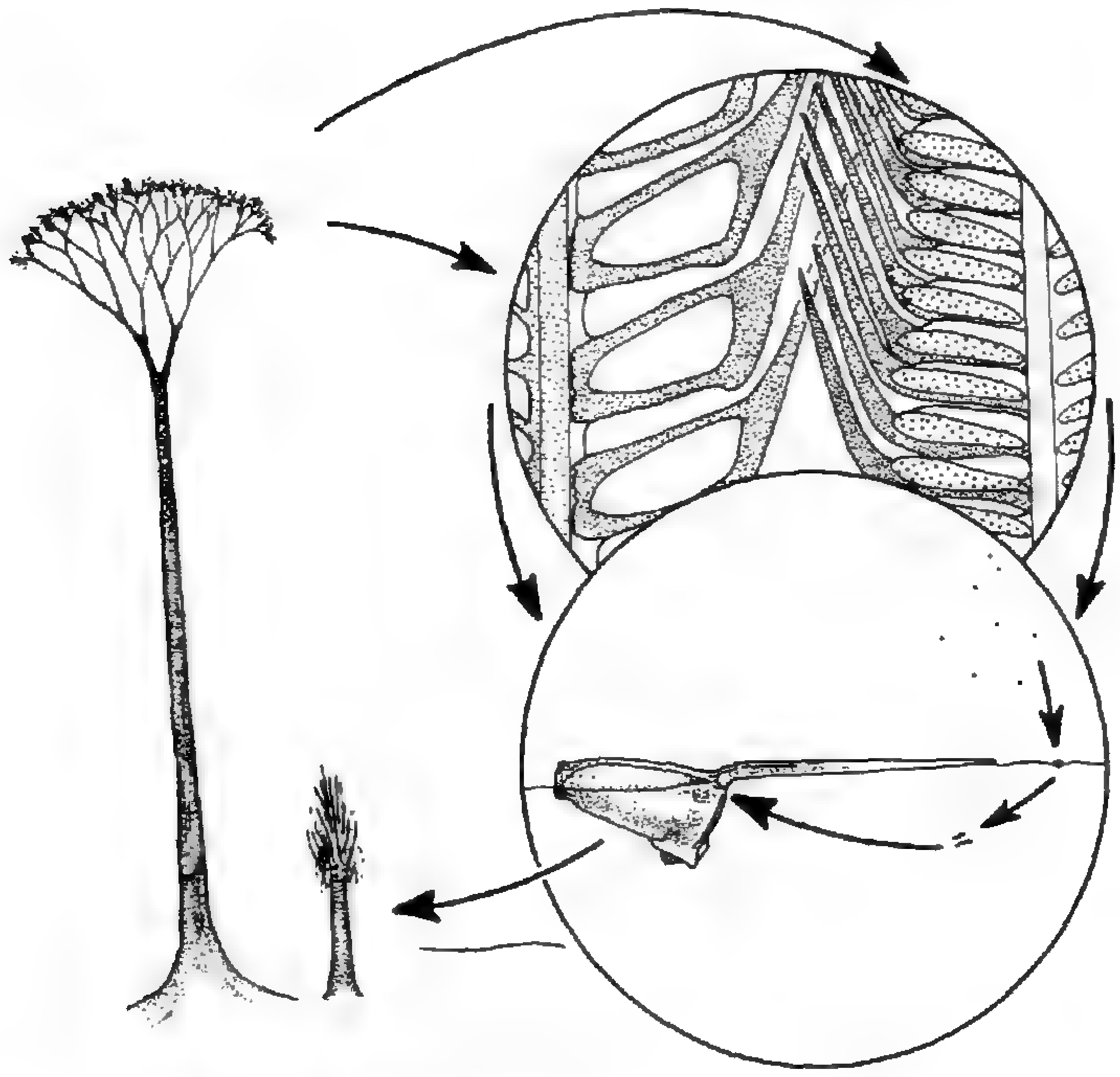

FIGURE 6. Inferred life history of *Lepidophloios* species. Major life cycle attributes include determinate habit and monocarpy of individual trees, separate megasporangiate and microsporangiate cones, and probable aquatic fertilization. Megasporangia were the largest ever to be produced by a lower vascular plant. With one spore per sporangium, and envelopment of the sporangium by sporophyll tissues, these aquacarps (*Lepidocarpon*) were the most complex produced by the lepidodendrids.

branchings. Microsporangia and megasporangia were produced in separate cones although their relative positions, or even if they were produced on the same tree, are unknown. This life history requires an environment free of major disturbances at least for the life of a tree. Given that, in some coals, *Lepidophloios* trees were abundant and *Lepidophloios*-dominated stands were common and repetitive in peat profiles, this tree may have reached its maximum abundance in peat swamps or parts thereof with relatively low disturbance frequencies.

The megasporangiate cones, *Lepidocarpon*, were constructed of a central axis bearing sporophyll units that abscissed from the cone axis. These units were morphologically complex, containing a large single functional megaspore and a megasporangium encased in integumentlike outgrowths. The similarity of these structures to ovules has been a subject of considerable discussion (Thomas, 1981); to differentiate them, the term "aquacarp" is suggested to reflect functional aspects of the *Lepidocarpon* on megasporangiate units. Aquacarp morphology suggests aquatic-based reproduction and dispersal (Phillips, 1979). The large distal lamina would have served as a wing to aid in wind dispersal away from the parent tree (Thomas, 1981) as well as a flotation device (Phillips, 1979). Juvenile sporophytes with exserted stigmarian axes (Phillips, 1979) suggest the potential for anchorage in a water-cover environment. The wide distribution of aquacarps in peat swamps (DiMichele & Phillips, 1985) and the density of *Lepidophloios* stands brings to mind the suggestion of Chaloner & Boureau (1967) that *Lepidocarpon* may have been carried by water and concentrated along margins of water bodies. Massive microspore and aquacarp production, the largely aquatic mode of dispersal, and tolerance of highly stressed physical conditions were the keys to the success of *Lepidophloios* in peat swamps.

ASPECTS OF REPRODUCTIVE BIOLOGY

Each of the lepidodendrid genera exhibited a distinctive combination of reproductive attributes including how cones were borne, cone structure, dispersal-unit morphology, and reproductive timing, as well as characteristic relative abundances of reproductive to vegetative biomass. As determinate and relatively short-lived, arborescent plants, lepidodendrids represent a spectrum of reproductive modes reflected directly in their architectures and autecologies.

Branching in lepidodendrids seems to be geared almost exclusively to reproduction or cone-bearing. The principal possible exception to this may be *Diaphorodendron scleroticum* with its extended branch development (DiMichele, 1981; Wnuk, 1985). Lepidodendrids are separated into polycarpic and monocarpic life histories by the types of branching, lateral versus terminal "crowns," and the associated timing of cone production. *Diaphorodendron* is the only genus that exhibits both polycarpy and monocarpy; aquacarpic *Lepidodendron* (except *L. serratum*) and *Lepidophloios* were exclusively monocarpic; free-sporing *Paralycopodites* and *Sigillaria* were polycarpic (Table 1).

REPRODUCTIVE ALLOCATION PATTERNS

As an approximate guide to relative reproductive allocations, biomass estimates of megasporangiate structures are divided by total aerial litter of a species. This is treated as the relative lifetime megasporangiate output. Despite many vagaries associated with such an indirect measure, based as it is on dispersed structures, these estimates provide a relative quantitative expression of differences. Relative microspore outputs are categorized as overrepresented or underrepresented, based on comparison of importance in peat versus palynological assemblages. It is well known from quan-

TABLE 1. Reproductive allocation patterns of Lycopsid trees.

Taxon	Reproductive timing	Lifetime megasporangiate allocation (♀/total aerial biomass)	Microspore (♂)/vegetative biomass pattern	Ecology
Diaphorodendron vasculare	Polycarpic	2–4%	*Granasporites:* under represented	Site occupier; disturbance tolerant
Diaphorodendron phillipsii	Polycarpic	1–2%	*Granasporites:* under represented	Site occupier; disturbance tolerant
Diaphorodendron scleroticum	Polycarpic	1–2%	*Granasporites:* under represented	Site occupier; disturbance tolerant
Sigillaria approximata	Polycarpic	3–5%	*Crassispora:* under represented	Site occupier; disturbance tolerant
Paralycopodites brevifolius	Polycarpic	4–7%	*Lycospora:* over represented	Colonizer; disturbance tolerant
Lepidophloios harcourtii	Monocarpic	3–4%	*Lycospora:* over represented	Site occupier; disturbance intolerant
Lepidophloios hallii	Monocarpic	6–7% (19%)	*Lycospora:* over represented	Site occupier; disturbance intolerant
Lepidodendron hickii	Monocarpic	?	*Lycospora:* ?	Site occupier; disturbance intolerant
Diaphorodendron dicentricum	Monocarpic	7–8% (22%)	*Granasporites:* ?	Colonizer; disturbance intolerant

titative biomass estimates of peat assemblages, compared to quantitative miospore floras from the same coals, that certain lepidodendrid genera are consistently either over- or underrepresented in spore floras (Phillips & Peppers, 1984). Some quantitative comparisons have been made by Peppers in Phillips & DiMichele (1981), Mahaffy (1985), and Willard (1990, in press). The *Lycospora* producers are overrepresented and the *Crassispora* and *Granasporites* (*Sigillaria* and *Diaphorodendron*) producers with larger microspores are underrepresented in spore floras.

Polycarpic. Lifetime megasporangiate reproductive allocation in *Paralycopodites brevifolius* ranges from 4–7% in Westphalian-age coal balls. This species was the only bisporangiate, free-sporing type, but was the most prolific polycarpic cone producer, which is consistent with its inferred role as a principal colonizer of disturbed ecotonal sites. This estimate probably is enhanced by more local distribution of cone fragments and megaspores. However, it rivals the megasporangiate outputs of the monocarpic forms, which are generally higher than polycarpic ones.

Sigillaria approximata from the lower Stephanian has a 3–5% megasporangiate allocation, which is also high. This estimate probably is affected by local conditions of accumulation, which could vary markedly within the Stephanian swamps, in which sigillarias were large and scattered; it may not be a typical estimate where cone fragments are aided in dispersal by sporadic sheet wash or intermittent floods.

Diaphorodendron species, except *D. dicentricum,* had lower reproductive outputs than the other polycarpic species: 1–2% in *D. phillipsii* and *D. scleroticum,* and 2–4% in *D. vasculare.* It should be noted that *D. vasculare* was typically a much smaller tree than any of the other *Diaphorodendron* species in the peat swamps sampled.

The estimates of reproductive allocations per relative units of time are portrayed graphically in Figure 7. *Paralycopodites* is thought to have begun cone formation earlier than other genera, rapidly attained a maximum reproductive output, and sustained that for variable but short life spans. Disturbances in its ecotonal habitats probably often altered the longevity of plants well below determinate limits. *Diaphorodendron* species exhibit the widest range of reproductive life spans; polycarpic ones probably started cone production slightly later than *Paralycopodites. Diaphorodendron* is the only genus containing a species with a continuous, low level of cone production over the life span of the trees; *D. scleroticum* represents potentially the longest sustained period of reproduction. Cone production by *Sigillaria* is the only distinctly sporadic or intermittent reproductive strategy detected; it is entirely conjectural how early reproduction

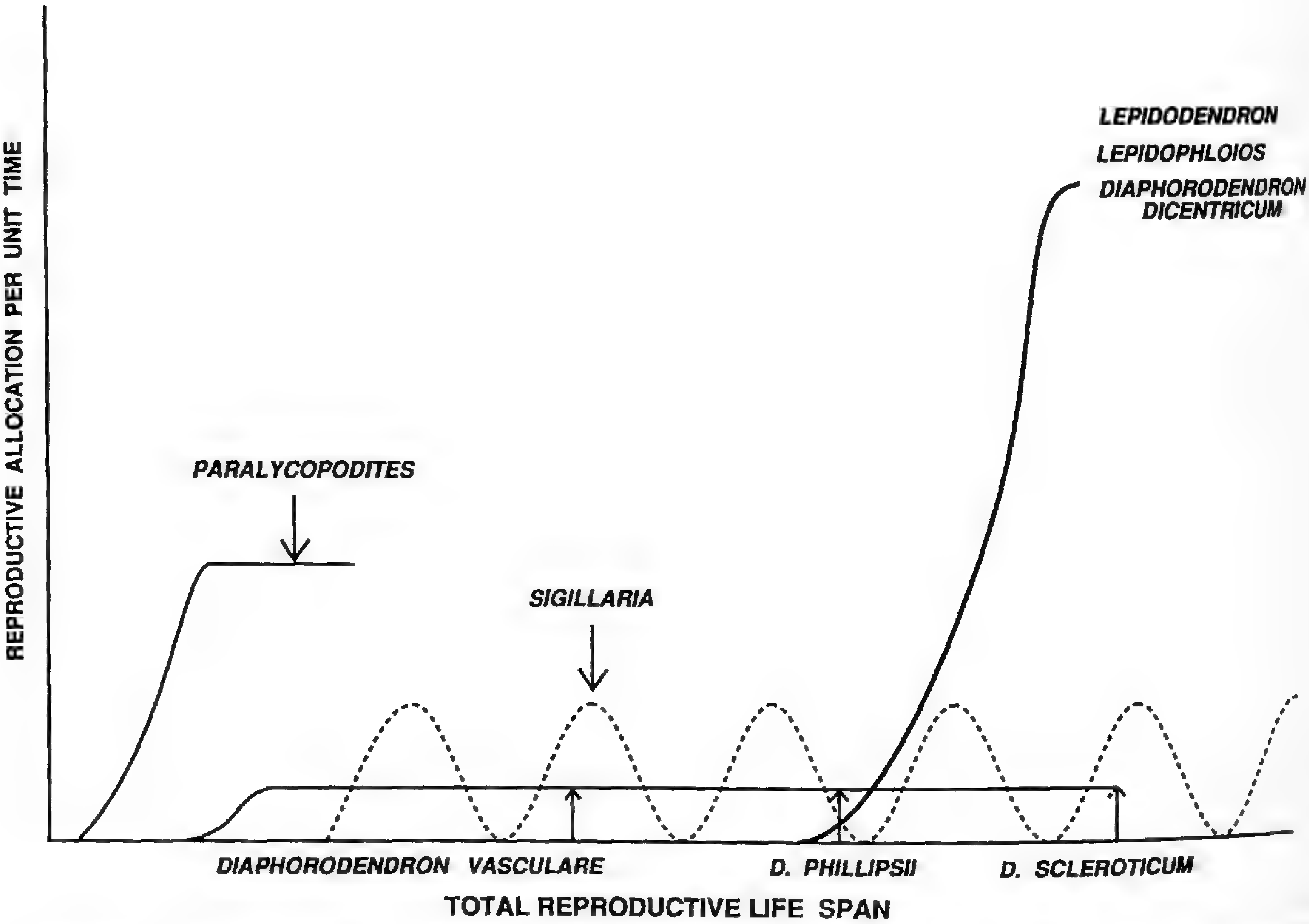

FIGURE 7. Reproductive patterns in the major lepidodendrid genera. Relative total reproductive life span is estimated from known maximum sizes of each species and the location and relative thickness of wood and periderm. *Paralycopodites, Diaphorodendron vasculare, D. phillipsii,* and *D. scleroticum* were all variants on a polycarpic life history with cones borne on lateral branch systems. The onset of branch production is thought to correspond to the beginning of reproduction. *Lepidodendron, Lepidophloios,* and *Diaphorodendron dicentricum* were monocarpic, with cone production limited to the determinate, terminal crown. Reproductive output appears to have been substantial in all of the monocarpic species based on quantitative analyses of coal balls and on morphological studies. *Sigillaria* was a diverse genus that cannot be summarized fully here; morphological evidence points to long life spans for trees, and periodic reproductive intervals, but qualitative evidence suggests only moderate productivity during any one event.

began and its establishment phase may have differed substantially from other genera. The symmetrical patterns of its reproductive cycles (Fig. 7) are intended to convey only repeated episodes of cone formation. While it is uncertain how *Sigillaria* cued reproductive cycles, it seems that they were likely geared to relative dry-wet conditions which could involve both seasonal and sporadic conditions of change. It is likely that *Sigillaria* had the potential for reproduction over a longer interval than most other genera. *Sigillaria* apparently produced only pedunculate branches until near its onset of determinate growth, and branching, then, was minimal at most.

Monocarpic. All the monocarpic lepidodendrids with essentially one terminal interval of cone production had aquacarps. They relied on determinate, terminal "crown" branching for cone formation and dispersal of microspores and megasporangium-sporophyll units. This constituted a massed reproductive phase near the end of the plant's life span. The estimates of megasporangiate allocations are the highest in *Diaphorodendron dicentricum* with 7–8%. *Lepidophloios hallii* is similar with 6–7% and *L. harcourtii* is 3–4%. Data are inadequate to make an estimate for *Lepidodendron.*

In the monocarpic time-abundance curve shown in Figure 7 all the taxa are represented by a common plot because of the lack of a temporal guide for distinct differences in life spans. However, it is likely that life span and timing of reproduction in *Diaphorodendron dicentricum* was distinct from that of *Lepidophloios,* probably geared to colonizing scattered habitats within the less-wet reaches of the swamp, as opposed to those in standing deeper water. The *D. dicentricum* trees do not appear in abundance until Westphalian C and apparently evolved monocarpic habit independently of *Lepidodendron* and *Lepidophloios*, perhaps rising in importance in large, variably disturbed planar swamps.

With the exceptions of *D. dicentricum* and the polycarpic *Paralycopodites brevifolius*, the lepidodendrids are termed site occupiers in the sense that they were generally capable of replacing themselves, conditions permitting. To a certain extent, all the polycarpic forms are regarded as disturbance tolerant because they could generally reproduce at least some before being killed by a major disturbance. The monocarpic forms were intolerant of disturbance levels that prevented the completion of their terminal reproductive phase.

It is not known whether all monocarpic species individually tended to be cohorts and, in turn, mass reproduced at about the same time. This is a cycle that certainly could have developed with *Lepidophloios* and probably differed within species. Despite the inherent drawbacks to such episodes and to monocarpy in general, it should be noted that this kind of reproduction was clearly related to a maximum mass dispersal capability from very elevated heights, utilizing both wind and water.

COMPARATIVE ECOLOGY: PERSPECTIVES AND IMPLICATIONS

At least five unusual circumstances provide important insights into and put constraints on our interpretations of stigmarian lycopsid ecology. The first and most important is that the lepidodendrids radiated within tropical wetlands and were confined to such habitats. That is to say, stigmarian lycopsids were the major trees in the tropical swamp-forests primeval. The pantropical distribution of principal genera resulted from tracking the expansion of the first coal age to its zenith in the Westphalian.

Second, the latest Devonian–earliest Carboniferous radiation of heterosporous arborescent lycopsids coincided with that of seed plants and apparently ferns. However, the lycopsids may have been the most conservative of these, establishing nearly all genera early in their radiation, rapidly in a geologic sense, attaining generic lines of remarkably distinctive bauplans and associated reproductive biology that persisted to extinctions, some over 100 million years later.

Third, only a small number of principal lepidodendrid genera spanned tropical wetlands. The five we have dealt with were widespread, although differentially abundant in different habitats. They occurred in both peat and clastic wetland environments and provide a means to contrast swamp types (see Gastaldo, 1987), as well as a means of tracking swamp structure over time using dispersed spore floras (see Kosanke & Cecil, 1989; Eble, 1990).

Fourth, exceptional in situ occurrences of swamp plants make the Westphalian one of the highest resolution windows on plant paleoecology in the entire geological record. This includes some of the enormous compression and cast/mold fossils of clastic deposits, the basis for the reconstructions of the trees and forests, and the vast numbers of occurrences of anatomical preservation in coal balls.

Fifth and last, these combined fossil records emphasize the generic paucity of Late Carboniferous tropical swamp floras as a whole, despite their maximum diversity in the Westphalian. Although we have avoided discussing the other kinds of trees that lived in the coal swamps with lepidodendrids, they are vitally important to our perspectives of the comparative ecology of the lycopsids. Every major group was represented, but commonly only by one or two arborescent genera. Thus, there were more genera of lepidodendrids in coal swamps than almost all the arborescent genera of other plant groups combined.

The extinct lepidodendrids and sigillarias have no modern analogues. Yet, they partitioned and characterized nearly the full spectrum of tropical wetland habitats. This is particularly evident in the early Westphalian A of Europe where lepidodendrids totally dominated the vegetation, and where their greatest generic diversity is found in peat swamps. Because the established stratigraphic ranges of the five principal genera extend back to the Tournaisian and Visean, it is reasonable to hypothesize that partitioning of swamp habitats occurred early in the Carboniferous and perhaps under circumstances where lycopsids were the principal or only arborescent occupants.

It was not until after the Westphalian A that other major groups (cordaites, ferns, pteridosperms) rose to codominant status or even as dominants (cordaites). Such vegetational changes may have taken place at the expense of lycopsids. However, in the late Westphalian D (uppermost Middle Pennsylvanian) of the United States, after most other plant groups had become well established in coal swamps, the five principal genera of lepidodendrids still dominated on a whole coal-swamp basis. Cordaites were the only other plants to hold a dominant ecological position within Westphalian coal swamps, but this was limited to the early Westphalian D and, as far as we know, to the western interior coal region of the United States (Raymond, 1988).

Late Westphalian D peat swamps indicate an

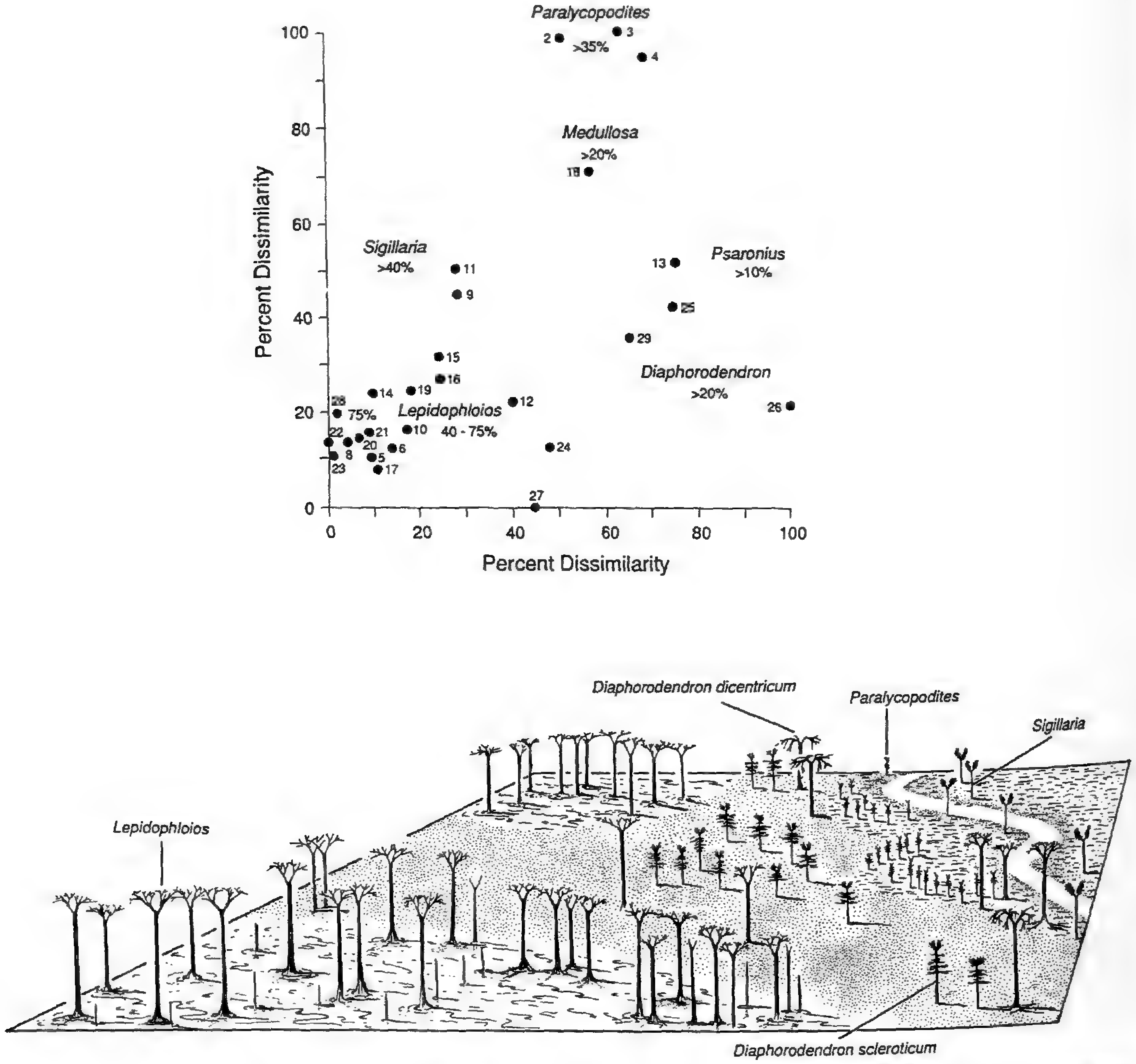

FIGURE 8. Patterns of distribution and association of major trees in the Herrin (No. 6) Coal of Illinois. Ordination, modified from DiMichele & Phillips (1988, fig. 10), is based on a profile of coal balls from the Old Ben No. 24 Mine (numbers refer to profile zones, beginning with 1 at the bottom of the seam). The lycopod distribution revealed in this ordination is characteristic of all late Westphalian D-age coals from the Illinois, Western Interior, and Appalachian coal regions studied to date. The distribution is depicted in the reconstruction: *Lepidophloios* occurred widely, but dominated flooded parts of the swamp (left corner). *Diaphorodendron* trees were site occupiers (*D. scleroticum*: center of diagram) or colonizers (*D. dicentricum*: top center, lower right corner) within parts of the swamp subject to minor disturbance. *Paralycopodites* (small trees along margin of drainage) occupied areas subject to clastic influx and disturbance; they frequently co-occurred with medullosan pteridosperms. *Sigillaria* may have grown along stream margins (sparsely branched trees along drainage margin).

increased diversity and abundance of non-lycopsids. In addition, most of the arborescent genera tended to be larger than their antecedents in older swamp floras, including the lepidodendrids. Some lepidodendrid forests became more storied-structured with increased shading by columnar tree ferns and seed ferns in some stands. In the Springfield and Herrin Coals, the best known from coal-ball studies, the habitat partitioning is perhaps even more clearcut because of the associated non-lycopsids that tend to cluster repeatedly in assemblages with particular lepidodendrids (Fig. 8; Phillips & DiMichele, 1981; DiMichele & Phillips, 1988). While *Lepidophloios* dominated the wettest and lowest diversity forest assemblages, *Psaronius* encroaches such habitats, as well as most others. *Diaphorodendron* species are associated with a variety of taxa but with a minimal overlap with *Paralycopodites* and *Lepidophloios*. *Paralycopodites* is often closely associated with *Medullosa*. In turn, *Sigillaria* is not generally a part of this array of coal-swamp assemblages. It rarely appears in relative high abundance, and then either with diverse, more non-swamp assemblages of seed ferns and ferns, or as simply repetitive sigillarian debris sometimes mixed with *Diaphorodendron.*

Coal swamps were edaphic islands because of the stressful physical attributes of an organic substrate (DiMichele et al., 1987). The appearances of other tree genera in what were nearly exclusively lycopsid-dominated habitats may reflect exploitation of the "colonizable-space" present at nearly all times in these environments. Drop in *relative* lycopsid abundance could result simply from the gradual accrual of new taxa that evolved the capacities to live in peat swamps, environments with low interspecific competition.

Our interpretation of such ordinations of profile data as well as gradient traverses (unpublished data) indicates that the key shifts of lepidodendrids in coal swamps are between ecotonal *Paralycopodites* and either *Lepidophloios* or *Lepidodendron.* These end point assemblages appear to define a marginal to deep-water gradient that probably existed for millions of years. The intercalation of *Diaphorodendron* may represent an originally short-term aquacarpic expansion into frequently disturbed environments where other factors preclude effective fertilization and/or dispersal. Most of the *Diaphorodendron* species, including the monocarpic *D. dicentricum,* manifest occupation of habitats with variable frequencies and intensities of disturbances, factors more important than the environmentally restricted conditions that defined the habitat limits of the other major genera. *Diaphorodendron* was probably as important in coal swamps of the Westphalian as *Lepidophloios,* and perhaps more so than *Lepidodendron.* The genus had a broader ecological amplitude because of the species differences in tolerances and reproductive strategies. These differences are still on a theme largely within the more physiologically water-stressed environments, not related to deeper standing water but in conditions of possible brackish influence, frequent edaphic substrate exposure and repetitive dry downs, all indicative of physiological drought stress at different temporal frequencies.

The ecological inferences for *Sigillaria* are quite different from the other "array of four" lepidodendrids. *Sigillaria* was essentially a marginal escapee of wetland environments labeled "swamps" and yet undoubtedly it was one of the characteristic wetland genera. *Sigillaria* represents the most xeromorphic of the lepidodendrids, unless *Sporangiostrobus* turns out to be stigmarian as suggested in Wagner's (1989) reconstruction. *Sigillaria* is so closely associated with the wetland tropics that it has rarely occurred to us that it may have occupied the drier, seasonally or intermittently wet habitats scattered along the streams and drainage areas where water availability was variable but subject to neither long-term flooding nor long periods of drought. In *Sigillaria* cone dispersal was apparently not so much a matter of high elevation, but of repeated dispersal in the same limited area.

ECOLOGICAL IMPACT ON SWAMP ENVIRONMENTS

The lepidodendrids may have altered their environments in profound ways. Here we consider how stigmarian lycopsids expanded their available habitats and contributed to stability of environments, how they may have affected nutrient and oxygen supply available to other plants, and how they contributed with litter and "self-burial" of roots to literally filling accumulation space and changing the water table of habitats.

The first and most striking comparative ecological feature of stigmarian lycopsids is how they dominated the available peat and water substrates and yet permitted extensive light penetration due to their open canopies. These two ecological patterns are compatible if our suggestions about diffuse photosynthesis are near the mark. They are compatible also with an extensive system of stigmarian axes and radiating appendages, which would act as both baffling and filtering systems in movement of transported sediment, modifying water flow itself. One might think of stigmarians as sort of botanical "beaver dams." If *Lepidodendron* and *Lepidophloios* were part of such a sediment baffling system they would constitute an important means of trapping mineral matter in the water and enhancing their nutrient supply, as well as ultimately adding to the stability of anchorage. The surficial flow of water in such swamps would have been more rapid along waterways unoccupied by impeding vegetation. The likely habitats of these genera extended to those waterways, no doubt utilizing them in reproductive dispersal. From the viewpoint of expanding lepidodendrid habitats, these open water areas were available for occupation up to depths that may have encroached the 2 m limits of semiaquatics and aquatics today. This would have been ideal for buoyant stigmarian appendages and potential exposure to sunlight. In this scenario, standing water is viewed as an area into which swamp plants encroached, particularly in clastic swamp settings. The lepidodendrids in these habitats impeded water and sediment flow, adding to swamp stability and garnering their resources into habitable substrates.

There are important consequences of such environmental alterations. If the flow of water were impeded by baffling and filtering, stigmarian lycopsids, with their dominance of many substrates, would have been a key nutrient filtering system. This amplifies the suspected differences in nutrient requirements between *Lepidodendron* and *Lepidophloios* with the latter more typical of lower nutrient, peat swamps, and the former centered in clastic-rich substrates.

The second aspect ties in with nutrient retention by stigmarian lycopsids. Surficial water, principally runoff from marginal watersheds, is apt to be quite varied in mineral nutrients, O_2, and CO_2. The effective acquisition of resources by stigmarian systems may have limited nutrients to other plant groups. In addition, lepidodendrids tend to tie up mineral nutrients with their large physical stature, extensive stigmarian systems, and decay-resistant litter. The most significant component is generally the periderm, parts of which are the most decay-resistant tissues found in peat deposits of the Upper Carboniferous. This sequestering of nutrients in organic matter prevents recycling in already very low nutrient environments, particularly in the *Lepidophloios* habitats and depositional environments. Coal geologists often associate high ash coals with most *Lycospora*-producing lepidodendrids and attribute this to planar swamp, eutrophic environments of habitation. This appears to be, in part, a circumstance of filtering out mineral matter and retarding its recycling by incorporating it into some organic matter that is highly decay resistant. This modifies the nutrient availability for plants that follow on these peat substrates.

Lepidodendrids may have partially structured the Westphalian coal swamps while serving their own peculiar adaptational strategies. The lush reconstructions of Late Carboniferous (Westphalian) lepidodendrid swamps are pictures of environmental uniformity and tranquility, not conveying that such an ecosystem may have been ever on the brink of disaster. These coal swamps were disturbance driven and abiotically controlled. The plants relied on highly dispersible sexual propagules for reproduction and colonization of available habitats. This system of reproduction was responsible for swamp persistence over short-term disturbances and following large areal disruptions where continuity had to be maintained from coal swamp to coal swamp.

We tentatively suggest that tropical Westphalian coal swamps defined a major coal age, in part, because of the ecology of the stigmarian lycopsids. Instead of being planar, eutrophic environmental indicators, these lycopsids might better be viewed as environmental stabilizers and hoarders of resources. Without these environmental framework builders, Westphalian peat formation may have been substantially diminished. Lepidodendrids formed an important part of the framework of Westphalian coal swamps by contributing to the stability of the wetland habitats and expanding the area of peat accumulation. The extinction of the principal genera in North America is tied perhaps to climatic changes and the consequent collapse of the entire ecosystem. With increasing taxonomic refinement (e.g., Lesnikowska, 1989) extinction can be documented for many other swamp-centered, allied plants. It is reasonable to suggest that it was the environmental importance of lepidodendrids that sustained the Westphalian coal age, and that their extinction, as an array, probably resulted in the loss of the many dependent non-lycopsids.

AQUACARPS

The concurrent radiation of lepidodendrids in wetlands and seed plants almost everywhere else during the latest Devonian–earliest Carboniferous presents unparalleled opportunities for comparison of independent, contemporaneous evolutionary radiations based on different fundamental architectures. Unfortunately, gymnosperm morphology has served as a reference base for assessing organizational grades that relate to wetland ecology. As a consequence, we spuriously, or for brevity of comparison, suggest that lepidodendrids mimicked the seed habit, bipolar "shoot and root" design, and, for want of the concept of the "lycopsid tree habit," "tree" architecture. The last appellation is most justified because of sheer size and a pole frame that usually branched. However, most such comparisons miss the mark in the questions asked because they are framed from preconceived notions that such comparative morphology can be taken out of evolutionary and ecological contexts and reduced to a seed-plant based reference.

A classic example of this, shared by most of us at one time or another, is, "How close did *Lepidocarpon* come to the seed habit?" This diverts the focus from how did it work in the life cycle ecologically to how should it have worked from a seed-plant perspective. Many of us have been taught that the homospory-to-heterospory-to-seed habit was *the* evolutionary sequence and that heterosporous lower vascular plants were stymied at free-sporing heterospory, a dead end. The dissections of this sequence (Sussex, 1966) indicated a slight spill over to heterangy by some heterosporous lower vascular plants, but there was not enough compelling data to suggest an alternative concept to the seed habit, along wetland ecological and evolutionary lines. The lepidodendrids demonstrate the further evolutionary elaboration of heterospory in directions other than the seed habit, an elaboration that is best represented by lepidodendrid structures such as *Lepidocarpon* and *Achlamydocarpon*. We have suggested the term aquacarp for these structures, incorporating the propensity for "carpon" names of such structures in wetland habitats. In an evolutionary and ecological sense such structures evolved toward the use of water in ways not found in their lower vascular plant ancestors, just as seed plants escaped from the constraints of aquatically mediated life cycles. In this sense, seeds and aquacarps are similar in grade and convergent in morphology, but are widely divergent in ancestry and function.

Aquacarpic lepidodendrid trees are viewed as the most highly derived, heterosporous lower vascular plants ever to exist within tropical wetlands. Consequently, they offer exceptional perspectives to the importance of heterospory in such environments. A striking feature about the late Paleozoic tropical wetlands is the diversity and relative abundance of heterosporous plants, especially lycopsids of most lineages.

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ADDENDUM

Since this manuscript was edited, the following relevant publications have appeared:

Rothwell, G. W. & J. S. Pryor. 1991. Development dynamics of arborescent lycophytes—apical and lateral growth in *Stigmaria ficoides*. Amer. J. Bot. 78: 1740–1745.

Winston, R. B. & T. L. Phillips. 1991. A structurally preserved, Lower Pennsylvanian flora from the New Castle Coal Bed of Alabama. Geological Survey of Alabama Circular 157, Tuscaloosa. (Plant source of *Lycospora pellucida*.)

EVOLUTION OF ISOETALEAN LYCOPSIDS[1]

Kathleen B. Pigg[2]

ABSTRACT

The recognition of numerous similarities between *Isoetes* L. and extinct arborescent lycopsids historically led to one of the best known phylogenetic lineages in vascular plant evolution. The lycopsid reduction series proposed the derivation of the extant quillwort *Isoetes* from the Carboniferous lepidodendrids through a progressive reduction in both stems and stigmarian rooting systems. New information gained in the past decade demonstrates that the history of this group is more complex than the linear reduction sequence suggests. Newly recognized isoetalean plants, such as *Protostigmaria* Jennings, *Chaloneria* Pigg & Rothwell, and *Cormophyton* Pigg & Taylor, establish the presence of isoetalean lycopsids in the Paleozoic. In Mesozoic strata, isoetaleans were widespread and diverse. They included woody plants, such as *Pleuromeia* Corda, that resemble the Carboniferous lycopsid *Chaloneria*, and smaller forms (*Isoetites* Münster) more similar to the extant *Isoetes*. In the Cretaceous and Tertiary, forms similar to the modern genus *Isoetes* were also widespread. Differences among "woody" isoetalean lycopsids such as *Chaloneria*, *Takhtajanodoxa* Snigirevskaya, and *Pleuromeia* are minimal; their differences with *Isoetes* are also relatively few. Trends that can be documented among isoetaleans include the reduction of axial elongation and vegetative growth, a change from trilete to monolete microspores, the development of sunken sporangia with a velum, and development of ligules with glossopodia. The relationship of these isoetalean plants to the lepidodendrids and other members of the rhizomorphic clade (sensu Rothwell and Erwin) is based on homologies between rooting structures and comparative ontogenetic studies. This new information suggests that lycopsid diversity is complex and that phylogenetic and ecological aspects of the rhizomorphic forms are closely intertwined.

RELATIONSHIP BETWEEN ISOETES AND FOSSIL LYCOPSIDS

Historically, the heterosporous lycopsid *Isoetes* L. has been an enigma to botanists. Most researchers agree that *Isoetes* is a lycopsid based on such typical lycopsid features as adaxial eusporangia, an exarch protostele, microphylls, ligules, and endosporic gametophytes (Paolillo, 1963; Bierhorst, 1971; Retallack, 1975; Gifford & Foster, 1989; but see Greguss, 1968). However, *Isoetes* also has a suite of features that are unusual among the pteridophytes, including bipolar growth, the production of apparently secondary vascular tissues, bilateral symmetry of the stem, and unusual rooting structures (Bierhorst, 1971; Karrfalt & Eggert, 1977a, b, 1978; Gifford & Foster, 1989). *Isoetes* further differs from other extant lycopsids in growth habit, the presence of sunken adaxial sporangia covered by a velum, sporangial trabeculae, transfusion tissue, and a ligule with a basal glossopodium (Bierhorst, 1971; Sharma & Singh, 1984; Gifford & Foster, 1989).

Although the complex morphology of *Isoetes* is difficult to interpret from extant plants alone, our understanding of this plant did not develop in a vacuum. Historically, *Isoetes* has been interpreted not just on the basis of extant species, but in the context of known fossil lycopsids. Anatomical similarities between *Isoetes* plant bases and the stigmarian rooting systems of the Carboniferous lepidodendrid trees led many authors to consider homologies between these organs (e.g., Williamson, 1887; Stewart, 1947, 1983; Chaloner, 1967; Frankenberg & Eggert, 1969; Karrfalt, 1980; Paolillo, 1982). In contrast to the typically unidirectional growth of pteridophytes, both *Isoetes* and lepidodendrids with stigmarian rooting structures have a type of bipolar growth. They also produce unusual rooting appendages with a char-

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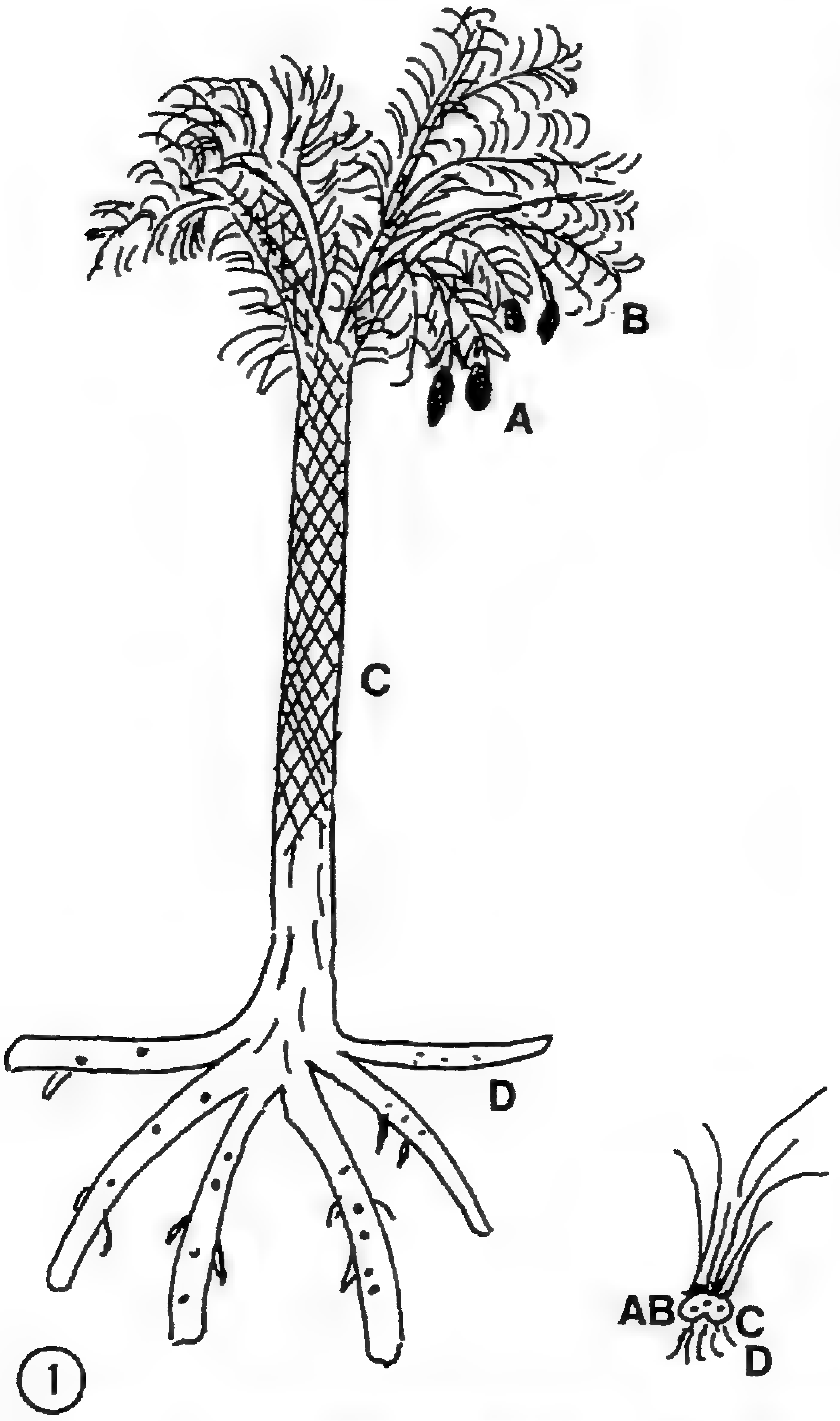


FIGURE 1. Morphological comparison of an arborescent lepidodendrid (left) and *Isoetes* (right). Proposed changes that occur in the lycopsid reduction series include (A) change from terminal cone to *Isoetes* sporophylls; (B) loss of branched crown and vegetative leaves in *Isoetes*, where all leaves are sporophylls; (C) loss of elongate stem; (D) reduction of axial stigmarian rooting system. Not to scale.

acteristic three-zoned cortex, aerenchyma, and an eccentric vascular bundle connected to the outer cortex by a narrow isthmus. Unlike typical roots, these bilaterally symmetrical rooting appendages are produced in a definite arrangement (taxis) and have been interpreted by many as leaf, rather than root, homologues (e.g., Stewart, 1947; Frankenberg & Eggert, 1969; Rothwell & Erwin, 1985; see also Charlton & Watson, 1982).

Similarities between *Isoetes* and *Stigmaria* Brongniart were used to support one of the best known lineages in paleobotany: the lycopsid reduction series (Figs. 1–8). Both Potonié (1894) and Mägdefrau (1931) proposed that *Isoetes* represented the end product of a linear reduction series that originated in the Paleozoic with a sparsely branched *Sigillaria* Brongniart tree bearing a stigmarian rooting system. In the Mesozoic, the lineage included intermediate-sized lycopsids with less lobed plant bases such as *Pleuromeia* Corda, *Nathorstiana* Richter, and *Nathorstianella* Glaessner & Rao (Mägdefrau, 1931, 1932; Karrfalt, 1984; Taylor, 1981). Later members of the sequence, *Isoetites* Münster and *Isoetes*, appeared in Mesozoic and Cenozoic strata. They shared the growth habit of extant *Isoetes* with cormose plant bodies that bear linear sporophylls at one end and rooting appendages at the other (Bock, 1962; Brown, 1939, 1958; Chaloner, 1967). Taken to its extreme, the lycopsid reduction series interpreted *Isoetes* essentially as a *Lepidostrobus* Brongniart (= *Flemingites* Carruthers sensu Brack-Hanes & Thomas, 1983) cone sitting directly atop a much reduced stigmarian plant base (Fig. 1; Stewart, 1947, 1983; Taylor, 1981).

The idea of a lycopsid reduction series culminating with *Isoetes* (Potonié, 1894; Mägdefrau, 1931; Stewart, 1947) has competed with a second, contrasting view that lepidodendrids and isoetaleans represent two parallel lineages, both established in the Paleozoic (Jennings, 1975; Stubblefield & Rothwell, 1981). This second view was supported by the presence of certain Paleozoic forms that lacked the stigmarian rootstock (e.g., *Lepidosigillaria* Kräusel & Weyland, *Protostigmaria* Jennings, *Paurodendron* Fry) and the description of fossil embryos of *Lepidocarpon* Scott and *Bothrodendrostrobus* Chaloner (Phillips et al., 1975; Phillips, 1979; Stubblefield & Rothwell, 1981). In the light of new information, neither of these views sufficiently deals with lycopsid complexity. In an alternative explanation, lepidodendrids, isoetaleans, and a variety of other forms such as *Oxroadia* Alvin (Long, 1986; Bateman, 1988) and *Paurodendron* (Phillips & Leisman, 1966; Rothwell & Erwin, 1985) comprise a plexus of related forms that can be recognized as a monophyletic clade. All of the members of this so-called "rhizomorphic clade" (sensu Rothwell & Erwin, 1985) share a suite of features including secondarily derived bipolar growth, the production of stigmarian appendages, and a heterosporous reproductive biology (Rothwell & Erwin, 1985). The variable expressions of form and function in this group are thought to reflect an interaction of genetic potential, developmental factors, and ecological parameters. In the present contribution I review the fossil record of isoetalean plants from the Paleozoic through Cenozoic. Aspects of morphology, reproduction, geographical distribution, and ecology are examined in order to evaluate which theories of lycopsid evolution most closely explain the currently recognized pattern.

PALEOZOIC ISOETALEANS

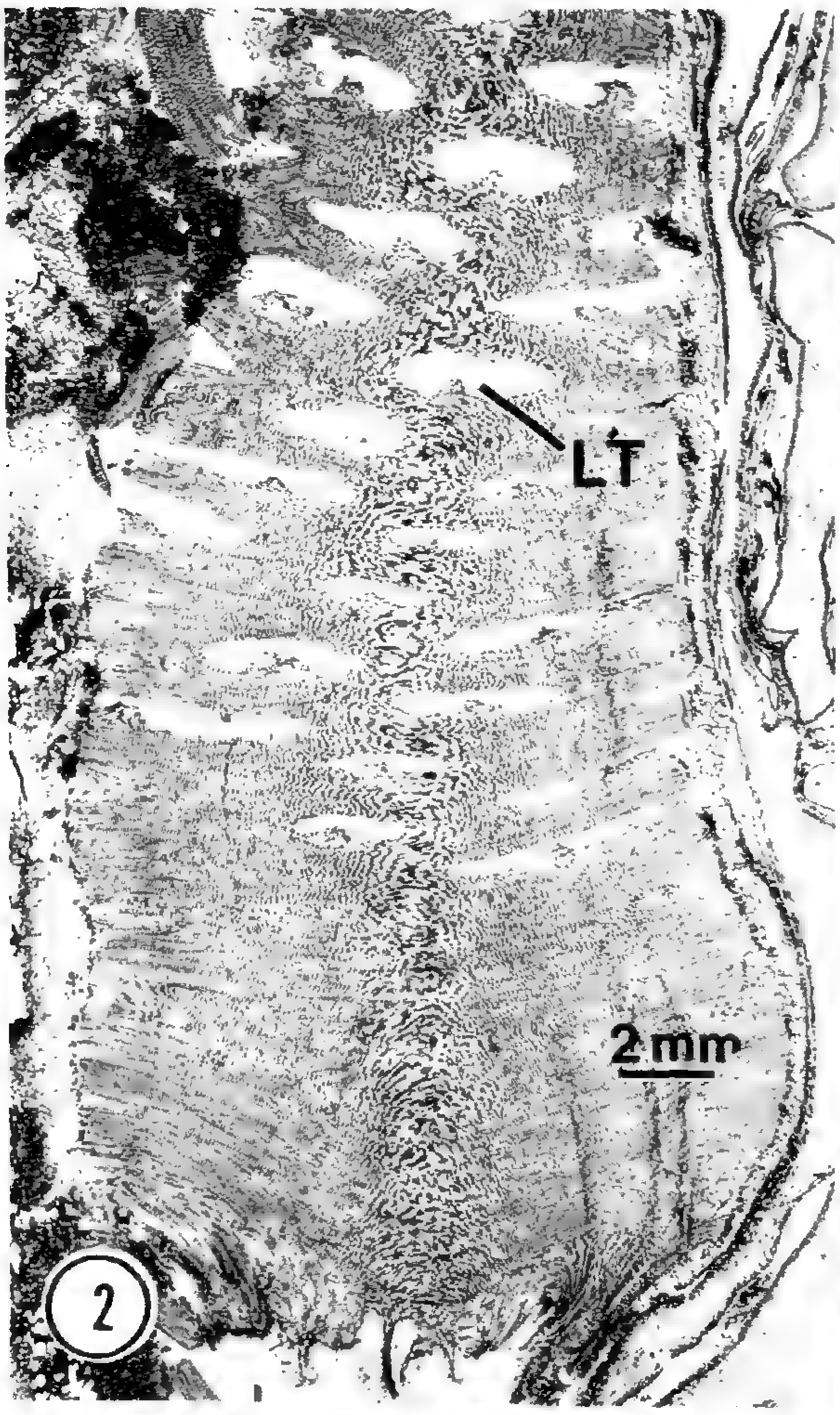
Although most arborescent lycopsids are associated with *Stigmaria*, a number of them lack an extensive branched rooting system. The Devonian lycopsid *Lepidosigillaria* is interpreted as a sparsely branched tree over 5 m tall that has a rounded plant base bearing characteristic stigmarian rootlets (Fig. 9A, Table 1; White, 1907; Kräusel & Weyland, 1949). Another Devonian form, *Cyclostigma kiltorkense* Haughton, has been reported to have a bilobed plant base (Fig. 9C, Table 1; Johnson, 1913; Schweitzer, 1969; Chaloner, 1984). Unfortunately, the basal part of the stem is abraded, and evidence for this interpretation is difficult to assess (Pigg & Taylor, 1985). An unnamed lycopsid in the Upper Devonian Cleveland Shale also has a lobed or rounded plant base (Fig. 9D, Table 1; pl. I of Chitaley, 1982, 1988). This slender plant is very similar to Mesozoic *Pleuromeia* stems and may represent some of the earliest evidence for the unbranched habit so common in isoetaleans (Chitaley, 1982, 1988). Also found in Devonian strata are stumps described as the bases of the progymnosperm *Eospermatopteris erianus* (Dawson) Goldring (Fig. 9B, Table 1; Goldring, 1924). These plant bases are remarkably similar to those of *Lepidosigillaria* (Fig. 9A, B, Table 1; Goldring, 1924; fig. 8.17 of Gensel & Andrews, 1984). Because these stumps have not been found attached to other parts of the plant, the possibility that some specimens belong to isoetalean, rather than progymnospermous, plants should not be overlooked.

Protostigmaria eggertiana Jennings, a plant base with up to 13 lobes, is known from Lower Mississippian strata in Virginia (Fig. 9E, Table 1; Jennings, 1975; Jennings et al., 1983). *Protostigmaria* is characterized by a basal pattern of lobes and furrows comparable to the pattern in the base of a multilobed *Isoetes*. In this pattern, cortical lobes occur between the juncture of three furrows. Apart from isoetalean and stigmarian-bearing lycopsids, this regular pattern of lobes and furrows is unknown in rooting systems of vascular plants. *Protostigmaria* presumably grew in a manner similar to that of a multilobed *Isoetes*, by adding new lobes between bifurcations of the furrows (Jennings et al., 1983). *Protostigmaria* has been found in attachment to the lepidodendrid stem *Lepidodendropsis* Lutz (Jennings et al., 1983). This tall, much-branched tree would have required an anchoring mechanism of some type. The plant may have accomplished this by effectively "burying" its rooting system, as does *Isoetes* (Karrfalt, 1977), with the production of new roots from the furrows and the resulting lateral displacement of older roots (Jennings et al., 1983).

While descriptions of *Lepidosigillaria*, *Protostigmaria*, and other forms demonstrate diversity in rooting structure among tree lycopsids (Fig. 9E), these plants are not known in anatomical detail. The relationship of these earlier lycopsids to later isoetalean/lepidodendrid lineages cannot yet be clarified. The discovery of internal anatomy and reproductive organs would greatly enhance our understanding of these plants and their role in rhizomorphic lycopsid radiation.

The presence of isoetalean lycopsids in the Carboniferous was clearly established with the description of the anatomically preserved lycopsid *Chaloneria cormosa* Pigg & Rothwell and the recognition of the Chaloneriaceae (Figs. 2, 3, 9F, Table 1; Pigg & Rothwell, 1979, 1983a, b; DiMichele et al., 1979). *Chaloneria cormosa* was described from the Upper Pennsylvanian coal ball flora of North America as a plant with internal tissues that are similar to those of the lepidodendrids but lacking a stigmarian rooting system (Figs. 2, 3, 9F; Pigg & Rothwell, 1979, 1983a). Instead, *C. cormosa* has a bilaterally symmetrical, cormlike plant base that resembles that of modern *Isoetes*.

Stems of *C. cormosa* are up to 10 cm in diameter and have an exarch protostele that begins at the base of the plant as a tiny rod of tracheids (Fig. 3) and expands distally, becoming medullated at higher levels (Pigg & Rothwell, 1979). No branching specimens are known. Primary xylem is somewhat fluted like that of *Sigillaria approximata* Fountaine & White (Delevoryas, 1957) and consists of metaxylem with tracheids with scalariform and reticulate wall thickening patterns separated by plates of xylem parenchyma, and protoxylem with helical wall thickening patterns (Pigg & Rothwell, 1983a). *Chaloneria cormosa* produces a thick zone of secondary xylem at the base (Figs. 2, 3) that is absent at distal-most levels. Since plant bases are decorticated, the entire size of the plant base and details of its external morphology are unknown. Wood of *Chaloneria* has uniseriate rays and tracheids with reticulate wall thickening patterns. Secondary tracheids in the basal region of the stem may be branched and contorted. To the outside of the xylem is a cylinder of phloem composed of



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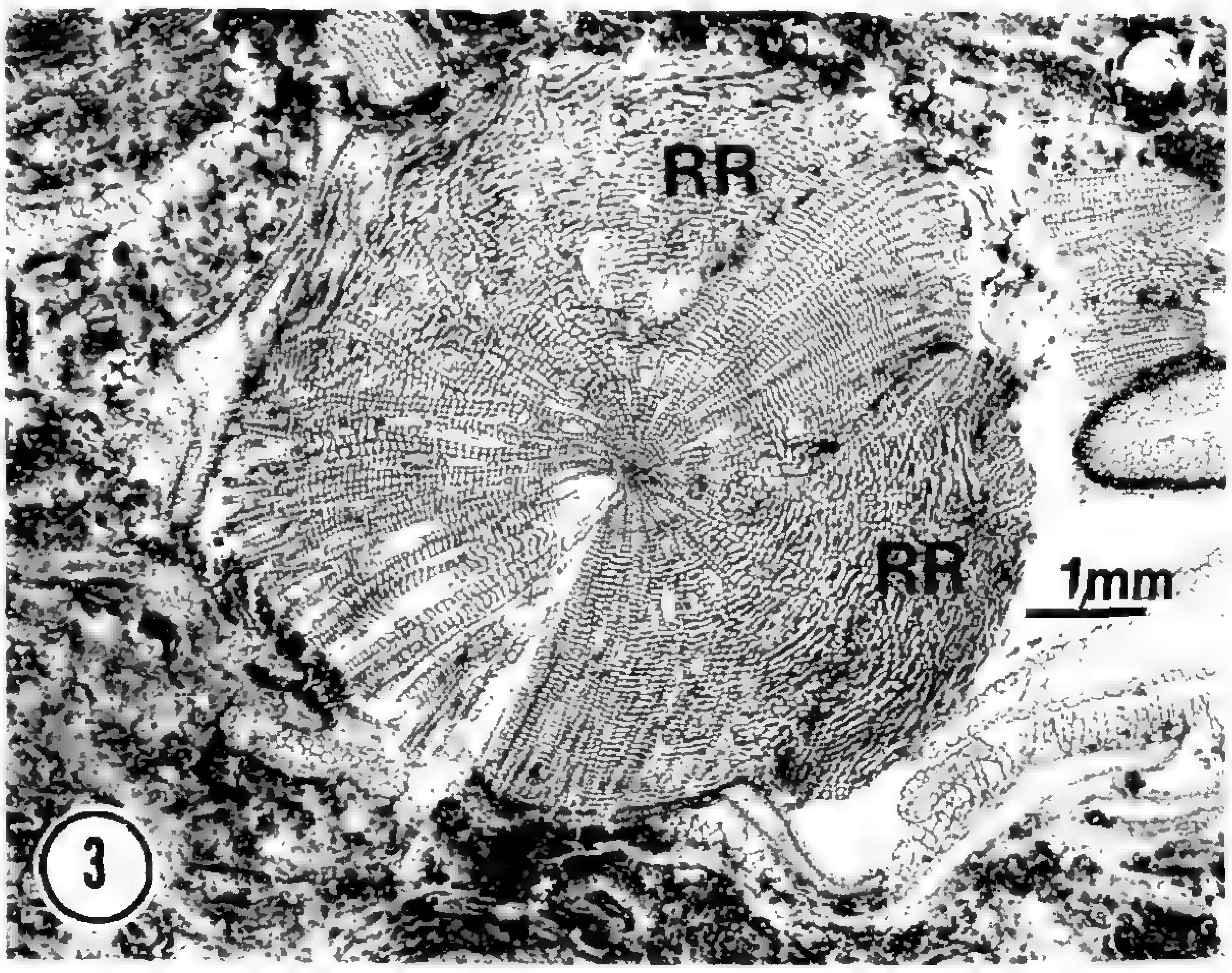

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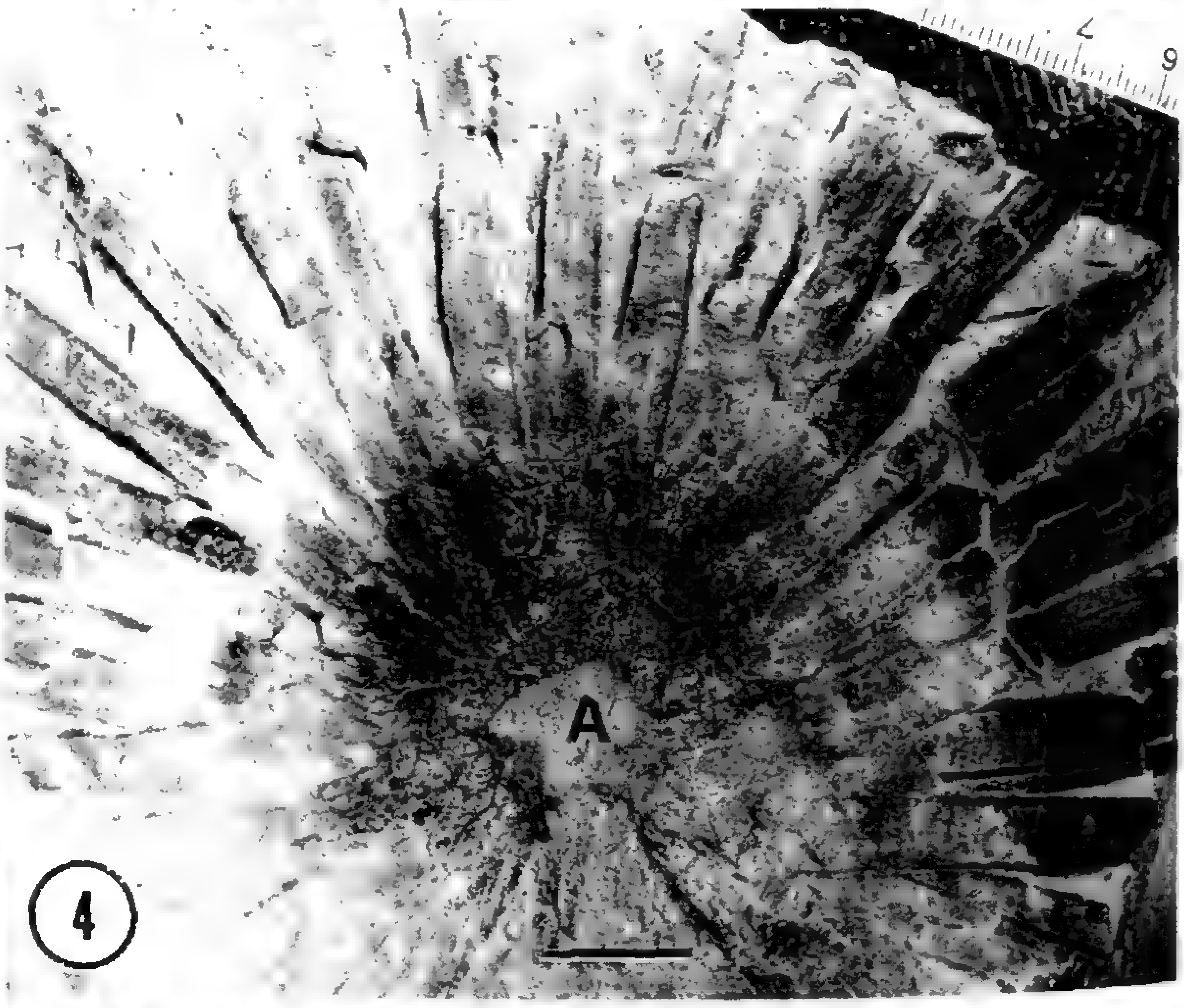

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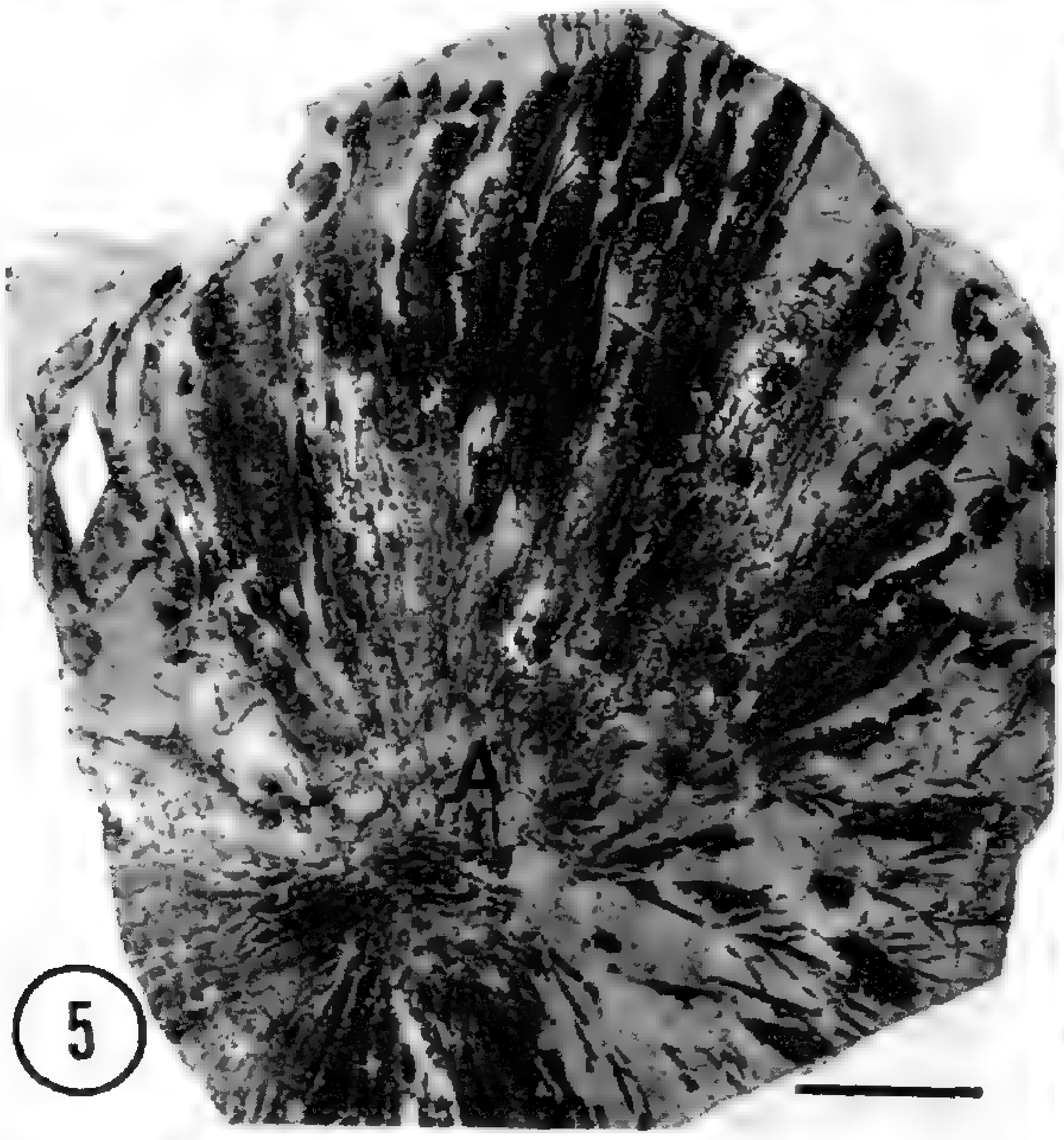

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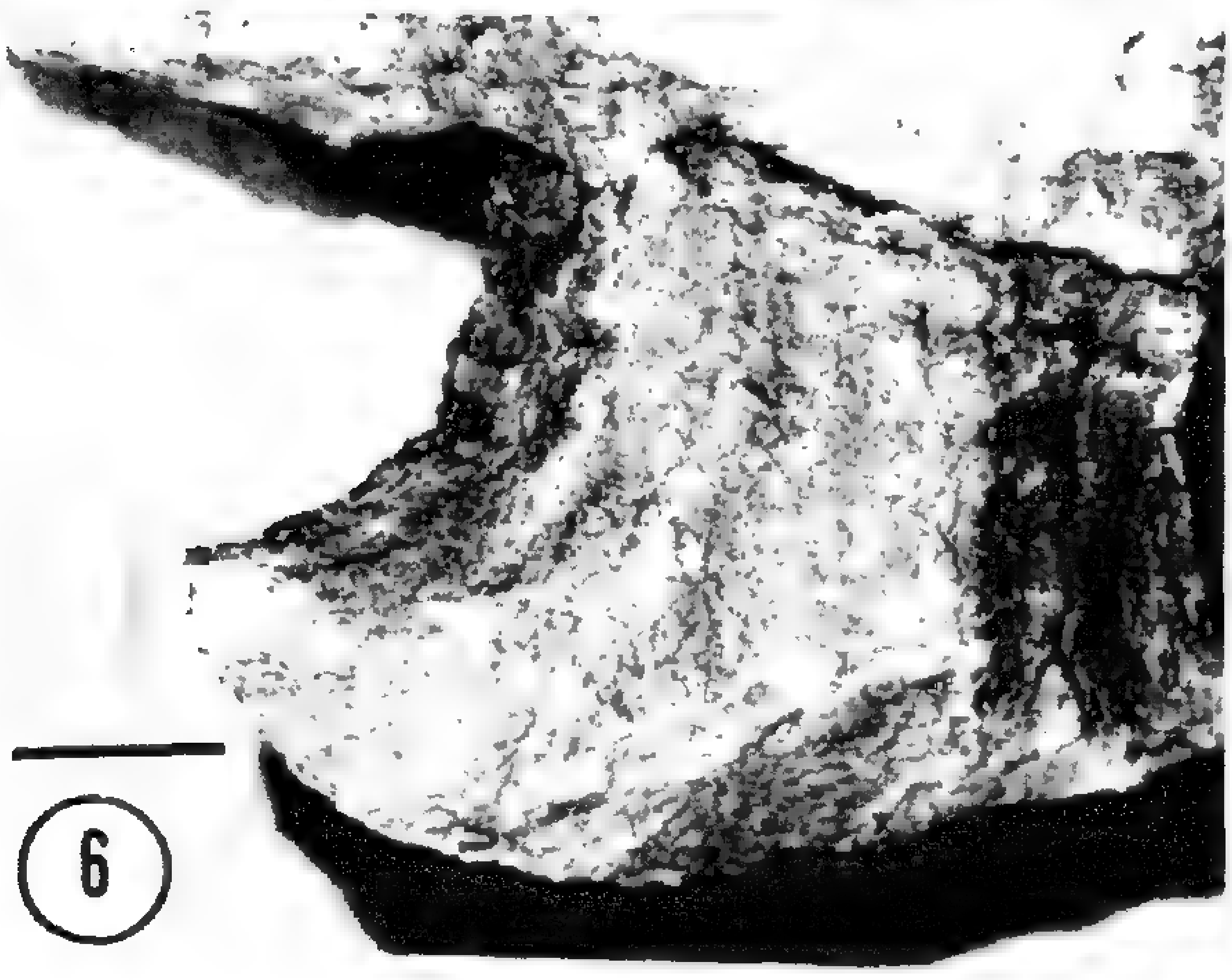

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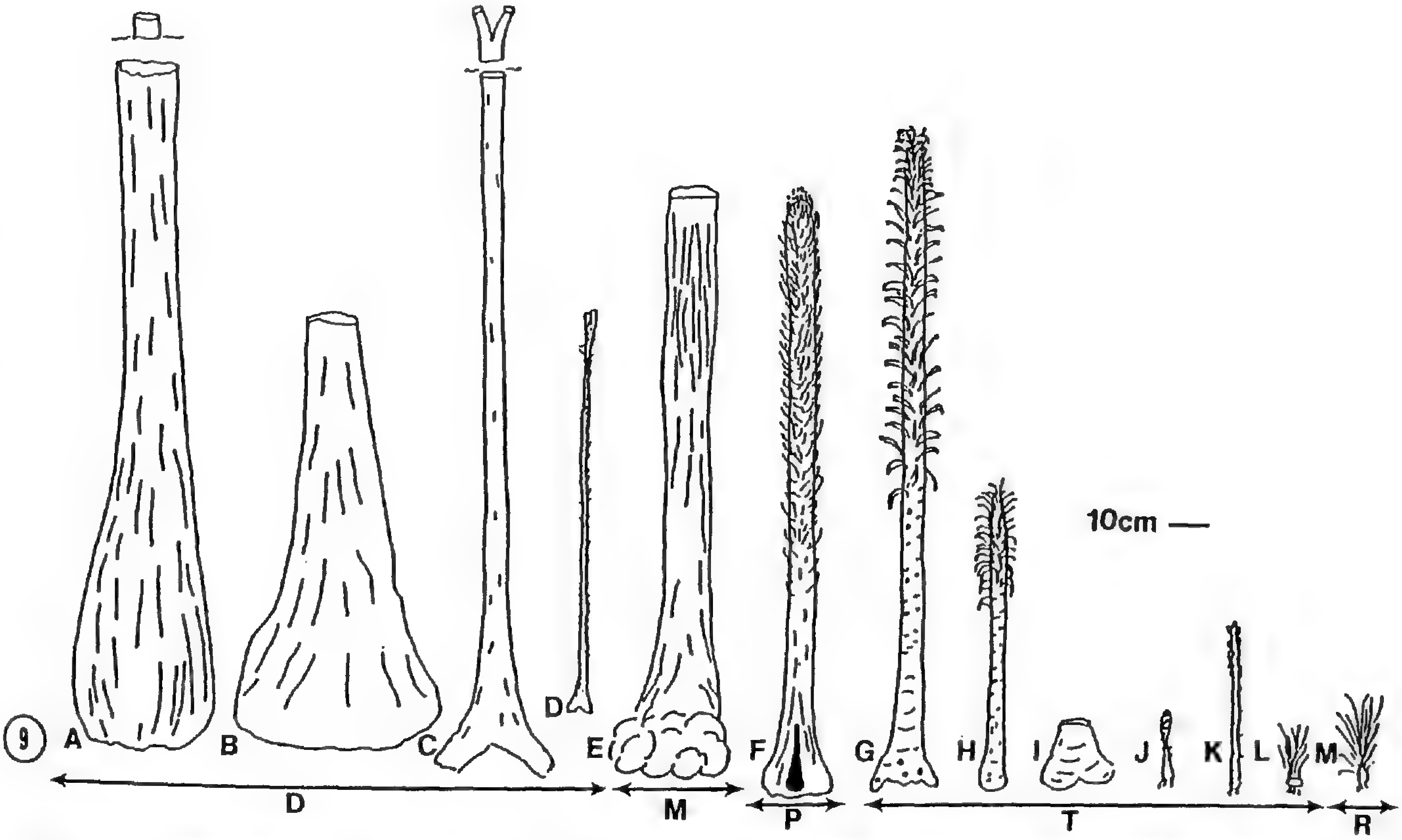

FIGURE 9. Reconstructions of isoetalean lycopsids from the Paleozoic, Mesozoic, and Cenozoic, drawn to scale (bar = 10 cm). A = *Lepidosigillaria whitei* (redrawn from White, 1907); B = *Eospermatopteris textilis* (redrawn from Gensel & Andrews, 1984); C = *Cyclostigma kiltorkense* (redrawn from Johnson, 1913); D = unnamed Cleveland Shale lycopsid (redrawn from Chitaley, 1982); E = *Protostigmaria eggertiana* (redrawn from Jennings et al., 1983); F = *Chaloneria cormosa* (redrawn from Pigg & Rothwell, 1983a); G = *Pleuromeia sternbergi* (redrawn from Mägdefrau, 1931); H = *Pleuromeia rossica* (redrawn from Neuburg, 1960); I = *Takhtajanodoxa* (redrawn from Snigirevskaya, 1980a); J, K = *Pleuromeia jiaochengensis* (redrawn from Wang & Wang, 1982); L = *Isoetes gramineoides* (redrawn from Bock, 1962); M = *Isoetes* sp., extant. Reconstructions are organized stratigraphically: D = Devonian, M = Mississippian, P = Pennsylvanian, T = Triassic, R = Recent. Dimensions were obtained from the literature. It should be pointed out that previously *Eospermatopteris* (B) has not been considered a lycopsid. The reconstruction of *Cyclostigma kiltorkense* (C) is highly conjectural because of the poor preservation of the material. The reconstruction of *Chaloneria cormosa* (F) is based on size estimated from external cortical tissues with the anatomically preserved woody base indicated by the shaded area.

sieve cells and parenchyma. Cortical tissues include a combination of primary, parenchymatous zones, secondary periderm from a distinct lateral cortical cambium, and irregular proliferations of secondary growth resulting from internal cell divisions of primary cortical cells. The last two cortical types, when seen together in tangential section, result in patterns referable to the decortication forms *Knorria* Sternberg and *Asolanus* Wood, respectively (Pigg & Rothwell, 1983a, 1985).

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FIGURES 2–8. Representative isoetalean lycopsids of Paleozoic, Mesozoic, and Cenozoic ages. 2, 3. *Chaloneria cormosa*.—2. Longitudinal section through decorticated plant base showing abundant secondary xylem, helically arranged leaf traces (LT), and root traces. 1423 E Bot. #23, PHOU, ×3.3.—3. Cross section through the base of the stem. Primary body is reduced to a tiny central point, areas of the rooting region (RR) extend upward on either side. 1387 Q(2) Top #2, PHOU, ×8.—4. Vertically compressed specimen of *Cylomeia* from the Triassic of Australia, showing a crown of vegetative leaves radiating from the axis (A). AMF 58791, AM, ×1.—5. *Isoetites serratus*, Cenozoic isoetalean from the Cretaceous of Wyoming. Crown of leaves that have been compressed vertically around plant axis (A). Type specimen. USNM 315170, ×1.—6. Plant base of *Cylomeia*-type Triassic lycopsid. AMF 59985, AM, ×1.—7. *Isoetites serratus* leaf. Higher magnification of Figure 5 to show detail of impressions of air channels (T) and serrate margin of sporophylls. Type specimen. USNM 315170, ×4.—8. Extant *Isoetes* sp. plant base with attached roots, ×2. Scale bars = 1 cm unless otherwise indicated. (PHOU = Paleobotanical Herbarium, Department of Botany, Ohio University, Athens, Ohio; USNM = U.S. National Museum, Smithsonian Institution, Washington, D.C.; AM = The Australian Museum, Sydney, New South Wales, Australia.)

TABLE 1. Paleozoic isoetalean lycopsids. Data taken from the following sources: [1] Kräusel & Weyland (1949); [2] Johnson (1913); [3] Chitaley (1982, 1988, unpublished data); [4] Goldring (1924); [5] Jennings (1975); Jennings et al. (1983); [6] Chaloner (1958); [7] Drābek (1976); [8] Pigg & Rothwell (1983a, b); [9] Pigg & Taylor (1985); [10] Leisman (1970); [11] DiMichele et al. (1979), Pigg & Rothwell (1983 a, b); [12] Abbott (1963); [13] Pigg & Rothwell (1983 a, b); [14] Remy & Remy (1975).

Taxon	Age	Occurrence	Extent	Preservation	Stem length and width (cm)	Rhizomorph shape
Lepidosigillaria whitei[1]	Devonian	New York, U.S.A.	Stem and plant base	Compression	>500 × 7	Rounded
Cyclostigma kiltorkense[2]	Devonian	Ireland	Stem and ?plant base	Compression	>800 × 7	Bilobed?
Unnamed lycopsid[3]	Devonian	Ohio, U.S.A.	Stem and plant base and attached fructification	Compression	119 × 1.5	Rounded
Eospermatopteris textilis[4]	Devonian	New York, U.S.A.	Stem and plant base	Compression	? × 25	Rounded?
Protostigmaria eggertiana[5]	Mississippian	Virginia, U.S.A.	Stem and plant base	Compression	>166 × 17	10–13 lobes
Polysporia mirabilis[6]	Westphalian A–C	England, Scotland, United States	Fructification with spores	Compression	Unknown	Unknown
Polysporia robusta[7]	Westphalian C	Central Bohemia	Fructification with spores	Compression	Unknown	Unknown
Chaloneria sp.[8]	Middle Pennsylvanian	Ohio, U.S.A.	Stem and plant base, spores	Petrifaction	Unknown	Rounded/lobed?
Cormophyton mazonensis[9]	Middle Pennsylvanian	Illinois, U.S.A.	Stem and plant base	Compression	Unknown	Rounded/lobed?
Sporangiostrobus kansanensis[10]	Middle Pennsylvanian	Kansas, U.S.A.	Stem; fructification with spores	Petrifaction	40 × ?	Unknown
Chaloneria periodica[11]	Middle Pennsylvanian	Kentucky, Illinois, Indiana, U.S.A.	Stem; fructification with spores	Petrifaction	>15 × ?	Unknown
Lepidostrobopsis missouriensis[12]	Middle–Late Pennsylvanian	Oklahoma, U.S.A.	Megasporophylls with spores	Compression	Unknown	Unknown
Chaloneria coromosa[13]	Late Pennsylvanian	Ohio, U.S.A.	Stem with plant base, attached fructification with spores	Petrifaction	>200 × 10	Rounded/lobed?
Sporangiostrobus puertollanesis[14]	Late Stephanian	Spain	Stem	Petrifaction	21 × ?	Unknown

TABLE 1. Continued.

Taxon	Rhizomorph width (cm)	Fertile zone length × width (cm)	Size sporangium length × width (mm)	Microspores	Micro-spore size (μm)	Megaspores	Megaspore size (μm)
Lepidosigillaria whitei[1]	38.5	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Cyclostigma kiltorkense[2]	24	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Unnamed lycopsid[3]	2.5	8.4 × 2	12 × 3	Unknown	Unknown	Immature?	400–475
Eospermatopteris textilis[4]	60	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Protostigmaria eggertiana[5]	32	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Polysporia mirabilis[6]	Unknown	>7 × 7	13–30 × 7	*Endosporites*	66–175	*Valvisisporites auritus*	520–1,360
Polysporia robusta[7]	Unknown	>14 × 5.5	6–10 × 4–6	*Endosporites*	61	*Pseudovalvisisporites* var. *sculptus*	1,200
Chaloneria sp.[8]	1.2 (decorticated)	Unknown	Unknown	*Endosporites*	Unknown	*Valvisisporites*	Unknown
Cormophyton mazonensis[9]	2.6	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Sporangiostrobus kansanensis[10]	Unknown	>16 × 12	11 × 7	*Densosporites*	39–57	*Zonalesporites*	2,500–3,000
Chaloneria periodica[11]	Unknown	>8 × ?	Unknown	*Endosporites globiformis*	67–140	*Valvisisporites auritus* var. *grandis*	900–1,560
Lepidostrobopsis missouriensis[12]	Unknown	Unknown	18–25 × 8–12	Unknown	Unknown	*Valvisisporites auritus*	1,000–1,500
Chaloneria cormosa[11]	1.9 (decorticated)	>21 × 10	6 × 2	*Endosporites globiformis*	48–87	*Valvisisporites auritus*; *Pseudovalvisisporites auritus*	430–670
Sporangiostrobus puertollanesis[14]	Unknown	? × 3	9–10 × 4–5	*Densosporites*	40–60	*Zonalesporites*; *Cristatisporites*	Unknown

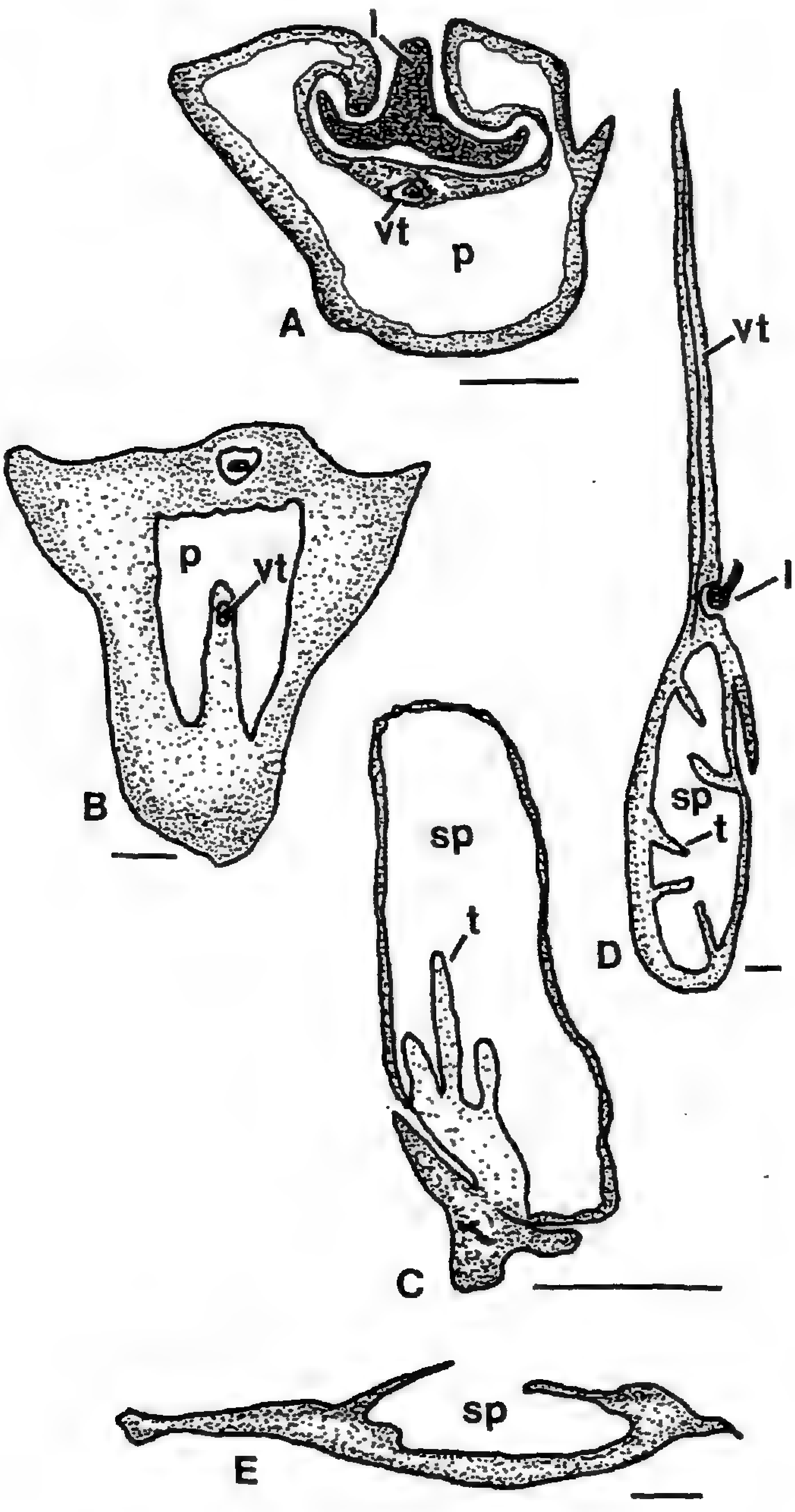

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FIGURE 10. Line diagrams of isoetalean leaf bases and sporophylls.—A. Transverse section through leaf base of *Takhtajanodoxa*. Note ligule (l) with glossopodium, vascular tissue (vt), and large air channel (p). Redrawn from Snigirevskaya (1980a) ×13.—B. Transverse section through leaf base of *Chaloneria cormosa*. Note small ligule (at top), bifurcating parichnos strand (p), and vascular tissue (vt) ×7.3.—C. Transverse section through sporophyll of *Chaloneria cormosa* showing position of trabeculae (t) in the sporangium (sp). B and C redrawn from Pigg & Rothwell (1983a).—D. Longitudinal section through sporophyll of *Isoetes* to show position of ligule (l) with glossopodium, vascular tissue (vt), sunken sporangium (sp) with trabeculae (t), and velum (at right) ×4.—E. Transverse section through sporangium (sp) of *Pleuromeia rossica* to show sunken nature of sporangium. Redrawn from Neuburg (1960) ×8. Scale bars = 1 mm on each figure.

Leaves of *C. cormosa* are ligulate and have a single bilobed, or double vascular trace accompanied by parichnos channels that bifurcate proximally and diminish distally (Fig. 10B). Abaxial, sunken stomata occur in rows. The fertile region of *C. cormosa* is up to 21 cm long and consists of broad zones of alternating micro- and megasporangia (Pigg & Rothwell, 1983a). Sporophylls bear sporangia 6 mm long × 2 mm wide on the adaxial surface. Microsporangia have abundant trabecular tissue (Fig. 10C) and bear hundreds of microspores, both singly and in tetrads, of the pseudosaccate *Endosporites* Wilson & Coe type (Wilson & Coe, 1940). Megasporangia, also with trabeculae, bear up to several hundred auriculate spores referable to *Valvisisporites auritus* (Zerndt) Potonié & Kremp that grade into the nonauriculate form *Pseudovalvisisporites* Lachkar (Drābek, 1976).

Cellular megagametophytes have been discovered within *Chaloneria* megaspores (Pigg & Rothwell, 1983b). They are composed of large central and small peripheral parenchymatous cells and contain up to about a dozen archegonia at various developmental stages showing two, three, or four tiers of neck cells. Mature gametophytes protrude out the trilete haptotypic mark and may produce a few rhizoids. Fungal hyphae also occur in the gametophyte tissue (Pigg, pers. obs.). The biological role of these fungi, that is, whether they were saprophytes, parasites, or mycorrhizae, has not been addressed. *Chaloneria* megagametophytes are very similar to those previously described for fossil and extant heterosporous lycopsids (La Motte, 1933; Brack, 1970; Galtier, 1970; Phillips, 1979; Stubblefield & Rothwell, 1981; Pigg & Rothwell, 1983b).

A second species, *C. periodica* Pigg & Rothwell (= *Polysporia mirabilis* Newberry sensu DiMichele et al., 1979) from Middle Pennsylvanian strata of the Illinois Basin, shares anatomical similarities with *C. cormosa* (Pigg & Rothwell, 1983a). This plant differs from the Upper Pennsylvanian form in having alternating vegetative and fertile zones, larger megaspores, and ligule pits lined with palisadelike cells (DiMichele et al., 1979). The smaller amount of secondary xylem found in this plant probably reflects the limited levels of the stem from which material is known. Basal parts of the plant have yet to be discovered (Pigg & Rothwell, 1983a). Similar permineralized *Chaloneria* fossils are also known from the Middle Pennsylvanian Anderson coal of Ohio (Pigg & Rothwell, 1983a) and have been observed in Lewis Creek, Kentucky (Copland coal) coal balls (Pigg, pers. obs.).

Because of the detailed information known for

Chaloneria, it has been possible to further correlate its structures with a number of less known, disarticulated fossils that also represent the Chaloneriaceae (Table 1). These include compressions of reproductive structures (*Polysporia*, *Lepidostrobopsis* Abbott; Chaloner, 1958; Abbott, 1963; Drābek, 1976), isolated sporangia (*Lepidocystis* Lesquereux; Gastaldo, 1981), isolated rhizomorphs (*Cormophyton* Pigg & Taylor; Pigg & Taylor, 1985), several taxa of decorticated stems (*Asolanus*, *Knorria*; Pigg & Rothwell, 1985), and the spores *Endosporites* (Brack & Taylor, 1972) and *Valvisisporites* (Gastaldo, 1981; Taylor, 1990). Based on the widespread distribution of these disarticulated organs in a variety of depositional environments (i.e., freshwater clastic swamp, peat-accumulating swamp, ironstone nodules), together with the stratigraphic record of the spores, it is obvious that *Chaloneria*-type, isoetalean plants were widespread components of the Pennsylvanian flora (Table 1).

Compressed fertile structures bearing *Valvisisporites* megaspores and *Endosporites* microspores were united under the genus *Polysporia* by Chaloner based on the presence of these characteristic spore types (Chaloner, 1958). *Polysporia mirabilis* is recognized in Westphalian A to Middle Pennsylvanian sediments in Scotland, England, and the Appalachian and Illinois Basins. Most of the specimens of *P. mirabilis* described by Chaloner (1958) were bisporangiate, although monosporangiate fructifications with these spore types cannot be precluded (Table 1). A second species, *P. robusta* Drābek, which is twice as large (14 cm long) and bears larger megaspores that lack well-defined auriculae (*Pseudovalvisisporites*), was later recognized from Bohemia (Table 1; Drābek, 1976). It is interesting that in both permineralized and compressed remains of the Chaloneriaceae, authors refer to the specimens as "fertile regions" rather than compact cones (e.g., Chaloner, 1958; Drābek, 1976; Pigg & Rothwell, 1983a). Often the distal lamina are missing and the large (1.3–3 cm long) sporangia give *Polysporia* a distinctive appearance (e.g., plate 31, fig. 7 of Chaloner, 1958). Pennsylvanian strata also contain isolated sporangia with *Valvisisporites* megaspores, assignable to the genus *Lepidocystis* (Gastaldo, 1981); detached sporophylls bearing sporangia with *Valvisisporites* megaspores, assignable to *Lepidostrobopsis* (Table 1; Abbott, 1963); and isolated sporangia with *Endosporites* microspores (e.g., Brack & Taylor, 1972). The characteristic spore types *Valvisisporites* and *Endosporites* have been described ultrastructurally by Gastaldo (1981) and Taylor (1990), and Brack & Taylor (1972), respectively. In addition to compressed fertile structures, *Cormophyton*, a mold-cast lycopsid plant base, has been described from the Middle Pennsylvanian Mazon Creek nodule flora (Table 1; Pigg & Taylor, 1985). This wide record of distribution indicates that Paleozoic isoetaleans may have occupied a number of depositional sites both within the peat-accumulating coal swamps and in other freshwater, clastic-dominated wetlands.

Anatomically preserved and compressed plant fructifications and vegetative stems described under the genera *Sporangiostrobus* Bode, *Puertollania* Remy & Remy, and *Bodeodendron* Wagner & Spinner have a suite of similar features when compared to the *Chaloneria/Polysporia* group (Table 1; Němejc, 1931; Leisman, 1970; Remy & Remy, 1975; Wagner & Spinner, 1976; Wagner, 1989). These fossils also are interpreted to represent unbranched or sparsely branched plants of about 1–2 m in height that bear fertile regions rather than compact cones (Wagner, 1989). *Sporangiostrobus* bears megaspores with an equatorial cingulum assignable to *Zonalesporites* Ibrahim and microspores of the widespread, cingulate trilete *Densosporites* Berry type (Leisman, 1970; Remy & Remy, 1975). Anatomically preserved stems originally recognized as *Lepidodendron dacrydioides* Leisman have been allied with *Sporangiostrobus kansanensis* Leisman fertile remains and share structural similarities with *Chaloneria* (Leisman, 1970; Leisman & Stidd, 1977). Because of all of these similarities, *Sporangiostrobus* was interpreted as a member of the Chaloneriaceae (Pigg & Rothwell, 1983b). *Sporangiostrobus* is known in considerably less anatomical detail than other members of the family, but the vegetative parts are found abundantly as compressions, allowing for a detailed description of vegetative form (Wagner, 1989).

Another Pennsylvanian fructification that may have some affinity with the Chaloneriaceae is the genus *Porostrobus* Nathorst. This bisporangiate lycopsid cone bears *Setosisporites* Potonié & Kremp megaspores and *Densosporites* microspores (Leary & Mickle, 1989). Although the microspores are similar to those of *Sporangiostrobus*, the megaspores have a prominent gula and equatorial hairs rather than auriculae like *Valvisisporites* or a flangelike cingulum like *Zonalesporites*. *Setosisporites* megaspores of *Porostrobus nathorstii* from early Pennsylvanian strata in Illinois resemble ultrastructurally the megaspores of *Setosisporites praetextus* forma *minor* Chaloner that characterize the cone of *Bothrodendrostrobus* *mundus*. This latter genus represents a Lower Pennsylvanian lycopsid cone from England containing megagametophytes with vascularized embryos that demonstrate reproductive biology and embryogeny very similar to that of extant *Isoetes* (Stubblefield & Rothwell, 1981). Although neither *P. nathorstii* nor *Bothrodendrostrobus mundus* can be unequivocally assigned to the Chaloneriaceae without further information, these reproductive structures appear to have some isoetalean relationship (Leary & Mickle, 1989).

Some Late Carboniferous Gondwana lycopsids can also be compared to the isoetaleans. Cormose plant bases found in association with *Bumbudendron* Archangelsky et al. are similar to *Chaloneria, Cormophyton,* and Mesozoic *Pleuromeia*-like plants in known features (Archangelsky et al., 1981). Similar lycopsid occurrences have been noted by Pfefferkorn & Alleman (1989) in Carboniferous strata of Peru.

ANATOMICALLY PRESERVED TRIASSIC ISOETALAEANS

Recently, significant anatomical information was added to our knowledge of Mesozoic lycopsids, with the description of the Russian taxon *Takhtajanodoxa mirabilis* Snigirevskaya (Snigirevskaya, 1980a, b). This Triassic plant is an apparently unbranched lycopsid 13–15 cm long and 3–20 cm in diameter that produced a medullated protostele surrounded by a small amount of secondary xylem and had a lobed, sometimes bifurcating rhizomorphic base (Fig. 9I, Table 2; pl. I, 3 of Snigirevskaya, 1980a). *Takhtajanodoxa* is similar anatomically to Carboniferous lepidodendrids and the members of the Chaloneriaceae for which anatomy is known (*Chaloneria*; Pigg & Rothwell, 1983a; *Sporangiostrobus*; Leisman, 1970). For instance, it produced leaf bases with broad parichnos strands and wedges of fimbriate secondary xylem tracheids that alternate with aerenchymatous rays, a fertile region rather than a compact cone, and auriculate, trilete megaspores. Microspores are unknown. *Takhtajanodoxa* is distinguished from *Chaloneria* by elaborate ligules that extend basally into glossopodia (compare Fig. 10A, B; pl. V, 1 of Snigirevskaya, 1980a). In this respect *Takhtajanodoxa* is more similar to extant species of *Isoetes* than is any other anatomically preserved fossil form (Snigirevskaya, 1980a, b; Sharma & Singh, 1984). As in *Chaloneria*, transfusion tissue occurs in the region between the ligule and the vascular bundle in the leaf base. The anchor-shaped, sometimes branched rhizomorph of *Takhtajanodoxa* bears typical stigmarian rootlets and has irregular lateral ridges resulting from secondary cortical tissue proliferation (Snigirevskaya, 1980a).

While Snigirevskaya (1980a, b) regarded *Takhtajanodoxa* as a member of a new order of lycopsids, the Takhtajanodoxales, Meyen (1987) suggested that this plant is probably related to the Isoetaceae. Thomas & Brack-Hanes (1984) placed the genus in the family Takhtajanodoxaceae in the Isoetales. *Takhtajanodoxa* differs from modern *Isoetes* in the production of an elongate stem, a radially symmetric rhizomorph, and the presence of sterile leaves. It cannot be compared in detail to *Pleuromeia*-type plants that lack anatomical features. Documentation of anatomically preserved ligules and parichnos strands in *Takhtajanodoxa* not only demonstrates heretofore uniquely *Isoetes*-like features in the Triassic, but also may prove valuable in interpreting the structure of leaf bases of other Angaran lycopsids previously thought to be eligulate (e.g., Meyen, 1972; Snigirevskaya, 1980a).

PLEUROMEIAN ISOETALEANS—MESOZOIC AND CENOZOIC FORMS

In contrast to the recently recognized, anatomically preserved Carboniferous Chaloneriaceae, the larger isoetalean forms of the Mesozoic have been known for many years as compressions (e.g., *Pleuromeia, Cylostrobus* Helby & Martin, *Nathorstiana, Nathorstianella* (Figs. 4, 6, 9G, H, J, K; Table 2)). Traditionally, these plants represented the intermediate members of the lycopsid reduction series (Potonié, 1894; Mägdefrau, 1931; Hirmer, 1933). They are variously included in their own order, the Pleuromeiales (Delevoryas, 1962; Taylor, 1981; Gifford & Foster, 1989), their own family, the Pleuromeiaceae (Retallack, 1975; Thomas & Brack-Hanes, 1984; Meyen, 1987), in the Isoetales (Smith, 1938; Bierhorst, 1971), or the Lepidodendrales (Neuburg, 1960, 1961; Chaloner, 1967; Retallack, 1975; White, 1981). These plant remains share a number of similarities with the Carboniferous Chaloneriaceae (Tables 1, 2, 4). Unbranched or sparsely branched stems bear helically arranged vegetative leaves that typically have bilobed vascular strands and may possess parichnos (Neuburg, 1960, 1961; Kon'no, 1973; Dobruskina, 1974). *Pleuromeia*-type plants may bear rounded (e.g., *P. jiaochengensis*; Wang & Wang, 1982), anchor-shaped (*Cylomeia* White; White, 1981), or four-lobed (*P. sternbergi* Münster; Mägdefrau, 1931) rhizomorphic plant bases, all of which produce rooting appendages with stigmarian morphology (Kon'no, 1973; Retallack, 1975). Distally, pleuromeians produce either a terminal cone (e.g., *Cylomeia, Skilliostrobus* Ash; Ash, 1979) or less compact fertile region (*Pleuromeia*), the latter sometimes described as pedunculate (Retallack, 1975). While fructifications of some species (e.g., *P. rossica* Neuburg, *Cylostrobus sydneyensis*) are clearly bisporangiate, those of other species (i.e., *P. sternbergi, P. obrutschewii* Elias, *P. jiaochengensis*) are presumably monosporangiate. Isolated fructifications thought to belong in this group (Table 2) include *Cylostrobus* (Helby & Martin, 1965), *Austrostrobus* Morbelli & Petriella (Morbelli & Petriella, 1973) (which has been synonymized with *Cylostrobus* as *C. ornatus* (Morbelli & Petriella) Batten & Kovach; Batten & Kovach, 1990), *Skilliostrobus* (Ash, 1979), *Tomiostrobus* Neuburg (Sadovnikov, 1982a), and possibly the enigmatic *Cidarophyton* Chaloner & Turner (Chaloner & Turner, 1987).

In contrast to Carboniferous forms that have relatively simple sporangia, Triassic isoetaleans have sporangia that are sunken into the sporophylls (Fig. 10E). This morphology, coupled with compression preservation in which sporangial cavities are preserved as coalified casts, led to the initial interpretation that *Pleuromeia* sporangia were abaxial (Mägdefrau, 1931). Reinvestigations have demonstrated the adaxial, sunken position of sporangia of this taxon (Neuburg, 1960, 1961; Dobruskina, 1974; Retallack, 1975). Megaspores are assignable to such *sporae dispersae* taxa as *Banksisporites* Dettman, cf. *Triletes* (Erdtman) Potonié, and *Horstisporites* Potonié (Neuburg, 1960; Helby & Martin, 1965; Retallack, 1975; Ash, 1979). Like Carboniferous spores they are trilete, with a granulate to smooth (e.g., Krassilov & Zakharov, 1975) or reticulate (Ash, 1979) exine. Microspores of Southern Hemisphere taxa and some Russian and European forms including *Tomiostrobus* Neuburg and *Annalepis* Fliche have been assigned to the monolete taxon *Aratrisporites* Leschik *mut. char.* Playford & Dettman (Retallack, 1975; Ash, 1979). Although microspores of *P. rossica* were originally described as monolete, Neuburg (1961) demonstrated that these were degraded trilete grains that have a layered exine, the outermost layer of which is often missing (Neuburg, 1960, 1961). Spores of this type are referable to cf. *Punctatosporites* (Ibrahim) Potonié & Kremp. A transition from trilete to monolete microspores like those that characterize extant *Isoetes* thus occurred among some pleuromeians in the Triassic (Yaroshenko, 1985).

Pleuromeia-type plants known from compressions show a wide range of variation. The initially described species, *P. sternbergi*, is known from Germany, France, Russia, and China (Fig. 9G, Table 2; Solms-Laubach, 1899; Seward, 1910; Mägdefrau, 1931; Hirmer, 1933; Neuburg, 1960; Chaloner, 1967; Fuchs et al., 1991). *Pleuromeia sternbergi* is characterized by a stem estimated to be about 1–2 m in maximum height and 5–10 cm in diameter and a plant base with four shortened rhizophoric lobes that bear stigmarian rootlet scars and attached rooting appendages (Mägdefrau, 1931). A terminal fructification 20 cm long is presumably monosporangiate and bears exclusively either micro- or megasporangia. This plant is reported to have produced basal leaves that were distinctly different from ones borne more distally (Fuchs et al., 1991).

The Russian species *P. rossica* is known in considerable detail (Fig. 9H, Table 2; Neuburg, 1960, 1961). In comparison to *P. sternbergi*, this Russian form is a smaller plant with a four-lobed rhizomorph with less extensive lobes. Parichnos strands are oval in comparison to the triangular strands of *P. sternbergi*, and fructifications are ovoid and bisporangiate rather than cylindrical and monosporangiate. Dobruskina (1985) recently proposed that *P. rossica* should be removed from the genus *Pleuromeia* and reassigned to a new genus, *Leiomeia*. The basis for this new genus is the apparent lack of sterile leaves in this taxon and the bisporangiate organization of the fructification (Dobruskina, 1985).

Other Russian forms include *P. obrutschewii*, *P. olenekensis* Krassilov, *P. taimyrica* Sadovnikov, and *P. jokvazhica* Dobruskina (Table 2; Krassilov & Zakharov, 1975; Sadovnikov, 1982b; Dobruskina, 1974, 1985). *Pleuromeia obrutschewii* is very similar to *P. sternbergi*, and according to Krassilov & Zakharov (1975) may be conspecific with the German taxon. *Pleuromeia olenekensis* can be distinguished from *P. sternbergi*, *P. rossica*, and other forms by its large (26 × 10 mm) megasporangia and large, reticulate megaspores (Krassilov & Zakharov, 1975). Megaspores have a three-layered wall, the outermost reticulate layer of which is easily removed from the spore body (Krassilov & Zakharov, 1975). Comparative study suggests that other taxa that lack the reticulate covering may bear similar spores that have become degraded during preservation. *Pleuromeia jokvazhica* is fairly well known from disarticulated vegetative and fertile remains, although details of plant base and spore types are obscure. Morphologically, this species is most similar to *P. sternbergi*, but has smaller and less compact fructifications (Dobruskina, 1985). *Pleuromeiopsis* Sixtel

TABLE 2. Mesozoic isoetalean lycopsids. Data taken from the following sources: [1] Snigirevskaya (1980a, b); [2] Kon'no (1973); [3,4] Krassilov & Zakharov (1975); [5] Mägdefrau (1931), Fuchs et al. (1991); [6] Neuberg (1960, 1961); [7] Sadovnikov (1982b), Dobruskina (1985); [8] Dobruskina (1974, 1985); [9] Wang & Wang (1982); [10] Wang (1991); [11] Retallack (1975); [12] Helby & Martin (1965), Retallack (1975); [13,14] White (1981); [15] Ash (1979); [16] Morbelli & Petriella (1973), Retallack (1975); Batten & Kovach (1990); [17] Grauvogel-Stamm & Duringer (1983); [18] Bock (1962, 1969); [19] Bock (1962, 1969); [20] Emmonds (1856), Brown (1958); [21] Walkom (1941); [22] Ash & Pigg (1991); [23] Münster (1842).

Taxon	Age	Occurrence	Extent	Preservation	Stem length and width (cm)	Rhizomorph shape
Takhtajanodoxa mirabilis[1]	Early Triassic	Russia	Stem and plant base, megaspores	Petrification	13–15 × 3–20	Radially symmetric (forked)
Pleuromeia hataii[2]	Early Triassic	Japan	Stem and plant base, megaspores	Compression	9.5 × 1.1–2.7	Forking, anchor-shaped
Pleuromeia obrutschewii[3]	Early Triassic	Russia	Stem, fructification with megaspores	Compression	Unknown	Unknown
Pleuromeia olenekensis[4]	Early Triassic	Russia	Fructification with megaspores	Compression	Unknown	Unknown
Pleuromeia sternbergi[5]	Triassic	Germany, France, Russia, China	Stem and plant base, fructification with spores	Compression	100–200 × 5–10	Four-lobed
Pleuromeia rossica[6]	Triassic	Russia	Stem and plant base, fructification with spores	Compression	100 × 4–5	Weakly developed four-lobed
Pleuromeia taimyrica[7]	Triassic	Russia	Fructification	Compression	Unknown	Unknown
Pleuromeia jokvazhica[8]	Triassic	Russia	Stem and plant base, fructification	Compression	>11 × 3–4	Unknown
Pleuromeia jiaochengensis[9]	Triassic	China	Stem and plant base, fructification with megaspores	Compression	20–50 × 1.5	Tuberous
Isoetes ermayinensis[10]	Middle Triassic	Northern China	Isolated sporophylls with attached sporangia containing spores	Compression	Unknown	Unknown
Pleuromeia longicaulis[11]	Triassic	Australia	Stem and plant base	Petrifaction	Unknown	Unlobed
Cylostrobus sydneyensis[12]	Triassic	Australia	Fructification with spores	Compression	0.8–5.8	Unknown
Cylomeia undulata[13]	Triassic	Australia	Stem, associated plant base	Compression	Unknown	?Anchor-shaped (associated)

TABLE 2. Continued.

Taxon	Age	Occurrence	Extent	Preservation	Stem length and width (cm)	Rhizomorph shape
Cylomeia capillamentum[14]	Triassic	Australia	Stem with fructification, associated plant base	Compression	Unknown	?Anchor-shaped (associated)
Skilliostrobus australis[15]	Triassic	Australia	Fructification with spores	Compression	1.5 × 2.5	Unknown
Cylostrobus ornatus[16]	Triassic	Argentina	Fructification with megaspores	Petrifaction	Unknown	Unknown
Annalepis zeilleri[17]	Triassic	France	Sporophylls with spores	Compression	Unknown	Unknown
Lepacyclotes americana[18]	Late Triassic	Virginia, U.S.A.	Rosette of attached leaves	Compression	? × 0.8	Unknown
Isoetes gramineoides[19]	Late Triassic	Pennsylvania, U.S.A.	Corm with attached roots, rosettes of leaves, isolated leaves and sporangia	Compression	0.8 × 1.2	Corm
Isoetites circularis[20]	Late Triassic	North Carolina and Arizona, U.S.A.	Corm with leaves, rosette of attached leaves	Compression	? × 10	Unknown
Isoetites elegans[21]	Jurassic	Western Australia	Rosette of attached leaves, sporangia with megaspores	Compression	? × 4	Unknown
Isoetites rolandii[22]	Middle Jurassic	Idaho and Oregon, U.S.A.	Corm with attached leaves, sporophyll bases, sporangia, megaspores?	Compression	0.6 × 1.5	Rounded/lobed?
Isoetites crociformis[23]	Late Jurassic	Germany	Corm (?)	Compression	Unknown	Lobed?

TABLE 2. Continued.

Taxon	Rhizomorph width (cm)	Fertile zone length × width (cm)	Size sporangium length × width (mm)	Microspores	Microspore size (μm)	Megaspores	Megaspore size (μm)
Takhtajanodoxa mirabilis[1]	3–20	Unknown	4–5	Unknown	Unknown	Unknown	300–500
Pleuromeia hataii[2]	3	>14 × 4	19 × 8	Unknown	Unknown	cf. *Triletes*	650–700
Pleuromeia obrutschewii[3]	Unknown	20 × 1.2–2.0	18–15	Unknown	Unknown	Unknown	370–390
Pleuromeia olenekensis[4]	Unknown	Unknown	26 × 10	Unknown	Unknown	Unknown	990–1,120
Pleuromeia sternbergi[5]	17	20 × 1.6–2.0	10–20	cf. *Laevigatosporites*	15–25	cf. *Triletes*	500–700
Pleruomeia rossica[6]	Unknown	>3.5 × 3	Unknown	cf. *Punctatosporites*	Unknown	cf. *Triletes*	300–340
Pleuromeia taimyrica[7]	Unknown	3.8 × 0.6–0.8	4–5 × 0.4–1.2	Unknown	Unknown	Unknown	Unknown
Pleuromeia jokvazhica[8]	Unknown	3–8 × 6–12	2–20	Unknown	Unknown	Unknown	Unknown
Pleuromeia jiaochengensis[9]	2.2	20 × ?	15 × 9	Unknown	Unknown	Unknown	300–500
Isoetes ermayinensis[10]	Unknown	N/A	7–20 × 2–5	*Aratrisporites*	20–30	*Dijkstraisporites*	288–611
Pleuromeia longicaulis[11]	Unknown	Unknown	? × 7.5	Unknown	Unknown	Unknown	Unknown
Cyclostrobus sydneyensis[12]	Unknown	0.8–5.8	Unknown	*Aratrisporites*	16–29	*Banksisporites*	350–512
Cylomeia undulata[13]	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Cylomeia capillamentum[14]	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown
Skilliostrobus australis[15]	Unknown	1.5 × 2.5	10 × 2	*Aratrisporites*	27–38 × 36–40	*Horstisporites*	800–1,000
Cylostrobus ornatus[16]	Unknown	? × 6	Unknown	Unknown	Unknown	Unknown	420–452
Annalepis zeilleri[17]	Unknown	N/A	25–45 × 10–20	*Aratrisporites*	28–33	*Tenellisporites*	600–700
Lepacyclotes americana[18]	3.8	N/A	Unknown	Unknown	Unknown	Unknown	400?
Isoetes gramineoides[19]	Unknown	N/A	Unknown	Unknown	Unknown	Unknown	Unknown
Isoetites circularis[20]	Unknown	N/A	Unknown	Unknown	Unknown	Trilete	600–700
Isoetites elegans[21]	Unknown	N/A	? × 1.2	Unknown	Unknown	Unknown	500
Isoetities rolandii[22]	2.5	N/A	10 × 10 associated	Unknown	Unknown	Round	440
Isoetites crociformis[23]	Unknown	N/A	Unknown	Unknown	Unknown	Unknown	Unknown

was originally described to represent a somewhat larger *Pleuromeia* plant of about 3 m in height (Sixtel, 1962; see also Chaloner, 1967, and Dobruskina, 1974). Dobruskina (1974) reevaluated this material and concluded that the genus had been based on a mixed assemblage of several types of plants. She proposed the name *Ferganodendron* Dobruskina for the lycopsid stem segments that were a part of this assemblage (Dobruskina, 1974). The relationship of these forms to isoetaleans is not clear.

Evidence of pleuromeian plants is abundant in Australia. Bisporangiate fertile structures bearing *Aratrisporites* microspores and megaspores assignable to *Banksisporites* were described by Helby & Martin (1965) as three species of *Cylostrobus* on the basis of differential spore size. Retallack (1975) united these three species into *C. sydneyensis* and documented the co-occurrence of this fertile material with vegetative remains of *Pleuromeia longicaulis* (Table 2; Retallack, 1975). He further recognized the permineralized cone *Austrostrobus ornatus* (Morbelli & Petriella, 1973) from Patagonia as an additional species of *Cylostrobus*. White (1981) suggested that this taxon and several additional Australian species were distinctive from Northern Hemisphere forms and proposed the generic name *Cylomeia* for Australian pleuromeian plants (Figs. 4, 6, Table 2). Her primary criterion for this assignment is the more compact, conelike nature of the Southern Hemisphere forms, in contrast to the looser, elongate fructifications of the northern forms. White (1981) further suggested that the lycopsid cone genus *Skilliostrobus* (Table 2; Ash, 1979) might be the reproductive structure of some of the *Cylomeia* types. *Cidarophyton* is a globose lycopsid fossil that is difficult to identify unequivocally as cone, stem, or rhizomorph (Chaloner & Turner, 1987). However, this specimen bears strong resemblance to *Skilliostrobus*, and if it is a fructification, most probably also has pleuromeian affinities. Sadovnikov (1982a) has suggested that the genus *Skilliostrobus* be united with the Russian genus *Tomiostrobus*, on the basis of similar sporophyll and spore morphology.

Species of *Pleuromeia* are also known from Japan (Kon'no, 1973) and China (Wang & Wang, 1982). *Pleuromeia hataii* Kon'no from the Triassic of Japan is most similar to *P. sternbergi* based on the presence of monosporangiate cones and the morphology of the leaf bases, which also have triangular parichnos strands. The stem, however, is considerably smaller (3 cm in maximum diameter) and bears smaller stigmarian appendages that leave scars only 0.5–0.8 mm in diameter (Table 2; Kon'no, 1973). The Chinese species *P. jiaochengensis* is characterized by entire, small plants 20–30 cm tall with swollen or tuberous rhizomorphs, and a large, terminal, spike-shaped strobilus (Fig. 9J, K, Table 2; Wang & Wang, 1982). Distinctive characters of *P. jiaochengensis* are the proportionally large fructification, sagittate sporophylls, and awl-like vegetative leaves. Isolated sporophylls assigned to *Annalepis* have been compared to species of *Pleuromeia* (Table 2; Grauvogel-Stamm & Duringer, 1983; Dobruskina, 1985; Meyen, 1987), and, more recently, to a newly described fossil species of *Isoetes* from the Cretaceous of northern China (Wang, 1991). Sporophylls of *Annalepis* bear large, elongate sporangia (2.5–4.5 × 1–2 cm) and have shortened distal laminae. Their fructifications are estimated to have been at least 14 cm wide (Grauvogel-Stamm & Duringer, 1983). Sporangia bear either trilete, spiny megaspores assignable to *Tenellisporites* Potonié or monolete *Aratrisporites* microspores. There is an intergradation in morphology between the sporophylls of *Pleuromeia*, *Annalepis*, and *Tomiostrobus*, and there is some suggestion these taxa might be congeneric (Dobruskina, 1985). Isolated sporophylls of *Lepacycloes* Emmonds are also similar (Table 2; fig. 93 of Bock, 1969). Wang (1991) has stressed the similarities of *Annalepis* and *Tomiostrobus* to material from the Triassic of China that he has named *Isoetes ermayinensis* Wang. He suggested that these taxa are more similar to modern *Isoetes* than they are to Triassic pleuromeians. It is interesting, though, that these Triassic isolated sporophylls are also quite similar to Carboniferous genera such as *Lepidostrobopsis*, which they strikingly resemble (compare plate 3, fig. 1 of Grauvogel-Stamm & Duringer, 1983, with figs. 2, 3, of Abbott, 1963). This suggests that some morphological features are characteristic of the rhizomorphic lycopsids as a whole and cannot be used to unite subgroups within the clade.

Opinions vary on systematic positions of the pleuromeian plants and whether they should be recognized as one or several genera. The proposals by White (1981) for the establishment of the genus *Cylomeia* for Australian forms and by Dobruskina (1985) that *Leiomeia* be named for the Russian *Pleuromeia rossica* emphasize the variability among pleuromeians as a whole and, in both cases, reveal a strong biogeographic basis. The naming of these new genera may be justifiable but should rest on comparative study of material from all the widespread localities. Clearly, a reassessment of all taxa of pleuromeian forms is needed.

Younger, Cretaceous pleuromeian plants include

TABLE 3. Cretaceous and Tertiary isoetalean lycopsids. Data taken from the following sources: [1] Mägdefrau (1932); [2] Glaessner & Rao (1955); [3] Drinnan & Chambers (1986); [4] Krassilov (1982); [5] Saporta (1894), Teixeira (1948); [6] Bose & Roy (1963); Banerji (1988); [7] Bose & Roy (1963); [8] Brown (1939); [9] Brown (1939); [10] Skog & Hill (1992); [11] Skog et al. (in press); [12] Hill (1987).

Taxon	Age	Occurrence	Extent
Nathorstiana arborea[1]	Early Cretaceous	Germany	Stem and plant base
Nathorstianella babbagensis[2]	Early Cretaceous	Australia	Stem and plant base
Isoetes bulbiformis[3]	Early Cretaceous	Victoria, Australia	Corm with attached leaves
Limnoniobe insignis[4]	Early Cretaceous (Aptian)	Mongolia	Stem and plant base, sporophylls, sporangia with megaspores
Isoetites choffati[5]	Early Cretaceous	Portugal	Corm and attached roots, isolated sporophyll bases, sporangia, spores?
Isoetites janaianus[6]	Early Cretaceous	India	Plant base with attached leaves and roots, microspores and megaspores
Isoetites serratifolius[7]	Early Cretaceous	India	Isolated leaves
Isoetites horridus[8]	Early Cretaceous–Paleocene	Western North America	Corm with attached leaves, megaspores
Isoetites serratus[9]	Early Cretaceous–Paleocene	Wyoming, U.S.A.	Corm and roots, rosettes of leaves
Isoetites new species[10]	Early Cretaceous	England	Plant base with attached leaves; megaspores
Isoetites new species[11]	Late Cretaceous (Cenomanian)	Kansas and Nebraska, U.S.A.	Corm with attached leaves
Isoetes reticulata[12]	Late Oligo–Miocene	Tasmania, Australia	Isolated sporophylls, megaspores

the genera *Nathorstiana* (Table 3; Mägdefrau, 1932; Karrfalt, 1984) and *Nathorstianella* (Glaessner & Rao, 1955). *Nathorstiana* is known exclusively from a large collection of over 200 specimens of vegetative remains from Quedlinburg, Germany (Mägdefrau, 1932; Karrfalt, 1984). Included in this collection are both small, presumably young plants with radially symmetrical plant bases and larger forms with four-lobed bases that resemble those of extant species of *Isoetes* (Karrfalt, 1984). It has been suggested that this material documents ontogenetic variability within *Nathorstiana*, presumably showing that plants initially had radially symmetrical rooting meristems that underwent a developmental change to bilateral symmetry during their life history. This proposed ontogenetic change in symmetry in *Nathorstiana* is further cited as evidence for the homology of radially symmetrical forms such as *Stigmaria* and *Paurodendron* with bilaterally symmetrical, lobed forms such as *Isoetes* and *Protostigmaria* (Jennings et al., 1983; Karrfalt, 1984; Rothwell, 1984; Rothwell & Erwin, 1985).

Nathorstianella, a Late Cretaceous taxon, is known from Australia from a cast of a robust (18 × 4–7.1 cm) stem with four rounded lobes on its plant base (Table 3). It has been suggested (Glaessner & Rao, 1955) that *Nathorstianella* may be identical with remains described as *Isoetites elegans* Walkom (Walkom, 1941). As with the Devonian forms, the discovery of fertile remains would aid in clarification of early Cenozoic Isoetales.

Other lycopsids whose affinities remain obscure and which may or may not be related to isoetaleans include four types of remains: (1) compressed cones that resemble *Pleuromeia*, i.e., *Lycostrobus scotti* Nathorst (Nathorst, 1908); *L. longicaulis* Burges (Burges, 1935) and *L. chinleana* Daugherty (Daugherty, 1941); (2) permineralized lycopsid stems of unknown affinities, i.e., *Chinlea campii* Daugherty and *Osmundites walkeri* Daugherty; (3) the large-diametered stem impression *Isoetodendron striata* Bock (Bock, 1969); and (4) *Selaginella*-like forms with characteristic spore types, i.e., *Selaginellites hallei* Lundblad (Lundblad, 1950), and *S. polaris* Lundblad (Lundblad, 1948).

TABLE 3. Extended.

Preservation	Stem length and width (cm)	Rhizomorph shape	Rhizomorph width (cm)	Size sporangium length × width (mm)	Megaspore size (μm)
Compression	10 × 3.8	Four-lobed	1–4	Unknown	Unknown
Mold-cast	18 × 4–7.1	Four-lobed	5.5	Unknown	Unknown
Compression	4 × 3 (+ leaves)	Unknown	Unknown	Unknown	Unknown
Compression	5.0 × 3.0	Unknown	Unknown	Unknown	Unknown
Compression	? × 1	Bulbous	Unknown	7 (diameter)	700–1,000
Compression	14 × 5–7	Five-lobed	5–7	3.5–6 × 2–3 megasporangia 4–5.5 × 3.5–4 microsporangia	285–430
Compression	Unknown	Unknown	Unknown	10–12 × 3	Unknown
Compression	Unknown	Unknown	Unknown	Unknown	477–606
Compression	Unknown	Unknown	Unknown	Unknown	Present
Compression	Unknown	Bilobed	Unknown	Unknown	Unknown
Compression	6.4 × 4.0	Conical, unlobed	Unknown	Unknown	Unknown
Compression	Unknown	Unknown	Unknown	Unknown	~606

Lycostrobus scotti is a bisporangiate cone from the Rhaetian of Sweden that is similar to *Polysporia* and *Sporangiostrobus* in having relatively large sporangia (1.5 cm long) with sporophylls that lack distal laminae (Nathorst, 1908; Chaloner, 1967). Megaspores are 550–600 μm and assignable to *Nathorstisporites hoplicus* Jung. Microspores are monolete, as are spores of the pleuromeians. They are compared with the genus *Chasmatosporites* Nilsson and *Aratrisporites*. This bisporangiate cone has little apparent organization to the distribution of mega- and microsporangia. Other species of *Lycostrobus* include *L. longicaulis*, with similar spores, from the Australian Triassic (Burges, 1935) and *L. chinleyana* from the Triassic Chinle formation of Arizona (Daugherty, 1941). The assignment of these last remains to *Lycostrobus* is somewhat in doubt (Chaloner, 1967).

Chinlea campii Daugherty and *Osmundites walkeri* Daugherty also from the Chinle Formation, were originally recognized as an osmundaceous fern from the Petrified Forest of Arizona (Daugherty, 1941). These permineralized axes were reinterpreted by Miller (1968) as lycopsids. He found them to be conspecific and united the two taxa under the name *C. campii*. Miller (1968) has further suggested that *Chinlea*, *Lycostrobus chinleyana*, and isolated *Lycopodites* leaves found together in the Chinle Formation could represent the same Triassic plant.

Isoetodendron striata Bock was named for an impression from the Upper Triassic of Virginia which Bock (1969) considered the remains of an arborescent lycopsid. It is not clear to me from the illustrated specimens what this material represents. The age and size of this fossil, together with the presence of trilete megaspores in the same matrix, suggest that *Isoetodendron* might represent a poorly preserved *Pleuromeia*-type plant found in a decortication state, but any taxonomic designations without further study seem premature.

Selaginellites hallei is of interest because although this plant has a megafossil habit similar to *Selaginella*, it bears spore types similar to those of the *Pleuromeia*-type plants (i.e., *Banksisporites pinguis* (Harris) Dettman and *Densosporites*

TABLE 4. Typical features of isoetalean lycopsids.

1. Heterospory, megaspore as propogule, often aquatic or semiaquatic reproductive biology.
2. Fructifications are bisporangiate (sometimes monosporangiate) fertile regions grading into cones—typically breaking up into dispersal units of sporophylls bearing sporangia.
3. Unbranched or sparsely branched stems—several centimeters to 2 m long.
4. Rounded or lobed rhizomorph.
5. Helically arranged microphyllous leaves with single or double vascular trace.
6. Parichnos/air channels in leaves.
7. Ligules present.
8. Leaf bases rather than leaf cushions, often nonabscising.
9. Rootlets with stigmarian anatomy borne in distinctive rhizotaxy.
10. Trilete megaspores.
11. Trilete or monolete microspores.
12. Endosporal megagametophytes.
13. Trabeculae/sterile tissue often present in eusporangium.
14. Secondary cortical proliferation, stems often preserved as decortication layers.

(Lundblad, 1950). Another species of *Selaginellites*, *S. polaris*, consists of a compressed cone and associated vegetative remains and also bears megaspores assignable to *B. pinguis* (Lundblad, 1950).

ISOETES-LIKE FORMS: MESOZOIC AND TERTIARY

Material described as *Isoetites* and *Isoetes* is the most similar in growth habit to the modern *Isoetes* (e.g., Figs. 1, 5, 7, 8, 9M; Bock, 1962, 1969; Brown, 1939, 1958, 1962; Drinnan & Chambers, 1986; Hill, 1987; Banerji, 1988; Ash & Pigg, 1991; Wang, 1991; Skog et al., in press; Skog & Hill, 1992). While most authors use the generic name *Isoetites* to designate fossil forms with an *Isoetes*-like habit, some (e.g., Bock, 1962, 1969; Drinnan & Chambers, 1986; Hill, 1987; Wang, 1991) prefer to equate fossils with the modern genus and name them as species of *Isoetes*. These fossils are widespread geographically and stratigraphically with approximately 16 species and over 30 occurrences represented from the Triassic to the Upper Tertiary (Tables 2, 3; Münster, 1842; Emmonds, 1856, 1857; Saporta, 1888, 1894; Fountaine, 1883, 1900; Seward, 1910; Brown, 1939, 1958, 1962; Daugherty, 1941; Teixiera, 1948; Bock, 1962, 1969; Bose & Roy, 1963; Krassilov, 1982; Drinnan & Chambers, 1986; Hill, 1987; Banerji, 1988; Ash & Pigg, 1991; Wang, 1991; Skog et al., in press; Skog & Hill, 1992). The considerable stratigraphic overlap between these smaller herbaceous forms recognized first in the Triassic, and the larger forms, which occur as late as the Lower Cretaceous (i.e., *Nathorstianella*; Glaessner & Rao, 1955) has always been problematic to the view of isoetalean evolution as a linear reduction sequence (Chaloner, 1967).

The genus *Isoetites* (Münster, 1842) was proposed for small cormlike plant bases that were referred to *I. crociformis* Münster (Table 3). This generic name was also used by Saporta (1894) for forms from France and Portugal he originally called *Isoetopsis* (Saporta, 1888) and also by Teixiera (1948) for the Portuguese fossils. Other *Isoetes* and *Isoetites*-like remains have been assigned to a variety of genera including *Yorkia* Wanner (Wanner, 1921; Bock, 1962, 1969), *Xantholithes propheticus* Ward (Ward, 1915), *Lepacycloes* (Daugherty, 1941), and *Limnoniobe insignis* Krassilov (Krassilov, 1982). Stems and their isolated sporophylls have been interpreted as grasses (*Yorkia*; Wanner, 1921; Bock, 1962), conifers (Emmonds, 1857), araucarians (Fountaine, 1883), cycads (Dawson, 1886), equisetoids (Fountaine, 1900), and bennettitaleans (Daugherty, 1941). Brown (1939, 1958, 1962) and Bock (1962) recognized the isoetalean affinities of these various fossils and renamed them as species of *Isoetites* or *Isoetes*, respectively (Ash & Pigg, 1991; Skog et al., in press). Vertically compressed specimens of *Isoetites* (Fig. 5) show radiating linear leaves surrounding an axis and are very similar in appearance to the vertically compressed specimens of the Australian pleuromeian plant *Cylomeia* (Fig. 4; White, 1981), or similarly preserved Carboniferous shoots (e.g., plate 28, figs. 1–4 of Abbott, 1963).

The most completely known *Isoetites*/*Isoetes* fossil plants are *Isoetites gramineoides* (Fig. 9L; Bock, 1962), *I. horridus* (Brown, 1939, 1962), *I. serratus* (Brown, 1939), *I. circularis* (Brown, 1958), *I. janaianus* (Banerji, 1988), *I. rolandii* (Ash & Pigg, 1991), *Isoetes bulbiformis* (Drinnan & Chambers, 1986), and *I. ermayinensis* (Wang, 1991). Because of their small size and probable in situ preservation, whole plants are often preserved (Bock, 1962; Brown, 1939; Drinnan & Chambers, 1986; Banerji, 1988; Ash & Pigg, 1991; Skog & Hill, 1992). Even when the morphology and anatomical details are not clear, a good idea of growth habit can often be obtained, especially from laterally compressed specimens (plate 14, fig. 1 of Bock, 1962; fig. 11B of Drinnan & Chambers, 1986; plate 1, fig. 11 of Banerji, 1988; fig. 2 of Ash & Pigg, 1991).

Information about the variability within this group has not been considered in detail. The most obvious variations within species of the fossil *Isoetes/Isoetites* group include details of plant size, and sporophyll and megaspore morphology. Leaf characters include the distinctiveness of vascular strand and air channels and presence and distribution of marginal teeth. Some species have completely or partly serrate margins (e.g., *I. serratus, I. serratifolium, I. circularis*), whereas leaves in others are entire-margined (e.g., *I. gramineoides, I. horridus, I. rolandii*). At least some of this vegetative variation may be explained by the differential preservational potential of different types of leaves. Some species of *Isoetes* and *Isoetites* have long, delicate, grasslike leaves, while others are quite strong and pointed (giving rise to the colloquial name "quillwort"). Presumably those more resistant leaves would be able to withstand the preservation process well enough to demonstrate the presence of rectangular pockets of air channels in their distal laminae (e.g., Fig. 7, *I. serratus*; *I. horridus*; Brown, 1939, 1962). On the other hand, in thinner and less resistant leaves, air channels and vascular strands are indistinct (Ash & Pigg, 1991). Megaspores are often found in situ or in direct association with isoetalean megafossils (Bock, 1962; Walkom, 1941; Bose & Roy, 1963; Hill, 1987; Banerji, 1988; Wang, 1991; Skog & Hill, 1992). Unfortunately, the in situ occurrence of microspores is especially rare (Banerji, 1988; Wang, 1991). In most cases they are poorly preserved, but in the best cases they can be identified to a *sporae dispersae* species. For instance, spores similar to *Minerosporites dissimilis* were reported in situ in megafossils of *I. horridus* (Hickey, 1977). Other *sporae dispersae* megaspore genera thought to have isoetalean affinities include several taxa from the Lower Cretaceous Dakota Formation of Kansas (Kovach & Dilcher, 1985, 1988). These include *Paxillitriletes vittanus* Kovach & Dilcher; *P. dakotaensis* (Hall) Hall & Nicolson, and *Minerisporites mirabilis* (Miner) Potonié and *M. dissimilis* Tschudy. These dispersed megaspores have been allied with the Isoetales on the basis of wall ultrastructure, spore morphology, and in some cases, correlation with similar spore types known in situ (Kovach & Dilcher, 1985, 1988).

With further investigation of Mesozoic and Cenozoic fossil *Isoetes*-type plants it may be possible to relate some fossil species to extant forms. Generally, extant *Isoetes* has posed difficulties for taxonomic study because of the lack of collections and the wide range of phenotypic plasticity (Hickey, 1986). Historically, leaf morphology, habitat preference, and megaspore ornamentation have been the primary characters used for classification (Pfeiffer, 1922; Hickey, 1986). Although recent studies show there is little cohesive correlation of systematically important characters, megaspore morphology does remain an important criterion (Hickey, 1986). Furthermore, because extant *Isoetes* species include many cases of hybridization and polyploidy (Hickey, 1986), interpretation of Mesozoic and Tertiary fossil species in a one-to-one relationship to extant forms is probably not tenable.

TRENDS WITHIN THE ISOETALEAN LINEAGE

A suite of morphological changes can be recognized in isoetalean lycopsids through time. These include a reduction in axial elongation, disappearance of vegetative leaf production (Fig. 1), trend from trilete to monolete microspores, production of a sunken adaxial sporangium with a velum (Fig. 10D), and elaboration of the basal portion of the ligule into a glossopodium (Fig. 10A, D, Table 5). It is interesting that, with the exception of the velum, all of these changes can be documented among forms that occur in the early Mesozoic. The earliest known plants with the small *Isoetes*-type growth habit occur in the Triassic of Pennsylvania (i.e., *Isoetes gramineoides*; Bock, 1969). Small plants lacking axial elongation (Fig. 9M) thus overlap in the Triassic with both larger "woody" plants of up to 2 m in height (*P. sternbergi*, Fig. 9G) and smaller forms with axially elongate stems (e.g., *P. jiaochengensis*, 20–30 cm tall, Fig. 9J, K). Monolete microspores are known in several species of *Pleuromeia* (Helby & Martin, 1965; Retallack, 1975), while other species retain trilete spores, and in still others spore morphology cannot be determined because degraded trilete spores may appear monolete (*P. rossica*; Neuburg, 1960, 1961). Sunken sporangia are common by the Mesozoic and occur in most of the *Pleuromeia*-type plants (Fig. 10E). Among fossil representatives, ligules with glossopodia are known exclusively in the permineralized Triassic *Takhtajanodoxa* (Fig. 10A; Snigirevskaya, 1980a, b). The presence of such structures has not been detected in compression taxa. Whether the absence of a velum among fossil isoetalean lycopsids is due to a lack of suitable preservation or because this structure evolved relatively recently cannot be determined at present.

It is interesting that the most obvious features

TABLE 5. Trends in the Mesozoic and Cenozoic Isoetales.

1. Reduction in axial elongation of the stem.
2. Reduction in amount of lateral growth.
3. Sporangia become increasingly sunken into sporophyll (*Pleuromeia* sporangia mistakenly thought to be abaxial).
4. Elaboration of ligular structure (glossopodium in *Takhtajanodoxa* and *Isoetes*).
5. Shift in microspore tetrad geometry resulting in change from trilete to monolete spores.
6. Decrease in number of vegetative leaves (most leaves of Isoetaceae are sporophylls).

in the stratigraphically youngest isoetaleans, the lack of axial elongation and vegetative leaves, have usually been considered as reductions, especially in reference to the traditional lycopsid reduction sequence (Fig. 1; Potonié, 1894; Mägdefrau, 1931; Stewart, 1947). In light of ontogenetic and evolutionary considerations, however, the process by which these "reductions" came into being may be more accurately considered a heterochronic process (Gould, 1977; Rothwell, 1987; DiMichele et al., 1989). Plants with the modern *Isoetes* growth habit effectively telescoped their life history by foregoing vegetative growth, stem elongation, and the production of vegetative leaves, and having an earlier onset of the reproductive phase of the life cycle. This life history was probably tied tightly to their frequently aquatic to marginal aquatic habitats and heterosporous reproduction (DiMichele et al., 1989). It would be interesting to consider further the environmental constraints that may have selected for this abbreviated vegetative sporophyte. One possibility might be the modification of the environment through competitive effects of other Mesozoic, and later, Cenozoic aquatic plants. Today, many species of *Isoetes* occur in disturbed habitats as pioneer species. Generally they compete poorly with aquatic angiosperms (W. Carl Taylor, pers. comm.). Isoetaleans may have been "driven" into restricted niche space by other plants.

Considered as a whole, isoetalean plants, whether Paleozoic, Mesozoic, or Cenozoic, have occupied a variety of ecologically similar types of environments. The Paleozoic Chaloneriaceae forms bearing characteristic spore types *Endosporites* and *Valvisisporites* are known from both freshwater, clastic wetland, and peat-accumulating swamps (in deltaic lobes; Chaloner, 1958; DiMichele et al., 1979; Pigg & Rothwell, 1983a, b). The abundance of *Endosporites* and *Valvisisporites* spores in the basal zones of a coal and in thin bony coals (the "*Polysporia* marshlands" of Phillips & Peppers, 1984) may imply that at least in some cases, *Chaloneria* was acting as a pioneer species in the Pennsylvanian (Debra A. Willard, pers. comm.). In the Mesozoic, pleuromeian forms often grew in monotypic stands in environments interpreted as coastal margins (Retallack, 1975) and are frequently found in association with marine fossils (e.g., Kon'no, 1973; Retallack, 1975). Smaller, Triassic and Jurassic *Isoetes*-like fossils are also reported as monotypic deposits of matted leaves or isolated sporophylls (Ash & Pigg, 1991; Wang, 1991). Cenozoic isoetaleans occur in low diversity floras in aquatic, or fluvial, types of sedimentation. It may be that isoetaleans have acted as "pioneer species" in various habitats throughout their history (Debra A. Willard, pers. comm.).

ISOETALEAN LYCOPSIDS AND THE RHIZOMORPHIC CLADE

Isoetalean lycopsids can now be recognized as a long-ranging group that extends from the Paleozoic (Fig. 9, Tables 1–4). They were present possibly by the Devonian or Mississippian, but certainly well established by the Pennsylvanian, as demonstrated by the Chaloneriaceae (Pigg & Rothwell, 1983a, b). The group persisted into the Mesozoic, where some forms became reduced in size and complexity like modern *Isoetes*. Other forms with axially elongate stems persisted until at least the Lower Cretaceous. Some authors (e.g., Wang, 1991) have recently questioned the relationships of pleuromeians and *Isoetes* forms, since monopodial pleuromeians and plants with a modern *Isoetes* aspect are both well known in the Triassic. Although clearly an ancestor/descendant relationship does not exist between contemporaneously living Triassic plants, separate phylogenetic origins for plants displaying these two types of habit need not be invoked. In my opinion, the morphologically similar characters of pleuromeian and Triassic *Isoetes/Isoetites* forms outweigh differences in growth habit, and, until more distinct differences can be delimited, they remain part of a single, variable, plexus.

Recent research suggests that we can no longer look at the isoetaleans as a distinct lineage, but rather as a part of a more complex group of heterosporous lycopsids, perhaps a rhizomorphic clade (Rothwell & Erwin, 1985). This plexus shares many similarities of vegetative details including stelar and cortical anatomy, the production of stigmarian rootlets, secondarily derived bipolar growth, and heterosporous reproductive structures. Further investigation in the following areas would greatly strengthen our understanding of the phylogeny of this group: (1) new information about reproductive structures and anatomy of late Devonian–Mississippian ancestral and/or early members of the isoetaleans; (2) understanding of the relationship of isoetalean and arborescent lepidodendrid radiations; (3) reexamination of the worldwide diversity of Mesozoic pleuromeian and *Isoetes* forms; (4) correlation of the ecology of extant *Isoetes* with the implied ecology and life history of fossil forms; and (5) formal phylogenetic analyses to test the strength of this proposed monophyletic group and its relationship to the rest of the Lycopsida.

The lycopsid reduction series has been a deeply entrenched concept in vascular plant evolution. However, with the removal of the constraints of thinking of rhizomorphic lycopsids as a linear transformation series, there is more room to consider this group as a plexus of related forms whose morphology reflects not only phylogeny, but also ecological constraints. Extant *Isoetes* clearly represents not a single homogeneous end product of a linear sequence, but the remnant of a morphologically variable mosaic that persisted in marginal aquatic environments since the Paleozoic.

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HABITAT, EVOLUTION, AND SPECIATION IN *ISOETES*[1,2]

W. Carl Taylor[3] *and R. James Hickey*[4]

ABSTRACT

Species of *Isoetes* are notorious for the difficulties they present in identification. These difficulties are attributable to a series of habitat adaptations that have resulted in morphological simplicity, homoplasy, and reticulate evolution. Internal air chambers in the leaves of all taxa indicate that primitive *Isoetes* was aquatic. During the breakup of Gondwana, ancestors of modern taxa appear to have passed through a terrestrialization phase, which was accompanied by development of several morphological novelties and reductions including the evolution of sclerotic phyllopodia. This adaptation appears to have evolved after separation of the Indian subcontinent. A new section of the subgenus *Isoetes* centered in India and possessing non-sclerified, persistent leaf bases is described. Following a terrestrialization phase, several lineages became secondarily aquatic and, in some instances, once again evolved a terrestrial habitat. As a result, the genus now occupies a variety of niches, from wholly aquatic to wholly terrestrial. Most terrestrial species, found as isolated populations of basic diploids, appear to be the result of gradual speciation via isolation and genetic divergence. Some aquatic species, often found in mixed populations containing taxa of different ploides, appear to have evolved abruptly via interspecific hybridization and chromosome doubling. Evidence from distribution patterns, megaspore morphology and viability, chromosome numbers, and electrophoretic profiles of leaf enzymes supports a hypothesis of allopolyploid speciation.

Isoetes L. is a cosmopolitan genus of heterosporous lycopsids comprising approximately 150 species. The generic limits of *Isoetes* are sharp, and while there is no difficulty in recognizing a plant as a member of the genus, there are difficulties with the identification of species and species relationships within it. Our studies indicate that these difficulties are attributable to (1) simplicity of form, (2) morphological convergence, and (3) allopolyploidy. Simplicity of form confounds species identification. Plants of *Isoetes*, often resembling tufts of grass, reveal few characters that can be used to distinguish species. Morphological convergence hinders phylogenetic reconstruction and obscures evolutionary relationships among species. Allopolyploidy results in a subtle mosaic of character state distributions, thus limiting our perception of both species and species relationships.

As a result of these difficulties, taxonomists of *Isoetes* traditionally have employed a simplistic approach to classification and phylogeny. Often single characters have been used as the primary basis for understanding the genus. Because students of *Isoetes* have had different points of view, their classification systems and species alliances have varied widely. For example, Pfeiffer (1922) revolutionized *Isoetes* taxonomy by proposing a classification system based primarily on megaspore morphology. Her scheme replaced the earlier systems of Baker (1880) and Motelay & Vendryès (1882), which were based on habitat preference and concomitant morphological adaptations. Pfeiffer (1922) pointed out that many species are highly variable in their habitat preference. Furthermore, she argued that there is often little correlation between morphology (e.g., presence or absence of stomata and fibrous bundles in leaves) and habitat. Since many early collections of *Isoetes* lacked adequate habitat data, species were often assigned to these habitat sections based solely on their morphology, a situation that led to an artificial suite of relationships. Although Pfeiffer's system improved upon earlier classification schemes, it is still fraught with problems such as convergence, reduction, and polymorphisms (Hickey, 1986a).

The replacement of earlier classification systems based on habitat preference by Pfeiffer's classification based on spore morphology resulted in de-emphasizing habitat preference as a feature of taxonomic value. Today, not only is habitat preference again recognized as a valuable diagnostic character, but there is also considerable evidence indi-

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cating habitat preference has played a major role in the evolution of *Isoetes* at two levels: major phylogenetic change and recent speciation. In the first part of this paper we will show that habitat shifts have been responsible for a number of major morphogenetic changes. Many of these changes are quite ancient and the current geographic distribution of the various morphological states can best be understood using a vicariance model. In addition to these morphological changes, numerous reversions to the ancestral, aquatic habitat have resulted in homoplasy. The second part of this paper outlines the relationships between a species habitat preference and its gregariousness in nature, which in turn dictates the dominant mode of speciation, either divergence or allopolyploidy.

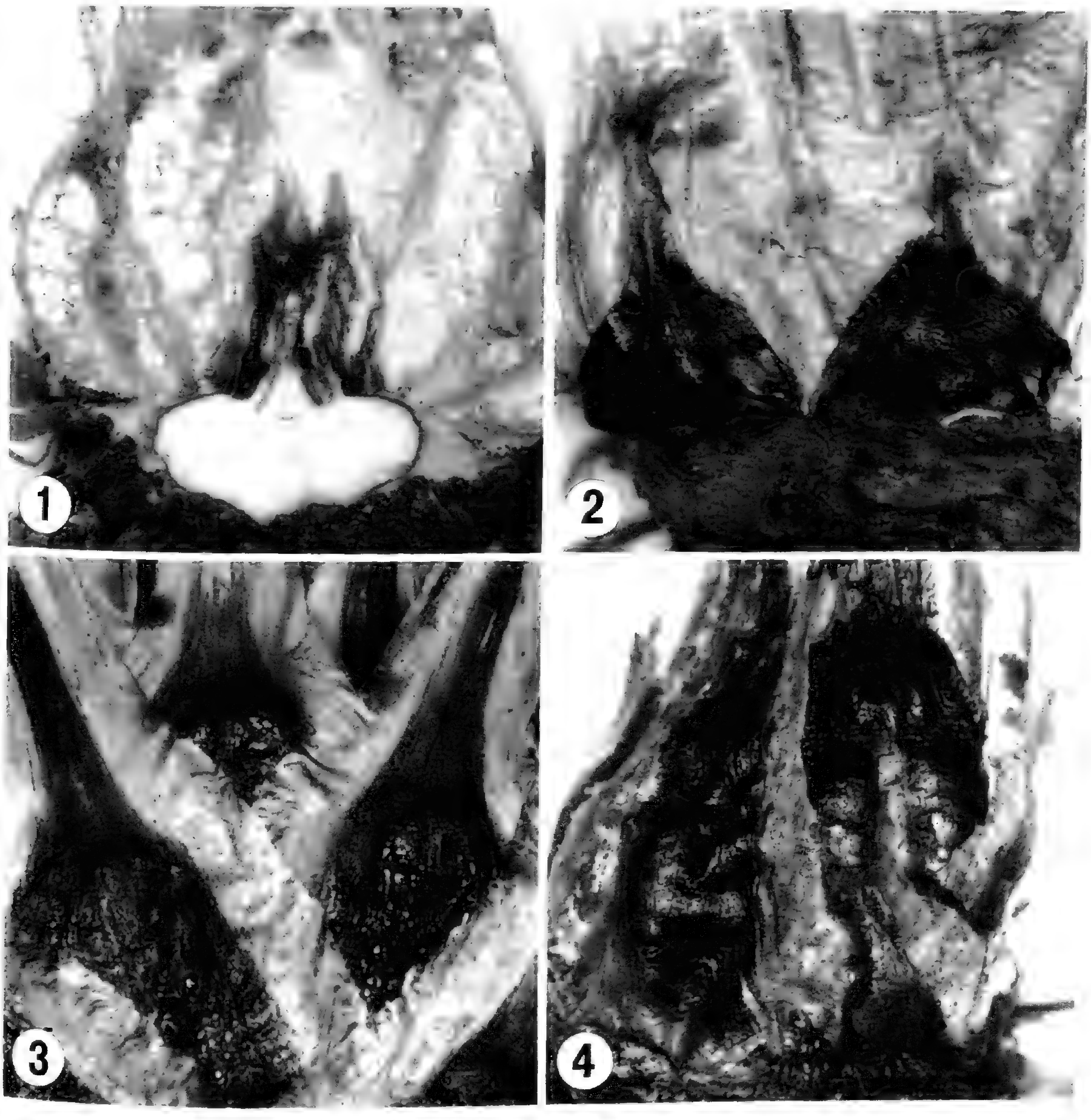
MAJOR PHYLOGENETIC CHANGE

The Isoetaceae (sensu Reed, 1953) can be characterized by the following synapomorphies: foliar embedded sporangia, labia, vela, indehiscent sporangia, trabeculae, multiflagellate sperm, lacunate leaves, and reduced axial growth. Based on these synapomorphies, the family represents a monophyletic assemblage that can be construed as primitively aquatic (Hickey, 1986b). Evidence supporting this contention comes from the presence of air chambers in the leaves of extant taxa and the fossil genus *Isoetites*. Such air chambers are generally regarded as providing buoyancy and an aeration mechanism for aquatic plants (Keeley, 1982). Certainly, the occurrence of air chambers in the leaves of all extant terrestrial *Isoetes* indicates that these plants had aquatic ancestors.

Isoetes includes species with alate leaves that are fully laminate and species with nonalate leaves that are nearly without blades. Alate leaves are universal in the Lepidodendrales, Lycopodiaceae, and Selaginellaceae, which are all close outgroups of the Isoetaceae. Therefore, alate leaves are inferred to be plesiomorphic in *Isoetes*. *Isoetites* may have arisen during the generally wetter conditions associated with the late Carboniferous and early Triassic. Species of *Isoetites* were alate. While the cosmopolitan distribution of this genus through the lower Tertiary suggests that it was rather successful, only three alate species have survived into modern times: *Isoetes baculata*, *I. gigantea*, and *I. bradei*. Of these, the latter two are probably now extinct. Together these three alate species of *Isoetes* and *Isoetites* represent *Isoetes* subgenus *Euphyllum* (Hickey, 1990). The other and far larger part of the genus, subgenus *Isoetes*, is characterized by a distal, three-dimensional subula and by alae that are restricted to the proximal portion of the leaf. In addition, many species of subgenus *Isoetes* have leaves with supporting fibrous bundles in the leaf. Such bundles are not found in species of subg. *Euphyllum*. Both the subulate condition and the presence of peripheral fibrous bundles are potentially adaptive because they provide stability and mechanical support for leaves in habitats that are ephemerally aquatic or terrestrial (Hickey, 1986b). Radiation from aquatic habitats may have occurred in response to the generally warmer and drier environmental conditions since the Cretaceous. Nearly all extant species of *Isoetes* have retained this essentially terrestrial habit, although some have again reverted to an aquatic habitat.

The development of a terrestrial habit resulted in an early morphological and systematic radiation, which apparently occurred subsequent to the fragmentation of Pangea. The transition from homogeneous, stable, aquatic environments to seasonally dry, terrestrial habitats resulted in additional problems for *Isoetes*, in particular that of desiccation during arid periods. Species of *Isoetes* have adapted to this situation in two ways, both of which involve protecting the apical meristem during drought conditions. In one group of species, unmodified leaf bases are retained throughout the dry season and form a scarious protective layer about the apex of the corm. Such modifications in *Isoetes* appear to be uniquely derived and thus represent a synapomorphy for the associated species. In general, this clade is restricted to the Indian subcontinent (Hickey, 1986b).

The second manner of protecting the corm apex during drought involves the sclerification of leaf tissue. In some species, leaf primordia become sclerified and their growth is arrested. This results in scales similar to those found on branches of temperate deciduous angiosperms. *Isoetes nuttallii*, of western North America, produces such scales (Figs. 1, 2). In other species, portions of the leaf bases become sclerotic and remain after the nonsclerotic portions of the leaves have eroded. This produces a distinctive ring of sclerotic phyllopodia covering the apex. Such phyllopodia are most extensively developed in certain European and African species, but sclerotic phyllopodia are found also in the North American species *I. howellii* and *I. melanopoda* (Figs. 3, 4). The geographic and evolutionary relationships of the species involved strongly suggest that scales and phyllopodia represent two independently derived states for resistance to desiccation. Furthermore, the absence of species with sclerified scales and phyllopodia on the Indian subcontinent suggests that these synapomorphies originated in Gondwana after separation of the Indian subcontinent.



FIGURES 1–4. Scales and phyllopodia in *Isoetes*.—1. Transection through corm and leaf bases of *I. nuttallii*. Scales surround corm apex during summer dormancy.—2. Leaf bases of *I. nuttallii* surrounded by scales. Near end of growing season, scales have been displaced to peripheral position by current season's growth.—3. Sclerified leaf bases of *I. howellii* near end of growing season.—4. Phyllopodia (remnants of sclerified leaves) surround corm apex during summer dormancy.

This group of nonsclerotic species, defined by scarious, persistent leaf bases, is centered in India and represents a distinctive element within subgenus *Isoetes*:

Isoetes sect. **Coromandelina** Hickey & Taylor, sect. nov.
TYPE: *I. coromandelina* L.f., Suppl. Pl. 447. 1781.

Species foliorum basibus scariosis, persistentibus.

The remaining species of subgenus *Isoetes* comprise section *Isoetes*, which is here redefined as those subulate taxa that have, or were presumably derived from taxa that had, the ability to produce sclerotic pigmentation in leaf primordia, leaf bases, or sporangial tissue. As so defined, section *Isoetes* contains most of the extant species of the genus. It is an extremely diverse assemblage including both terrestrial and aquatic species, which are found throughout Africa, Australia, Europe, Asia, and the New World. By comparing the morphology of these species with that found in subgenus *Euphyllum* and section *Coromandelina* of subgenus *Isoetes*, we can polarize several included characters (Watrous & Wheeler, 1981). Notable among these are velum and labium development. Analyses in-

TABLE 1. Polyploid series for North American aquatic species of *Isoetes*.

Species	Chromosome number (2*n*)
I. lacustris	110
I. occidentalis	66
I. maritima, I. riparia, I. tuckermanii	44
I. bolanderi, I. echinospora, I. engelmannii, I. prototypus	22

dicate that the absence of a velum and the presence of a large, well-developed labium are plesiomorphic conditions (Hickey, 1985). In addition, the generalized condition of tuberculate (sensu Pfeiffer, 1922) megaspores is likewise plesiomorphic. When section *Isoetes* is analyzed for these character state distributions, two facts are immediately evident. First, species retaining all plesiomorphic conditions are terrestrial or amphibious; and second, nearly all aquatic species have derived or intermediate states for these characters, regardless of their geographic location. These data strongly suggest that the aquatic condition seen in most temperate and high-altitude tropical species is a secondarily derived condition that has evolved independently in unrelated lineages (Hickey, 1985).

The more plesiomorphic taxa of section *Isoetes* show a distinctly southern or Gondwana distribution, most evident in Africa and South America, whereas derived members of the section are generally Laurasian, but with close affinities to species of proximate Gondwana landmasses. These observations, coupled with data on section *Coromandelina*, suggest that subgenus *Isoetes* had its origin within Gondwana and subsequently radiated northward into Laurasia. Such hypotheses are strongly corroborated by the distribution of other character states, including the persistence of leaves during cold and drought periods, megaspore surface morphology, and electrophoretic anomalies such as the migrational location of TPI-2 (triosephosphate isomerase-2) and the presence or absence of anomalous TPI-3 activity (Hickey et al., 1989a).

RECENT SPECIATION

In North America, species of *Isoetes* vary in habit from ephemeral terrestrials to evergreen aquatics. Terrestrial *Isoetes* are found in seasonally wet soils where, in general, plants are active in spring when the soil is saturated with water and dormant in summer when the soil is dry. In the southern United States, terrestrial species may be found as isolated populations in soil pockets on sandstone, limestone, or granite. *Isoetes melanopoda* is widespread in the central and eastern United States where it is found in meadows, fields, and soil pockets on sandstone outcrops. *Isoetes butleri* occurs in the south-central and southeastern United States in calcareous soils over limestone. *Isoetes piedmontana* grows in soil pockets on granite outcrops in the southeastern United States. *Isoetes melanospora* inhabits shallow pools on isolated granite domes and flatrocks in the Piedmont of Georgia and South Carolina. *Isoetes tegetiformans* occurs in pools on porphyritic granite flatrocks in the Piedmont of Georgia (Rury, 1985). *Isoetes lithophila* is found in temporary pools on granite domes in central Texas. In the western United States, *I. howellii* and *I. nuttallii* inhabit seasonally wet meadows, lake margins, and vernal pools and streams. All of these terrestrial species have the lowest diploid chromosome number found in the genus ($2n = 2x = 22$). These basic diploids appear to represent examples of gradual speciation due to spatial isolation of ancestral populations followed by genetic divergence.

Aquatic *Isoetes* occur mostly in glacially formed lakes, ponds, and streams. In contrast to the terrestrial species, which occur mainly as isolated populations, two or more aquatic species frequently grow together. For example, in the northeast, *I. echinospora, I. engelmannii, I. riparia, I. tuckermanii*, and *I. lacustris* may all grow in the same body of water. Likewise, in the northwest, *I. echinospora, I. bolanderi, I. maritima*, and *I. occidentalis* could occur in the same lake. Such assemblages, which might have resulted as divergent species of *Isoetes*, were brought together by foraging water fowl, which carried spores into bodies of water left by retreating glaciers. Because gametes of different species can readily mingle in these aquatic habitats, the potential exists for interspecific hybridization. The existence of a polyploid series among the aquatic taxa (Table 1) implies that some species could be allopolyploids, which have evolved through interspecific hybridization and chromosome doubling. In addition to cohabitation and chromosome numbers, further evidence for hybridization and allopolyploidy come from spore morphology and viability, *in vitro* hybridizations, and electrophoretic profiles of leaf enzymes. How these sources of evidence support an allopolyploid mode of evolution in aquatic *Isoetes* are shown by two examples, the evolution of *I. riparia* in eastern North America and the evolution of *I. brochonii* in western Europe.

THE EVOLUTION OF *ISOETES RIPARIA* IN EASTERN NORTH AMERICA

In the early summer of 1895, A. A. Eaton discovered unusual plants of *Isoetes* growing along the Powwow River in southeastern New Hampshire. Dodge (1897) described these unusual plants as a new species, *I. eatonii.* Dodge noted his new species to be "peculiar" in several ways. First, he mentioned that *I. eatonii* "seldom is found growing very near another of its species" and that plants "are from a foot to ten feet apart." By contrast, he noted the associated species *I. echinospora, I. engelmannii,* and *I. riparia* grow "for the most part gregariously." Dodge also reported his new species to be exceptionally vigorous. He mentioned vernal leaves attaining a length of 28 inches and the plants producing from 50 to nearly 200 leaves. Further, Dodge noticed the "straightness" of the radial ridges on the proximal side of the megaspore and "the low angle they form with the equatorial plane." Such a configuration imparts a proximally flattened, nearly lenticular form to the megaspore. Species of *Isoetes* typically have curvilinear radial ridges conforming to a rounded proximal hemisphere and a globose megaspore.

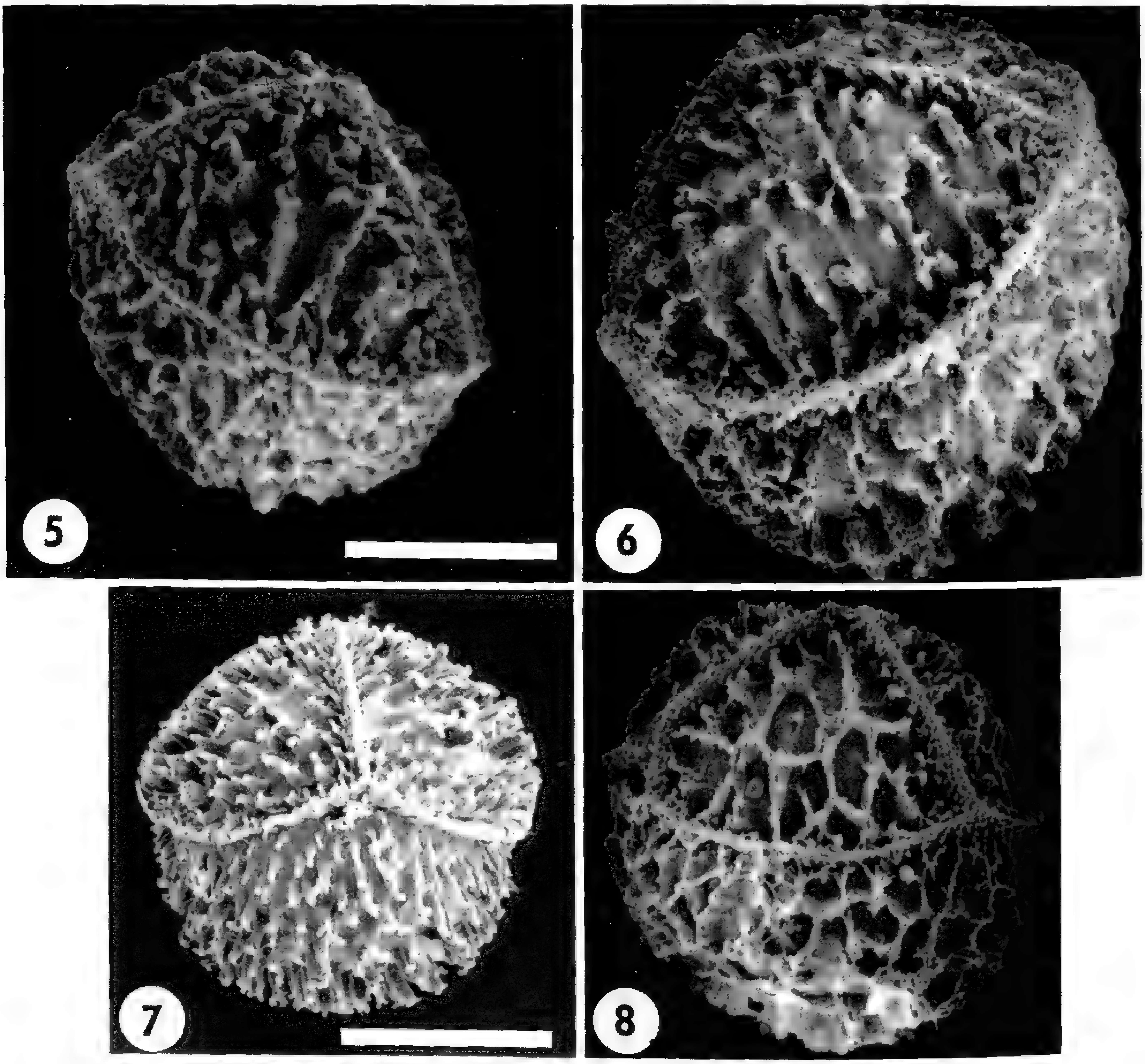
Taylor et al. (1985) reported that the megaspores of *I. echinospora, I. engelmannii,* and *I. riparia* readily germinated and formed megagametophytes in culture, but megaspores of *I. eatonii* did not germinate. They also showed that *I. eatonii* had been found almost entirely within the overlapping ranges of *I. echinospora* and *I. engelmannii* and that hybrids between these two species are readily produced in culture. They concluded that *I. eatonii* ($2n = 2x = 22$) represented a sterile, basic diploid hybrid between the basic diploids *I. echinospora* and *I. engelmannii* (both $2n = 2x = 22$).

Although the megaspores of *I. eatonii* are described most often as small and flattened, with a labyrinthiform-convolute (brain coral) surface texture, larger, globose megaspores are produced occasionally (Fig. 5). The cristate surface texture of the larger, globose megaspore of *I. eatonii* appears intermediate between the echinate megaspore of *I. echinospora* (Fig. 7) and the reticulate spore of *I. engelmannii* (Fig. 8). Furthermore, the larger, cristate megaspore of *I. eatonii* resembles the even larger, globose megaspore of *I. riparia* (Fig. 6), a fertile tetraploid ($2n = 4x = 44$) occurring in northeastern North America, throughout the range of *I. eatonii.* If *I. eatonii* is the sterile, diploid hybrid between *I. echinospora* and *I. engelmannii,* could *I. riparia* be its fertile, allotetraploid derivative?

Electrophoretic profiles of triosephosphate isomerase (TPI) from *Isoetes* leaves help to answer this question. Leaves of *I. echinospora, I. engelmannii, I. eatonii,* and *I. riparia* were crushed and ground in Tris-HCl buffer-PVP solution. The resulting mixtures were absorbed onto filter paper wicks and subjected to horizontal starch gel electrophoresis. Electrophoretic procedure, composition of grinding, gel, and electrode buffers, and staining method follow Soltis et al. (1983). Electrophoresis was conducted using electrode and gel buffer system 7 in a 12% starch gel at 4°C with a constant current of 35 mamp for 8.5 hr. Wicks were removed from the gel after 15 min. The gel was sliced, incubated in substrate at 37°C for 1 hr. in the dark, rinsed in distilled water, and photographed.

Electrophoretic profiles of *I. echinospora, I. engelmannii, I. eatonii,* and *I. riparia* support the hypothesis that *I. eatonii* is a sterile hybrid between *I. echinospora* and *I. engelmannii* and that *I. riparia* could be an allotetraploid derivative of *I. eatonii.* In Figure 9, TPI, a dimeric enzyme, requiring the combination of two subunits to form an active enzyme, is expressed by two loci, TPI-1 and TPI-2. TPI-1 appears single-banded, and invariant for the taxa sampled. TPI-2, composed of subunits designated "a" and "b," shows variability that distinguishes *I. echinospora* and *I. engelmannii* and relates *I. eatonii* to *I. riparia. Isoetes echinospora* expresses the band "aa," whereas *I. engelmannii* expresses the band "bb." *Isoetes eatonii* and *I. riparia* express bands "aa" and "bb" in addition to the heterodimeric band "ab," which is not present in either parent. The profiles of TPI-2 for *I. eatonii* and *I. riparia* are similar and additive for *I. echinospora* and *I. engelmannii.* Lighter bands cathodal to bands "aa" and "ab" may represent subbands. A subband is formed when an additional, charged component attaches to an enzyme thereby changing its charge, possibly its size and shape, and thus its migration (Buth, 1990). Subbanding for "bb" is not evident in Figure 9.

Evidence from distribution patterns, spore morphology and viability, *in vitro* hybridizations, and electrophoretic profiles of leaf enzymes supports the hypothesis that *I. echinospora* has crossed with *I. engelmannii* to form the sterile hybrid *I. eatonii,*



FIGURES 5–8. Scanning electron micrographs of *Isoetes* megaspores.—5. *I.* × *eatonii.*—6. *I. riparia.*—7. *I. echinospora.*—8. *I. engelmannii.* Scale bar = 0.25 mm.

which then doubled its chromosome number to form the fertile allotetraploid *I. riparia.*

THE EVOLUTION OF *ISOETES BROCHONII* IN WESTERN EUROPE

In October 1983, a mass collection of *I. echinospora* and *I. lacustris* was made from Neva Lake in northern Wisconsin to obtain spores for germination and hybridization experiments. Neva Lake is a small, glacially formed, soft-water lake with a sand, gravel, and muck bottom. Examination of plants from this collection revealed several individuals bearing megaspores that were far more variable in size, shape, and surface texture than typical megaspores of *I. echinospora* or *I. lacustris.*

Isoetes echinospora and *I. lacustris* grow together in many lakes in northeastern North America and Europe. Although they can look alike vegetatively, these two species are readily distinguishable by their spores, which differ in size and surface texture. *Isoetes echinospora* produces echinate megaspores about 400–500 μm in diameter, whereas *I. lacustris* bears cristate megaspores mostly 600–800 μm in diameter. Scanning electron photomicrographs show that megaspores from the unusual Neva Lake plants bear a spine and ridge texture that seems to combine the patterns of *I. echinospora* and *I. lacustris* (Fig. 10).

Megaspores from these plants are not viable. Using the procedure described by Taylor & Luebke (1986) for germinating spores of aquatic *Isoetes, I. echinospora* and *I. lacustris* megaspores germinated and formed megagametophytes in culture, but megaspores from the unusual Neva Lake plants did not germinate.

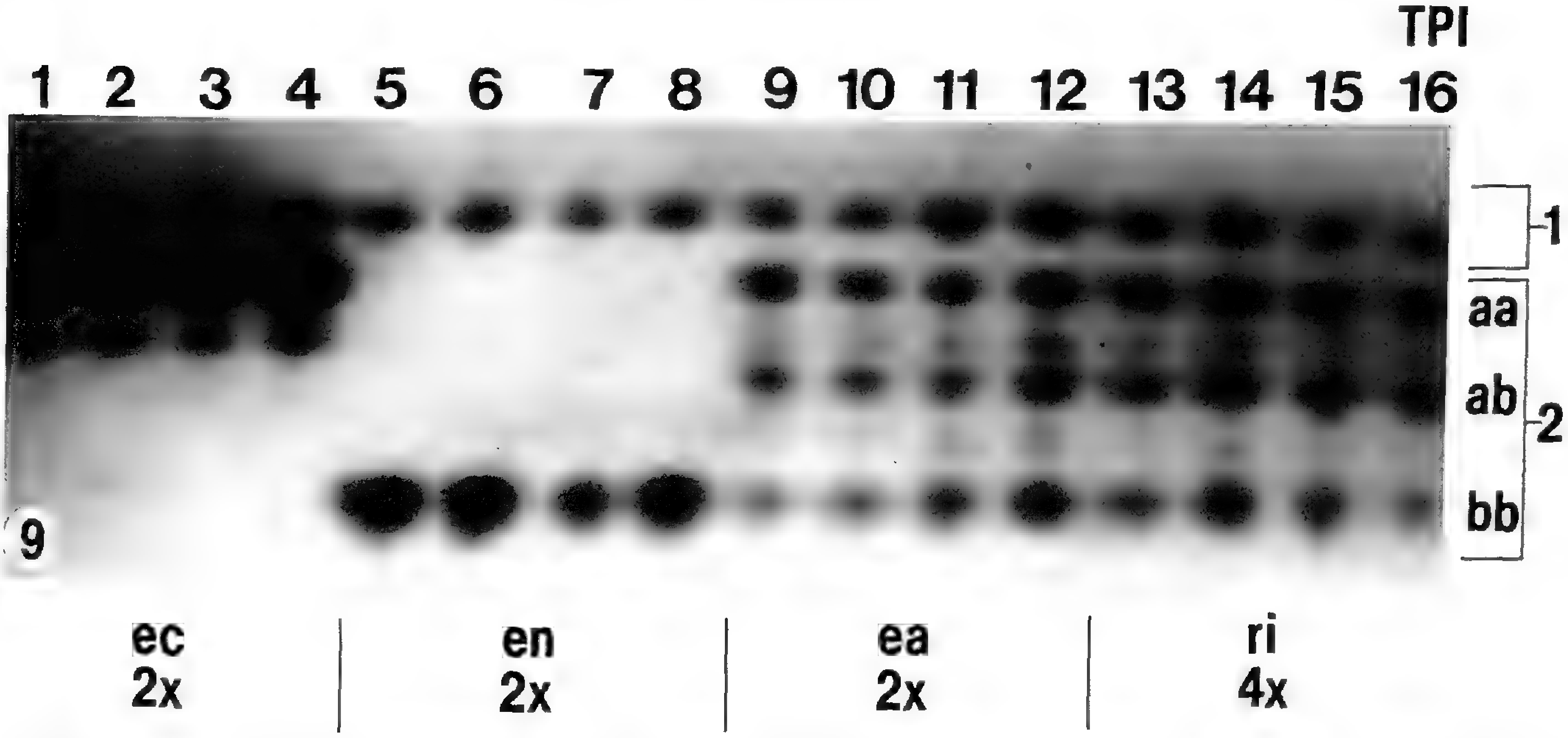
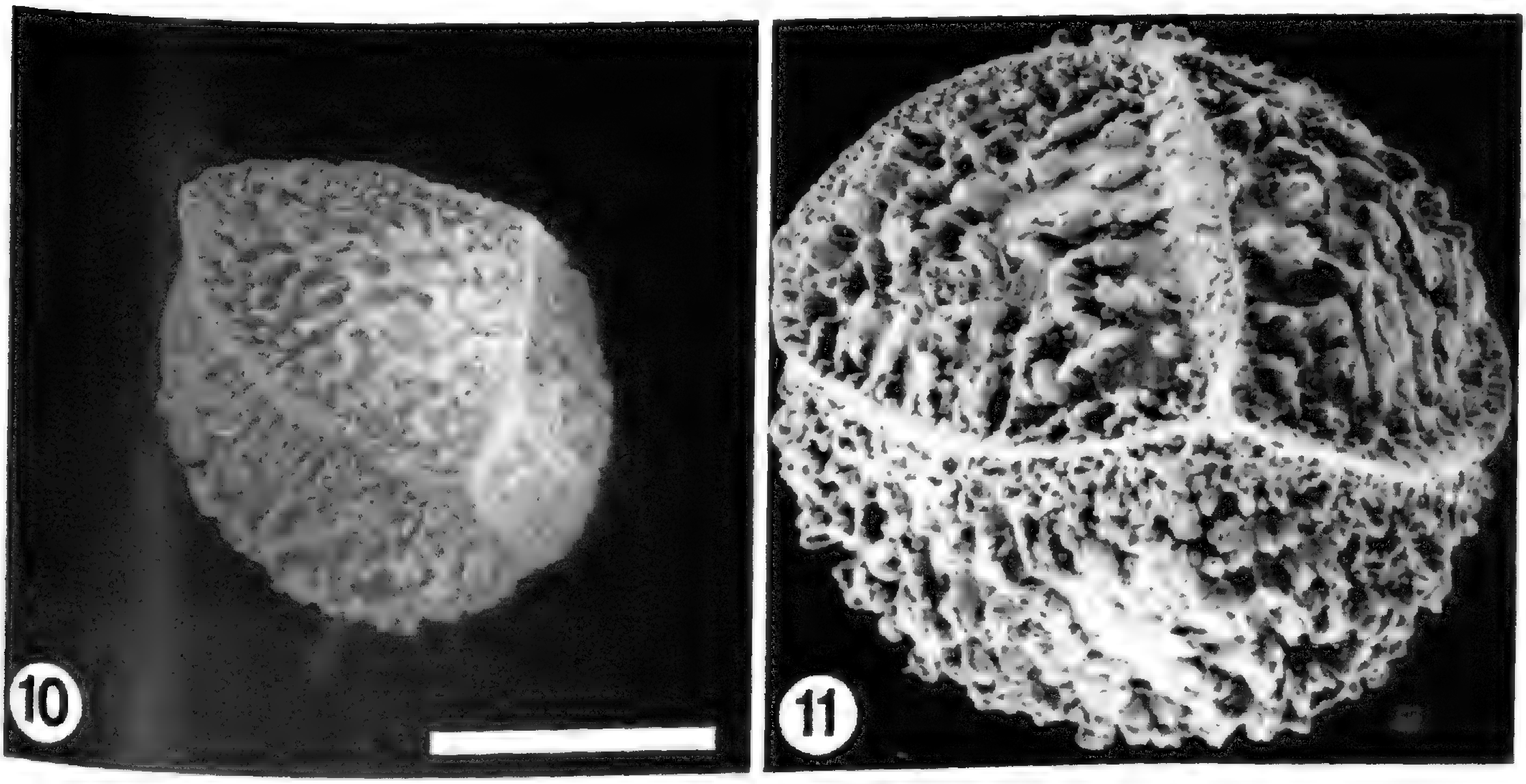


FIGURE 9. TPI (Triosephosphate isomerase) zymogram of *Isoetes* leaves.—Lanes 1–4. ec = *I. echinospora*.—Lanes 5–8. en = *I. engelmannii*.—Lanes 9–12. ea = *I.* × *eatonii*.—Lanes 13–16. ri = *I. riparia*. $x = 11$, chromosome base number for *Isoetes*.

A hybrid between the basic diploid ($2n = 2x = 22$), *I. echinospora*, and the decaploid ($2n = 10x = 110$), *I. lacustris*, should have a chromosome number of $2n = 6x = 66$, the sum of 11 chromosomes from a haploid gamete of *I. echinospora* and 55 chromosomes from a haploid gamete of *I. lacustris*. Root tip squashes of the unusual Neva Lake plants show cells containing the predicted 66 chromosomes for a hybrid between a diploid and a decaploid (Taylor & Luebke, 1988).

Based on megaspore morphology, production of nonviable megaspores, and chromosome number, it appears that these unusual Neva Lake plants are sterile, interspecific hybrids between *I. echinospora* and *I. lacustris*. This hybrid has been named *I.* × *hickeyi* (Taylor & Luebke, 1988).

Isoetes brochonii, a poorly known taxon, has been collected from several lakes in the Pyrenees of France where it grows with *I. echinospora* and *I. lacustris*. Since its description by M. L. Motelay (1892), the taxonomic status of *I. brochonii* has been debated, and it has been treated as a distinct



FIGURES 10, 11. Scanning electron micrographs of *Isoetes* megaspores.—10. *I.* × *hickeyi*.—11. *I. brochonii*. Scale bar = 0.25 mm.

species or it has been variously allied to either *I. echinospora* or *I. lacustris* (Prelli & Bock, 1989).

In August 1987, *I. brochonii* was collected from Lac Vivé, just west of Lac Bouillouses in the western Pyrenees of France. Specimens from this collection were cultured to provide root tips for chromosome counts and leaves for enzyme electrophoresis. Of initial interest in this collection was the surface texture of *I. brochonii* megaspores (Fig. 11). Although they were globose, and uniform in shape, size, and surface texture, these megaspores had a surface texture like many of the megaspores of *I.* × *hickeyi* from Neva Lake, Wisconsin. Chromosome counts from root tip squashes revealed *I. brochonii* to be dodecaploid ($2n = 12x = 132$), double the chromosome number of *I.* × *hickeyi.* If *I.* × *hickeyi* is the sterile, hexaploid hybrid between *I. echinospora* and *I. lacustris,* could *I. brochonii* be the fertile, allododecaploid derivative?

Electrophoretic profiles of malate dehydrogenase (MDH) from *Isoetes* leaves help to answer this question. Leaves of *I. echinospora, I.* × *hickeyi, I. brochonii,* and *I. lacustris* were crushed and ground in phosphate-PVP buffer solution. The resulting mixtures were absorbed onto filter paper wicks and subjected to horizontal starch gel electrophoresis. Electrophoretic procedure and composition of grinding buffer and staining method follow Soltis et al. (1983). Electrophoresis was conducted using an electrode and gel buffer system by Clayton & Tretiak (1972) adjusted to pH 6.0 with N-3 (3-aminopropyl)-morpholine in a 12% starch gel at 4°C at a constant current of 40 mamp for 6 hr. Wicks were removed from the gel after 30 min. The gel was sliced, incubated in substrate at 37°C for 30 min. in the dark, rinsed in distilled water, and photographed.

Electrophoretic profiles of *I. echinospora, I.* × *hickeyi, I. brochonii,* and *I. lacustris* support the hypothesis that *I.* × *hickeyi* is a sterile hybrid between *I. echinospora* and *I. lacustris* and that *I. brochonii* could be an allododecaploid derivative of *I.* × *hickeyi.* In Figure 12, MDH profiles of *I.* × *hickeyi* and *I. brochonii* appear similar and additive for their suspected parents *I. echinospora* and *I. lacustris,* but it is impossible to precisely interpret the MDH band patterns until variation in parental species is identified and segregation studies are conducted.

Isoetes × *hickeyi* has recently been collected from Lac Long and Lac Font Vivé in the western Pyrenees of France, within the range of *I. brochonii* (Carmen Prada, pers. comm.). Prada's plants are hexaploid and have the variable spores characteristic of *I.* × *hickeyi.* This is the first report of *I.* × *hickeyi* in Europe, and these collections represent a geographically closer link to *I. brochonii.*

Evidence from distribution patterns, spore morphology and viability, chromosome numbers, and electrophoretic profiles of leaf enzymes supports the hypothesis that *I. brochonii,* like *I. riparia,* is an allopolyploid species formed through interspecific hybridization and chromosome doubling.

In addition to the allopolyploid evolution of *I. riparia* and *I. brochonii* described here, allopolyploid origins for several other polyploid taxa are being disclosed as we learn more about *Isoetes.* With nearly 60 percent of the known species being polyploid, allopolyploidy may be a significant speciation mechanism in this genus.

Thus, species of *Isoetes* appear to have evolved in two ways. First, species have developed gradually by isolation and genetic divergence as taxa adapted to terrestrial and aquatic habitats. Second, species have formed through interspecific hybridization and chromosome doubling as divergent species migrated into the same aquatic habitats. Interspecific hybridization produces plants of more or less intermediate morphology and the inclusion of such hybrids within species descriptions has confused species distinctions. Allopolyploidy fixes this intermediate, hybrid morphology in fertile, polyploid species (Hickey et al., 1989b).

CONCLUSIONS

The role of habitat in explaining the phylogeny of *Isoetes* has only recently been recognized, but there is a growing body of evidence indicating that the major clades of the genus radiated subsequent to environmental shifts. Initially *Isoetes* species were evergreen aquatics with lacunate, laminate, nonsclerified leaves without peripheral fibrous bundles. The evolution of novel character states occurred as members of the genus radiated into terrestrial habitats following the Cretaceous. Peripheral fibrous bundles for support, sclerified leaves and leaf bases for protection, subulae, and ephemeral leaves to reduce water loss were derived as plants adapted to more xeric environments. Subsequently, many of these novel states were lost as plants reverted to aquatic habitats perhaps during wetter periods. These serial environmental shifts resulted in a tremendous amount of parallelism and convergence as characters or character states were gained, lost, or modified.

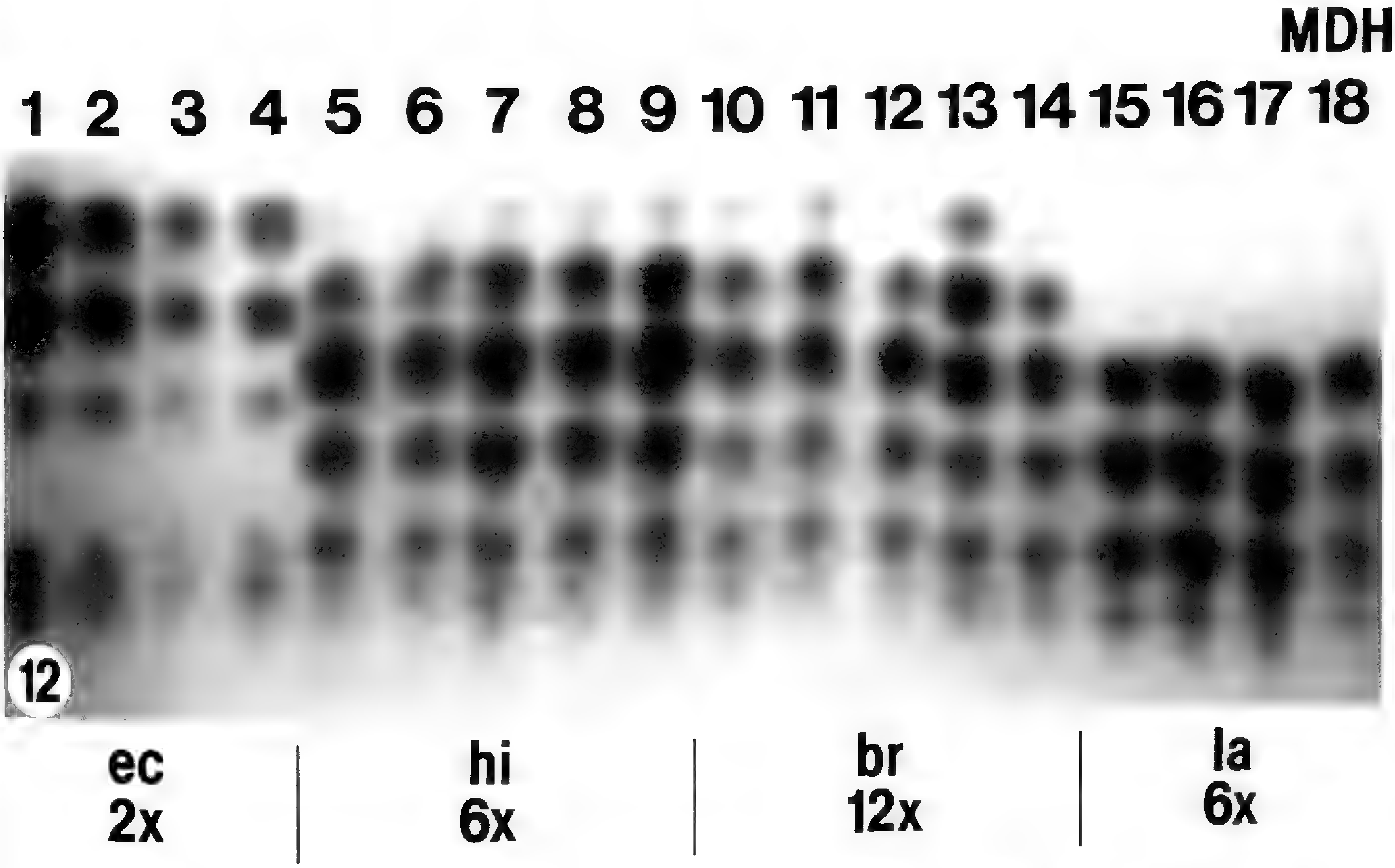


FIGURE 12. MDH (Malate dehydrogenase) zymogram of *Isoetes* leaves.—Lanes 1–4. ec = *I. echinospora.*—Lanes 5–9. hi = *I.* × *hickeyi.*—Lanes 10–14. br = *I. brochonii.*—Lanes 15–18. la = *I. lacustris. x* = 11, chromosome base number for *Isoetes.*

Because of their terrestrial habit these species had little or no long-range dispersal ability during continental movements, and their geography can be explained largely on the basis of vicariant events.

Extant species can be viewed loosely as being either terrestrial or aquatic. The assemblage (nonphylogenetic) of extant aquatic species can be characterized as being highly polyploid, "social" (coexisting with one or more additional taxa), and promiscuous. The terrestrial taxa are quite the opposite. These taxa are generally diploid, often exist in monospecific populations, and rarely hybridize. These differences appear to be tied to the mode and frequency of dispersal events. Ponds and lakes may be good "visual targets" for migrating waterfowl that carry spores of *Isoetes.* This increases the opportunity both for long-distance dispersal and for commingling of species. This sociality of aquatic *Isoetes* species in turn leads to a greater opportunity for hybridization and evolution via subsequent polyploidy. Terrestrial species, by contrast, produce mature spores as or when their habitats, ephemeral ponds or moist glades, are drying out. The habitats of terrestrial species may then be poor "visual targets" for waterfowl, at least during the time of year necessary for dispersal. This would lead to a reduced number of dispersal events and a decrease in sociality of species.

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PALEOZOIC HERBACEOUS LYCOPSIDS AND THE BEGINNINGS OF EXTANT *LYCOPODIUM* SENS. LAT. AND *SELAGINELLA* SENS. LAT.

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ABSTRACT

Devonian and Carboniferous herbaceous Lycopsids are reviewed to illustrate their diverse morphologies. The problem of interpreting small fragments of Lycopsids as either the remains of herbaceous plants, or as terminal portions of much larger plants, is highlighted. Lycopsids resembling the extant genera *Lycopodium* and *Selaginella* are known from the Carboniferous onward. The problems of assigning these herbaceous taxa to extant genera are discussed. The presence of both isophyllous and heterophyllous *Selaginella*-like plants in the Carboniferous supports the idea that the genus should be divided into at least two genera.

Any paleobotanical study, unlike that of extant plants, involves plant remains that are nearly all isolated organs or fragments of the whole plant. Much effort is expended trying to reconstruct whole plants from these remains, often with quite striking and valuable results. People should not, however, become accustomed to looking at plant fossils as though they are all fragments of large plants. This is clearly not the case; herbaceous plants were probably present in large numbers in most of the many diverse floras that have existed from the late Paleozoic onward. They would have formed the ground cover in open habitats or the floor layer of the more closed forest communities. Unfortunately, remains of these herbaceous plants might easily be misidentified as fragments of much larger plants, or just overlooked.

LOWER PALEOZOIC LYCOPSIDS

Herbaceous lycopsid-like plants are known from the Upper Silurian onward. The earliest, *Baragwanathia* Lang & Cookson, 1935, came from Upper Silurian strata of Victoria, Australia (Garratt et al., 1984). It was very similar to *Drepanophycus spinaeformis* Goeppert, 1852, and *Asteroxylon mackiei* Kidston & Lang, 1920, from the Lower Devonian of the present Northern Hemisphere, in having a partly creeping and partly erect habit with lateral branching and spirally arranged microphylls. They must have been very similar to living *Huperzia selago* (L.) Bernh. ex Schrank & Mart., 1829, in size and general morphology and, as far as we know, in stelar anatomy and in being homosporous. The problem, however, is that although these early land plants resembled lycopsids vegetatively, their sporangia were cauline rather than being on the adaxial surfaces of sporophylls. This cauline arrangement is more like that of such plants as *Zosterophyllum* Penhallow, 1892, and *Sawdonia* (Dawson) Hueber, 1971, which are included in the Zosterophyllophytina. One other genus very similar to *Asteroxylon* is the Lower/Middle Devonian *Kaulangiophyton* Gensel, Kasper & Andrews (1969). It was described as having prostrate, dichotomously branching rhizomes and dichotomizing aerial axes with scattered spiny leaves. The ovoid sporangia borne on some of the upright branches terminated well-developed lateral stalks. They were not associated in any regular manner with the sterile spines. Schweitzer (1980), however, concluded that the type species, *K. akantha*, was conspecific with *Drepanophycus devonicus*, so that *Kaulangiophyton* should be regarded as a synonym of *Drepanophycus*.

Various suggestions have been made about the taxonomic relationships of these early lycopsid-like forms. Banks (1968) described them as transitional between the Zosterophyllopsida and the Lycopsida. Bierhorst (1971) argued that they should be placed in a new order, the Asteroxylales, within the class Zosterophyllopsida. Rayner (1984) stressed their dissimilarities even further by suggesting that a new class, the Drepanophycopsida, is needed for

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plants intermediate in organization between the Zosterophyllopsida and the Lycopsida. It may, however, be a little premature to accept this new class because most species of *Drepanophycus* have been included in the genus solely on vegetative characters; the genus could easily represent several unrelated species. Grierson & Banks (1983) implied this by segregating *D. gaspianus* as a new genus, *Haskinsia*.

The recognition of the first undisputed lycopsid is difficult, as only a relatively simple change of sporangial position was needed to derive the first lycopsid from its drepanophycopsid ancestor. The earliest homosporous lycopsids diversified and radiated in many ways, as hybridization was probably easily accomplished through the plants' relatively simple genetic make-up (Banks, 1968). Some forms of plants seem to have continued almost unchanged to the present day. Others evolved into further homosporous herbaceous forms or into heterosporous ones, while some evolved along quite different paths that gave rise to the arborescent Carboniferous lycopsids and eventually to the extant *Isoetes* (Snigirevskaya, 1980; Pigg & Rothwell, 1983; Karrfalt, 1984).

Lycopsids are perhaps the most common plant fossils found in Devonian rocks around the world. This may reflect a greater tolerance of climatic and other ecological conditions, and/or their better potential for fossilization. Nevertheless, this wider distribution is generally taken as evidence for a uniform worldwide flora in mid-Devonian times (Fairon-Demaret, 1974; Gould, 1975; Anderson & Anderson, 1985, Edwards & Benedetto, 1985).

Many of these Devonian and subsequent Carboniferous adpression lycopsids have been described as herbaceous, although they are known only as fragmentary remains of leafy axes or even axes with scars marking the former attachment of leaves. For example, Grierson & Banks (1963, 1983) described *Archaeosigillaria* Kidston, 1901, *Protolepidodendron* Krejci, 1880, *Colpodexylon* Banks, 1944, *Eleutherophyllum* Stur, 1877, *Sugambrophyton* Schmidt, 1954 and *Zimmermannia* Gothan & Zimmermann, 1932, as herbaceous on such evidence.

The recent description of pyritic axes from the Tournaisean of Ireland (Matten, 1989) highlights the similar problem of recognizing herbaceous lycopsids when they are preserved as permineralizations. The specimens, described as a new genus *Wexfordia*, have only primary tissues and a combination of characters intermediate between the Devonian Protolepidodendrales and the Upper Carboniferous Lepidodendrales. However, these features are not reliable enough to prove that the fragments came from a herbaceous plant for, as Matten has indicated, *Wexfordia* might instead represent the distal portions of a larger plant such as *Cyclostigma* or even fragments of a rhizome.

LIGULES AND TAXONOMIC PROBLEMS

In living lycopsids ligules are restricted to heterosporous genera. However, in fossils it is often impossible to determine whether leafy shoots are ligulate or eligulate. One exception is the Lower Carboniferous eligulate leafy shoot *Stansburya petersenii* Tidwell & Jennings (1986). There is a general assumption that fossil lycopsids that are known to be ligulate are also heterosporous and vice versa, even though the homosporous Devonian *Leclercqia* has been shown to be ligulate (Grierson & Bonamo, 1979; Bonamo et al., 1988). This genus has been described from several North American localities (Kasper & Forbes, 1979) and from Australia (Fairon-Demaret, 1974) and was evidently widespread.

Ligulate lycopsids continued to evolve rapidly during the Carboniferous. There were a number of recognizably different forms. The morphologically simplest erect isophyllous axes, with unknown reproductive features, were worldwide during the Lower Carboniferous, but became more restricted during the Upper Carboniferous and Permian. Large numbers eventually survived only in the colder area of what is now Siberia (then Angaraland). Meyen (1976) suggested that they may have escaped competition here from more vigorous plants that were evolving elsewhere. Similar genera have been described from the northern slope of Alaska, which suggests that this area of land was once closer to, or part of, Angaraland (Thomas & Spicer, 1986; Spicer & Thomas, 1987).

Such sterile axes are referred to genera solely on morphological characters related to phyllotaxy, leaf morphology, or to features visible after leaf fall such as the leaf cushion, leaf scar, ligule pit, and infrafoliar bladder (Thomas & Meyen, 1984a). This is a workable system provided that its more important limitations are understood. These are: (1.) The systematic, taxonomic, and evolutionary relationships of fragmentary adpression axes are impossible to assess accurately without details of any reproductive organs. An overly simplistic approach can lead to generalized comparisons and statements that are impossible to prove. For that reason, Thomas & Brack-Hanes (1984) suggested an alternative method of classifying lycopsids where only bisporangiate whole plants or fructifications, megasporangiate fructifications, or isolated megasporangiate organs could be assigned to families. All other organs are then described as satellite taxa assigned either to a family or to an order, as seems most appropriate in each case. (2.) An assumption that placing different species in the same genus implies phylogenetic relationship rather than mere phenetic similarity can influence the conception of plant communities, distribution patterns, and paleogeography. (3.) It is difficult to know whether many specimens are from herbaceous or arborescent lycopsids, and it is easy to make assumptions that are untestable on limited evidence.

When further evidence is found of larger, more complete, specimens, or of attached reproductive organs, the possible interpretations must be treated with care. For example, the Lower Carboniferous European genus *Eskdalia* Kidston emend Thomas & Meyen (1984b), also described from South Africa (Brown & Lemoigne, 1977) and Siberia (Thomas & Meyen, 1984b), has generally been regarded as a taxon of comparatively small lycopsids (Thomas, 1968; Meyen, 1976; Thomas & Meyen, 1984b). Rowe (1988a), however, redescribed and renamed some specimens of *Scutellocladus variabilis* Lele & Walton (1962) from the Visean Drybrook Sandstone of the Forest of Dean, Gloucestershire, United Kingdom, as *E. variabilis*, which he believed to be the terminal shoots of an arborescent lycopsid because of its branching pattern and its possession of terminal cones. This species underlines the dangers of making generalized inferences from comparison of species based on vegetative axes. The type specimens of *Eskdalia variabilis* were originally assigned to the monotypic genus *Scutellocladus* Lele & Walton (1962), but were later included in *Tomiodendron* Radczenko emend. Meyen, 1972, by Thomas & Purdy (1983); a genus that has also been described from Alaska (Spicer & Thomas, 1987), North Africa (Lejal-Nicol & Massa, 1980) and Siberia (Meyen, 1976). The use of either of the widely distributed genera *Eskdalia* or *Tomiodendron* for these fertile British Visean shoots could be misinterpreted as implying that all species included within it are taxa of the terminal branches of arborescent lycopsids. *Scutellocladus*, redefined to include the terminal reproductive organs, should not be misinterpreted in this way.

THE BEGINNINGS OF MODERN HERBACEOUS LYCOPSIDS

What then can be interpreted from the fossil record that might give some indication of the evolutionary relationships within the herbaceous lycopsids, or the evolutionary history of the modern herbaceous genera *Selaginella* sens. lat. and *Lycopodium* sens. lat.?

Available evidence suggests that the extant herbaceous lycopsids most probably had their origins in the same Upper Carboniferous equatorial region where the arborescent lycopsids were reaching their zenith. In contrast with the Euramerican equatorial region, the northern Angaran Upper Carboniferous and Permian floras showed increasing endemism. There were large numbers of lycopsids in the Angaran Carboniferous that Meyen (1972) described as a cheerless and monotonous "brush" of fairly short straight sticks and suggested that the scanty vegetation was associated with lakes and rivers. There were no truly herbaceous forms; the lycopsids were represented by such genera of shrubby plants as *Lophiodendron* Zalessky, 1936, *Tomiodendron* Radczenko emend. Meyen, 1972, *Angarophloios* Meyen, 1972, *Ursodendron* Radczenko emend. Meyen, 1972, *Angarodendron* Zalessky, 1918, *Tunguskadendron* Thomas & Meyen, 1984c, and *Eskdalia* Kidston emend Thomas & Meyen, 1984b.

Similarly, there were no herbaceous forms in the Upper Paleozoic tundra vegetation of Gondwanaland (Retallack, 1980). There were instead very small trees or shrubs such as the Argentinian *Bumbudendron* and *Malanzania* described by Archangelsky et al. (1981) and the Brazilian Permian *Brasilodendron* Chaloner et al., 1968. Archangelsky et al. (1981) showed that *Bumbudendron paganzianum* had fertile branch structures rather than strobili, and Chaloner et al. (1968) suggested similar fertile structures for *Brasilodendron pedroanum*. Such simple reproductive structures were common world-wide in the Lower Carboniferous but later seem to have become restricted to the equatorial belt.

HOMOSPORY

Lycopodites Brongniart, 1822, or *Lycopodites* Lindley & Hutton, 1833, is a name that has been given to small, presumed herbaceous, leafy lycopsid shoots. Species based on vegetative axes alone have also been included. Pal & Ghosh (1990) have discussed the problems emanating from Brongniart's (1822) use of *Lycopodites* for a type species whose affinites are confused and argued the case for preferring Lindley & Hutton's usage of the generic name.

Species of *Lycopodites* have been described from the Upper Devonian onward and some of these are known to be fertile. For example, *Lycopodites* *oosensis* Kräusel & Weyland, 1937, from the Upper Devonian of Germany has globose sporangia on unspecialized sporophylls and spores that are 90–120 μm in diameter. Other species are merely vegetative shoots with no indication of their reproductive organs. Some of these vegetative shoots assigned to *Lycopodites* are isophyllous, such as *L. pendulus* Lesquereux, 1880, from the Upper Carboniferous of Illinois, U.S.A., *L. arberi* Edwards, 1934, from the Jurassic of New Zealand and *Lycopodites hannahensis* Harris, 1976, from the English Wealden. This last species, based on a large number of erect, dichotomizing vegetative stems preserved in a fine-grained sandstone was interpreted by Harris as a slender, upright, reedlike plant. I have found a similar specimen in fine-grained sandstone in the Yorkshire Jurassic. Such plants might well have been common on sandy mud flats on riverbanks and deltas throughout the Mesozoic. Other species of *Lycopodites* are anisophyllous, possessing two lower ranks of larger leaves and two upper ranks of smaller leaves. The type species, *L. falcatus* Lindley & Hutton (1833; reexamined by Harris, 1961), is of this form. This character is not restricted in extant species to *Selaginella*; there is a form of anisophylly occasionally present in *Lycopodium* resembling that of *Selaginella* (e.g., *Lycopodium carolinianum* figured in Troll, 1937). This clearly has implications for the use of anisophylly as an aid to generic distinction, and the problem will be discussed later in the section on the "generic assignment of herbaceous fossil lycopsids."

Carinostrobus foresmanii was the name given by Baxter (1971) to a single lycopsid cone from the Pennsylvanian of Kansas. It was only 2.3–3.0 mm in diameter, suggesting that it might have been the fructification of an herbaceous species. The spores were all of one type and 20–22 μm in diameter, indicating that the cone was either homosporous, microsporangiate, or a fragment of a heterosporous cone. Baxter, however, stated that *Carinostrobus* clearly lacked a ligule. Unfortunately, we have no knowledge of the plant that bore the cone.

HETEROSPORY

Heterospory is presumed to have developed in several groups of plants during the late Devonian, for the record of fossil spores shows a rapid increase in the number and diversity of presumed megaspores during this period (e.g., Chaloner, 1967). A few heterosporous Devonian fructifications probably belong to herbaceous lycopsids. For example, *Barsostrobus famennensis* Fairon-Demaret (1977) from the Upper Devonian of Belgium is an isolated portion of a cone with narrowly triangular and toothed sporophylls, each bearing a stalked, slightly reniform sporangium. The spores are all 240–320 μm in diameter and are interpreted as small megaspores. However, no ligules have been observed. These morphological characters, and details of its anatomy and vascular bundles, suggest that *B. famennensis* is closer to Carboniferous lycopsids than to the early Devonian forms. Unfortunately, once again the vegetative organs of the plant are unknown.

Other herbaceous forms from the Euramerican Upper Carboniferous Coal Measures were very similar to extant species of *Selaginella*. Some are known to have been heterosporous, but others are known to resemble *Selaginella* only in morphological characters of vegetative shoots. Both isophyllous and anisophyllous species are known from the Carboniferous onward.

The fairly rare anisophyllous shoots either have been placed into *Lycopodites* (as mentioned above), included in the genus *Selaginellites* Zeiller, 1906, or even regarded as species of *Selaginella* sens. str. *Selaginellites* was first used by Zeiller for a specimen from the Upper Carboniferous of the Blanzy Coalfield, France that he named *Selaginellites suissei*. This lycopsid had a dichotomously branched stem, dimorphic leaves, and a distinctive bisporangiate cone with apical microsporangia and basal megasporangia. *Selaginellites suissei* is therefore very similar to many living anisophyllous species of *Selaginella* that have tetragonous strobili (e.g., *Selaginella vogelli* Spring, *S. cathedrifolia* Spring and *S. pervillei* Spring: Quansah, 1988).

There are several other species of anisophyllous *Selaginellites* that have been described from the Carboniferous Coal Measures. I have reexamined the remarkable specimen of *Selaginellites gutbieri* (Goeppert) Kidston, 1911, from the Westphalian D of the Zwickau Coalfield, Poland, which was refigured by both Schimper (1870–1872, pl. 57, fig. 4) and Hirmer (1927, fig. 327). It is truly anisophyllous with terminal cones. Microspores (of the *Ciratriradites* form) were recovered from several of the cones, although megaspores were not found. It is, however, quite possible that the plant had only microsporangia similar to the condition found in some individuals of many living anisophyllous species of *Selaginella* (e.g., *S. versicolor* Spring, *S. vogellii* Spring and *S. leonensis* Hieron. (Quansah, 1988)). *Selaginellites elongata* Goldenberg, 1855, is, however, rather different. It was reexamined by Halle (1907), who described the sporangia as occurring in the axils of ordinary vegetative leaves. This condition is found in living species such as *Selaginella denticulata* (L.) Link and *S. pallidissima* Spring, where there are two sizes of sporophylls arranged in four ranks. In these living species the smaller sporophylls are in the same plane as the smaller median vegetative leaves, and the larger sporophylls are in the same plane as the larger lateral vegetative leaves (Quansah, 1986). This gives the superficial appearance of there not being a discrete cone. Kidston (1911) also described some fertile specimens from the Westphalian B of the Belgium Coalfield as *Selaginellites gutbieri*, although his plate figures are labeled as *S. primaevus* Goldenberg. There are, however, several characters that distinguish the Belgian cones from *S. gutbieri*. The most obvious differences are that the larger leaves are much more dentate and the sporophylls are approximately the same size as the larger vegetative leaves. It is therefore very similar to *S. elongata*, although a reexamination of the Belgian material is necessary before any firm identification can be made.

I have also seen other specimens of late Carboniferous herbaceous anisophyllous shoots, from Poland and Germany, that have distinctly different leaf shapes, leaf orientations and leaf outlines. Such characters are remarkably consistent in living species of *Selaginella* (Quansah, 1986; Dahlen, 1988), so it is reasonable to assume that they can be used for distinguishing species of fossils.

Anisophyllous forms have also been described from Mesozoic strata, and many of these have been shown to be heterosporous; examples include *Selaginella anasazia* Ash, 1972, from the Trias of New Mexico, *Selaginella hallei* Lundblad, 1950b, from the Rhaetic of Sweden and *Selaginella dawsoni* Watson, 1969, from the Wealden of England. There are also vegetative shoots such as *Selaginella dichotoma* Velenovsky & Viniklav, 1931, from the Jurassic of Siberia and *Selaginellites nosikovii* from the Cretaceous of Czechoslovakia.

The earliest isophyllous specimens of *Selaginella* (= *Selaginellites*) are known from the Lower Carboniferous. These, called *Selaginellites resimus* Rowe (1988b), came from the Drybrook Sandstone. They are both herbaceous and isophyllous, with small terminal strobili showing impressions of megaspores in several sporangia.

Isophyllous forms such as *Selaginella fraipontii* (Leclercq) Schlanker & Leisman, 1969, are also known from the Upper Carboniferous Euramerican Coal Measures, although they are similarly rare. This species has been described as sparsely branched, sprawling and possibly of determinate growth. The terminal cones had sporophylls arranged in alternating pairs of verticels. It is very similar in morphology to some extant species of *Selaginella* (e.g., *S. selaginoides* L.), except for not having a distinctive basal root-bearing organ. It also shows a very close similarity in stelar anatomy, change in the number of protoxylem points, secondary growth in the base of the stem, and in the change from centrarch to exarc steles.

Isolated cones are also included in *Selaginellites*, such as *S. polaris* Lundblad, 1948, from the Trias of Greenland. We know nothing of their axes, and their assignment to this genus is therefore tenuous.

Miadesmia membranacea Bertrand (Benson, 1908) is an isolated cone of a rather different structure. Its small size suggests that it might belong to an herbaceous lycopsid, although there is no other evidence. It is megasporangiate: a single large megaspore occupies each sporangium, which in turn is enclosed by integuments, suggesting an analogy in its structure with that of *Lepidocarpon* Scott, 1900.

THE GENERIC ASSIGNMENT OF HERBACEOUS FOSSIL LYCOPSIDS

Lycopodites is generally used to encompass homosporous lycopsids, or just vegetative axes, bearing a resemblance to living species of *Lycopodium*. Although the usage of the name *Lycopodites* varies, there is no strong argument for any of the fossils to be included within *Lycopodium* sens. str. *Lycopodites* seems to be a problematic taxonomic unit; some specimens have even been subsequently shown to be twigs of larger lycopsids or even of conifers. When Harris (1961) redescribed the type species of *Lycopodites*, *L. falcatus* Lindley & Hutton (see Pal & Ghosh, 1990, for a discussion on generic priority), from the Yorkshire Jurassic, he not only confirmed its anisophyllous structure but showed there to be twice as many larger lateral leaves as smaller leaves. *Lycopodites falcatus* was, however, solely vegetative. It might therefore be better to consider restricting the use of *Lycopodites* to that of a form-genus of sterile axes and to accept that it is delimited by artificial parameters. Harris's (1969) classification of Mesozoic conifer shoots offers a precedent for this practice.

There has, however, been intense debate about the necessity of using another generic name in preference to *Selaginella* for fossil plants resembling this genus. Zeiller (1906) originally suggested that the presence of more than four megaspores in each megasporangium was a distinguishing character of his new genus *Selaginellites.* Halle (1907) did not accept that this character was essential and used *Selaginellites* for all heterosporous fossils. Subsequently, Duerden (1929) and Quansah (1988) showed that living species of *Selaginella* can possess more than four megaspores per sporangium. Seward (1910), Harris (1935), Hirmer (1941), Chaloner (1967), and Rowe (1988a) used *Selaginellites* for all fossil shoots that were closer to *Selaginella* than any other genus. In contrast, Darrah (1938), Lundblad (1950b), Townrow (1968), Schlanker & Leisman (1969), Watson (1969), and Ash (1972) used *Selaginella* for fossil shoots because they could not demonstrate any real morphological differences from the extant species of that genus. The problem of using generic names of extant plants for fossil specimens is a major one encountered throughout palaeobotany (e.g., Collinson, 1986). In the case of the herbaceous anisophyllous axes, further complications can arise during attempts to include fossil species of *Selaginella* in the described subgenera, or to incorporate them into the various genera suggested for splitting *Selaginella.* This problem will be discussed in the following section.

Fossil plants are usually incomplete fragments of whole organisms, which pose even more problems for generic assignment. For example, Lundblad (1948) assigned a small detached heterosporous cone to *Selaginellites* with no knowledge of vegetative morphology, even though the cone was broader than those of all living species of *Selaginella.* This approach may be the simplest way of dealing with the situation but, when the fossils are merely vegetative axes, taxonomic decisions have to be made without knowledge of their reproductive organs.

It is interesting to note how the use of these generic names can vary, even within a single publication. For example, Lundblad (1950a) named an isolated cone from the Rhaetic of Sweden *Selaginellites hallei* sp. nov. but referred the associated vegetative, anisophyllous axes to *Lycopodites scanicus* Nathorst ex Halle. Later, Lundblad (1950b) found fertile specimens sharing the characters of both these species and named them *Selaginella hallei* comb. nov., presumably preferring to use the cone name rather than taxonomically uniting the two species and using the rules of priority (cf. Greuter et al., 1988).

Many systematists have followed Bower (1935) in arguing that *Selaginella selaginoides* L. is a primitive form because of its radial construction and the lack of aerial roots. However, the anisophyllous heterosporous forms appeared in the fossil record soon after the isophyllous forms, implying that plants with the *Selaginella selaginoides* morphological form may not be ancestral to all *Selaginella*-like fossils. It is possible that an ancestral group of both the isophyllous and anisophyllous lycopsids might be eventually recognized in the late Devonian or very early Carboniferous lycopsids. However, it is also possible that these plants are much less closely related than has been previously thought.

Fossil Evidence for the Generic Assignment of The Extant Species of the Selaginellaceae

Early classifications (e.g., Wildenow, 1810; Sprengel, 1827) placed *Selaginella* within the genus *Lycopodium,* though Spring (1850) presented the major monograph of the genus *Selaginella* as it is presently understood. Even though most workers have generally understood and agreed on the parameters delimiting the genus *Selaginella,* there have been many attempts to express taxonomically groups of species that have distinctive morphologies. The taxonomic divisions of the genus by various authors differ in the number of subgenera or genera that they accept.

A study of African species of *Selaginella* (Quansah, 1986) and a preliminary review of approximately 100 South American species (Quansah & Thomas, 1985) suggest that the genus should be divided into at least two genera or subgenera: those with isophyllous leaves and those with anisophyllous leaves. This is supported by several recent studies, including Jermy et al. (1967), Crabbe & Jermy (1976), Alston et al. (1981), and Tryon & Tryon (1981), whose authors have recognized two subgenera, *Selaginella* and *Stachygynandrum,* within the genus. The two groups originate from Baker's (1883, 1887) classification. The other two subgenera, recognized by Baker and by Walton & Alston (1938), *Homostachys* and *Heterostachys,* are best recognized at a lower hierarchical level within the group containing all the anisophyllous species.

Jermy (1986) has, however, proposed five subgenera within *Selaginella.* The two subgenera of anisophyllous species differ in several characters, including their cone morphologies. It is interesting to note that Carboniferous *Selaginellites* could be included in both of these subgenera; *S. gutbieri,* with its uniform and tetrastichous sporophylls, could be included in Jermy's subgenus *Stachygynandrum* (P. Beauv.) Baker, while the Carboniferous *Selaginellites elongata* could be included in Jermy's subgenus *Heterostachys* Baker. Work in progress on the Carboniferous species may give further evidence in support of Jermy's idea of creating five subgenera.

It is, at least, clear that both isophyllous and anisophyllous *Selaginella*-like plants are known from the Carboniferous onwards and that some of these have been thought even to be generically indistinguishable from extant *Selaginella*. The origin of isophyllous and anisophyllous lycopsids at approximately the same point in geological time can be taken as additional evidence for regarding the two groups of plants as taxonomically distinct. Indeed, the recognizable division into two different morphologies, which has existed for approximately 300 million years, strengthens considerably the argument for making the division at generic rather than subgeneric level.

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DEVELOPMENTAL PROBLEMS IN *SELAGINELLA* (SELAGINELLACEAE) IN AN EVOLUTIONARY CONTEXT[1]

Terry R. Webster[2]

Abstract

The antiquity and diversity of *Selaginella* species attest to the evolutionary success of the genus. This success may be attributed, in part, to certain morphological and anatomical features that characterize *Selaginella*. Recent developmental studies of anisophylly, monoplastidy, the ligule, the rhizophore, marginal warty cells, and marginal teeth of the leaves, as well as aspects of the heterosporous life cycle are discussed. Unresolved questions concerning vegetative features include the function of the ligule, morphological interpretation of the so-called rhizophore, and a possible role of distinctive leaf ornamentations in water economy. Among unresolved questions concerning reproductive morphology are the basis of heterospory, control of sporangial development, spore dispersal mechanisms as they affect inbreeding and outcrossing, and other details of the reproductive process. It is concluded that the genus *Selaginella* offers numerous opportunities for future research.

From the standpoint of both development and evolution, the genus *Selaginella* raises a number of intriguing questions. In this regard the following quotation from Bierhorst (1971) seems appropriate:

> The family Selaginellaceae includes *Selaginella* and several very closely related fossil forms which are known from Lower Carboniferous and more recent strata. *Selaginella* is probably one of the oldest of all extant genera of vascular plants, second only to *Lycopodium*. Despite its great antiquity, which might lead one to expect specialization and relative genetic stagnation, there are approximately 700 extant species and much evidence for recent speciation.

The key elements of this statement are the antiquity and diversity of the genus and the probability that *Selaginella* is presently undergoing active speciation. Years ago, the prominent morphologist C. W. Wardlaw (1925) also alluded to the evolutionary status of *Selaginella*:

> The genus is represented by a large number of species, many of which are polymorphic. They have a wide geographical distribution, and in some floras they dominate the ground vegetation. Further, they show adaptation to all degrees of xerophily and hygrophily. It would appear from these facts that the genus is successfully retaining its position in the midst of the more highly differentiated Phanerogams.

With our current state of knowledge, the reasons for the apparent evolutionary success exhibited by *Selaginella* are far from obvious. It is my contention that, at least in part, the reasons may be found in the genus's unique combination of vegetative and reproductive features. These include anisophylly, the ligule, the presence of certain foliar epidermal ornamentations, the aerial root (rhizophore), monoplastidy, and certain aspects of the heterosporous life cycle (Fig. 1). It should be emphasized that although each of these features may be found in other plant groups (for example, the ligule is found in *Isoetes* as well as in *Selaginella*), it is the combination of features that is unique to *Selaginella*. It is the purpose of this paper to discuss these features and to point out certain controversies and questions, which may lead to further discussion and future studies. Although some older references from the literature have been included where appropriate, this paper mainly considers work of the past 30 years.

Vegetative Morphology

Certain vegetative features of *Selaginella* have intrigued students of the genus for many years. For example, the ligule and the so-called rhizophore are two enigmatic structures that are familiar to students of plant morphology. Yet, despite numerous studies, the morphological interpretation and evolutionary significance of many of the vegetative features of *Selaginella* remain a mystery. An examination of the vegetative plant body reveals

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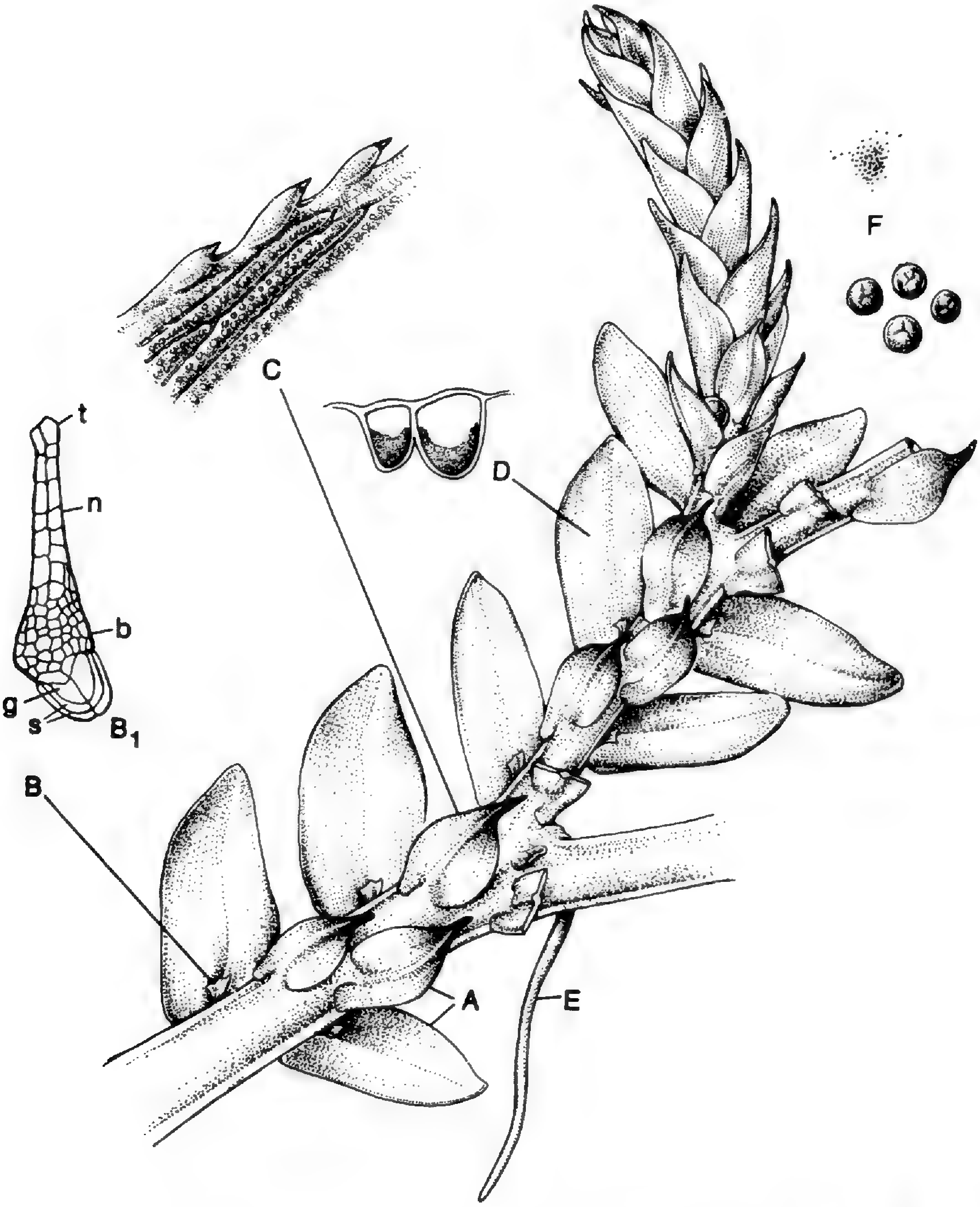

FIGURE 1. Diagram of structural features of *Selaginella*.—A. Anisophylly.—B. Ligule.—B1. Ligule, in section. t = tip, n = neck, b = base, g = glossopodium, s = sheath.—C. Marginal warty cells and marginal teeth.—D. Monoplastidy.—E. Aerial root (rhizophore).—F. Heterospory.

a basic simplicity of design, which would seem to make the evolutionary success exhibited by the genus that much more interesting. A critical examination of certain key vegetative features may provide insights into this apparent contradiction.

ANISOPHYLLY

Perhaps the most obvious vegetative feature found in most species of *Selaginella* is anisophylly. According to Dengler (1983a), the term anisophylly refers to differences in leaf form related to the transectional symmetry of the shoot and most often occurs in plagiotropic shoots from shaded situations in which the foliage leaves on the upper side of the stem are smaller than those on the lower side. In several detailed studies, Dengler (1980, 1983a, b) investigated anisophylly in *S. martensii*. Unlike many plants that are anisophyllous, *Selaginella* (sect. *Heterophyllum*) exhibits no transitional leaf forms, but rather shows two distinct leaf types borne in pairs along the stem. At each node one smaller dorsal leaf and one larger ventral or lateral leaf are initiated as an opposite pair (Fig. 1). Leaf dimorphism in *Selaginella* is generally considered to be related to efficient trapping of light in shady habitats with low light intensity. Dengler (1980) noted that certain anatomical features are related to orientation of the shoot to light. Most notably, the abaxial (aligular) epidermis of the dorsal leaf and the adaxial (ligular) epidermis of the ventral leaf consist of nearly isodiametric cells, each containing a single large chloroplast. These surfaces are directed toward light. The shaded epidermal layers (adaxial or ligular surface in dorsal leaves and abaxial or aligular surface in lateral leaves) consist of elongate tabular cells with numerous small plastids. Certain other features of the leaves of *S. martensii* do not exhibit a relationship to light. For example, stomates occur primarily on the aligular (abaxial) leaf surface regardless of orientation to light (Dengler, 1980).

Dengler (1983a, b) sought to determine the developmental basis for anisophylly in *S. martensii* by carefully following leaf initiation, development, and histogenesis. She concluded that, although the general pattern of growth is similar for both dorsal and lateral leaves, the two leaf types diverge early in development and can be distinguished at inception. She argued against Goebel's theory of developmental arrest to account for the differences between dorsal and ventral leaves. Goebel (1895) proposed that all leaves of a heteroblastic series share the same early stages of development and differ in mature form through a process of arrest at a particular developmental stage and subsequent divergence of ontogenetic pathways. In contrast, Dengler argued that the dorsal leaf of *S. martensii* should not be regarded as an arrested form of the ventral leaf, since critical morphological differences are initiated at inception. Two distinct leaf forms result, which can be distinguished in the primordial stage rather than differentiating late in development.

In a recent series of experiments with *S. kraussiana,* which exhibits anisophyllous dorsiventral shoots typical for section *Heterophyllum,* Bilderback (1984a, b) demonstrated the effect of the small dorsal leaves on the response of the shoot to phototropism and in maintaining a plagiotropic growth habit. He used excised shoot tips that were placed in sterile culture and oriented with respect to light. When placed in a normal position, with the dorsal leaves illuminated, shoot bending was slightly below the horizontal position, and the normal plagiotropic habit occurred (Bilderback, 1984a). Curvature resulted from asymmetric growth of the stem in a region just behind the apex, where cortical cells on the dorsal stem surface underwent greater elongation than ventral cortical cells. When the ventral surface was illuminated, the shoot exhibited a strong phototropic response so that the dorsal leaves eventually were reoriented toward light. The phototropic response was negated by application of phenylacetic acid (a known inhibitor of phototropism) to the dorsal leaves. Results of dark experiments indicated that the growth response was not affected by gravity.

Surgical removal of young dorsal leaves strongly inhibited phototropic curvature of the shoot (Bilderback, 1984b). Replacement of dorsal leaves with auxin in lanolin paste restored the phototropic response, whereas application of triiodobenzoic acid (TIBA), an auxin transport inhibitor, to dorsal leaves resulted in a significant reduction in phototropic stem curvature. The author concluded that phototropic sensitivity allows *Selaginella* to maintain its orientation with its environment. The dorsal leaves act as an auxin source to the dorsal portion of the stem, which results in greater cell elongation and stem bending. Light to the dorsal surface inhibits the bending, so that the shoot maintains its typical dorsiventral orientation.

LIGULE

Another interesting morphological feature in *Selaginella* is the ligule, a tiny appendage attached to the base of each leaf on the adaxial surface (Fig. 1). In addition to its universal occurrence in living species of *Selaginella*, the ligule has been described for extinct members of the genus, including *S. fraiponti*, a fossil of mid-Pennsylvanian age (Rock & Segal, 1973). The recent discovery (Grierson & Bonamo, 1979) of a ligule in *Leclercqia*, a fossil homosporous lycopsid from the Devonian, has resulted in a reevaluation of the concept that the ligule is always linked with heterosporous plants. Although the ligule in *Selaginella* has been the subject of numerous investigations, its function remains a mystery. It has been suggested that the ligule may function in secretion of mucilage or water, absorption of water, mucilage accumulation, production-collection-transport of materials, or that it may represent a vestigial organ (Horner et al., 1975).

Horner et al. (1975) examined the development of the ligule in *S. pilifera* and *S. uncinata* at the light microscope and ultrastructural levels. They divided the ligule into tip, neck, and basal regions (Fig. 1). They described the ligule of *S. pilifera* as being shaped like a curved hand; that is, the broad tip consisted of fingerlike unicellular papillae, the neck resembled appressed fingers 1–2 cells thick, and the base was broad and bulbous, like a swollen palm. In contrast, the ligule of *S. uncinata* was shaped like a slightly flattened bowling pin, with no distinct papillae. In agreement with earlier studies, Horner et al. (1975) pointed out the precocious development of the ligule and indicated that the entire structure stained intensely for RNA early in development, whereas only the polygonal basal cells of older ligules stained intensely. In the basal region, the bottommost layer of sheath cells was separated from the leaf vascular strand by one or two layers of mesophyll cells. Thus, the vascular strand was not in direct contact with the ligule. The entire ligule was covered with a cuticle continuous with the cuticle on surrounding surfaces of the leaf.

In their ultrastructural study, Horner et al. (1975) noted that the cells of the ligule possessed plastids that contained only a few internal lamellae and that the ligule never became green. The authors agreed with Sigee (1974) that the central cells gave the appearance of highly active cells and that their ultrastructure was similar to that in certain plant secretory systems; that is, the cells were dense and contained numerous ribosomes, Golgi bodies and associated vesicles, mitochondria, and plastids. Although the presence of callose was noted in the polygonal base cells, the authors found no evidence for the secretion of mucilage.

The glossopodium and sheath cells (Fig. 1) differed anatomically from the central cells. At maturity the large glossopodial cells were vacuolate and were subtended by two layers of bricklike sheath cells. Prominent ingrowths occurred on the lower glossopodial wall and on the upper wall of the adjacent sheath cell. Horner et al. (1975) suggested that these cells with wall ingrowths might be involved in the movement of solutes. The walls common to the upper and lower sheath cells lacked ingrowths but contained numerous plasmodesmata. Although the ligule base was separated from the leaf vascular strand by one or two mesophyll cells, the authors pointed out that there is no reason to believe that the mesophyll cells would inhibit the movement of materials in either direction.

As had been found in previous studies, Horner et al. (1975) noted that ligule development and maturation occurred rapidly. In *S. uncinata* the tip and neck cells appeared to senesce soon after maturation, whereas the polygonal basal cells, glossopodium, and sheath cells remained unchanged for a number of dichotomies back from the tip.

Based on their observations on *S. uncinata* and *S. pilifera*, Horner et al. (1975) contended that the ligule is physiologically active and contains cells that may be involved in the movement of certain substances through the ligule. As another possibility, they suggested that the ligule may represent a vestigial organ that still retains certain properties of a once functionally active state.

In a series of studies, Sigee (1974, 1975, 1976) examined the structure and function of the ligule of *S. kraussiana*. In an ultrastructural study, Sigee (1974) noted that the central cells of the ligule displayed an extensive endoplasmic reticulum and Golgi system, which produced large numbers of Golgi vesicles. He proposed that the central cells could be involved in the elaboration or secretion of materials. A comparison with known secretory systems in other plants, however, suggested that the ligule is not active in the mass secretion of mucilage. He noted the presence of a continuous cuticle, which lacked cuticular pores and with no signs of rupture—further indications that the ligule is a nonsecreting structure.

Using histochemistry and light and transmission electron microscopy, Sigee (1975) was able to show that there was no significant accumulation of mucilage within the cells or on the surface of the ligule. He suggested that the Golgi system in the ligule, rather than secreting mucilage, contributed to cell wall formation. In another study, Sigee (1976) showed the incorporation of tritiated glucose into cells of the central region of the ligule, with particular accumulation in the Golgi bodies. The uptake and retention of label was cited as evidence that the Golgi bodies were active in the synthesis of complex carbohydrates, but did not pass these substances to the cell surface. Sigee (1976) concluded that the relatively inactive Golgi system in the ligule may be derived phylogenetically from a more active one and suggested that the ligule could be a vestigial organ, derived from a primitive secretory structure.

Jagels & Garner (1979) compared callose deposition in ligules of seven species of *Selaginella*. Using aniline blue stain and fluorescence microscopy, they determined that callose was localized in the basal region of the ligule and that the amount of deposition could be related to habitat. Species from dry, sunny habitats (the isophyllous *S. rupestris* and *S. densa* and the anisophyllous *S. lepidophylla*) exhibited heavy callose deposits, whereas species from moist, shady habitats (*S. kraussiana*, *S. martensii*, *S. apoda*, and *S. uncinata*—all anisophyllous species) had a light to moderate deposition of callose.

Recent evidence has been presented for the secretion of mucilage by ligules in several species of *Selaginella* (Bilderback, 1987). Putative mucilage bodies were shown to be associated with ligules of greenhouse-grown *S. kraussiana* and in ligules of *S. wallacei* and *S. oregana* from nature. When shoot tips of *S. kraussiana* and *S. douglasii* were grown in sterile culture with sucrose in the medium, massive amounts of mucilage were found around the apical meristem and coating the youngest leaves. The mucilaginous material in *S. kraussiana* was composed of protein and polysaccharide. In contrast, no mucilage was associated with ligules of *S.*

douglasii, *S. densa*, or *S. apoda* from nature, nor was mucilage produced when shoot tips of *S. wallacei*, *S. densa*, or *S. apoda* were grown in sterile culture. Because mucilage was found to be closely associated with the ligules of several species, Bilderback (1987) concluded that the ligule of *Selaginella* may be glandular.

In order to understand better the possible role of the ligule in mucilage secretion, Bilderback & Slone (1987) investigated the ultrastructure of the ligule in cultured shoot tips of *S. kraussiana*. Polysaccharide bodies similar to those seen in the mucilage believed to be secreted by ligules also were observed in apical cells of ligules from cultured shoot tips. Although no pores or breaks in the cuticle were seen, the cuticle of the apical cells was distended and separated from the cell wall, and electron-dense granules were present in the space thus formed. Although the apical cells lacked dictyosomes, they did possess dilated endoplasmic reticulum. Dictyosomes were present in the cells of the basal portion of the ligule. The ultrastructure of the ligule was compared to that of secretory structures in angiosperms, and Bilderback & Slone (1987) concluded that the ligule in *S. kraussiana* is a structure that produces and secretes extracellular mucilage.

Kohlenbach & Geier (1970) used selective staining of leaves with berberine sulfate to study the function of the ligule in *S. kraussiana* and presented evidence that the ligule is a site for absorption of liquids. They suggested that the ability of the ligule to absorb liquids is related to special qualities of the thin cuticle at the ligule apex.

Lafont & Lemoigne (1965), using light microscopy, reported a system of canals in the rather large ligule of *S. willdenovii*. They described a principal canal and occasional connecting secondary canals. The canals were reported sometimes to open directly to the surface of the ligule. The canals occurred only in the basal part of ligules in an advanced stage of development. Although the exact significance of this system of canals is unknown, the authors suggested that they might serve as a pathway for the emission of products to the exterior environment, and that a role in water absorption for the ligule is debatable. The ultrastructure of the plastids in the ligule of *S. willdenovii* was also studied by Lafont & Lemoigne (1966). The small achlorophyllous plastids were found to contain vacuoles and associated amorphous material, and the authors suggested that these plastids might be associated with a secretory function.

Despite the considerable attention that has been paid to the ligule of *Selaginella*, the function remains a mystery. Suggestions that it is an organ involved in water absorption, water or mucilage secretion, mucilage accumulation, or the production-collection-transport of materials have been made, as well as the possibility that the ligule is a vestigial organ (Horner et al., 1975). Much of the evidence presented to date is contradictory, so that a definitive interpretation for the function of the ligule must await further investigation.

FOLIAR EPIDERMAL ORNAMENTATIONS

Recent studies have shown the presence of distinctive epidermal ornamentations in leaves of *Selaginella* species. These ornamentations are evident as so-called warty cells and teeth that are prominent along the leaf margins (Fig. 1). Waterkeyn & Bienfait (1967) first described the interesting method of development of these cells in leaves of *S. kraussiana*. Using the dyes resorcinol blue and aniline blue and fluorescence microscopy, they were able to show that the outer walls of these specialized cells undergo callose deposition, which is then gradually degraded and replaced with silica. Differentiation in leaves of *Selaginella* is basipetal, so that the development of marginal teeth and warty cells can be followed sequentially. Thus, in a differentiating leaf, the teeth and warty cells at the leaf apex possess silica walls; in subjacent regions of the leaf, teeth and warty cells contain both callose and silica; and at the base of the leaf, these cells possess callose but no silica in their outer walls. Concerning a possible function for these distinctive cells, Waterkeyn & Bienfait (1967) noted that plants that are strongly mineralized often have a particularly high rate of cuticular transpiration, and they suggested that the marginal warty cells and teeth might somehow be involved in the control of foliar transpiration in *Selaginella*.

Waterkeyn et al. (1982) expanded their study of foliar emergences in *S. kraussiana* to similar structures in several angiosperms, including *Cannabis sativa*, *Urtica dioica*, *Campanula persicifolia*, and *Blumenbachia hieronymi*. In all of these cases it was shown that a callose phase occurred before or during silicification of the walls of these epidermal cells. They determined that callose deposition resulted in a thinning of the wall and overlying cuticle, and that the fluorescent dye, berberine sulphate, accumulated in the cells possessing callose, but not in those that had become silicified. They also presented evidence that these epidermal cells are regions where absorption is favored owing to the greater permeability of the cuticle. Their results indicated that the epidermal appendages in the plants investigated, including the foliar marginal warty cells and teeth of *S. kraussiana*, are regions of active transpiration. Based on their study, they suggested that callose might play two roles: (1) to control somehow the movement of water by a nonosmotic mechanism; and (2) to provide a favorable matrix for silica deposition during wall formation.

LeCoq et al. (1973) used scanning electron microscopy, fluorescence microscopy, and the electron microprobe to trace the development of the marginal teeth and warty cells in *S. kraussiana* and confirmed the earlier observations of Waterkeyn & Bienfait (1967) of a callose phase that preceded silicification in these cells. They also noted that, in addition to marginal teeth and warty cells, certain other cells of the leaf epidermis possessed mamillae, smaller silicified leaf ornamentations. They also found that the outer cell walls of the entire leaf epidermis eventually became covered with a continuous layer of silica. Robert et al. (1973) continued the study of leaf ornamentations in *S. kraussiana* by using transmission electron microscopy. As a result of their investigation, they proposed five phases of silicification in the external walls of leaf epidermal cells in *S. kraussiana*: (1) a pectic-cellulose phase; (2) a callose phase during which the marginal teeth and warty cells achieve their final shape and size; (3) a cellulosic phase, which isolates a callose plug; (4) silicification of the teeth and warts, during which callose is gradually replaced; and (5) a new phase of silicification over the entire outer wall.

Robert & Laroche (1979) later described the development of the marginal warty cells of *S. kraussiana* in detail. As seen with the transmission electron microscope, a wart first appeared as a raised area resulting in a space between the outer cell wall and the plasmalemma. This space, the central region of the wart, then became filled with callose. Below this space, the cytoplasm was rich in endoplasmic reticulum, which the authors suggested may be important in the formation of callose. Once the wart attained its final size, a new pectocellulose wall was formed beneath the raised area, thus isolating the callose plug from the cytoplasm. During these changes in wall structure, the cuticle covering the wart became thinner and was structurally disrupted. These localized disruptions of the cuticle appeared to the authors to result in an increased flow of water at these particular points (Robert & Laroche, 1979). Finally, there was a breakdown of the central callose plug, accompanied by a gradual replacement of the callose with silica.

Dengler & Lin (1980), using scanning electron microscopy and X-ray microanalysis, studied the distribution of silica in the ventral (lateral) leaves of *S. emmeliana*. High levels of silica were found in the marginal warty cells (termed "marginal sclereids" by the authors) and in approximately half of the abaxial epidermal cells. Stomates were confined to a broad band of cells on the abaxial (aligular) surface overlying the single vascular strand. Although most cells of the stomatal band did not accumulate significant amounts of silica, approximately 6% of the stomata possessed high levels of silica and exhibited a constricted aperture. Epidermal cells that were unprotected by adjacent ventral leaves and were thus exposed to light were the ones that developed warty projections and accumulated silica. Dengler & Lin (1980) suggested that higher rates of transpiration might be expected from the exposed portion of the leaf, which could account for the observed pattern of silica distribution. The authors concluded that although the function of silica in *Selaginella* is unknown, it is possible that it may play an important role in support of the leaf. They also pointed out that others (Kaufman et al., 1972) have suggested that hydrated silica gel in the epidermal walls may provide water to a leaf or stem during periods of drought or when transpiration causes loss of turgor.

Based on a comparison of several species of *Selaginella*, Bienfait & Waterkeyn (1974) concluded that the morphology and distribution of marginal teeth and warty cells in leaves could be useful in taxonomic determinations.

Although the structure of these distinctive leaf epidermal cells of *Selaginella* has been carefully documented, their function has yet to be determined. Based on the recent studies cited above, a role in water economy would seem to be a reasonable possibility.

MONOPLASTIDY

Another interesting feature of leaf anatomy in *Selaginella* pertains to the chloroplasts of the epidermal cells. Typically for leaves of *Selaginella*, the epidermal cell layer directed toward light (aligular surface in dorsal leaves, ligular surface in lateral leaves) is composed of conical or bowl-shaped cells, each containing a single large chloroplast (Fig. 1). In recent years there have been several studies on the structure and development of these plastids (Jagels, 1970a, b; Webster & Tanno, 1980; Tanno & Webster, 1982b). Despite their size, these chloroplasts exhibit normal ultrastructure, with distinct grana, stroma, and starch grains. It would appear that these plastids represent the major light-absorbing region of the leaf, and also show a remarkable adaptation for shady habitats. It has been shown that these plastids are able to move in response to light direction and intensity (Zurzycki & Zurzycka, 1951; Mayer, 1971; Haupt, 1973, 1982). For example, when leaves of *S. martensii* are exposed to diffuse daylight, the chloroplast lies at the base of the cell and occupies the whole area of the cell. If the leaf is illuminated with intense white light, the first chloroplast movements are detectable after 10–20 minutes. The chloroplast moves to a side wall, leaving the base and opposite wall uncovered. This movement of the chloroplast onto the side walls is accomplished after two or three hours (Zurzycki & Zurzycka, 1951). According to Haupt (1973), who discussed chloroplast movement in several plants:

> The biological significance of these light-dependent arrangements seems self-evident: The low intensity arrangement enables the chloroplasts to absorb as much light for photosynthesis as possible, but the high intensity arrangement protects them against the absorption of damaging amounts of light.

In recent years there has been considerable interest in monoplastidy and its association with cell division mechanisms. As part of a series of studies on cell division mechanisms in monoplastidic plants, Brown & Lemmon (1984, 1985, 1990) have pointed out that among vascular plants, *Selaginella* and *Isoetes* possess meristematic cells that are monoplastidic. Cell division in such cells is subject to certain constraints that result in each daughter cell receiving a plastid, thereby avoiding the apoplastidic condition. In a recent study of cell division in root meristems of *Selaginella* and *Isoetes*, Brown & Lemmon (1984) noted the precise orientation of the dividing plastid relative to the preprophase band. Specifically, the plastid is oriented with the long axis perpendicular to the preprophase band, and the isthmus of the dividing plastid is in the plane of the preprophase band and, in turn, the mitotic equator. The regular positioning of the plastid during cell division is obviously an important part of morphogenesis in monoplastidic cells. The orientation of both the preprophase band and the dividing plastid predict the plane of cell division.

In another study, Brown & Lemmon (1985) examined cell division and plastid movements in stomates of *S. erythropus*. They noted the same spatial relationship between the preprophase band and dividing plastid in the guard mother cell as was found for root meristematic cells (Brown & Lemmon, 1984), but they also described postcytokinetic plastid migrations during guard cell differentiation. The authors (Brown & Lemmon, 1985) stated that plastid behavior in developing stomates of *Selaginella* is the most complex yet demonstrated for monoplastidic cells. The observed plastid movement in guard cells is related to cytoplasmic polarity and is clearly a different phenomenon than photo-induced plastid movement seen in normal photosynthetic leaf cells of *Selaginella*. These observations suggest the need for further study to determine the mechanisms of plastid movements in *Selaginella*. The recent studies of variation in cell division mechanisms in monoplastidic plants, which include numerous algae, certain bryophytes, and, among vascular plants, *Isoetes* and *Selaginella*, seem certain to have important evolutionary implications.

ROOT (RHIZOPHORE)

One of the most controversial organs of *Selaginella* is the leafless cylindrical structure arising at the angle of shoot branching (Fig. 1). This structure is positively geotropic, green for much of its length, and lacks a root cap and root hairs until it strikes the soil. In addition, the angle-meristem from which it arises may, under certain conditions, develop into a leafy shoot. Nageli & Leitgeb (1868) coined the term "rhizophore" (root bearer) for this organ, since they believed true roots were produced endogenously behind the tip of the rhizophore. Since then, the morphological nature of this curious organ has been a source of continued debate. Over the years, the rhizophore has been interpreted as a modified root, shoot, or an organ sui generis.

In a series of studies involving four species, Webster & Steeves (1963, 1964, 1967) examined the morphology and development of the organ in question, and determined that it is a root throughout its development. They provided evidence that refuted the early interpretation that endogenous roots are produced behind the tip of a so-called rhizophore. In *S. kraussiana* (anisophyllous), *S. densa* and *S. wallacei* (both isophyllous), all species with a creeping habit, root caps are formed when the root is less than 1 mm long. In *S. martensii*, an ascending species, the leafless structure arising at the angles of shoot branching grows for several centimeters before forming a root cap. Root caps are produced as the tips of the branching root strike the soil. In all four species root hairs are produced as the tips enter the soil, soon after root cap formation. The root cap is formed when the apical cell of the root meristem, in addition to producing lateral segments, begins to cut off cells from its distal face as well. Thus no evidence for a "root bearer" (rhizophore) was found by Webster and Steeves, and the organ was interpreted as a root.

In a recent study of *S. uncinata*, Imaichi & Kato (1989) refuted the interpretation by Webster & Steeves (1963, 1964, 1967). According to Imaichi & Kato (1989), subterranean roots of *S. uncinata* are derived endogenously behind the apex of a rhizophore. The initial of the rhizophore apex is divided by periclinal divisions into rectangular and prism-shaped cells and becomes indistinguishable from neighboring cells. Apical cells of endogenous roots are then formed from inner cells near the apex of the rhizophore. A similar interpretation for endogenous root origin behind the rhizophore apex resulted from the study of three large tropical species with branched rhizophores (Imaichi & Kato, 1991). Their studies thus support the earlier view of Bruchmann (1905).

Despite considerable study of the leafless cylindrical structures that arise at the angles of shoot branching in *Selaginella*, the morphological interpretation of these structures remains an open question. Final resolution of the root–rhizophore controversy must await further investigation.

Webster & Jagels (1977) investigated the development of aerial roots in *S. martensii* grown under experimental conditions. Aerial roots (capless, hairless, and with green tips) were directed into moist bottles so that the tips were prevented from touching a solid surface as they grew through the air. Under the humid conditions produced inside the bottle, the roots grew, branched dichotomously, and formed root caps followed by root hairs. During development there was a gradual loss of pigmentation in the root apices, so that by the time caps and hairs were formed, the tips were colorless. Sections showed that the green color of aerial root tips resulted from chloroplasts in the cortex, whereas the same region in colorless root tips (with caps and hairs) contained amyloplasts. Developmental changes in plastid structure were also followed with the transmission electron microscope. From their observations, Webster & Jagels (1977) concluded that the leafless cylindrical organs arising from angle-meristems of *S. martensii* are roots, and they refuted the concept of a rhizophore. They also suggested that the presence of a root cap may be necessary in order for root hairs to be formed and showed that neither physical contact nor darkness are necessary conditions for caps and hairs to be formed.

A study by Grenville & Peterson (1981) provided further details of the root cap and apical meristem in aerial and subterranean roots of *S. kraussiana*. They noted the presence of a thick cuticle over the surface of the bulbous root cap of the aerial root and suggested that its role might be to prevent desiccation as the root grows through the air toward the soil. They also noted a lack of statolith starch in the root cap of aerial and subterranean roots, both of which are positively geotropic. They pointed out that a study of the mechanism of geotropism in *Selaginella* is needed. Although their study showed certain structural differences between aerial and subterranean roots of *S. kraussiana*, Grenville & Peterson (1981) concluded that the organ is a root throughout its development, an interpretation that agrees with that of Webster & Steeves (1964).

Bilderback (1985, 1986) recently reported on tropic responses of rhizophores (aerial roots) of *Selaginella kraussiana*. When branching shoot tips bearing young rhizophores were oriented in a horizontal but inverted position on nutrient agar and illuminated from above, erect rhizophores grew away from light and toward gravity. In darkness, rhizophores grew in wide arcs toward gravity. Bilderback (1985) concluded that the weak geotropic response of the rhizophore is intensified by light. In another study, Bilderback (1986) oriented shoots so that the rhizophores were in a horizontal position, and illumination was from below. After five hours the tips bent 90° away from light. When placed in darkness, the rhizophore tips bent only 30° toward gravity. Removal of 2–3 mm of the tip prevented bending of the rhizophore away from light; however, decapitated rhizophores treated with abscisic acid in lanolin did bend away from light. Bilderback (1986) suggested that the strong negative phototropic reaction of the rhizophore may be mediated by abscisic acid.

Karrfalt (1981) studied the root system of *S. selaginoides*. As in other species of *Selaginella*, the first three roots are produced from the young sporeling. However, unlike typical species of *Selaginella*, subsequent roots arise from a swollen root-producing meristem at the base of the hypocotyl, and no roots are formed from angle-meristems along the shoot. Thus, a total of only 8–10 roots are produced in *S. selaginoides*. Karrfalt (1981) considered earlier comparisons of *S. selaginoides* with certain fossil arborescent lycopsids (e.g., *Stigmaria*) as invalid; rather, he considered *S. selaginoides* to represent a condition in which the juvenile (sporeling) method of root formation, which normally accounts for only the first three roots, is retained in the adult plant. A thorough reinvestigation of the morphology of *S. selaginoides*, including both vegetative and reproductive organs, is in order. Whether the unusual morphology seen in this isophyllous species represents a primitive or an advanced condition is not clear at this time. The relationship of *S. selaginoides* to the other isophyllous species of *Selaginella* and to the genus as a whole is poorly understood and in need of further investigation.

The angle-meristem of *Selaginella* is one of the few examples of a truly undetermined meristem—one that has the potential to develop as either a root or as a shoot (Halperin, 1978). This morphogenetic plasticity may be indicative of a primitive nature and thus have a bearing on certain phylogenetic questions in *Selaginella*. Several recent studies have examined the developmental potential of angle-meristems.

Webster (1969) examined the effect that auxin has on angle-meristem development in *S. martensii*. In this study, Y-shaped shoot segments, each bearing a dorsal and a ventral angle-meristem, had either plain lanolin or lanolin containing auxin applied at the distal cut surfaces. In the presence of exogenously supplied auxin, angle-meristems developed as roots, whereas in the absence of auxin, shoots were formed. The results also showed that precocious development of a ventral angle-shoot could influence the dorsal angle-meristem to develop as a root. Destroying the ventral angle-meristem by puncturing resulted in development of a dorsal angle-shoot. Presumably the ventral angle-shoot acted an an auxin source to control dorsal development.

Cusick (1953) analyzed the shoot system of *S. willdenovii* and noted that at each bifurcation of the main shoot axis a dorsal and a ventral angle-meristem are present. For any given shoot branching, the ventral angle-meristem is the first to develop and produces a rhizophore (aerial root); the corresponding dorsal angle-meristem is delayed in its development and produces a shoot. In isolated shoot segments of *S. willdenovii*, Cusick (1954) was unable to alter, by surgical treatments, the position of leaf primordia arising on ventral angle-shoots. He reasoned that growth centers for leaf primordia were already present in the dormant angle-meristem; therefore auxin, either from the intact axial shoot or applied distally to isolated stem segments, must allow the development of the apical but not appendicular growth centers, and a rhizophore results. In the absence of auxin, appendicular growth centers are no longer inhibited, leaf primordia develop, and an angle-shoot results. Based on his experiments with *S. willdenovii*, Cusick (1954) suggested that, in ontogeny, the angle-meristem is basically an embryonic shoot, and rhizophore formation involves a secondary change in the pattern of growth.

In a series of articles, Wochok & Sussex (1973, 1974, 1975, 1976) further examined morphogenesis in the root and shoot system of *S. willdenovii*. Using ^{14}C-indoleacetic acid they traced auxin transport in the shoot system and developed a hypothesis for auxin regulation of angle-meristem development in *S. willdenovii*. As will be recalled from the previous work by Cusick (1953, 1954), at each bifurcation of the main shoot axis, a dorsal and a ventral angle-meristem are formed. The ventral angle-meristem is the first to develop and forms a root; the dorsal angle-meristem develops later and produces a shoot. In a study of auxin transport in the stem, Wochok & Sussex (1973) found that auxin transport was polar through the stem axis, but in the region of shoot branching there was lower auxin concentration on the ventral side of the shoot and a higher concentration on the dorsal side. These findings were related to the observed development of angle-meristems. Wochok & Sussex (1973) hypothesized that in the region just behind the shoot apex, the high auxin concentration inhibits development of both angle-meristems. Further behind the apex, the reduced auxin concentration on the ventral side initiates development of the ventral angle-meristem, and the auxin level results in determination as a root. In branchings still further behind the apex, the auxin concentration to the dorsal surface is decreased, and the dorsal angle-meristem is stimulated to develop as a shoot because of a lower auxin level. This hypothesis was further related to the complex stelar pattern in *S. willdenovii*, which includes a tristelic condition in the main axis of the shoot.

An examination of auxin transport in the root showed that auxin moved predominately in an acropetal direction (Wochok & Sussex, 1974). This was cited as physiological evidence that the leafless cylindrical organ arising at the angles of shoot branching in *S. willdenovii* is a root and not a shoot.

In another study of angle-meristem development in *S. willdenovii*, Wochok & Sussex (1975) used triiodobenzoic acid (TIBA), an auxin inhibitor. When TIBA was applied in lanolin paste around the stem in a region just behind the shoot tip of intact plants, both dorsal and ventral angle-meristems in the vicinity developed as leafy shoots. When dorsal angle-meristems were excised and grown in sterile culture, they developed as leafy shoots on an auxin-free medium and as roots on a medium containing auxin. Dorsal angle-meristems transferred after excision from auxin-free to plus-auxin medium on successive days showed an increasing tendency to develop as shoots. From these results the authors suggested that dorsal angle-meristems undergo a change in developmental potential. That is, after 1–3 days in culture most dorsal angle-meristems could still be influenced by exogenous auxin to develop as roots. However, after 5 days a majority of dorsal angle-meristems had been determined as shoots and could not be "redetermined" by auxin as roots.

Wochok & Sussex (1976) also studied the developmental potential of excised root tips of *S. willdenovii*. When roots approximately 20 mm or less in length were grown in sterile culture on an auxin-free medium, approximately 20% of them developed as leafy shoots. When root tips were grown on a medium containing auxin, only roots were produced. Thus it was shown that auxin prevents redetermination of the root apex as a shoot, and the reason redetermination does not occur in the intact plant may be that auxin is transported toward the root tip where it exerts its control.

Finally, Jernstedt & Mansfield (1985) used a chemical approach to interpret the nature of the so-called rhizophore. Using two-dimensional gel electrophoresis, they compared polypeptides from the vegetative organs of *S. kraussiana*. Of the more than 600 polypeptides resolved, 18% were found in all four vegetative organs (leaves, stems, roots, and rhizophores). Comparisons between pairs of organs revealed that stems and rhizophores showed the greatest similarity with 58% of their polypeptides in common, while for rhizophores and roots, 42% of their polypeptides were similar. They also found that stems and rhizophores had the largest number of polypeptides unique to a pair of organs (95), while rhizophores and roots shared fewer unique polypeptides (5). Jernstedt & Mansfield (1985) concluded that, at the abundant gene-product level, stems and rhizophores are more similar than are rhizophores and roots. Further, the results contradict the view that the rhizophore is simply an aerial phase of the root system, but, rather, indicate that the rhizophore is sufficiently distinct to be placed in the organ category. Finally, the results refute the interpretation that rhizophores and roots are homologous organs.

The above studies indicate that organography in *Selaginella* is somewhat plastic, so that the same meristem (angle-meristem) may develop as either a root or a shoot, depending on the conditions of growth. This, along with the other unusual features of the aerial root or rhizophore indicate that in *Selaginella* root and shoot are not so distinct and suggest a somewhat primitive state of organography. Such a conclusion seems reasonable in view of the antiquity of the genus. In this connection, it should be pointed out that in certain Devonian fossils, branchlike structures (called axillary tubercles) have been found associated with angles of shoot branching. Banks & Davis (1969) hypothesized that the axillary tubercles of *Gosslingia* and *Crenaticaulis* may represent rhizophorelike branches similar to those in modern *Selaginella*. However, in a general discussion of axillary tubercles, Edwards (1970) suggested that the structure probably represents the base of a branch, which was either abscised prior to preservation or was lost during preservation.

REPRODUCTIVE MORPHOLOGY

HETEROSPORY

An important feature in the reproductive biology of *Selaginella* is heterospory (Fig. 1). Despite the fundamental importance of heterospory to plant evolution, neither the physiological basis nor the origin of this phenomenon are presently well understood. Sussex (1966) has discussed the origin and development of heterospory in general, and Pettitt (1971, 1977) has investigated certain aspects of heterospory for *Selaginella*, specifically, megasporocyte degeneration and post-meiotic regression of megaspores and microspores. Recently, Haig & Westoby (1988) proposed a theoretical model to account for the origin of heterospory. However, despite these and other discussions, many critical questions about heterospory remain unresolved.

SPORANGIAL DEVELOPMENT

Horner & Beltz (1970) studied the early stages of sporogenesis in *S. pilifera* and compared developing microsporangia and megasporangia with respect to certain features. They noted that, in pairs of sporangia, megasporangia were slightly larger than microsporangia from an early stage of development. In the microsporangium, sporogenous tissue stained intensely for RNA, whereas in the megasporangium of corresponding age, only a single cell of the sporogenous tissue stained. Furthermore, whereas each sporogenous cell in the microsporangium was surrounded by callose, in the megasporangium only the RNA-positive (functional) sporocyte developed a callose wall. Based on these findings, the authors suggested that the formation of a callose wall around the single functional sporocyte serves to isolate that cell in the sporangium, resulting in differentiation in a new direction. A causal mechanism for the determination of megasporogenesis versus microsporogenesis is as yet unclear, however.

Using length of sectioned sporangia as an index, French (1972) examined growth relationships in developing megasporangia and microsporangia of *S. bigelovii*. Strobili of *S. bigelovii* usually contain two vertical rows of megasporangia and two rows of microsporangia, and, at each node, a megasporangium is opposite a microsporangium. French (1972) discovered that for a pair of decussate sporangia, prior to sporocyte formation the megasporangium was larger and elongated more rapidly than the corresponding microsporangium. Also, although there was an increase in the number of sporogenous cells in both sporangial types in early development, this increase in sporogenous cell number ended at a lower growth index in megasporangia than in microsporangia. Thus the differences in growth relationships observed by French (1972) indicate that events that ultimately lead to the development of microsporangia and megasporangia occur prior to the onset of sporocyte degeneration.

Brooks (1973) studied the effects of ethylene on the determination of sporangia in *S. wallacei* and *S. pallescens*. In plants sprayed with distilled water, strobili produced a high proportion of microsporangia, whereas plants sprayed with Ethephon, an ethylene-releasing compound, produced a high proportion of megasporangia. Brooks (1973) speculated that sporangial determination in *Selaginella* may rely on the effects of ethylene on plant cells. He noted that ethylene is known to inhibit or retard cell division as well as accelerate or induce cell degeneration in certain plant tissues. Therefore, a high endogenous level of ethylene could result in one less division in cells of the sporogenous tissue, producing fewer sporocytes per sporangium, and in the degeneration of most of them. Eventually sporocyte degeneration would result in one functional megasporocyte, which would produce four megaspores by meiosis. In the absence of an inhibitory level of ethylene, the final cell division would occur in the sporangium, followed by very little sporocyte degeneration, and ultimately result in numerous sporocytes in a microsporangium. Further work is necessary to prove this hypothesis, and future investigations should include the effects of other growth regulators on sporangial development.

Horner & Arnott (1963) examined sporangial arrangement in strobili from 30 North American species of *Selaginella* and described four patterns:

I. Basal megasporangia and apical microsporangia;
II. Two vertical rows of microsporangia and two vertical rows of megasporangia;
IIa. Two vertical rows of microsporangia and two vertical rows containing a mixture of microsporangia and megasporangia;
III. Wholly megasporangiate strobili.

They concluded that arrangement of sporangia can serve as a taxonomic tool. Of particular interest is *S. rupestris*, which exhibits patterns I and III; the populations exhibiting these two patterns can be separated geographically. Pattern I plants occur in the Appalachian mountain region and are presumably sexual, whereas Pattern III plants occur throughout the rest of the range and are apomictic. Horner & Arnott (1963) also suggested that the primitive condition is represented by Pattern I, from which the other patterns are derived.

An unusual variation of sporangial development was reported by Webster (1974). In *S. umbrosa* grown under greenhouse conditions, cones were microsporangiate but also exhibited an abundance of abortive sporangia. In addition, occasional small green vegetative outgrowths ("sporangioids") were found in the position of sporangia. These small cylindrical structures contained tissues resembling epidermis and cortex, as well as a central strand of tracheids. The exact nature and significance of sporangioids remain to be determined, as are the possible factors that account for their occurrence.

Recent studies on the morphology of microsporangia in *Selaginella* have provided insight into mechanisms of spore dispersal. Somers (1982) examined the microsporangium of series *Articulatae*, a group of approximately 40 species including *S. kraussiana* and *S. diffusa*, and concluded that the microsporangium in *Articulatae* is more complex than that found in the nonarticulate species. The microsporangium of *Articulatae* is characterized by two broad annuloid bands of thick-walled cells that play an important role in dehiscence. The presence of these bands suggests a more advanced condition not found in the microsporangium of other species of *Selaginella*. Somers (1982) argued that the highly developed microsporangium, together with several other characteristics, is sufficient to elevate the *Articulatae* to the status of subgenus.

In an examination of 53 species of *Selaginella*, Koller & Scheckler (1986) recognized five types of microsporangia that exhibit three spore dispersal mechanisms. In the passive type, there is little cell modification among the cells of the sporangium.

Dehiscence occurs along the distal surface and continues down the sides, resulting in two valves that bend outward, and the microspores simply sift out passively between the two valves. Most species exhibiting this mechanism are isophyllous and inhabit xeric environments. *Selaginella wallacei* is an example of the passive type of microsporangium. The spore-ejector type relies on a distinct area of dead water-filled cells within the sporangial wall. Koller & Scheckler (1986) recognized two subtypes within this category: the central subtype, characterized by an ovoid region of dead water-filled cells in the center of each valve; and the basal subtype, characterized by a reniform region of dead water-filled cells in the basal half of each valve. In each subtype, sporangial cells exhibit uneven wall thickenings resulting in active dispersal of microspores. As the sporangium dries and dehisces, the two valves bend away from each other, sometimes reaching an angle between them of 150°. The valves then snap back toward their original positions, ejecting a large portion of microspores. The valves may reflex and snap several times, effectively ejecting all the spores from the sporangium. After dehiscence is complete, the cells previously filled with water contain gas bubbles. The spore-ejector type of sporangium was observed in a number of anisophyllous tropical or subtropical species. *Selaginella emmeliana* is an example of the central subtype, and *S. plana* represents the basal subtype.

The sporangium-ejector type was found only in series *Articulatae* and was described previously by Somers (1982). The prominent feature of this sporangial type is the raised band of large cells extending around the sporangium. Koller & Scheckler (1986) noted that these cells are dead and water-filled, with uneven thickenings. At the time of dehiscence the two valves bend with such force that the microsporangium is torn from the strobilus and ejected for a distance up to 20 cm. A series of snapping motions completes spore ejection from the dispersed microsporangium. Once dehiscence is complete, the raised band of cells contains gas bubbles instead of water. Koller & Scheckler (1986) distinguished two subtypes based on minor anatomical differences, with *S. kraussiana* considered to be distinct from other members of *Articulatae*.

The authors suggested that the spore-ejector types have a dispersal mechanism similar to that of a fern leptosporangium, which relies on an annulus of distinctive cells. It was further suggested that the dispersal mechanisms described, particularly the sporangium-ejector type, enhance outcrossing in *Selaginella*. The passive type, which results in spores shed near the base of the parent plant, would be more likely to restrict the amount of outcrossing.

A recent study by Page (1989) described the dispersal mechanisms for both the microsporangium and megasporangium of *S. selaginoides*. Whereas microspore dispersal is passive in this species, megaspore dispersal is active, and, under experimental conditions, may result in discharge of megaspores for distances of over 2 m from the parent cone.

The studies by Somers (1982) and Koller & Scheckler (1986) have added significantly to our understanding of microspore dispersal in *Selaginella*. Further studies comparing dispersal mechanisms for both microsporangia and megasporangia of the same species, such as the recent investigation by Page (1989), are needed.

GAMETOPHYTE DEVELOPMENT

The gametophyte generation of *Selaginella* has received far less attention than the sporophyte. The small size of the endosporic microgametophytes and megagametophytes makes them more difficult to study and perhaps gives the impression that there is little variation in gametophyte morphology throughout the genus. In recent years, Robert has studied the development of the gametophytes of *S. kraussiana* in some detail. In his study of the microgametophyte of *S. kraussiana*, Robert (1973) described a two-staged ontogeny: (1) the formation of the antheridium and divisions resulting in a number of spermatogenous cells (spermatids), and (2) the differentiation of spermatids into spermatozoids. The mature microgametophyte consists of a single lenticular prothallial cell and an 8-celled antheridial jacket surrounding 256 spermatids. This study of the general organization of the male gametophyte was followed by a detailed description of spermatogenesis (Robert, 1974). The mature spermatozoid is 25 μm in length with two asymmetrical flagella. The organelles in the narrow sperm are linear. These include an anterior centriole, an elongate mitochondrion, and a nucleus. Toward the posterior pole is a posterior centriole and flagellum, a plastid, and a mitochondrion. In comparing the sperm of *S. kraussiana* to sperm in other archegoniates, Robert (1974) noted similarities to those of bryophytes. On the other hand, the sperm of *S. kraussiana* does not seem to have features in common with other pteridophytes, a conclusion also reached in an earlier study by Yuasa (1933).

Robert (1971a, b, 1972a) also provided a detailed account of megagametophyte development in *S. kraussiana.* The megagametophyte of this species is unusual in that a thickened diaphragm divides the gametophyte into two distinct regions: the reproductive tissue from which archegonia and rhizoids form, and a food reserve region rich in lipids and proteins (Robert, 1971a). Robert went on to describe these regions in detail (Robert, 1971b, 1972a). He pointed out that, although large numbers of archegonia are formed, at any given time only one or two, sometimes none, have their necks open and thus are capable of being fertilized. He also described certain complexities exhibited by the egg, features not found in the eggs of other archegoniates. During oogenesis there is a redistribution of organelles, resulting in a marked polarity of the mature egg. There is an apical region of mitochondria, a peripheral and median region of Golgi bodies, and a basal region rich in endoplasmic reticulum. The plastids that occur around the nucleus also undergo certain changes during oogenesis. He also noted the occurrence of certain structures of undetermined origin. The result is a highly polarized egg cell of considerable complexity, the significance of which will be discussed later.

Wetmore & Morel (1951) were able to maintain sterile cultures of megagametophytes of *S. pallescens* and *S. flabellata.* They cultured the megagametophytes on Knudson's medium supplemented with 2% glucose and a mixture of vitamins. At the end of six months a globular mass of tissue approximately 1 cm diam. was obtained. By subculturing every three months they were able to maintain the tissue cultures for two years. Under the culture conditions employed, the prothallus lost its normal organization; that is, after their initial appearance, rhizoids and archegonia failed to be produced, and only unpigmented parenchyma cells were formed. The culture was thus similar to higher plant tissue cultures lacking organization, i.e., a callus.

Bruchmann (1912) studied embryology in a number of species of *Selaginella,* including *S. kraussiana.* The embryology of *S. kraussiana* is of particular interest because of certain unusual developmental features. Soon after fertilization of the egg, the basal wall of the archegonium elongates to form a tube. This "embryo tube" carries the zygote to the center of the reserve tissue where the embryo is initiated. Robert (1972b) speculated that this unusual development may result from certain structural complexities of the egg of *S. kraussiana* discussed above (Robert, 1972a). Further embryological studies of *Selaginella* using modern techniques are needed because, as noted by Gifford & Foster (1989), most of our present knowlege is based on a few early studies.

Finally, recent studies (Webster, 1979; Webster & Tanno, 1980; Tanno & Webster, 1982a, b) have used artificial crossing techniques to determine the inheritance of pigmentation in *Selaginella.* In *S. kraussiana* var. *aurea,* the *aurea* character is controlled by a single nuclear gene exhibiting incomplete dominance, whereas *S. martensii* forma *albovariegata,* a variegated variety, exhibits maternal cytoplasmic inheritance of pigmentation. The crossing technique (Webster, 1979) used in these studies allows for direct observation of certain aspects of the life cycle of *Selaginella* and raises several questions for future investigations. For example, the most dramatic feature observed during hybridization experiments with *Selaginella* is the strong chemotactic response. Almost immediately after megagametophytes and sperm are mixed in a droplet of water on a depression slide, attraction of sperm to the archegonial region of the megagametophyte can be detected with the light microscope. Within minutes, a sizable cloud of swimming sperm is visible around the archegonia. The chemical nature of the chemotactic principle in *Selaginella* has yet to be identified. Preliminary observations (Webster, unpublished) suggest that the chemotactic response is rather general, because for example, sperm of *S. kraussiana* are readily attracted to megagametophytes of *S. martensii,* an unrelated species (and sporelings fail to result). More detailed studies of the specificity of the chemotactic response in *Selaginella* should yield interesting results. Also, the details of fertilization have yet to be examined; this would be an ideal subject for an ultrastructural study.

CONCLUDING REMARKS

The genus *Selaginella* has existed since the Lower Carboniferous (Bierhorst, 1971). Today, this remarkable assemblage of approximately 700 species is distributed worldwide and occupies a wide range of habitats from tropical to temperate, rainforest to desert. One would have to conclude that *Selaginella* is indeed an evolutionary success story. The longevity and apparent success of *Selaginella* is even more remarkable given its rather simple morphology. In the present paper an attempt has been made to call attention to certain structural features that may hold the key to a better understanding of the evolutionary status of *Selaginella.* If the basic morphology of *Selaginella* has remained essentially unchanged since the Carboniferous, then the study of extant forms of *Selaginella* should yield insights into certain aspects of early land plant evolution. Developmental studies on such enigmatic structures as the ligule, "rhizophore," and angle-meristem, and phenomena such as anisophylly, monoplastidy, and heterospory may be as relevant to the evolutionist as to the developmental botanist. Modern selaginellas lend themselves to experimentation. They are readily grown and manipulated under greenhouse and laboratory conditions. Through continued developmental studies of the vegetative and reproductive organs of *Selaginella*, insights may be gained into some of the reasons underlying the longevity and survival of this unique group of plants. Coupled with the study of extant forms should be a reinvestigation of existing fossil material of *Selaginella* to determine the extent to which the genus has changed in its morphological and anatomical details through the ages. Whether the genus *Selaginella* represents an evolutionary dead end or a group that led to higher plant forms, its modern and past history is interesting and offers ample opportunity for fruitful research in the future.

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THE MESOZOIC HERBACEOUS LYCOPSIDS

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ABSTRACT

Occurrences of lycopsid megafossils and their spores in the Mesozoic are reviewed. Subarborescent lepidodendralean forms diversified in the early Mesozoic before going extinct in the early Jurassic, although herbaceous, *Isoetes*-like forms—considered here also to be lepidodendraleans—survived to the present day as represented by the sole surviving genus *Isoetes*. Records of *Isoetes*-like forms from Triassic strata are considered questionable; the earliest good-quality examples that can currently be accepted are in the late Jurassic/early Cretaceous. The two other major groups of lycopsids that also survive today—the lycopodialeans and selaginellaleans—were present throughout the Mesozoic as entirely herbaceous forms. Some of them closely resemble extant species but most are less similar and some, such as *Synlycostrobus* with its apparently compound strobili, greatly extend our knowledge of lycopsid diversity. A few of the Mesozoic species appear to provide important and hitherto unsuspected links between these two major groups. Increasingly refined knowledge of late Paleozoic through Mesozoic lycopsids and their spores is contributing to growing precision in biostratigraphy and also in environmental changes that have affected our planet in the geological past, particularly the protracted interval of global warming that began in the late Paleozoic and continued throughout the Mesozoic. New information is presented on Mesozoic lycopsids from the United States and England, including a new species of *Isoetites* of Cretaceous age with well-preserved spores in situ.

The late Paleozoic through Mesozoic was an exciting time of transition between ancient and modern floras, bridging the gap between the Paleozoic, which had relatively few plants like those we know today, and the Tertiary (especially the late Tertiary), by which time many plants were essentially modern in appearance. Lycopsids did not escape this phase of intense biotic change; within the Mesozoic timespan of 170 million years the great tree lycopsids of the Paleozoic, i.e., the lepidodendraceans and other families, finally died out, leaving only the diminutive *Isoetes*-like forms to survive to this day. These sole survivors, still largely inhabitants of pools and swamps, bear witness to a once mighty group of swamp-forest and lacustrine organisms. On the other hand the Selaginellales and Lycopodiales, which also had their origins in the Paleozoic, continued to diversify throughout the Mesozoic as indeed they still do today. They were represented by a core of forms similar to extant species with a range of extinct forms that were more or less intermediate and some that are simply bizarre. These evolutionary changes that took place in the Mesozoic were results of global environmental changes, especially the intense climatic warming that occurred between the glaciations of the late Paleozoic and the greenhouse conditions that mark most of Mesozoic time. The dramatic effects of this warming on arborescent lycopsids in the Pennsylvanian, the Permian, and especially the early Mesozoic provide an excellent example of how ancient plants can be used as mirrors of ancient climate change, and, in the case of lycopsids, also of edaphic change. Conversely, an understanding of the effects of climatic change on ancient vegetation is contributing to increasing precision and sophistication in our awareness of how plant ecosystems have changed and developed through geologic time.

The detailed picture of lycopsid evolution in the Mesozoic is currently far from complete. The paleobotanical data base needs focussed attention if we are to appreciate relationships and climate-related global changes in vegetation through geologic time. In Mesozoic lycopsids much important material languishes unexploited in museum cabinets, while poor or poorly described material has been widely and rather uncritically accepted as providing satisfactory evidence, for example of the appearance of extant taxa such as *Isoetes*. An example to which we will draw attention in this survey is Bock's (1962) record of supposed *Isoetes* from the Triassic of North America. This is not to say that *Isoetes*-like forms definitely did not occur in the Triassic; what we conclude is that the evidence as currently expressed in the literature is unconvincing. There are many other such instances where a critical reexamination of the orig-

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inal material is needed, using modern laboratory techniques and fresh collecting.

Although this means that Mesozoic lycopsids present an especially promising area for research, they also represent an area beset with a number of challenging problems. First, although lycopsids are not especially uncommon in Mesozoic rocks (though much scarcer than in the Carboniferous), relatively few occurrences are of the quality of preservation needed to identify the material as lycopsid, let alone to characterize it properly; many of the plants were herbaceous forms that tend not to fossilize well, and important characters for their classification, such as the presence or absence of a ligule on the leaf, can be notoriously difficult to assess. As noted by Seward (1910), there is danger of confusion between lycopsids and such other contemporary groups of plants as conifers and bryophytes, when not enough characters can be seen. Second, this problem is exacerbated in the lycopsids by an asymmetry in the quality and quantity of preservation of dispersed spores versus megafossils, and conversely by the importance of in situ spore characters in identifying and characterizing megafossils. There is a wide diversity and rich abundance of dispersed megaspores worldwide throughout the Mesozoic, but the affinities of many of them remain obscure in the absence of knowledge of the megafossils and hence of the plants that produced them. Equally, there are many records of heterophyllous *Selaginella*- and *Lycopodium*-like megafossils of which the exact affinities can only be determined by reference to evidence from in situ spores as well as their vegetative characters. However, although there is an argumentatively tight circle here, it is not in practice a vicious one. The real problem is that good-quality megafossils in which both spores and vegetative parts are well preserved are uncommon, and, of those that are known, few have as yet been documented adequately using modern techniques. The solution lies in focussing future work on quality megafossils that have in situ spores preserved.

A primary objective of any review is to present and summarize the information that is reasonably well known, representing achievements that have already been made. There have been considerable advances both in the breadth and depth of knowledge of Mesozoic lycopsid diversity in recent years. Moreover, although important recent studies of Paleozoic lycopsids have cast doubt on Mägdefrau's (1956) simple picture of the arborescent lepidodendraleans evolving by reduction through *Pleuromeia* and *Nathorstiana* to *Isoetes* (see also Chaloner & Boureau, 1967), there is no doubt that whatever their botanical affinities, the intense global warming of the late Paleozoic and early Mesozoic led to the extinction of all arborescent and subarborescent lycopsids, at first in the then equatorial everwet regions sensu Ziegler (1990). All currently known fossil species of lycopsids surviving into or newly evolving in the mid-Jurassic through Cretaceous were herbaceous, at least to the extent that all extant lycopsids can be regarded as herbaceous. Among the objectives of the review, therefore, is an attempt to comment critically on available records as reported in the literature, so far as is possible without direct examination of the specimens themselves, and thus to focus on especially worthwhile material for future research (whether from renewed collecting or in existing collections). Utilizing our own research material, an additional objective is to illustrate directly the range in quality of preservation of Mesozoic material and some of the successes as well as difficulties attendant on its study. Reflecting the major floristic change, this review begins with the mainly subarborescent lepidodendralean forms of the early Mesozoic, followed by a discussion of the dispersed spore record of Mesozoic lycopsids in general and then by the herbaceous fossils of the Lycopodiales and Selaginellales, which are mostly of later Mesozoic age, and ending with Isoetales and allied forms. Thus, the *Isoetes*-like lepidodendraleans are treated separately from the arborescent ones, on purely arbitrary grounds. The review is concluded with a brief discussion on phylogenetic relationships.

The Subarborescent Lepidodendraleans of the Early Mesozoic (Triassic–Early Jurassic)

ANNALEPIS-LEPACYCLOTES

Annalepis is represented by large, well-preserved sporophylls with pointed apices, 2.5–4.5 cm long, 1–2 cm wide, described in detail from the middle Triassic of France by Grauvogel-Stamm & Duringer (1983). The sporophylls are monosporangiate and have yielded either megaspores of *Tenellisporites/Dijkstraisporites* type or monolete microspores referable to *Aratrisporites*, a miospore (spore less than 200 μm, see Traverse, 1988) that is stratigraphically useful and which occurs widely as a dispersed spore in Triassic rocks. Although the authors' estimate of at least 14 cm diameter for the reconstructed strobilus may be too large, the cone was certainly no less than 9 cm wide at its widest point and thus represents the largest of any known Mesozoic lycopsid. Comparable but less complete and somewhat smaller sporophylls from China, also with in situ spores, have been identified with *Annalepis* by Wang & Lou (1990). In addition, it seems possible that the vertically compressed strobilar discs named *Isoetites* (*Lepacyclotes*) *circularis* (Emmons) by Brown (1958) may be generically equivalent (Bock, 1969), and possibly the material of Daugherty (1941: pl. 12, figs. 1, 2, but not pl. 15, figs. 1, 2). These specimens deserve fresh study.

If the North American material proves congeneric with *Annalepis*, it may be significant that there is a regional association with structurally preserved axes 1–2 cm wide described by Daugherty (1941) as *Chinlea* and *Osmundites walkeri* and referred to the lycopsids by Miller (1968). Other rare early Mesozoic stems such as *Grammaeophloios* (up to 3.5 cm wide) of Harris (1935) and the considerably larger *Ferganodendron* Dobruskina (1974) represent more substantial axes of the kind that might have been necessary to support *Annalepis/Lepacyclotes* sporophylls.

PLEUROMEIA

The "classic" subarborescent lycopsids of the Triassic, figured in almost every textbook on paleobotany, are those attributed to *Pleuromeia* (Fig. 1). This genus, often preserved spectacularly in permineralized form, is known from many mid-latitude Northern Hemisphere localities of early to middle Triassic age (see Mägdefrau, 1931; Neuburg, 1960; Dobruskina, 1974; Wang & Wang, 1982; but cf. Retallack, 1975, who includes the Southern Hemisphere genus *Cylostrobus* and other non-pleuromeian material). The plants ranged from 2–30 cm in height, i.e., distinctly herbaceous (Wang & Wang, 1982), to more typically 2–3 m. They were heterosporous but the strobili were monosporangiate, with rounded, partly sunken sporangia borne adaxially on sporophylls of a distinct broad ovate form unique to the genus. The sporophylls were crowded to give the strobilus an imbricate appearance. In situ spores were trilete and have been described by Neuburg (1960), Chaloner & Boureau (1967), and Yaroshenko (1975). Anatomical structure was studied by Snigirevskaya & Srebrodolskaya (1986). Srebrodolskaya (1988) showed that cambial activity at certain levels in the axis was lacking. This suggests an herbaceous to suffrutescent habit even for the larger species. Although the basal anchoring organ of the larger forms was four-lobed, like a highly reduced lepidodendralean rhizophore, that of the diminutive herbaceous (though fully fertile) forms is simply bulbous, with no apparent lobing.

As noted by Retallack (1975), rooted plants at Bernberg were almost certainly growing in freshwater, as were those described by Wang & Wang (1982). Evidence that some stands or species grew in, as opposed to being deposited in, brackish environments as claimed by Retallack (1975) is in need of critical reappraisal. The common environments of deposition that are preserved in the sedimentary record for most Mesozoic plants were coastal plain/deltaic or shallow marine. Monodominant assemblages may be locally or regionally derived, that is, of two distinct types. Although they may indicate actual growth in brackish environments such as marine embayments, discrimination of the exact situation for *Pleuromeia* is not entirely clear from the evidence Retallack presented. For organic remains, as with inorganic clastic particles, a resulting assemblage may merely reflect the characteristics of the sediment supply. If *Pleuromeia* stands formed the dominant vegetation over large areas within the drainage basin, they would also, inevitably, form the dominant fossils in a range of depositional settings. Such an example is often provided by *Equisetum* in Mesozoic rocks. Accordingly, the reconstruction in Figure 1 presents *Pleuromeia* as a plant of freshwater clastic swamps rather than coastal brackish ones. Whether such places in the Triassic may have been saline in the sense that inland lakes of arid regions today can be saline is not addressed. It is clear that *Pleuromeia* grew in inorganic clastic, rather than organic-rich, dominated swamps.

CYLOSTROBUS-SKILLIOSTROBUS-TOMIODENDRON-LYCOSTROBUS

A number of large cones and stem remains, known best from the Southern Hemisphere, have been described. Currently, the most useful account is that of Ash (1979) for *Skilliostrobus.* Known essentially from isolated rounded to ovate strobili, *Skilliostrobus* contrasts markedly in shape and sporophyll form with the more elongate strobili of *Pleuromeia.* They were heterosporous and bisporangiate, and the wedge-shaped unisporangiate sporophylls bore, in *Skilliostrobus* and in some of the species referred to *Tomiostrobus,* a narrow distal limb unlike sporophylls of *Pleuromeia.* Some of the figured sporophylls look remarkably like *Isoetes* sporophyll bases (Neuburg, 1936).

The in situ megaspores of *Skilliostrobus* appear similar to *Horstisporites/Maiturisporites* and the monolete microspores are of *Aratrisporites* type as in *Annalepis*, both types of spores being quite unlike those of *Pleuromeia.* Whether *Skilliostrobus* strobili were genuinely pedunculate as de-

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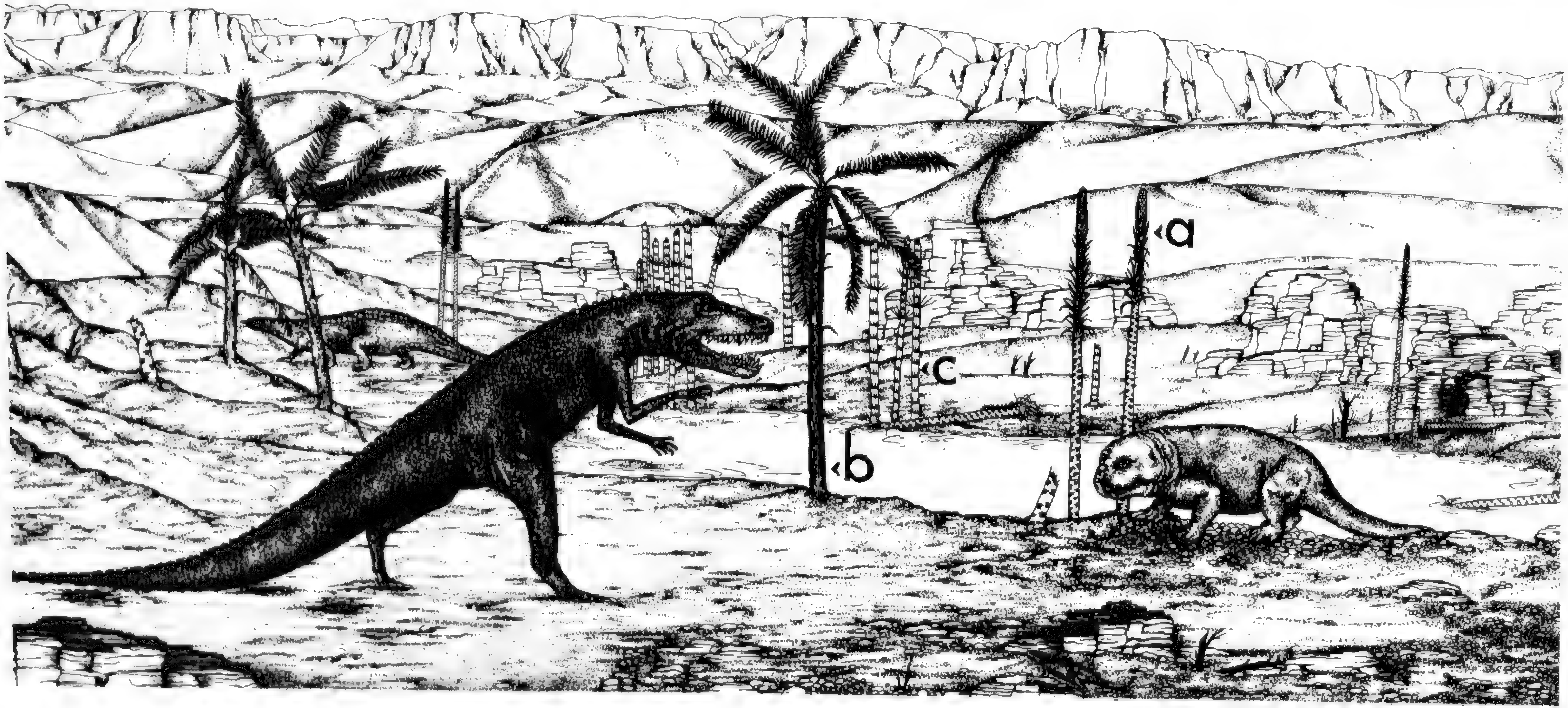

FIGURE 1. Reconstruction of Triassic landscape showing *Pleuromeia* (a) in its likely habitat, together with *Leptocycas* (b) and *Equisetum* (c). Drawing by P. Laird based on information collated by C. R. Hill.

scribed by Ash is, we believe, unlikely. As is often the state of preservation in *Pleuromeia, Skilliostrobus* may have been borne on a broader axis than figured by Ash, with a wide cortex that tended to rot away, leaving the woody stele in the center. Mature strobili may have been abscised, as appears to have been the case in *Pleuromeia.*

It is likely that the structure described by Chaloner & Turner (1987) from Queensland is a denuded permineralized cone of *Skilliostrobus* type. Comparable structurally preserved material currently under study by D. Cantrill, Melbourne, will undoubtedly advance our knowledge of Australian Triassic lycopsids. This material may help to clarify the uncertain relationship of *Skilliostrobus* to the other large, similar but more elongate Triassic cones and plants from the Southern Hemisphere. One of these plants is described under the name "*Pleuromeia longicaulis* (Burges)" by Retallack (1975), which has stems of broadly pleuromeian/*Nathorstiana* type, up to ca. 1 m long and ca. 2.5 (?) cm broad. Others are *Cylostrobus* Helby & Martin and *Cylomeia* White. White (1981) illustrated a series of fine vegetative specimens bearing long microphylls that in one species appear to have been clearly trabeculate as in *Isoetes.* She presented evidence that the leafy stems bore *Cylostrobus* strobili, with which they are intimately associated, at their apices. It should be noted that this material is well preserved, with in situ spores (Helby & Martin, 1965). It clearly deserves further detailed study using modern techniques and thorough nomenclatural revision.

In comparison to this promising Australian material, most other records of similar-looking strobilar fragments and isolated sporophylls are of relatively little significance as presently described (see e.g., Sadovnikov, 1982, and Neuburg, 1936) except as indicators of geographical distribution. Sadovnikov (1982) assigned *Skilliostrobus* to *Tomiostrobus* without any evidence other than broad similarity in morphology of the sporophylls. Nevertheless, some of the Russian specimens do indicate the widespread occurrence of material broadly like that from Australia. *Austrostrobus ornatum* is a strobilus from Argentina described by Morbelli & Petriella (1973), which is undoubtedly similar to *Cylostrobus* and the two genera were formally synonymized by Retallack (1975).

Nathorst's (1908) beautifully illustrated *Lycostrobus scottii* from the Rhaetic (or Liassic) of Sweden (see Chaloner & Boureau, 1967) is a cylindrical strobilus with highly distinctive megaspores unlike those of the Australian material. It also deserves additional study.

SPORE DATA: DISPERSED SPORES

Dispersed spores attributable to the lycopsids are widespread throughout the Mesozoic. Although quantitatively they are usually a minor component of the total palynomorph assemblage, they are often biostratigraphically useful (Traverse, 1988; Kovach, 1988; Kovach & Batten, 1989; Batten & Kovach, 1990). They can be locally abundant, but they never form spore-dominated coals as in the Paleozoic. The increasing quality of the megafossil record and of studies on in situ spores contained within megafossils means that an increasing range of dispersed Mesozoic spores can now be attributed directly to the parent plants. Thus, of the Triassic lycopsids reviewed above, several species enable contemporary dispersed spores to be related to megafossils. Conversely, for example, the global and biostratigraphically limited occurrence during the Triassic (Traverse, 1988; Grauvogel-Stamm & Duringer, 1983) of the cavate monolete spore *Aratritriletes* Leschik (produced by *Cylostrobus, Skilliostrobus,* and *Annalepis*) underscores the widespread occurrence of the various parent plants, even though their megafossils are known from relatively few localities.

MEGASPORES AND MICROSPORES

Several dispersed megaspore genera that have been used extensively in Mesozoic biostratigraphy (see e.g., Marcinkiewicz, 1981; Fuglewicz, 1980) are now known in situ from Triassic material, notably: *Tennellisporites* (in *Annalepis* from France); *Dijkstraisporites, Banksisporites,* and *Laevigatisporites* (*Annalepis* from China, see Wang & Lou, 1990); *Horstisporites* and *Maiturisporites* (in *Skilliostrobus*); and *Banksisporites* (from *Cylostrobus*). In addition, Scott & Playford (1985) reported occurrences of *Aratrisporites* microspores attached to the surfaces of *Banksisporites* and *Nathorstisporites* dispersed megaspores.

The position in the Jurassic and Cretaceous is less satisfactory because relatively few lycopsid spores of the later Mesozoic have been linked directly to megafossils as in situ occurrences, principally the megaspore *Minerisporites* to *Isoetites* megafossils, and various trilete small spores named *Lycospora* (Traverse, 1988) or *Lycopodiumsporites* (Couper, 1953). Monolete dispersed spores have been named *Monolites* (Couper, 1953).

However, since most of the currently known Jurassic–Cretaceous megafossils are fairly similar to extant lycopsids, it is also reasonable to take a different approach: to postulate affinities of the dispersed spores *indirectly*, by reference to in situ spores of the extant taxa, such as Hueber (1982) did for megaspores of the Lower Cretaceous Potomac Group. Such comparison has been undertaken with increasing precision in recent years by Batten (1988), Kovach & Dilcher (1988), Kovach (1989), and Koppelhus & Batten (1989). As Batten has pointed out, the problems in this regard are illuminating in that they reflect as much on the current limited state of knowledge of extant spores as on that of the fossils. Moreover, particular problems arise with extant *Isoetes*, in which the megaspores may possess a silicified perispore that is often not preserved in fossil megaspores. Thus, although there are several exemplary studies of the megaspores of the extant plants (e.g., by Hickey, 1986a), the data are rarely in a form suitable for comparison with fossil spores and vice versa (see also Pant & Srivastava, 1962). Added to this, in past treatments of the extant spores (and to an extent of fossil ones following the system of Potonié, 1956), a narrow range of such characters as surface sculpture has been emphasized at the expense of other characters with the predictably unfortunate consequence of holding up scientific progress for many years (Hickey, 1986a). Once a wider range of characters was employed an important biological reality became clear, that megaspore variation in *Isoetes* can be considerable within "species" and within populations, leading to convergence of spore characters in many cases. The biological basis for this lies in growing chromosomal, ecological, and morphological evidence for frequent hybridization and allopolyploid speciation indicating a highly complex evolutionary history for *Isoetes*. This is only now beginning to be clarified (Hickey, 1986b; Hickey et al., 1989; Taylor & Hickey, 1992). Additional work is needed on extant spores in the context of this growing knowledge of the biological relationships of *Isoetes*, with reference to a wide range of spore characters such as the "secondary ornamentation" features referred to by Hickey (1986a) as well as to those of surface sculpture, and, if comparisons with fossil spores are to be effective, both before and after removal of the siliceous perispore with hydrofluoric acid.

A more sophisticated recent approach by leading fossil megaspore workers is a critical assessment of the infrastructure of lycopsid megaspore exines. Stimulated by pioneering transmission electron microscope (TEM) studies of sectioned extant material, undertaken in Europe during the 1960s and 1970s by Martens, Pettitt, and Stainier (see Koppelhus & Batten, 1989, for references), Kovach and Batten have recognized that a fundamental difference in exospore construction exists between megaspores of extant *Isoetes* and selaginellaleans at the ultrastructural level. In *Isoetes* the megaspore exospore is composed dominantly of a three-dimensional reticulate network of threads in which the main orientation of the threads and airpores between them is more or less parallel with the spore surface, whereas in selaginellaleans much of the exposure is usually constructed from a mesh of tightly packed threads and/or robust rods, with less intervening porespace than in *Isoetes* exospores and with the elements at more variable angles to the spore surface. Additionally, in some selaginellaleans the exospore is constructed of tightly packed granules that are organized into distinctive geometrical patterns (Kovach & Batten, 1989).

Kovach (1989) described a relatively simple laboratory procedure for obtaining megaspore exospore sections for examination by scanning electron microscopy (SEM). Using such sections he selected two consistently measurable infrastructural characters for quantitative study: (a) porosity, and (b) variability in orientation of the elongate pores (airspaces)—measured as angles relative to a baseline drawn perpendicular to the spore surface. The results indicate consistently higher dispersion of angle of the pores around the mean (= lower r values) and consistently lower porosities in a sample of extant selaginellalean versus *Isoetes* megaspores. Differences in the r values appear to be more powerfully diagnostic than porosity. Kovach showed that two Cretaceous dispersed megaspore genera relate as would be expected on the basis of general morphological comparisons with extant species: *Erlansonisporites* to the extant selaginellaleans and *Paxillitriletes* to extant *Isoetes* (Kovach & Dilcher, 1985; Kovach, 1989).

Utilizing such approaches, together with other indirect indicators (for example, occurrence of associated or adherent microspores—monolete in *Isoetes*, trilete in selaginellaleans), Jurassic and Cretaceous megaspores can now be attributed as shown in Table 1.

As Batten (1988) pointed out, some megaspores regarded as probably selaginellalean are zonate, that is, they have an equatorial flange as in *Isoetes* and therefore their general morphology resembles that of *Minerisporites* and *Henrisporites*. This underscores that the kind of convergence in characters detected among species within extant genera may also apply between genera in the fossil record. In this respect the ultrastructural evidence appears to take on added significance.

Table 1 is not intended to be exhaustive, and it refers mainly to Cretaceous taxa. However, it presents a start that we hope will be built on rapidly

TABLE 1. Megaspores attributable to lycopsid orders.

Isoetaleans, sens. lat.	Selaginellaleans
Minerisporites (including *M. mirabilis* and *Minerisporites* species A known in situ)	*Erlansonisporites* (*E. spinosus, E. erlansonii, E. scanicus, E. septus, E. sparassis*; see Harris, 1961)
Dijkstraisporites	*Ricinospora cryptoreticulata*
Henrisporites	*Thylakosporites retiarius*
Herbosisporites	*Rugotriletes diktyotus*
Paxillitriletes (including *P. phyllicus*; see Harris, 1961: 44)	*Rugotriletes costatus*
	Trileites persimilis, known in situ
Sepisporites	*Trileites murrayi* (Harris, 1961: 44)
Tenellisporites pro parte	*Cabochonicus carbunculus*
Scabratriletes pro parte	*Verrutriletes dubius*
	Verrutriletes compostipunctatus
	Bacutriletes nanus
	Bacutriletes majorinus
	Horstisporites species
	"*Triletes*" *onodios* (Harris, 1961)

in the future. Although inadequate, it summarizes the considerable recent progress that has been made, representing a broad attribution of some 17 out of the 70 or so Mesozoic genera of dispersed megaspores that have been recognized to date. Since several of these 70 genera represent plants other than lycopsids (mainly water ferns), the 17 genera probably represent about a third of the known lycopsid megaspore diversity. It is interesting to compare this general picture emerging today with that of Harris (1961), who was unable to attribute any of the Yorkshire Jurassic megaspores other than in the broadest of terms.

Environmental significance. Harris (1961) pointed out that dispersed megaspores are moderately abundant in Yorkshire Jurassic plant localities. Although few megafossils are known from Yorkshire, the nonuniform megaspore composition of the localities suggests that the parent plants did not live far from the various coastal plain environments in which they were deposited. Batten (Koppelhus & Batten, 1989) noted that in horizons with podsols and evidence of fluvial activity, inferred selaginellalean megaspores are the most abundant spores, indicating a likely growth environment that could have ranged from low-growing streamside vegetation to nearby interfluvial forest or scrub environments, directly comparable to environments occupied by most selaginellalean species today. Probable *Isoetes*-group megaspores were associated with low energy environments of deposition; the inferred parent plants and the sedimentological evidence both indicate that the plants lived in a floodplain marsh to lacustrine habitat as occupied by *Isoetes* today. Significantly, Batten drew attention to the fact that several megaspore genera attributed to *Isoetes*-like plants can occur locally in large numbers in Cretaceous sediments known to have accumulated in freshwater, suggesting a likely freshwater environment of growth for the parent plants. This view is supported by occurrences of little-drifted megafossil remains as virtually whole plants in such environments, e.g., *Isoetites choffatii* (see below) and *Isoetites* sp. nov. (see below), that are very similar to species growing today in freshwater.

MIOSPORES

Miospores attributable to the lycopsids are found in almost all the Mesozoic strata that have been analyzed for spores and pollen. Although usually a minor component of the flora, they are present throughout the world and apparently occur in most of the examined deposits. For example, some reports of the Cretaceous miospores from various areas are eastern Australia (Cookson & Dettman, 1958), southeastern Australia (Dettman, 1963), western Canada (Singh, 1964, 1971), southeastern United States (Phillips & Felix, 1971), and New Zealand (Couper, 1953). Because the host plants rely mainly on wind dispersal, the worldwide distribution of their miospores (spores in the case of Lycopodiales and microspores in the case of Selaginellales) is not surprising. For most of these miospores the host plants are unknown and, in view of the depauperate record of fertile lycopsid remains in the Mesozoic, there is probably little hope of assignment to host plants for these spores until modern approaches similar to those utilized for megaspores are attempted. The main Sporae Dispersae genera that have been recognized as spores of lycopsids are *Lycopodiumsporites, Lycospora, Lycopodiacidites, Reticulatisporites* (Phillips & Felix, 1971), and *Acanthotriletes* for *Selaginella* (Singh, 1964). These genera appear in most of the spore references where lycopsid spores have been described.

Spore data thus show that the three lycopsid lines continue throughout the Mesozoic worldwide as a minor component of the flora, but as yet give no clues regarding significant evolutionary changes in the groups.

HERBACEOUS FORMS

Many herbaceous forms similar to those of extant lycopodialeans and selaginellaleans have been described from the Carboniferous onward (Thomas, 1992). However, the Mesozoic fossils either rarely preserve sufficient detailed information of the kind required for accurate identification, or have not been studied sufficiently to illustrate such details. There is real danger of confusion of isophyllous forms with conifer shoots, fern rhizomes, and bryophytes (Seward, 1910: 74–75), and also a frequent inability to tell whether the material was lycopodialean as distinct from selaginellalean. As is the situation for Mesozoic lycopsid megaspores discussed above, the generally limited state of present knowledge of these forms necessitates heavy reliance on characters of the extant taxa—for example, that selaginellaleans have ligulate leaves and sporophylls whereas lycopodialeans lack ligules, and that selaginellaleans are heterosporous with usually four megaspores per megasporangium whereas lycopodialeans are isosporous. In all extant species of these orders the isospores or microspores are trilete, as opposed to the monolete microspores of *Isoetes*-like forms. There are also a number of detailed vegetative differences, although both of the living orders include some forms that are isophyllous, considered the plesiomorphic condition for lycopodialeans by Øllgaard (1987), as well as a range of more or less anisophyllous ones, although selaginellaleans are usually more regularly anisophyllous (Harris, 1961).

Heavy reliance on comparison with extant forms inevitably means that the law of the excluded middle applies (Davis & Heywood, 1963: 34–35; Hill & Crane, 1982: 322–324), such that any genuinely intermediate forms might well be overlooked by being forced into a category, i.e., selaginellalean versus lycopodialean, in which they do not really belong. Additionally, where detailed preservation of vegetative characters is limited, which is often the case, there is a marked asymmetry in ability to recognize Selaginellales when relying on spore characters. Thus, the occurrence of in situ megaspores is a clear indication of selaginellalean affinity, whereas if only small spores (miospores) with trilete laesurae are found (especially if they are poorly preserved) they could indicate identity of the parent plant as either lycopodialean or selaginellalean.

LYCOPODIALEAN LINE

Because of the fragmentary condition of these plants when found as fossils, few of the characters considered important by Øllgaard (1987, 1989) in classifying extant lycopodialeans can be recognized in fossil material. These characters relate to branching pattern (isotomous, anisotomous, flabellate), stem and rhizome anatomy, sporophylls (paleate to peltate) with a sporangium near the axil that may be displaced, and sporangia of equal valves or unequal valves, in addition to particular characters of leaf variability such as those to do with leaf form and attachment mentioned above. Adding these to the considerations already mentioned, it is hardly surprising that there are currently no unequivocal records of Mesozoic lycopodialeans, and none that can be characterized in terms of the genera now in use for extant lycopodialeans. If anything, it is perhaps surprising that at least a few are convincingly, even if not certainly, lycopodialean in a broad sense.

The quality of these records ranges widely. At worst are those such as "*Lycopodium* sp." of Drinnan & Chambers (1986) from the early Cretaceous of Victoria, which appears to have no characters diagnostic of Lycopodiales. A number of other species known solely as vegetative material are lycopsids and may be lycopodialean, but detailed evidence is lacking: anisophyllous species such as *Lycopodites victoriae* of Seward (1904) from the Jurassic of Victoria, and isophyllous ones such as *L. arberi* Edwards from the Jurassic of New Zealand (Edwards, 1934), and *L. sewardi* Nathorst from the Mesozoic of Spitzbergen (Nathorst, 1897). Some other occurrences of anisophyllous forms, such as *Lycopodites gracilis* from the Mesozoic of India figured by Seward & Sahni (1920), are similar to *L. falcatus* from the Yorkshire Jurassic, discussed below, and thus can also probably be considered lycopodialean. Moreover, *L. gracilis* occurs in the same series of beds as small, 2-mm-wide axes named *Lycoxylon*, which have distinctly lycopodialean anatomy (Srivastava, 1946).

To our knowledge, this leaves few species of

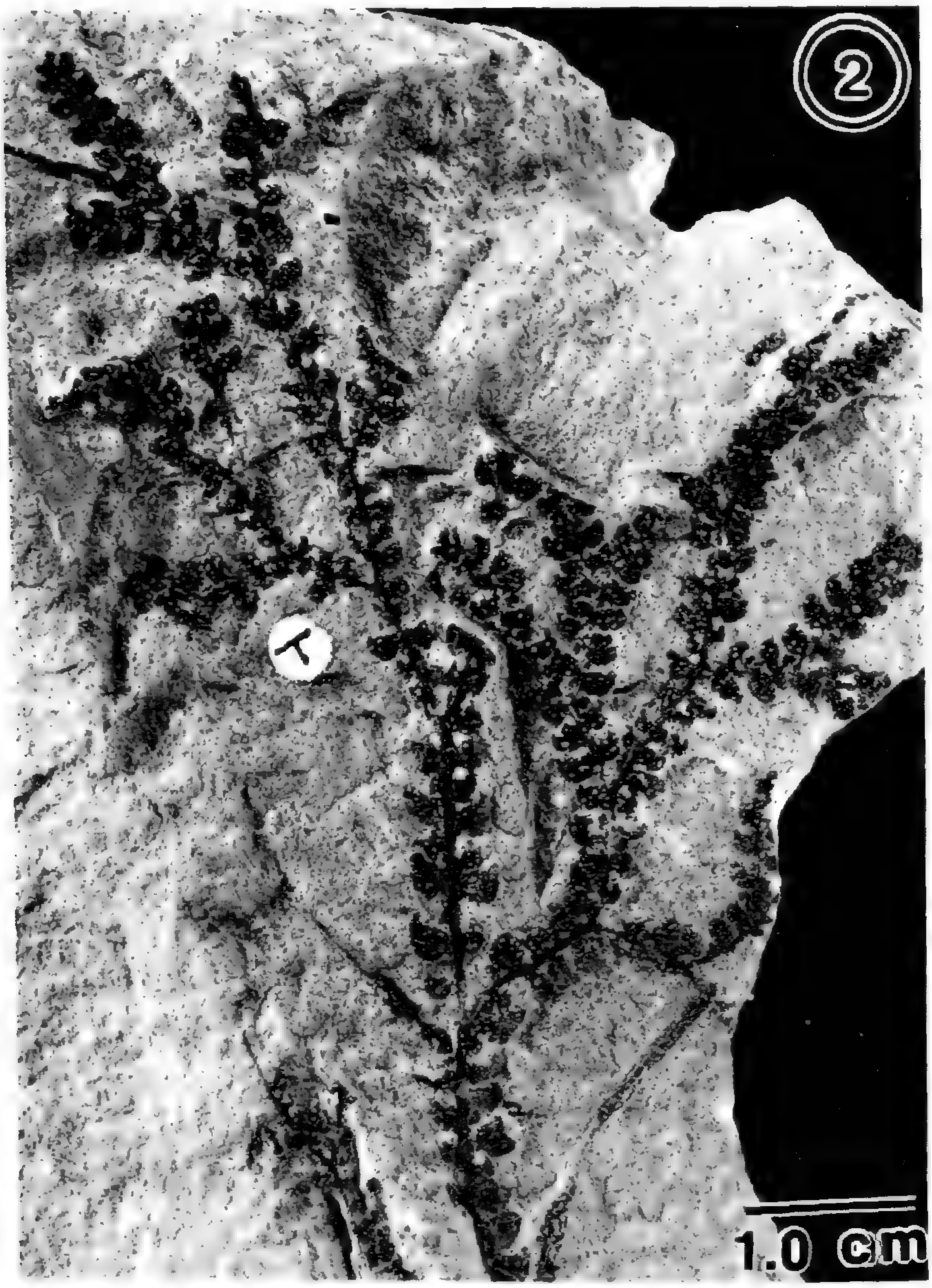

FIGURE 2. *Lycopodites falcatus* Lindley & Hutton. Holotype of Lindley & Hutton (1831–1833) volume I, plate LXI, figures 1,2. Specimen v. 39314 in British Museum (Natural History).

compression fossils that can be accepted on currently available evidence as definitely lycopodialean. The best known is *Lycopodites falcatus* Lindley & Hutton (Fig. 2), which was described and discussed in depth by Harris (1961). It has isophyllous main stems up to 2 mm wide, bearing dichotomizing branches that are complanate and distinctly anisophyllous. Like extant genera of lycopodialeans but unlike extant selaginellaleans, there is no leaf in the angles of dichotomy of the branches; there is a lower number of small versus the larger leaves; the shape and attachment of the large lateral leaves is as in lycopodialeans, to reiterate Harris's words, "entirely foreign to *Selaginella*," as is the broad distribution of the leaf stomata (see also Thomas & Masarati, 1982). However, the exact combination of vegetative characters seen in *L. falcatus* is not one that is seen among extant lycopodialeans. It is also significant that strobilar material is poorly known even for this otherwise well-characterized species. Harris described some detached strobili in close association with the vegetative branches, but while they are broadly lycopodialean in appearance they are poorly preserved and have yielded only a few spores on maceration. A comparable strobilus in attachment to vegetative shoots has been illustrated by Hill et al. (1985). This may prove to yield spores, although morphologically it too is poorly preserved. Further collecting is required if knowledge of this "classic" but incompletely known species is to be improved. This species has been proposed as the basis for conservation of the generic name (Pal & Ghosh, 1990).

Another convincing record of a complanate but isophyllous lycopodialean is *Lycopodites multifurcatus* of Li et al. (1986, excluding their pl. 38, figs. 3, 3a), from the early Cretaceous of northeastern China. As in the Yorkshire Jurassic species, preservation is sufficiently good to be certain that leaves are lacking from the angles of dichotomy of the branches. The main stems and strobili are not known.

Skog (1986, 1990) has described *Wathenia*, another complanate isophyllous form. It is based on some newly collected material from the English early Cretaceous and on some formerly attributed to *Hymenopteris psilotoides.* Other specimens referred to *Onychiopsis psilotoides,* but probably representing the German and Japanese material of *O. elongata* Yokoyama, have been recognized as a dicksoniaceous fern by Friis & Pedersen (1990). If *Wathenia* is actually a lycopodialean, then it is of considerable interest in representing a possibly epiphytic species resembling extant species from the tropics. Certainly the combination of characters is of an advanced complex close to modern species of *Lycopodium* and *Huperzia,* and not of the generalized type associated with those extant species considered primitive by workers such as Øllgaard. The fertile phyllotaxis of the somewhat flattened branches is helical, sporophylls are paleate, and the spores, numbering about 200 per sporangium, are similar in structure to those of extant lycopodialeans. Sporangia are elongate, a condition not known in extant lycopodialeans but found in selaginellaleans. As with *Lycopodites falcatus,* there is a hint from this fossil of characters that are intermediate between those of extant selaginellaleans and lycopodialeans.

Finally, Harris's (1976) *Lycopodites hannahensis,* if correctly attributed, would greatly extend the scope of lycopodialeans to encompass slender, upright, evidently aquatic plants—unlike any surviving today. While Thomas (1992) accepts *L. hannahensis* as convincingly lycopodlike and believes that comparable forms occur in the Jurassic, we are inclined to be more skeptical. The material is exceedingly poorly preserved and compares favorably in almost every respect with vertical in situ roots known to have been produced by fossil *Equisetum* species, especially *E. columnare* (Harris, 1961). In the field such roots often appear to branch upward as in *L. hannahensis,* but when traced a sufficient distance in the rock they converge again at a higher level; we suggest that this represents the effects of decay of the roots into separate strings that then were pulled apart by soft sediment. Whatever the merits of our suggestion or of Thomas's appraisal, however, insufficient knowledge exists to make a firm judgment at this time; further study material based on additional carefully controlled collecting, together with detailed evaluation of extant *Equisetum* rooting systems, is required.

The meager fossil record of Mesozoic lycopodialeans indicates that new forms were appearing at the end of the Jurassic and through the Cretaceous. We hypothesize that the modern lines of lycopodialeans were established during late Jurassic–Cretaceous times and that their diversity today may result from the same events which led to the increasing diversity of the angiosperms and the modern fern families (i.e., Polypodiaceae). Many of the modern lycopodialeans are associated with angiosperm dominants as terrestrial or epiphytic plants. While the fossil record is not strongly supportive of such a hypothesis, it does not negate it. Much more work with existing and new collections is needed on the critical ages of the late Jurassic and Cretaceous with the lycopodialeans in mind.

SELAGINELLALEAN LINE

Evidence for herbaceous, ligulate, and heterosporous forms, often attributed to the genus *Selaginellites,* occurs from the Carboniferous onward. The general situation of Mesozoic selaginellaleans is similar to that of lycopodialeans in that a number of forms comparable with living ones are known, but few are exactly like any living species or group of species. A few, such as *Synlycostrobus* and *Lycopodites macrostomus,* are unlike any extant members. The situation is a little more satisfactory than for lycopodialeans partly because it is based on more definitive evidence of ligules, strobili, and spores.

Isophyllous forms similar to *Huperzia selaginoides,* such as *Selaginella harrisiana* from the Permian of Australia (described in detail by Townrow, 1968), were clearly well established by the outset of the Mesozoic. Townrow's material is important because it has a long, apparently leafless rhizome like that of *Asteroxylon,* corroborating Karrfalt's (1981) view based on developmental anatomy that the rooting pattern of extant species of *Huperzia selaginoides* type is highly derived rather than representing the generalized condition.

Subsequently, critically recognizable isophyllous forms are unknown until the occurrence of *Lycopodites macrostomus* Krassilov from the middle Jurassic (Callovian) of Siberia (Krassilov, 1978). This species is well preserved, with evidently ligulate leaves, although details of the ligulelike structures are obscure. Epidermal features, however, are clearly illustrated by Krassilov. This species is interesting in that the shoot morphology, the lack of a leaf in the angle of shoot dichotomy, and the distribution of stomata scattered over both surfaces of the leaf are distinctly lycopodialean rather than selaginellalean in terms of extant analogues. Unfortunately, the strobilus and spores are as yet unknown or unrecognized. We include *L. macrostomus* here under Selaginellales purely because by reference to extant species the law of the excluded middle could be taken to enforce consideration of all such ligulate Mesozoic lycopsids as selaginellalean. However, such a view is not favored by the balance of the evidence, as Krassilov pointed out; we might just as appropriately have included this species under Lycopodiales. Moreover, studies of the Devonian *Leclerqia* have made clear that there are other ancient plants with strongly lycopodialean characteristics that possessed a ligule (Grierson & Bonamo, 1979).

Judging by the currently available evidence, *Lycopodites macrostomus* is of considerable importance in demonstrating that at least in their vegetative characteristics the selaginellalean and lycopodialean clades were not yet fully distinct in the Jurassic. In other words, this species appears to represent an important missing link between the two clades. It underscores the importance of finding well-preserved strobilar material of both *L. macrostomus* and *L. falcatus* if we are to obtain a better overview of lycopodialean/selaginellalean relationships.

Vegetative material considered to represent an isophyllous lycopsid from the middle Jurassic (Aalenian), which Black (1934a, b) collected from Loftus Alum Quarry in Yorkshire and described under the name of the coniferous shoots *Pagiophyllum peregrinum*, was mentioned by Harris (1979: 57). Although morphologically broadly resembling *P. peregrinum*, Harris recognized that Black's material is very different from that species, not least in failing to yield a cuticle on maceration, and he indicated possible lycopsid affinity. A well-preserved portion of shoot from additional material, collected by C. Hill and Ronald Williams at Loftus Alum Quarry in 1984, is illustrated here in Figure 3, showing coaly spots suggestive of ligule pits situated near the bases of the leaflike appendages. Further study of this material, however, has shown that the appendages in Figure 3, which look broadly like *Pagiophyllum* or lycopsid leaves, are, in fact, the scaly bases of quite different organs. As illustrated, they closely resemble scaly appendages on osmundaceous fern stems and rhizomes attributed to *Todites princeps* (Schweitzer, 1978). The appendages narrow at their apices and are produced into elongate petiolar extensions several centimeters long. The surface throughout the scaly bases and these apical extensions shows only uniformly narrow elongate cells and lacks any evidence of midrib or stomata. Two other factors that also argue against a lycopsid affinity are the steeply inclined spiral of attachment of the scales (low spirals are typical of lycopsids), and the position of the apparent ligule pits, which is too low in relation to the free part of the appendages to fit any known lycopsid. These probably represent points where roots left the rhizome. When compressed vertically they would form coaly plugs.

All other Mesozoic records of selaginellaleans known to us represent anisophyllous or vegetatively indeterminate forms. One of the best preserved and best described is *Selaginella anasazia* Ash from the late Triassic of Arizona (Ash, 1972). The dichotomizing branches bore leaves like those of many living species in four ranks, two ranks of large spreading leaves up to 2.3 mm long and two of small leaves up to 1.2 mm long. The leaves are so well preserved that tracheid anatomy of the midvein and epidermal details of the lamina could be illustrated clearly. The leaf form resembles that of extant species such as *S. krausiana* and *S. abysinica*, which today live in moderately moist shady habitats. Although the strobili of *S. anasazia* are poorly preserved, they include in situ megaspores and, like the vegetative shoots, appear to resemble those of extant Selaginellales.

Other well-preserved late Triassic material from Sweden, named *Selaginella hallei*, was studied by Lundblad (1950b) based on anisophyllous shoots bearing leaves in four ranks. Attached strobili bore sporophylls in a tightly imbricate spiral as occurs in some extant species. They were heterosporous, with four megaspores per megasporangium as in most extant species; microspores were trilete with an annular ring, which is also characteristic of such extant species as *S. scandens* and *S. parkeri*. The megaspores are attributable to *Trileites persimilis*.

Lundblad (1950a) also described other broadly comparable vegetative material as *Lycopodites scanicus*, which requires revision using modern techniques. There is some indication from her illustrations that vegetative branches attributable or potentially attributable to *S. hallei* may have been variable in form, ranging from 4-ranked anisophyllous to isophyllous with the leaves in an imbricate spiral; if not, it would appear that distinct isophyllous selaginellaleans may have occurred in the same deposits. In either case, additional knowledge would be of considerable value in clarifying relationships between the Swedish material and extant species.

We include mention here of an isolated strobilus yielding spores, named *Selaginellites polaris* by Lundblad (1948). This is more for completeness of coverage than from the conviction that on present evidence it is better placed here than with the subarborescent lycopsids we reviewed earlier in this paper (see also Chaloner & Boureau, 1967, for discussion).

Fossils closely resembling anisophyllous selaginellaleans do not reappear significantly in the fossil record until the early Cretaceous, when there is evidence of considerable diversity. Watson's (1969) revision of *Selaginellites dawsoni* from the English Wealden demonstrated heterospory and showed that the megasporangia had four megaspores. Material was not abundant, and no spore relationships were suggested. Comparisons were made with extant *Selaginella sanguinolenta* and *S. emmeliana,* although the fossil is not identical with either species in all its characters. Most other Cretaceous species of *Selaginellites* are vegetative shoots with a leaf arrangement that suggests assignment to *Selaginella* rather than *Lycopodium* (see also Seward, 1910, 1913). Many are poorly preserved fragments. One such example, *Selaginellites marylandica* Fontaine (Ward, 1905), was apparently so poorly preserved that it can no longer be found in the collections at the United States National Museum of Natural History.

As part of the work for this review, J. Skog has reexamined a strobilus of early Cretaceous age from South Carolina described by Berry (1910) as *Lycopodium cretaceum.* Although Berry described 17 specimens in his paper, only the one illustrated here in Figure 4 remains in the collections today. His description of the sporophylls appears to be more or less accurate, but the specimen has suffered degradation over time and now the specimen is too poorly preserved to confirm the accuracy of his description. The sporangia are attached to the leaves in Berry's reconstruction, but he indicates that the drawings are "somewhat diagrammatical." In our opinion, it is impossible to confirm the position of the sporangia on the sporophylls or whether they are borne on stalks (Figs. 5, 6). Sporophylls are thicker at the base and acute at the apex (Fig. 5). Careful examination of the strobilus reveals that there are poorly preserved large dark areas among the leaves (Fig. 6), and these rounded areas may be the sporangia that Berry reconstructed. Material that appears to be carbonized from these areas has been removed and prepared in different ways. Attempts to extract spores were unsuccessful. Part of the material was placed in hydrofluoric acid to see if any plant material could be isolated, but only small fragments appeared. These have been removed and examined with light and scanning electron microscopy (Figs. 7–9). Because of the poor preservation, assignment is questionable at best. The structure they most resemble, although they are clearly different and smaller, is the palynomorph *Dictyothylakos* Horst (1954), described from the Cretaceous by a number of authors (Hughes, 1955; Singh, 1964; Kovach & Dilcher, 1988; Hueber, 1982). Hueber's description includes SEM illustrations, which are comparable to the SEM material here. The network of primary strands reinforced by secondary strands characteristic of Hueber's material can be seen in Figure 9 (arrow). The material here is much smaller than

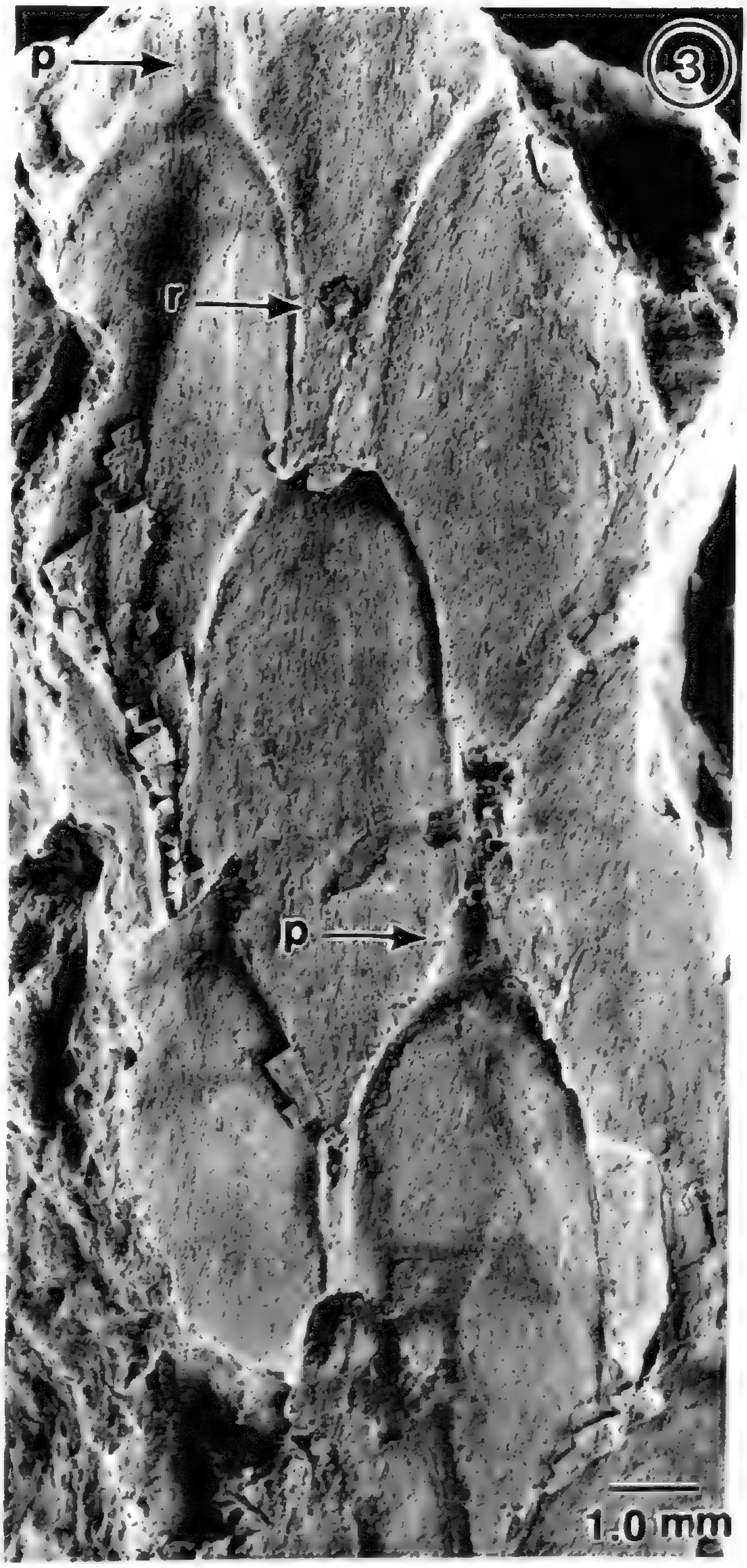

FIGURE 3. Lycopodlike axis from Loftus Alum quarry, interpreted here as a fern stem. British Museum specimen v. 63453. (p) = petiolar extensions; (r) = coaly plug probably the site of a root.


4
6505
1.0 cm


5
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6
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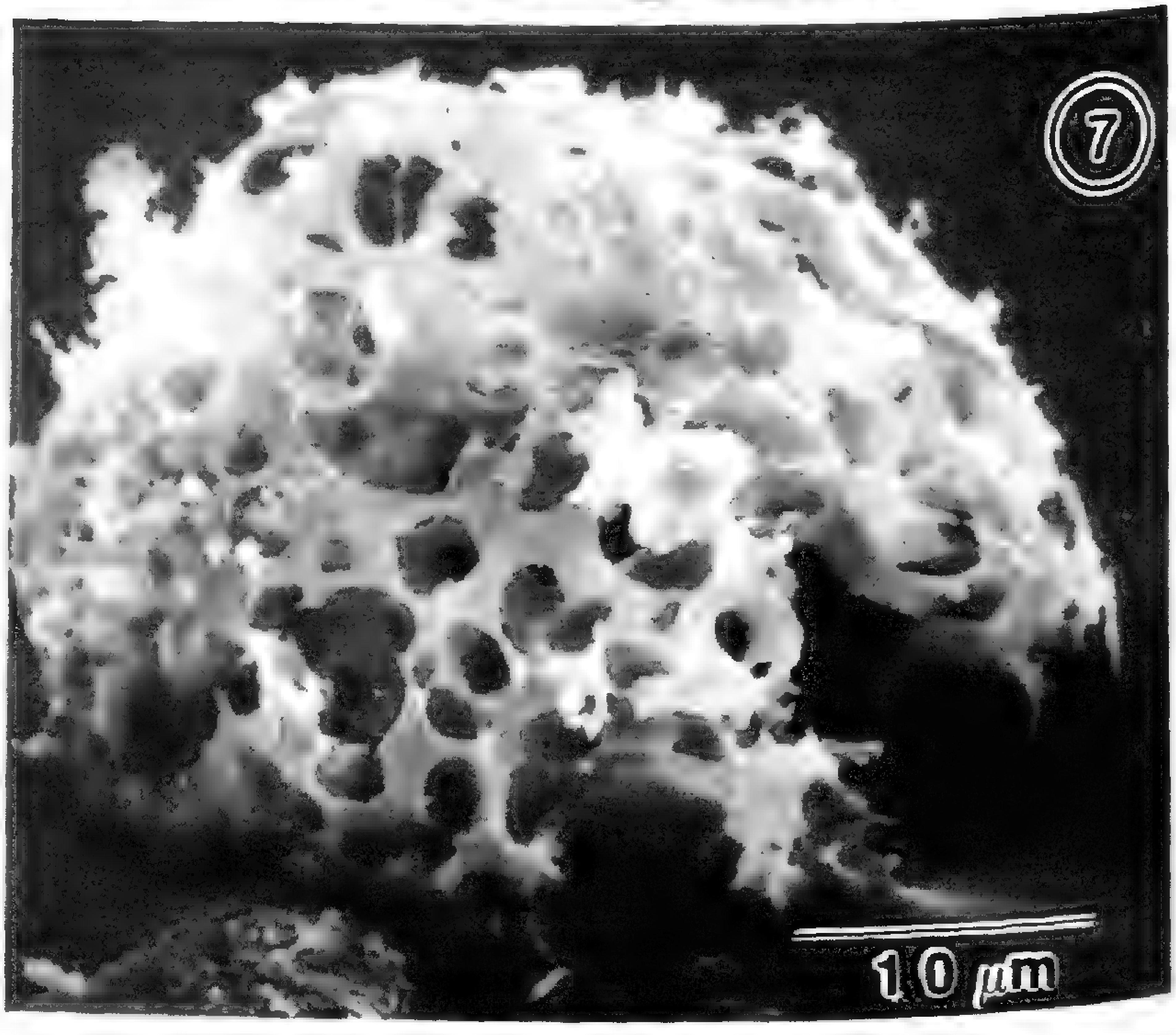
7
10 μm

that of Hueber, but since these represent fragments the size is not critical. However, Hueber's material is flat and not rounded, and the material extracted from *Lycopodium cretaceum* appears to be a round structure (Figs. 7, 8). Hueber suggested it could represent the operculum of a selaginellalean sporangium, since the similarity in ornamentation and structure to parts of the spore *Thylakosporites* were obvious not only to him but to Hughes (1955). The granular surface is evident in the material shown in Figure 9. Because the material seen here was obtained from a lycopodiaceous strobilus and isolated from the region of the putative sporangia, the suggested identity with the lycopsids may be more substantiated, but the structure remains as elusive as ever. It probably represents some part of a degraded lycopsid strobilus, but whether operculum, spore, or cuticular portion of the wall is not clear. This material illustrates that even when modern techniques are utilized some poorly preserved material remains enigmatic.

As presently described, *Limnothetis gobiensis* of Krassilov (1982) from the early Cretaceous of Mongolia is another enigmatic, poorly preserved lycopsid. Krassilov reconstructed the vegetative shoots as bearing ligulate leaves, isophyllous and two-ranked on main axes and anisophyllous, four-ranked on lateral branches (with two sets of broadly ovate imbricate leaves and two of small pointed leaves). He reconstructed the fertile zones of these branches (there appear to be no definite strobili) as bearing crowded lateral condensed branches, each in turn bearing a single terminal sporangium surrounded by pointed leaves. The sporangia are stated to be dimorphous. Presumed megaspores (occurring in association and not in situ) are large and have a regularly reticulate sculpture; microspores are stated to be trilete and apparently were extracted in situ.

It is difficult to assess this intriguing but inadequately described material. If indeed a selaginellalean it is of a highly specialized form that, like *Synlycostrobus* (see below), may be unique to Selaginellales. However Krassilov's photographic illustrations and written description do not provide evidence to justify arriving at the detailed reconstruction in his textfigure 2. On the evidence currently available the possibility cannot be excluded that the plant may be a conifer, e.g., badly preserved *Elatides* or *Geinitzia* shoots, or a pteridosperm; if it is a selaginellalean lycopsid, the fertile "short shoots" of Krassilov may actually represent germinated megaspores with small viviparous plants as occur, for example, in extant *Selaginella rupestris.*

The situation is very different for Krassilov's (1978) description of *Synlycostrobus tyrmensis* from the latest Jurassic to earliest Cretaceous of the Bureja Basin. As reconstructed from associated fertile and vegetative remains, the *Synlycostrobus* plant comprised main stems about 1 mm thick with widely spreading lateral leaves borne helically or in two ranks. The branch systems are anisophyllous and bear more closely spaced ligulate leaves in four ranks. As in extant anisophyllous selaginellaleans there are two ranks of large leaves and two of smaller ones. The fertile branches, unlike any extant selaginellalean, are compound and thus bear strobili laterally in the axils of so-called bracts or alternating with leaves, with the stalks of the strobili "fused" with the bracts. Only the microspores are known in situ; they were apparently cavate and trilete. Megaspores referable to *Bacutriletes onodios* occur monodominantly in association with the fertile shoots, including a detached megasporangium in which there are four megaspores. The strobili have paleate, keeled sporophylls, of which the detailed structure is poorly preserved, although they are typically lycopodialean/selaginellalean in form.

Although the vegetative and fertile remains of *Synlycostrobus* occur in one locality, they are preserved in different bedding planes rather than in intimate association or attachment. The possibility that the strobilar branches might have been borne on leafy shoots like those of *Lycopodites macrostomus* (although known from a different locality) cannot be ruled out; the "bracts" of *Synlycostrobus* look similar to the leaves of *L. macrostomus.* Krassilov commented, however, that occasional leaves of the strobilar branches of *Synlycostrobus* resemble those of the vegetative branches to which he attributed them.

Regardless of which vegetative shoots are the

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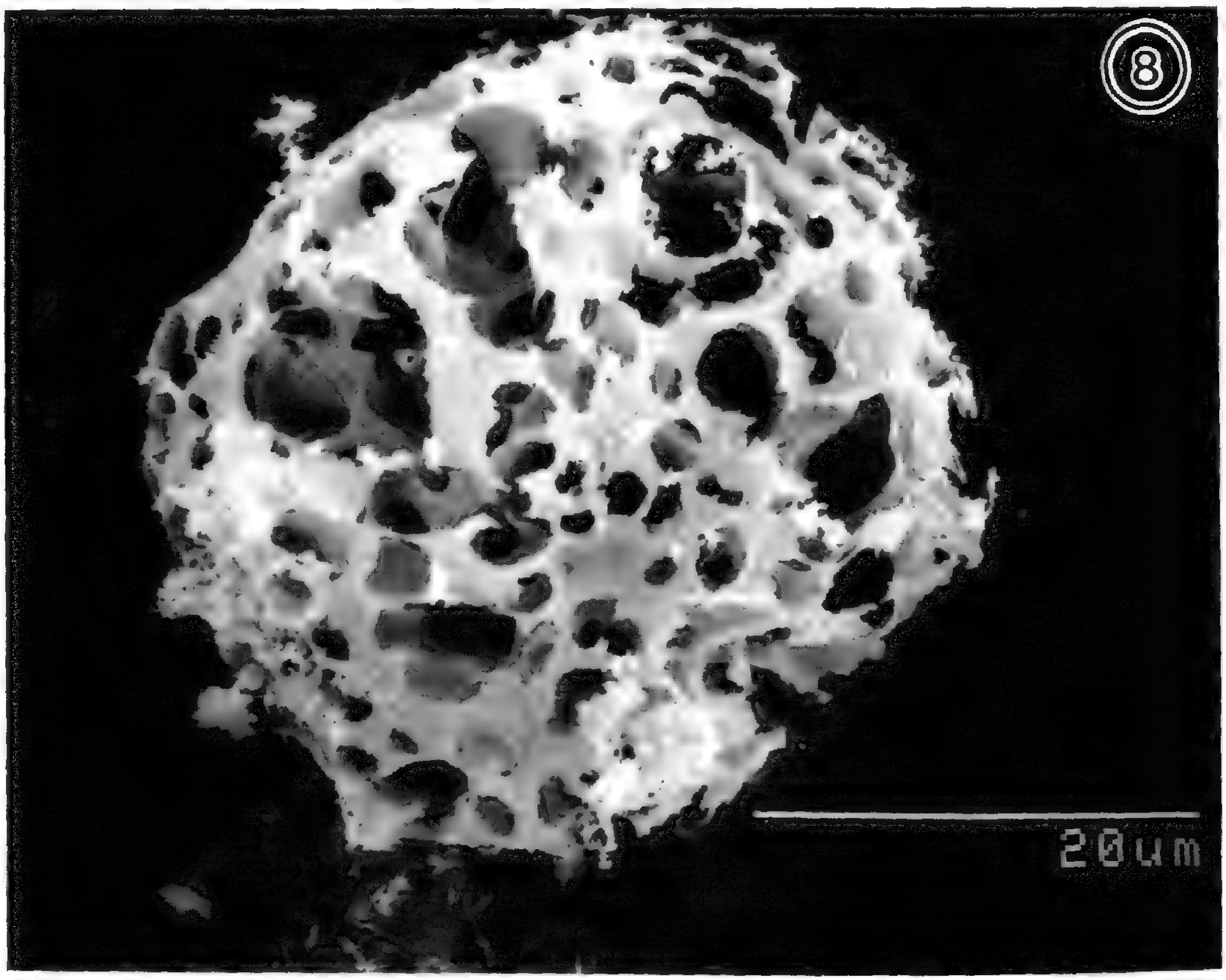
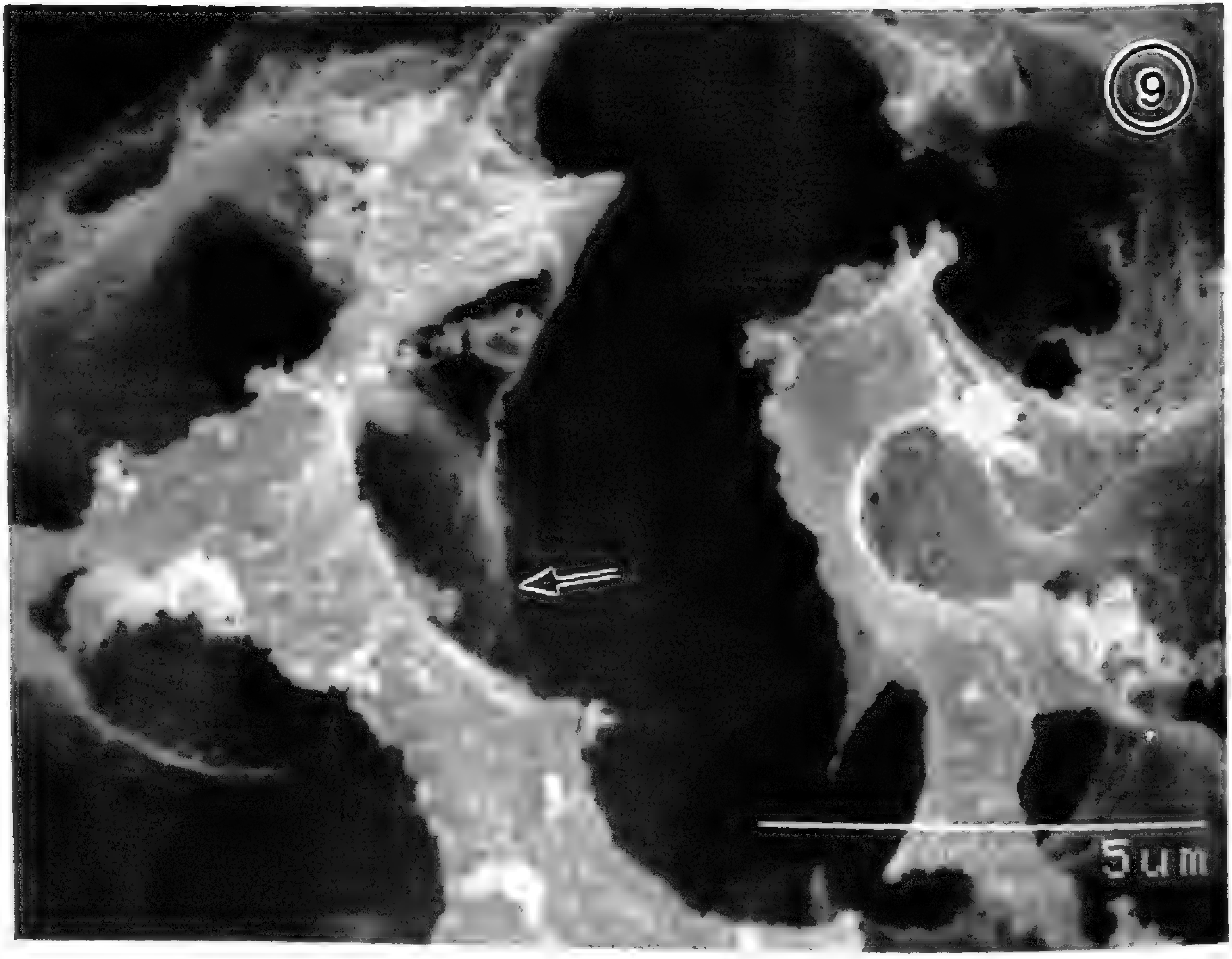
FIGURES 4–7. *Lycopodites cretaceum* Berry, United States National Museum specimen USNM 38199.—4. Complete specimen.—5. Enlargement of upper portion of specimen in Figure 4 showing leaves (l) in a helical arrangement, acute tips and enlarged bases of leaves and a thicker structure (t) that appears to be in the axil of the leaves.—6. Enlargement of right side of Figure 4 with leaves at the left side clearly shown. Pieces of the carbonized material in the leaf axils (arrows at center and left) were removed for microscopy.—7. Scanning electron micrograph (SEM) of round structure obtained from carbonized fragments. Three-dimensional shape can be seen in this view.





FIGURES 8, 9. Fragmented piece of carbonized material from *Lycopodites cretaceum* Berry.—8. SEM showing network arrangement and layers of material as well as rounded shape.—9. Enlargement showing granular surface and interconnections of the network (arrow to secondary strands).

most appropriate, *Synlycostrobus* is certainly a lycopsid. As such it extends the known diversity of reproductive branch morphology within the herbaceous lycopsids, both living and fossil. Within the fertile branches, the apparent fusion of "bracts" and strobilar stalks can be interpreted as a result of condensation of a set of more elongate lateral leafy shoots, each bearing a terminal strobilus. Condensation, effectively removing nearly all the vegetative regions of the lateral axes, would bring their terminal strobili back virtually onto the axis of the next order of branching. The length of the "bracts" is greater than that of the vegetative leaves. This length is appropriate if it represents in its proximal region a foreshortened shoot axis bearing distally a single remaining leaf; the leaf would then equate more readily in size with those on vegetative axes, and the whole "bract-like" structure thus interpreted is clearly not a bract but is itself compound, a reduced shoot. If this speculation is correct it provides an interesting parallel with the evolution of the coniferous female strobilus.

SUMMARY: LYCOPODIALEANS AND SELAGINELLALEANS

Although their fossil record offers only occasional and incomplete glimpses of these lycopsids in the Mesozoic, the fossils nonetheless represent a wide diversity of forms. There are those, especially selaginellaleans, essentially like extant species or groups of species, a situation first seen in the Paleozoic. Others, however, such as *Synlycostrobus,* and also *Limnothetis* and *Lycopodites hannahensis* if accepted as lycopsids, represent degrees of specialization unknown among extant taxa. Finally, there are those such as *Lycopodites macrostomus* that appear to provide persistent links between the two clades, even though they had begun to diverge millions of years earlier.

The environmental significance of these lycopsids is difficult to assess from the scattered records of megafossils. However, Ash (1972) pointed out that the leaf form of *Selaginella anasazia* resembles that of extant species such as *S. krausiana* and *S. abysinica,* which today live in moderately moist shady habitats. By extension and on a broadly uniformitarian basis it can be assumed that species such as *Lycopodites falcatus* probably occupied a similar habitat in the Jurassic. Most records of these forms are from mid- to high-latitude floras and few from the then-equatorial regions. Finally, an additional reason for our poor understanding or recognition of Mesozoic lycopodialeans versus selaginellaleans may be that they rarely got the chance to be preserved, for environmental reasons. Many extant lycopodialean species are robust enough to make potentially excellent fossils, e.g., *Lycopodiella cernuum,* but most of them today grow far from suitable depositional settings for preservation, certainly more the case than for selaginellaleans.

LEPIDODENDRALEANS CONTINUED: ISOETALEAN(?) LINE

Included in this section are a number of the squatter herbaceous forms, ranging from *Nathorstianella,* which we might equally have included with the subarborescent lepidodendraleans, to forms so similar to *Isoetes* that they could be accommodated in a slightly enlarged circumscription of that genus. As indicated previously, certain, if not all, species of the Triassic genus *Pleuromeia* could have been included here in the sense that they were herbaceous to suffrutescent.

The earliest Mesozoic records of *Isoetes*-like plants are of *Isoetes* (*Yorkia*) *gramineus* (Ward) Bock (1962, 1969) from the late Triassic of Pennsylvania. Although widely accepted in the literature, Bock provided no convincingly illustrated evidence that these intriguing fossils are like *Isoetes.* Our investigations of the original specimen, reillustrated in Figure 10, indicate that it is most likely an osmundaceous fern stem with attached petiole bases, such as that described by Schweitzer (1978) and similar to the rhizome material in Figure 3 of this paper. Most importantly, the tips of the petioles (i.e., Bock's leaves) indicate that pinnate divisions characteristic of fern fronds were attached (Fig. 12 and Schweitzer, 1978: pl. 2, fig. 4, textfig. 12). The attachment of these upper regions was not clear in the specimen until a fragment of rock was found in the drawer, which fit between the base and the divided tips. Once this was replaced on the specimen (Fig. 11), the attachment of the alternately divided tips of the petioles (leaves) to the rhizome base became clear. The high angle spiral of attachment of the appendages in Bock's (1962) textfigure A:B and our Figure 13 is more suggestive of a fern stem than a lycopsid shoot, and the broad scaly bases of the petioles are exactly like those described by Schweitzer for *Todites* stems. Furthermore, there is strong evidence that the petiole bases are stipulate (Fig. 13) and that the wiry roots extend away from the rhizome.

This leaves other material figured by Bock (1969) that may well be lycopsid but is certainly not of *Isoetes*-like form: his *Isoetodendron striata* and *Triletes isoetodendron. Isoetites circularis* (Emmons) Brown from the Triassic of North Carolina (Brown, 1958) also is untenable as an *Isoetes*-like plant, although it too is probably a lycopsid and further research is clearly needed.

With the possible exception of the poorly dated Indian material referred to below, records from the Jurassic are also unconvincing. They include the type species of the genus *Isoetites,* the aptly named *I. crociformis* Münster, from Daiting in Bavaria (Münster, 1842; Fig. 14). Apart from a superficial similarity to *Isoetes* its affinities are entirely unknown, and it may well represent something similar to a *Czekanowskia* short shoot. Should any reader know of the existence of Münster's material, C. Hill would like to know its location, as it clearly

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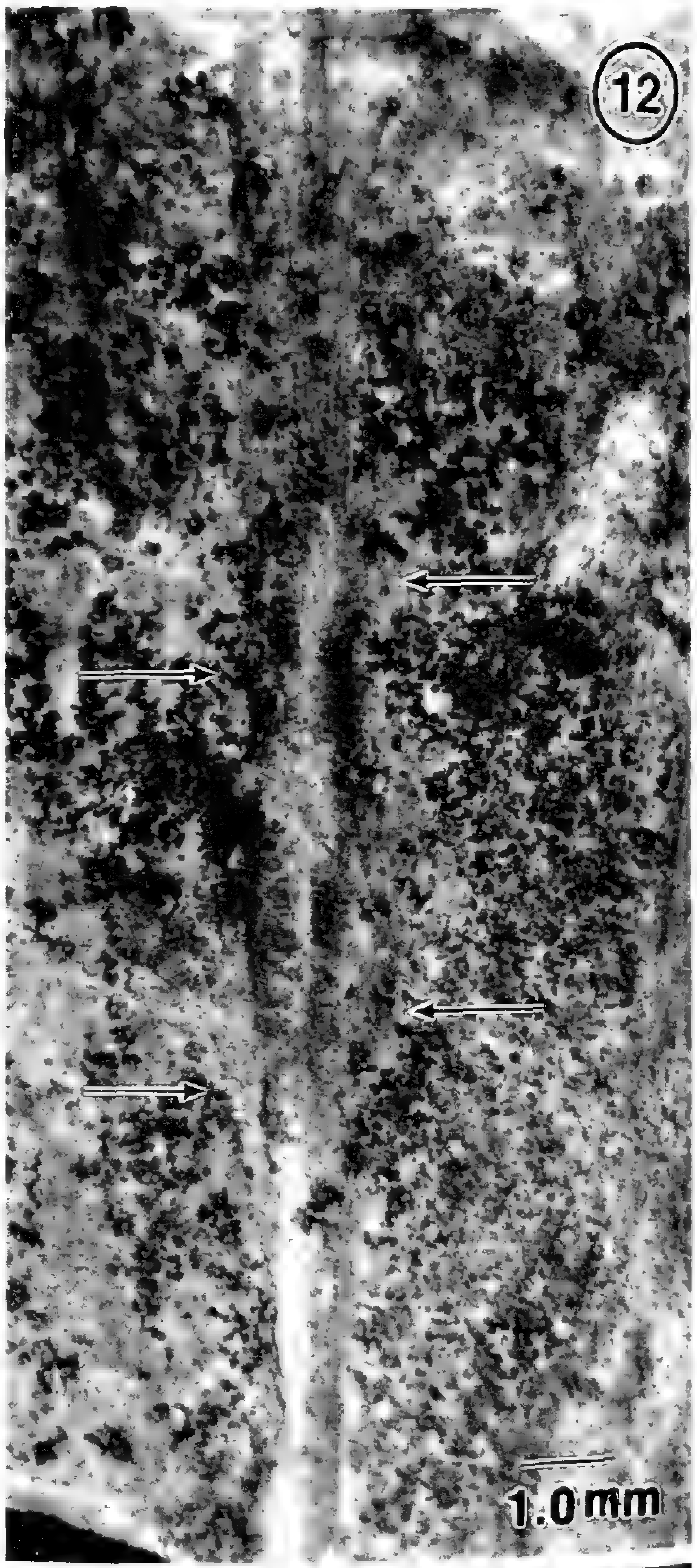

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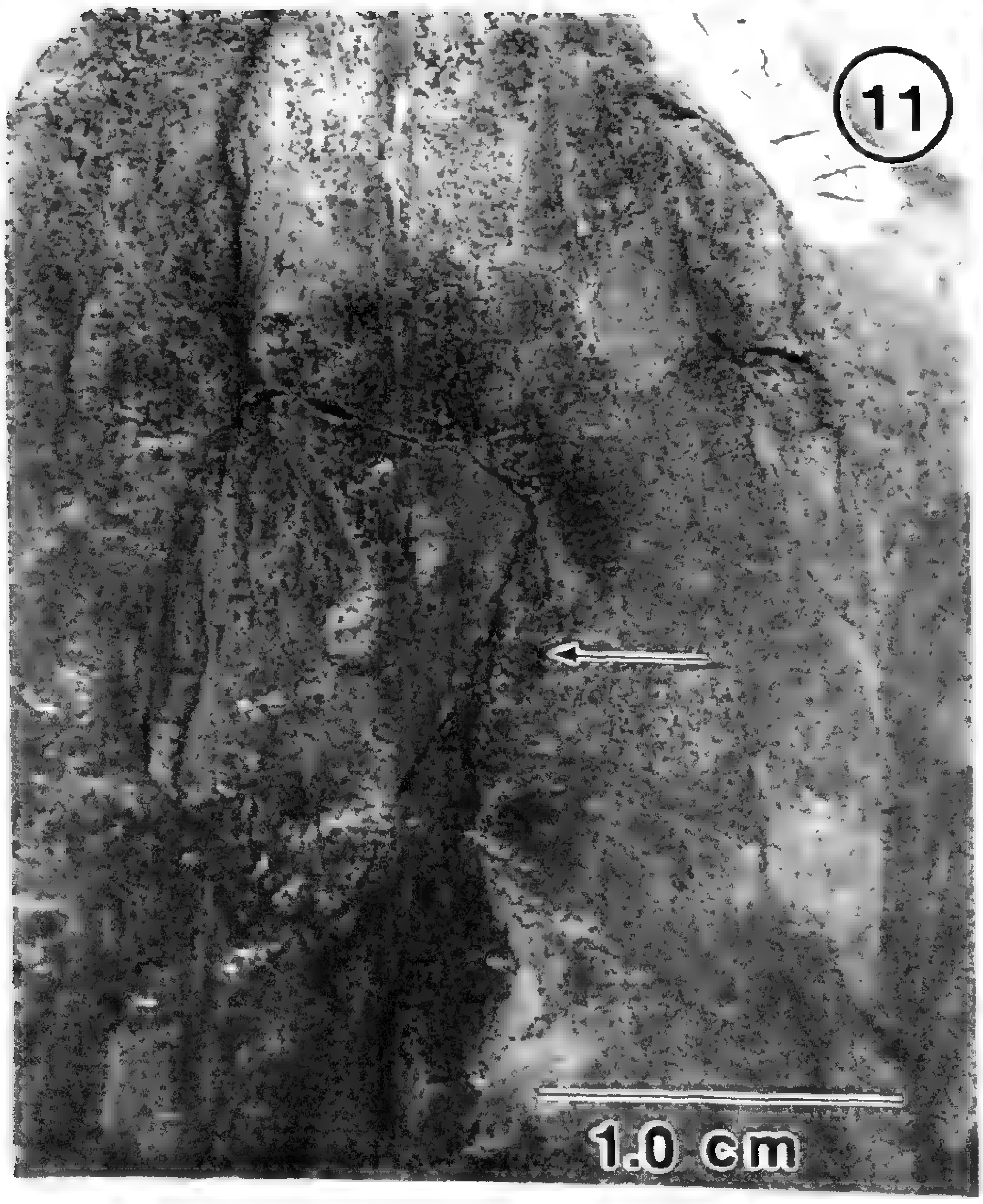

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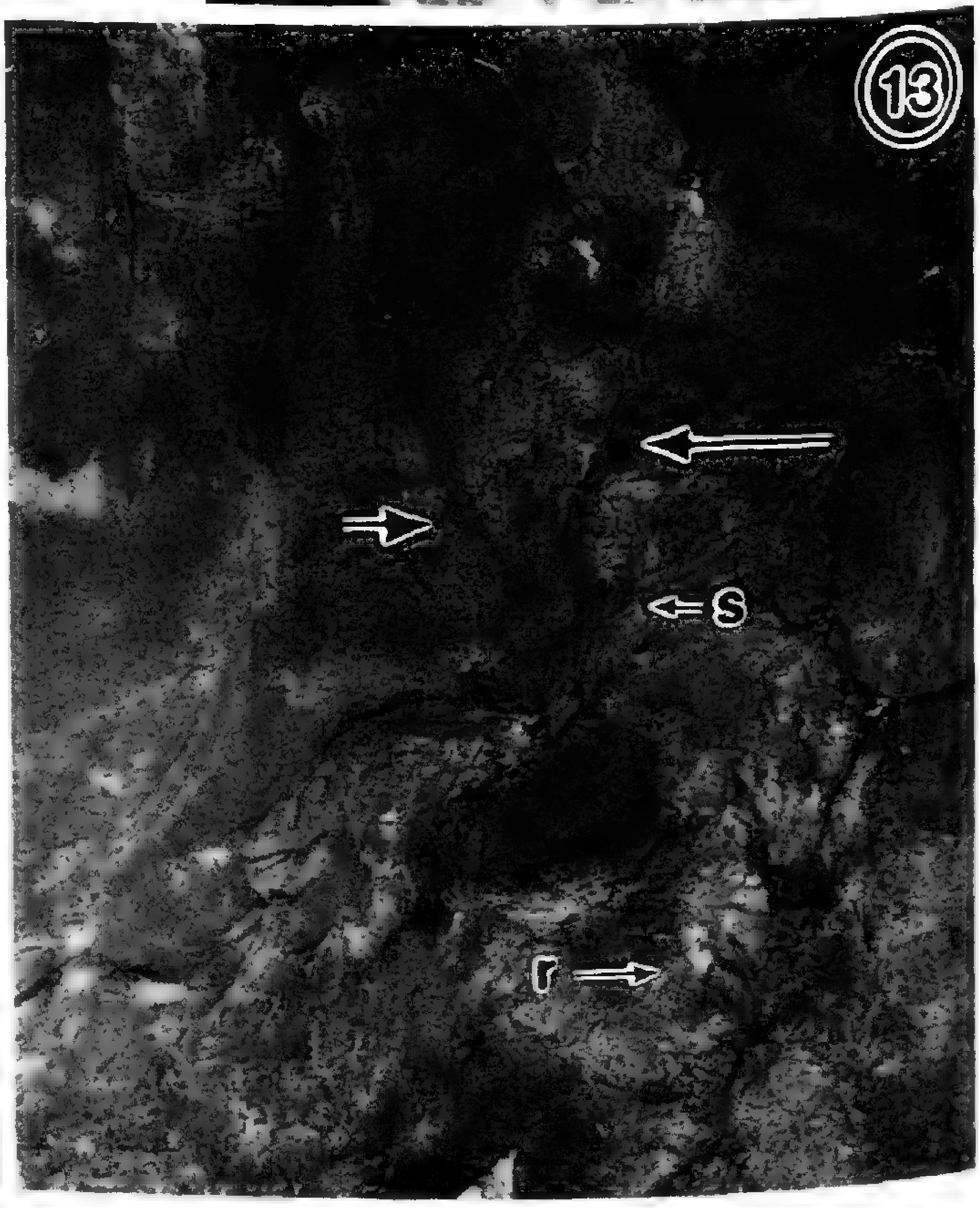

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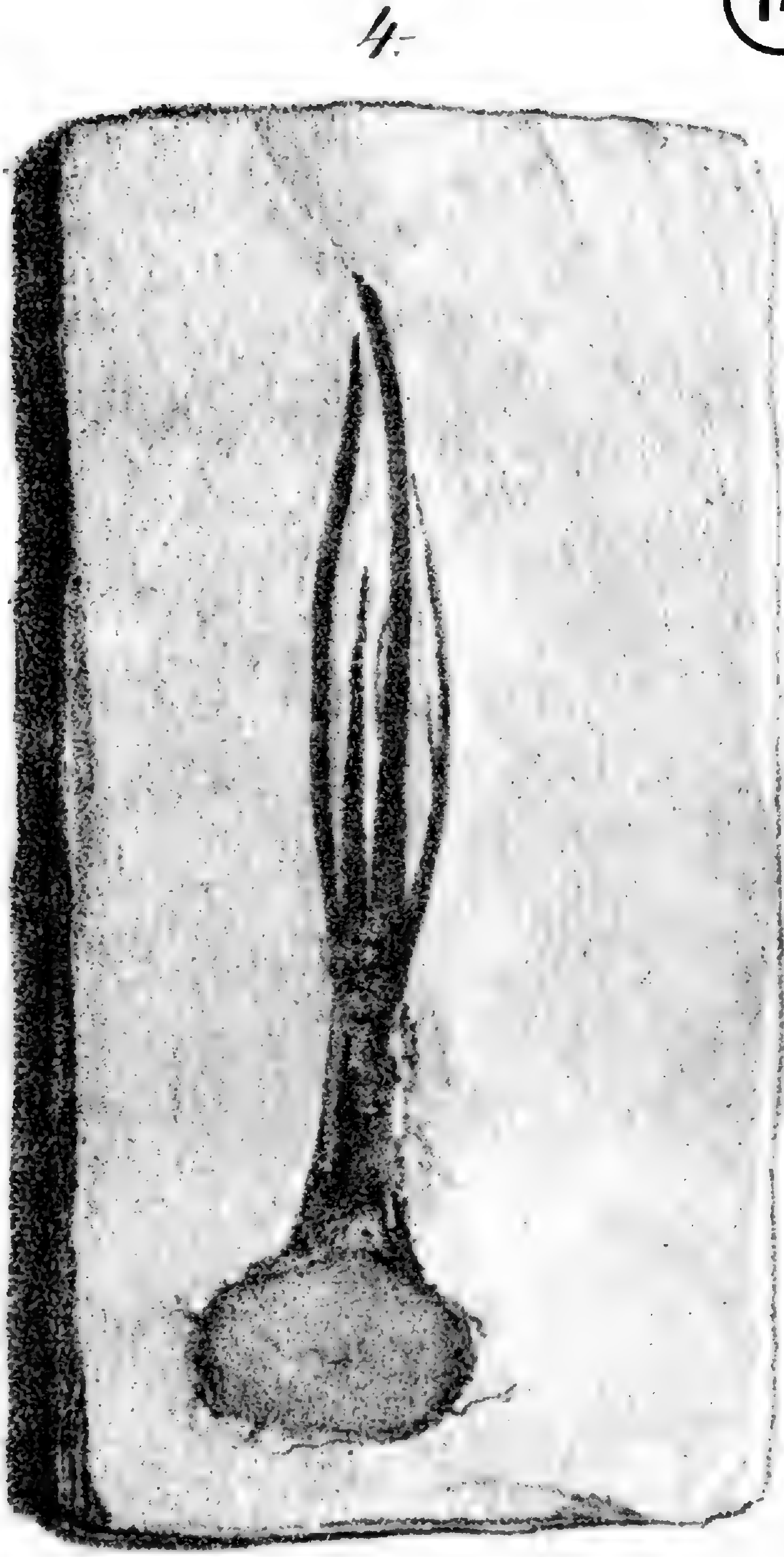

FIGURE 14. *Isoetes crociformis* Münster (1842), Tafel IV, figure 4, shown here at 2.25× the original illustration.

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FIGURES 10–13. *Yorkia gramineoides* Ward.—10. Holotype specimen USNM 41228 showing rhizome at arrow with elongate petioles (p) extending upward from it.—11. Enlarged portion of Figure 10 showing broken piece at arrow that was replaced from the drawer. Connections of the petioles above and the rhizome below can now be seen.—12. Upper portions of the petioles with pinnate side divisions at arrows. The lower left is the clearest.—13. Enlarged basal rhizome portion of Figure 10 showing the stipules (s), roots (r), and petioles (large arrows).

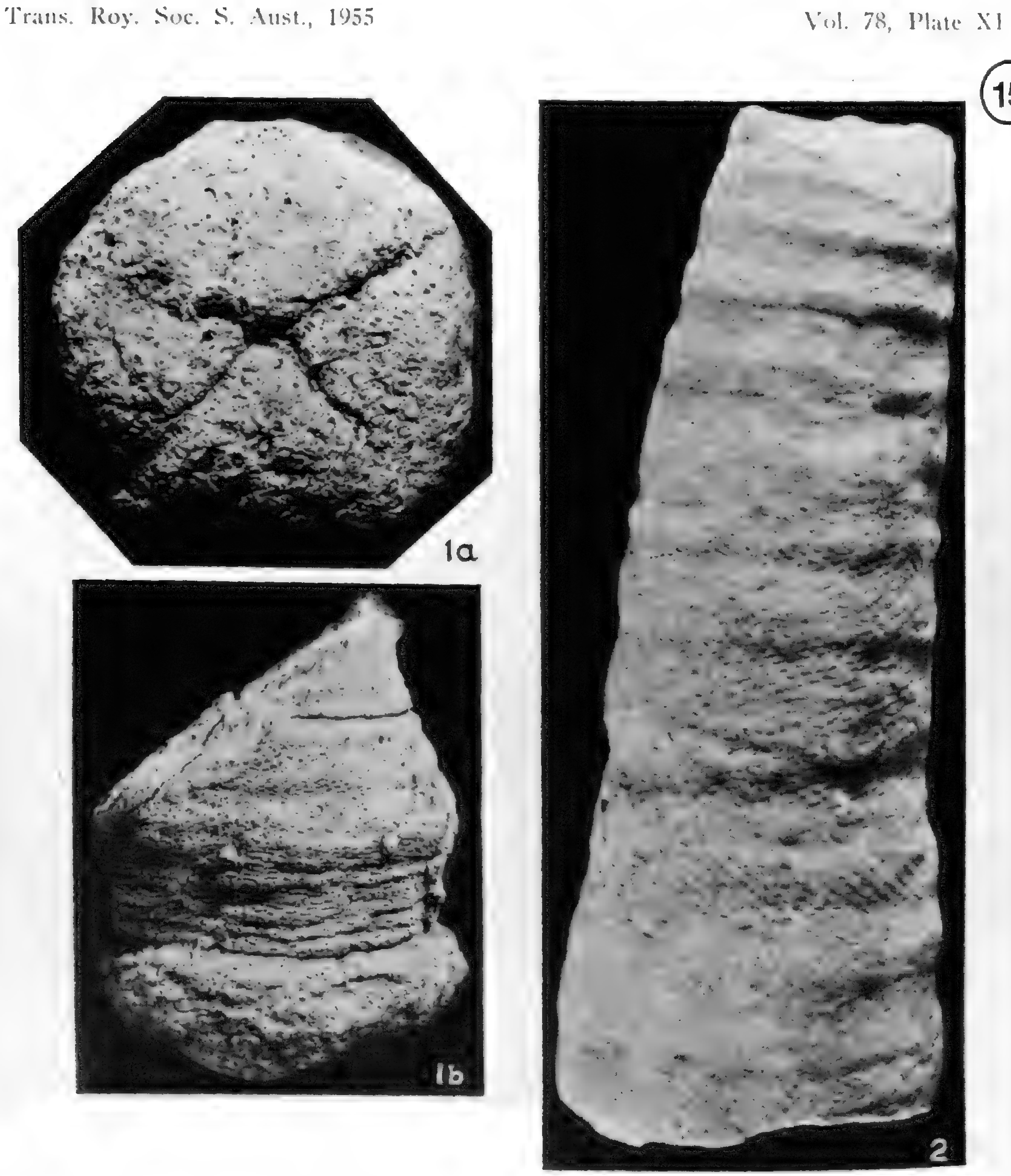

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FIGURE 15. *Nathorstianella* Glaessner & Rao, original illustrations from Transactions Royal Society South Australia, 78, plate XI, 1955.

deserves proper study, and adequate typification of the genus depends on this.

This unsatisfactory situation changes dramatically in the early Cretaceous, when good *Isoetes*-like forms appear in force in the fossil record from both hemispheres. The largest and least like *Isoetes*, with elongate stems, are those named *Nathorstianella* from South Australia (Glaessner & Rao, 1955; Fig. 15). The stems were substantial, known from fragments 3–18 cm long and up to 7 cm wide. The slightly expanded basal region bore rootlet scars and was divided into four lobes, while the erect part shows numerous closely crowded leaf base scars with a pattern of annular banding, which may reflect alternating periods of differential growth. Although no leaves or sporophylls are known from South Australia, Walkom (1944) described a crown of elongate tapering sporophylls from the Cretaceous of western Australia, each sporophyll up to 12 cm or longer. At their bases they have either well-preserved megasporangia (with in situ spores preserved) or presumed microsporangia. To our knowledge the spores have not been studied in detail. Glaessner & Rao (1955) indicated that sporophylls like Walkom's may have been borne on *Nathorstianella* stems, and this may be correct. However, as will be evident from the following, records of Cretaceous *Isoetes*-like stems are now sufficiently diverse to suggest that other forms of stem are equally possible candidates. Conversely, in the absence of attached sporophylls, *Nathorstianella* may represent persistence into the Cretaceous of subarborescent plants such as *Cylostrobus.*

Limnoniobe insignis Krassilov from the early Cretaceous of Mongolia is represented by stem fragments up to 5 cm or more long and 3 cm wide. The stem surface has similar features to *Nathorstianella,* including apparent differential growth increments and it shows both root and sporophyll scars that have a single vascular strand. The sporophylls were more than 7 cm long, were clearly trabeculate, and have *Isoetes*-like epidermal features. Details of attachment of the sporangia are obscure. The large megaspores, however, are well preserved and appear to be referable to the dispersed spore genus *Minerisporites*; they have a very broad zona and relatively subdued acrolamellae. Microspores occur adherent to the megaspores and appear to be monolete (Krassilov, 1982).

Limnoniobe was about the same height as the inaptly named *Nathorstiana arborea* Richter, described by Mägdefrau (1932), the entire plant of which reached up to 10 cm in length with leaves about 5 cm long. Sporangia and spores are unknown. The root-bearing bases were somewhat swollen and were marked by longitudinal furrows. Karrfalt's (1984) detailed study of the stems suggested that the basal swelling may be more apparent than real, resulting from decortication above the base. He detected a developmental sequence from radial (juvenile) through bilateral two-lobed to quadrangular four-lobed forms.

Isoetites choffatii (Figs. 16–19) from the Aptian–Albian of Cercal, Portugal, has been illustrated by Saporta (1894) and Teixeira (1948). Certain specimens named *Delgadopsis rhizostigma* Saporta probably represent more mature material of the same species. The following summary is based partly on material in the paleontological collections of the Natural History Museum, London.

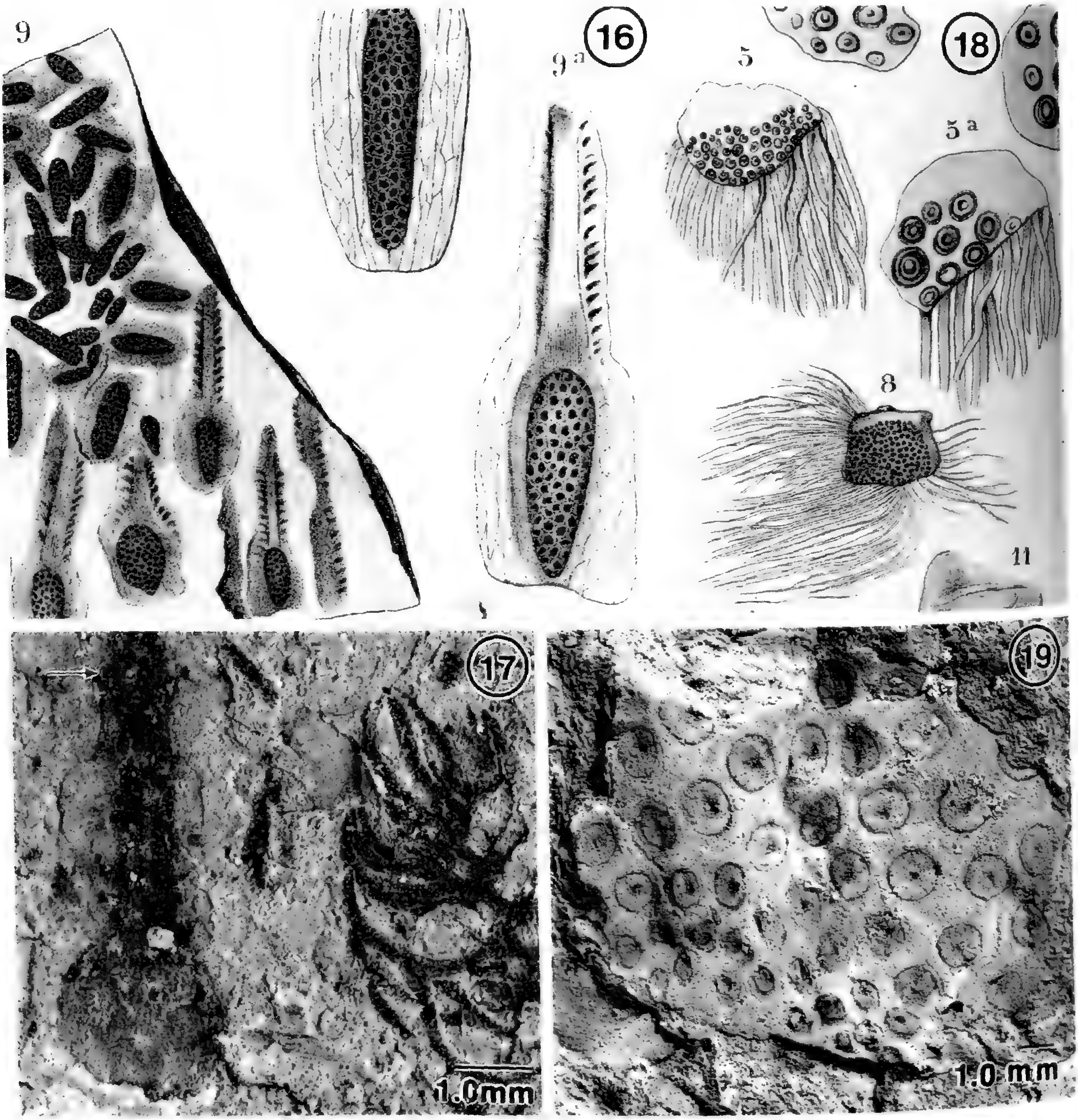
The stems of *Isoetites choffatii* were radial in end view and also appear rounded in lateral view, narrowing upward to a stem about 1 cm wide of unknown length. The bulbous base bears abundant roots, and the stem has numerous crowded scars of attachment, apparently of sporophylls. The overall appearance of these stem bases resembles that of the Paleozoic genus *Cormophyton* and, equally, is not unlike the base of *Nathorstiana* but lacks vertical ribs and displays no evidence of stem decortication or lobing; however, there is a hint of bilateral symmetry. The associated sporophylls are small, 2–3 cm long, with a pointed lamina; they are trabeculate and of typical *Isoetes*-like form. Compressed megaspores are preserved both in situ and closely associated with the sporophylls, but their detailed morphology has yet to be examined.

Specimens from the early Cretaceous of Victoria referred to *Isoetes bulbiformis* by Drinnan & Chambers (1986) are probably pentoxylalean fertile short shoots (A. Rozefelds, pers. comm.). There is no detailed evidence that they represent *Isoetes*-like fossils.

All of the Cretaceous species discussed so far had more or less elongate stems; some, such as *Nathorstianella* and *Limnoniobe,* were rather longer and wider than their nearest extant analogues such as *Isoetes andicola,* the others were apparently well within or matching the size limits of extant species. Since no widely ranging studies have been made of the form of stems of extant species stripped of their appendages at various stages of development and decortication, it is difficult to compare the fossil stems with those of extant species or vice versa.

For the remaining Cretaceous species there is direct evidence that their stems were "corm"-like as in many extant species, or else their preservation as compact crowns without stems suggests indirectly that the stems were cormose.

Isoetites sp. nov. C. Hill (Figs. 20–30) from the Cretaceous of southeastern England is preserved as permineralized crowns, some of which are borne on a small, essentially bilobed corm (not illustrated here) bearing poorly preserved root scars. Only the bases of the sporophylls are preserved in the crowns, but because they are up to 7 cm long, this suggests that the original length of the complete sporophylls was considerably longer, perhaps up to 15–30 cm. The sporophylls were rounded or angular in section, trabeculate, with typically *Isoetes*-like epidermal cells (Fig. 26). Their expanded bases were ligulate and apparently had a velum partly covering the oval sporangia. These were trabeculate, large (about 8–13 mm long by 3–5 mm wide). They yield either many thousands of monolete microspores (Fig. 30) or several hundred trilete, rounded to subangular megaspores (Figs. 27–29) about 425 × 450 μm



FIGURES 16–19. *Isoetes choffatii* Saporta. Figures 16, 17. Sporophylls. —16. Selected drawings reproduced from Saporta (1894), plate XXIV, figure 9 at natural size, the other figures being enlargements showing evident cellular details and spores. —17. At left of photo, an actual sporophyll base from Cercal, with a few adherent megaspores (one of which is at arrow), at right a *Lycopodites* shoot, v. 23601. 18, 19. Corms with rootlets and rootlet scars. —18. Selected drawings reproduced from Saporta (1894), plate XXV, figures 5 and 8 at natural size, the others enlarged. —19. An actual corm from Cercal with rootlet scars, v. 23596, collected by W. N. Edwards in 1934.

wide in polar view. The megaspores are zonate, of *Minerisporites* form with rather subdued acrolamellae; their sculpture is reticulate, normally of low muri bearing spines; they are not attributable to any described dispersed species known to us.

This *Isoetites* compares favorably in its general morphology with several extant tropical lacustrine species. It differs from all extant species, however, in having a larger megaspore productivity per sporangium, and, to the extent that knowledge of

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FIGURES 20–25. *Isoetes* sp. nov. C. Hill. All scale bars = 1 cm. —20. v. 63454, side view. —21. v. 63456, basal view showing corm. —22. v. 63454, longitudinal medial section of Figure 20. —23. v. 63455, side view showing sporophyll lamina impression, as longitudinal furrow. —24. v. 63458, basal view showing ring of fertile basal regions of sporophylls. —25. v. 63459, transverse section.


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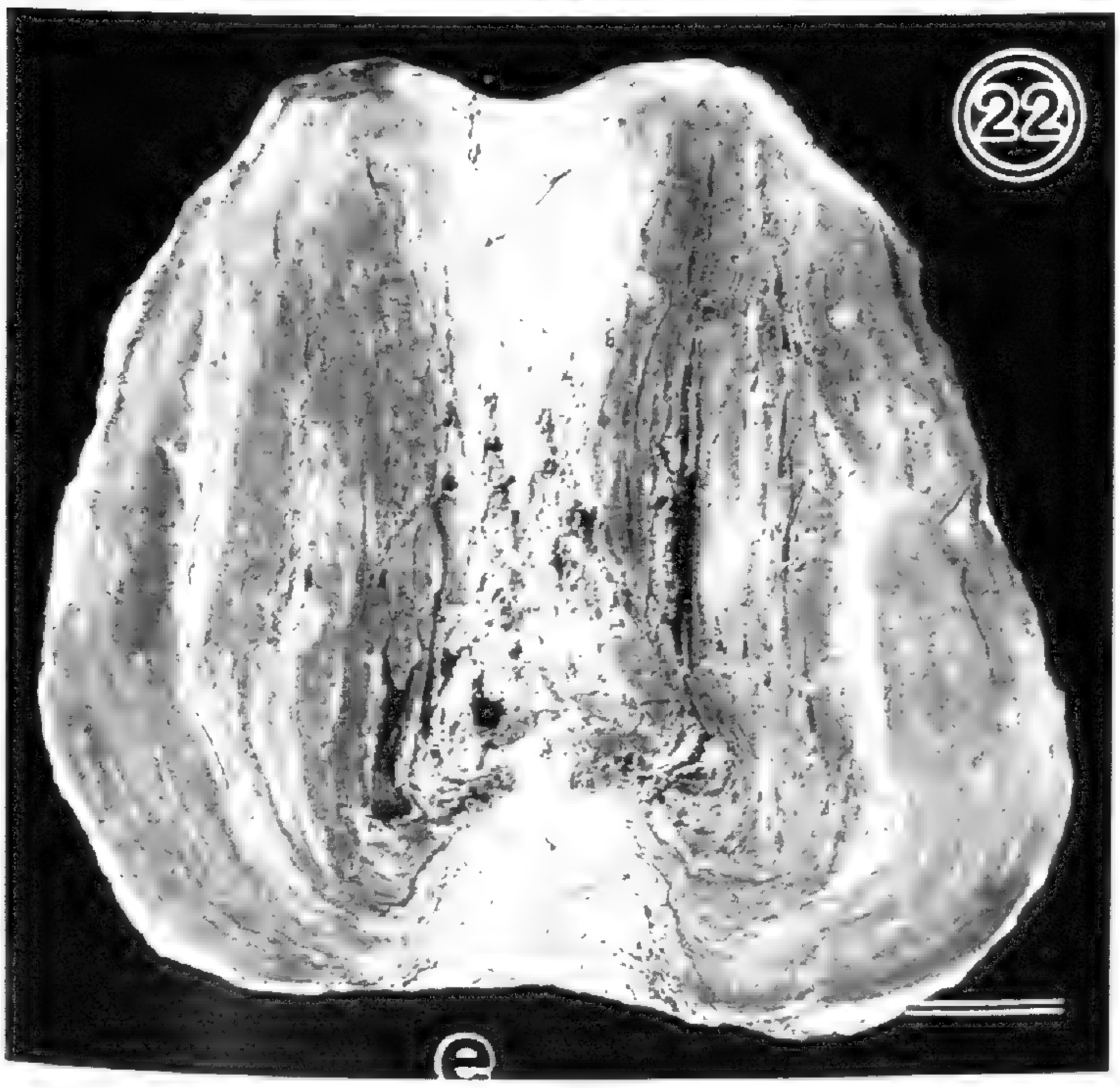
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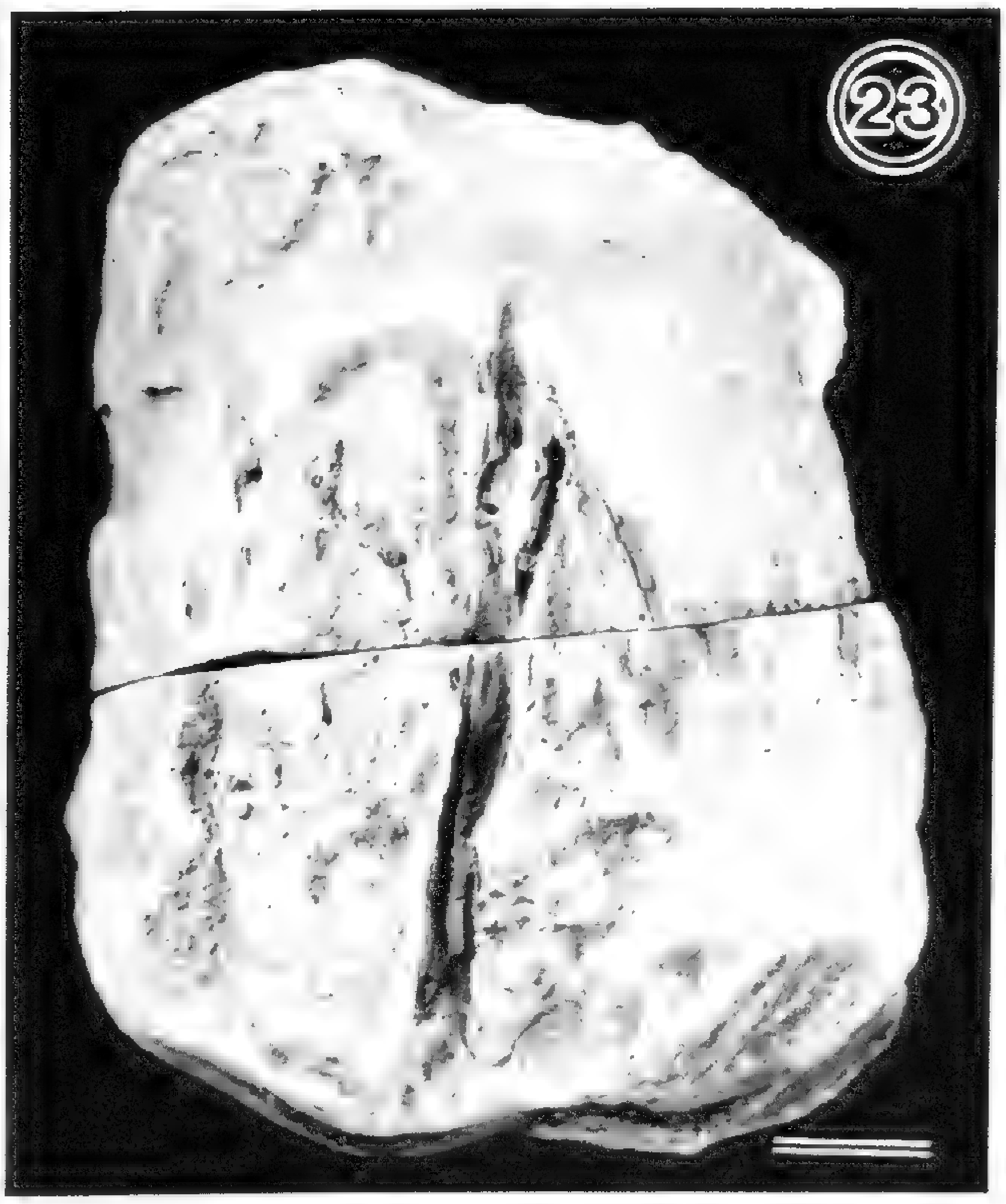
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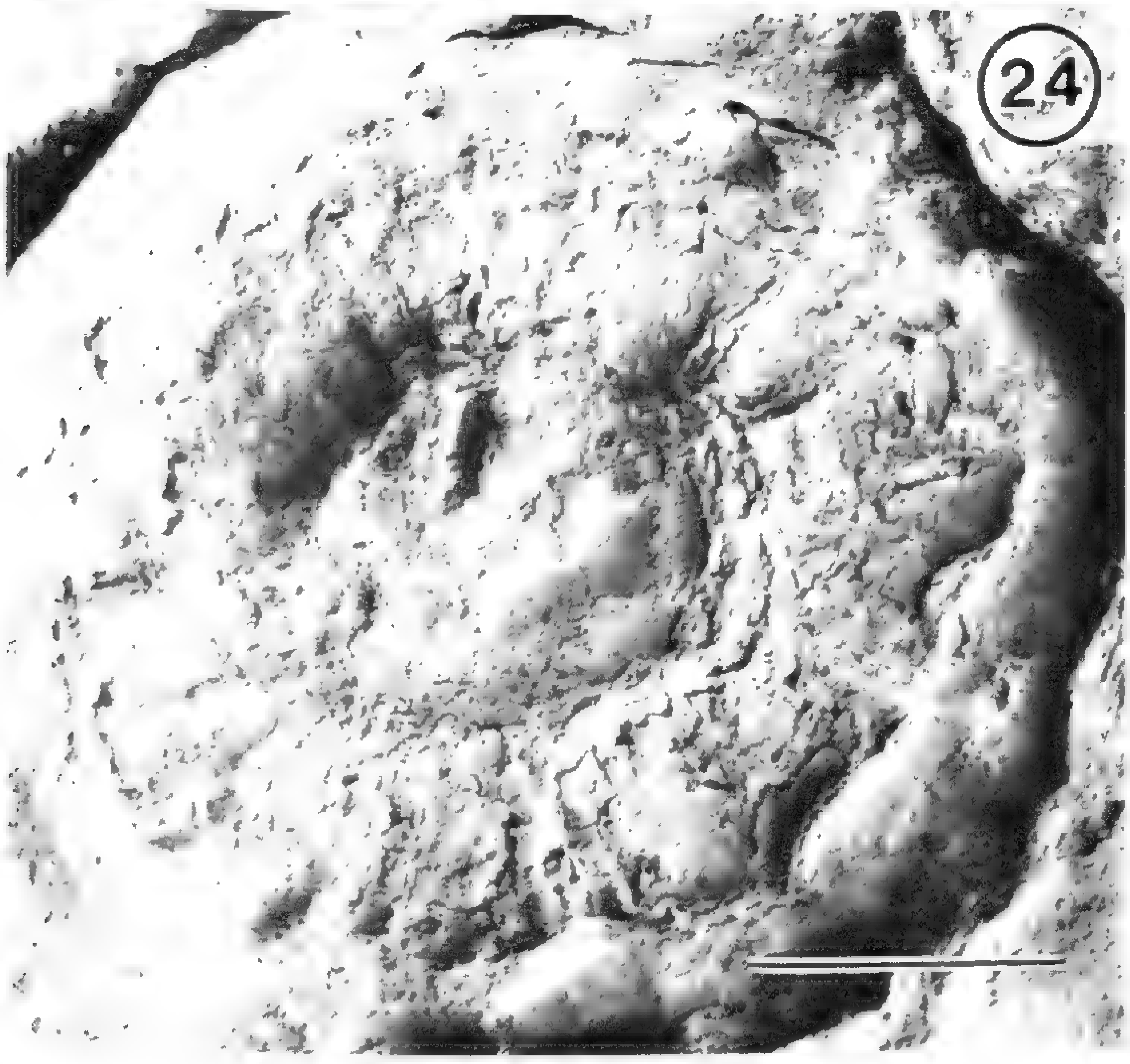
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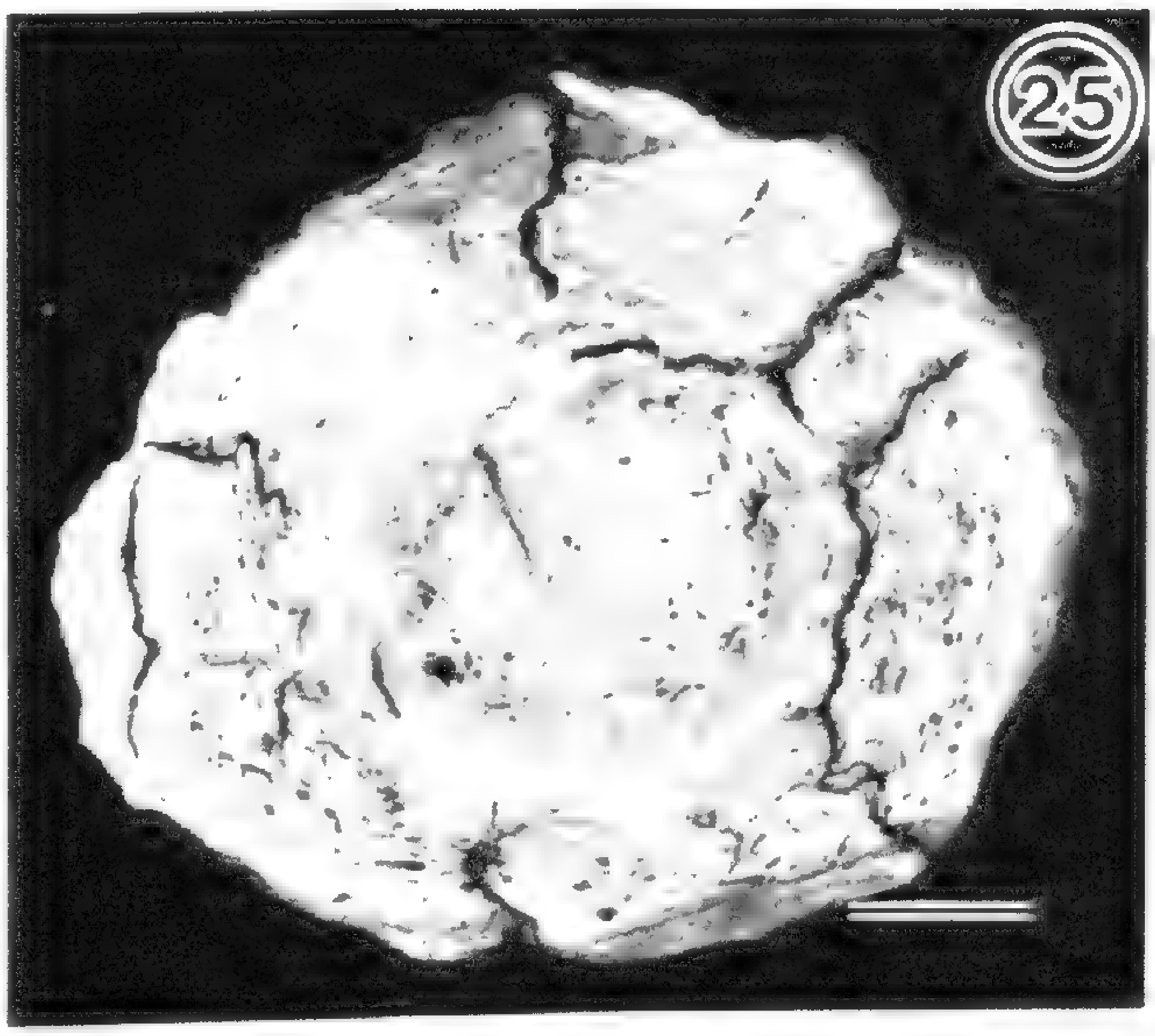
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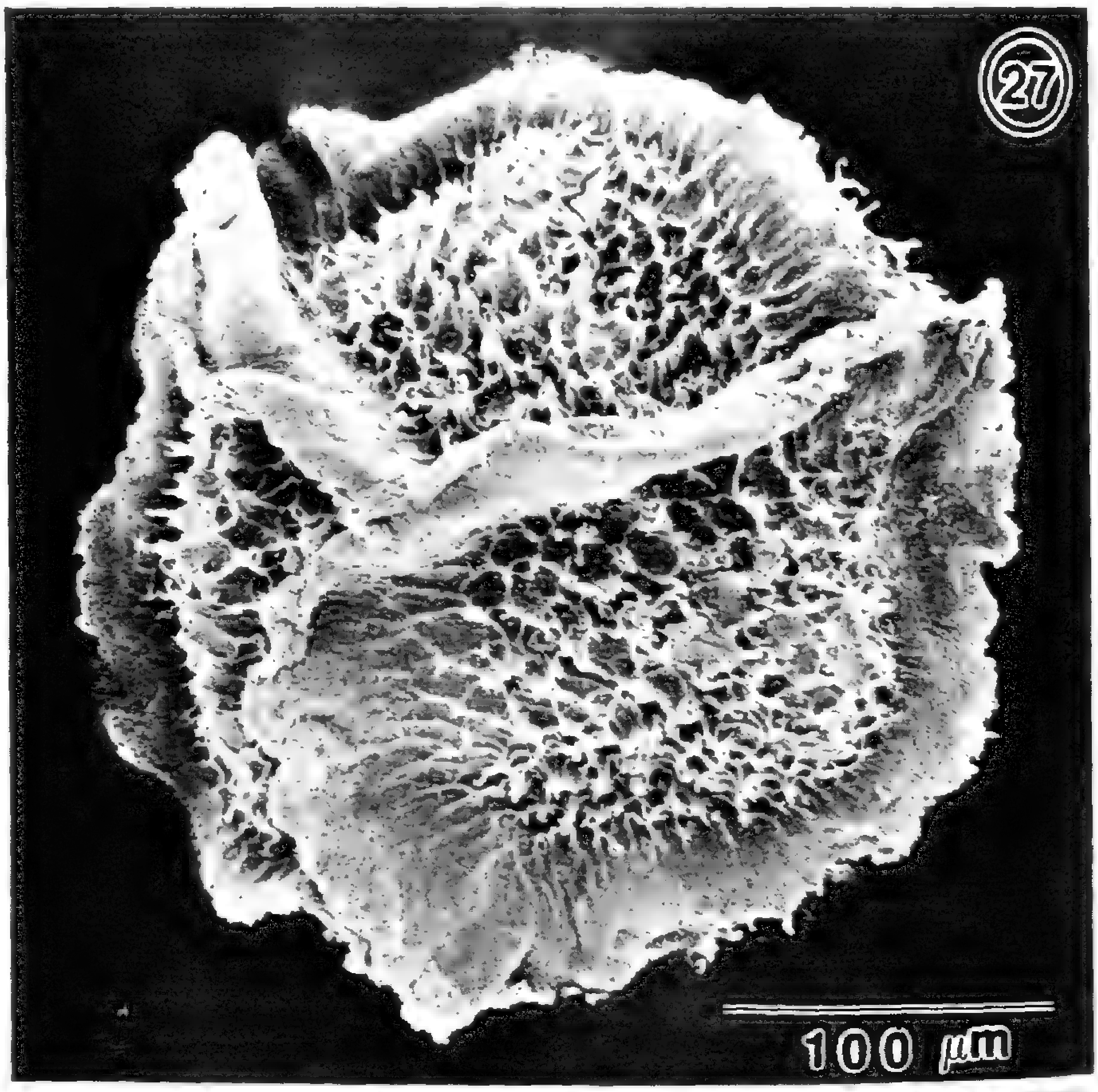
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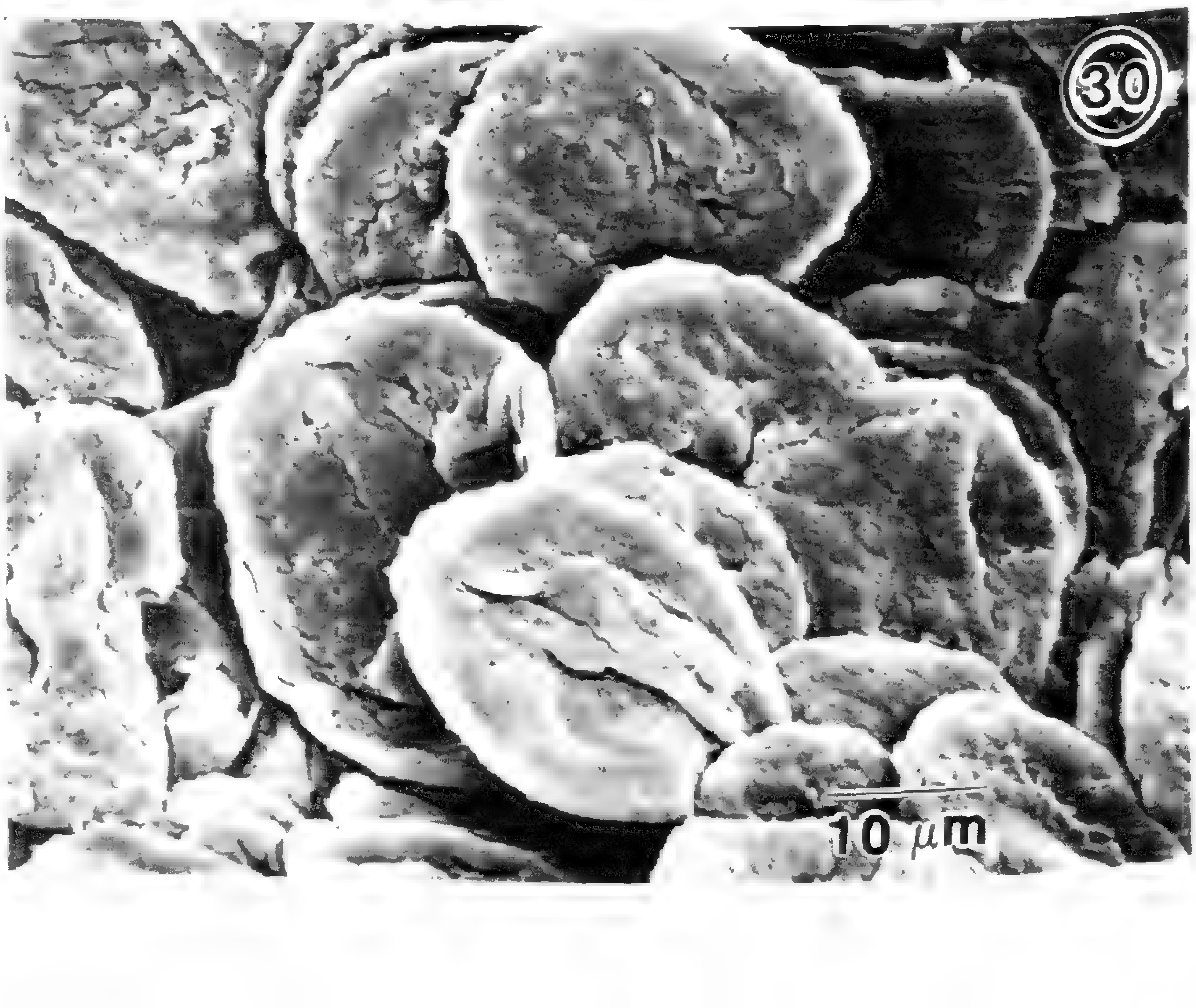
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corms of extant species permits comparison, the aerial apex of the corm in the fossil is more elongated, so that it appears more acutely conical in section. To the extent that the spores can be compared, the fossil ones also resemble those of some extant species.

A comparable species to the British *Isoetites* is *Isoetes janaianus* Banerji, previously described as *Isoetites indicus* Bose & Roy (1964) from the ?middle to late Jurassic (Banerji, 1989) to (more likely) early Cretaceous of northwestern India (see also Bose & Banerji, 1984; Sukh-Dev, 1980). Although it has a five-lobed corm and is smaller than the British material, it is otherwise very similar. It too has yielded megaspores of *Minerisporites* form produced in large numbers (Bose and Roy estimated more than 1,500 per megasporangium; Banerji, 1989, reported 100–1,500). The most comparable dispersed megaspores appear to be *Minerisporites cutchensis* and *M. auriculatus* (Banerji et al., 1984; Sukh-Dev, 1980). These have a fine reticulum like the in situ spores of *Isoetes janaianus* and similar to the spores of the British fossil.

A coeval *Isoetites* species from India is *I. serratifolius* Bose & Roy (see also Bose & Banerji, 1984 who provide a partial reconstruction of the parent plant). It has large, well-preserved laminate sporophylls up to 1.5 cm wide that had serrate margins to the distal region beyond their expanded bases. Such margins are unknown in any extant species. Unfortunately, no material has yet been found with in situ spores, and this material is known only from detached sporophylls (Bose & Roy, 1964). The sporangia were large, up to 12 mm long. The basal parts of the sporophylls have a remarkably similar outline to those of Triassic lepidodendraleans such as *Skilliostrobus* and certain species currently referred to *Tomiostrobus*.

A distinctive pair of *Isoetites* species that also had serrate sporophylls is known from the late Cretaceous to early Tertiary of North America. However, these were even less like extant *Isoetes* than the Indian material just mentioned. In the Upper Cretaceous *Isoetites serratus* Brown (1939, 1958), the strongly trabeculate sporophylls not only had minutely serrate distal margins but were also markedly spatulate distally. Collinson (1988, 1992) drew attention to the possibility that the spatulate distal regions of the sporophylls in this and especially the next species were dehiscent—quite unlike extant *Isoetes*. Other characters of *I. serratus* were similar to those of extinct species and extant *Isoetes*; for example, although a corm is not known preserved, the sporophylls were evidently disposed around a corm to form a crown and they had typical epidermal cells apparently without stomata.

Isoetites horridus (Dawson) Brown (see also Melchior, 1977 and Hickey, 1977) from the late Cretaceous to Eocene of North America also had markedly trabeculate and distally expanded sporophylls Brown (1939, 1958). It is thus similar morphologically to *I. serratus*, although the sporophyll margins are entire and a corm or short stem is preserved. In situ spores have been well described and illustrated by Hickey (1977) and Melchior (1977), who attributed them to the dispersed spore species *Minerisporites mirabilis* (Miner) Potonié. This North American material requires fresh study using modern techniques.

Since we have now digressed into the early Tertiary, we should mention the record of sporophylls with ?*Minerisporites* megaspores from the Oligocene to Miocene of Tasmania, named *Isoetes reticulata* by R. S. Hill (1987).

SUMMARY: ISOETALEANS

These records of Mesozoic and early Tertiary *Isoetes*-like forms encompass several species that, at least in principle, may be related to groups of species within the extant genus. Others extend the range of form of *Isoetes* to greater or lesser extent. Although knowledge of these fossils is growing rapidly, it is clear that much further, carefully focussed work needs to be done on them and on extant species if comparisons are to be effective.

Environmentally, the evidence is slim but suggests that these forms have always occupied the same niches as their living descendants. Apart from the indirect evidence supplied by megaspores (noted previously), the rarity of the megafossils suggests that they were not immediate occupants of the high-energy fluvial environments of deposition fa-

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FIGURES 26–30. *Isoetes* sp. nov. C. Hill.—26. v. 63455, surface details indicating cell outlines.—27. v. 63455, SEM of trilete megaspore, proximal view.—28. v. 63455, SEM enlarged of Figure 27 showing ornamentation of spines.—29. v. 63455, SEM enlarged showing reticulate pattern of exine below ornamentation.—30. v. 63457, SEM of cluster of microspores.

vored in the sedimentary record of plants, but that they grew instead in associated low-energy lacustrine and marsh settings. Although there is no absolute correlation even among extant species (Thomas & Masarati, 1982), the apparent lack of stomata from any of the fossil sporophylls so far known suggests that the plants we know as megafossils were growing more or less submerged in water as lacustrine forms; this makes sense in terms of sedimentological bias and should not be taken as evidence that there were no species growing coevally in more exposed marshy environments. Indeed, it is these that are likely to be represented indirectly, by those megaspores that cannot be linked to megafossils. At present the lacustrine species are virtually cosmopolitan in distribution, but those of larger size comparable to *Isoetites* sp. nov. are mainly tropical; on uniformitarian grounds this indicates that Cretaceous lowland Britain was likely to have been warm and, despite many other indicators of widespread seasonally moderately arid or salt-stressed conditions, was at least locally sufficiently wet to sustain shallow freshwater lakes.

PHYLOGENY

Any account of Mesozoic lycopsid phylogeny cannot adequately be divorced from an understanding of lycopsid relationships as a whole. This must be based on detailed knowledge of extant as well as of extinct forms, including extinct plants from as far back as the Devonian in geologic time, as is obvious from the papers in this collection. Hence, our treatment here of wider aspects is brief and provisional. Some of the main points of interest are as follows.

(1) As was recognized by Townrow (1968), *Selaginella harrisiana* possessed many derived characters but it retained several generalized characters in its evidently leafless rhizome, which thus resembled the rhizomes of more plesiomorphous lycopsids. This is of considerable value in indicating the likely generalized condition of the main rooting system in *Selaginella* as a whole.

(2) The apparently rather confusing admixture of characters in Mesozoic *Lycopodites* species such as *L. macrostomus* and *L. falcatus* can be reconciled if related to the selaginellaleans. Thus, for instance, *L. macrostomus*, while vegetatively *Huperzia*-like, had apparently ligulate leaves. Several such extinct species may have retained many "lycopodialean" features together with a few "selaginellalean" ones, in contrast to those at the other end of this apparently paraphyletic spectrum of forms, such as *Selaginella harrisiana*, which retained just a few "lycopodialean" features. To that extent, when interpreted in a cladistic sense, these forms are "selaginellalean" rather than "lycopodialean." In this light it may not be surprising if either *Lycopodites macrostomus* or *L. falcatus* prove to be heterosporous. These Mesozoic species appear to provide hitherto unrecognized evidence, albeit tentative, of links and/or homoplasies between the extant selaginellaleans and lycopodialeans that may call into question their apparent monophyly as represented by the surviving species.

(3) A growing number of accurately identified *Isoetes*-like forms is becoming better known. Together with permineralized Mesozoic specimens of such genera as *Pleuromeia* and in particular *Takhtajanodoxa* (Snigirevskaya, 1980), this provides a promising basis for improved comparison with Paleozoic material, and this, in turn, is leading to greater clarity in our present understanding of the origin of *Isoetes*.

SUMMARY

Following the extinctions of the Paleozoic lycopsids, the Mesozoic is perceived as a time of comparative silence regarding the evolution of this major group of plants. Yet when the record is critically examined there is evidence of diversity among the now mainly herbaceous lycopsids. The three main lines that have continued into the Recent (Isoetales, Selaginellales, and Lycopodiales) are well established within various habitats. Problems arise because of the scarcity of known megafossils, specimens that are poorly known, confusion between the lycopsids and other groups of plants when not enough characters can be seen (gymnosperms and bryophytes in particular as Seward noted in 1910), and difficulty in correlations between the palynological and megafossil records. In this paper we have tried to summarize the state of knowledge for the Mesozoic lycopsids, to indicate trends of evolution that may have been occurring during this time interval, to offer some new information on lycopsids represented as megafossils, and especially to suggest some critical areas for future research.

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GENERIC CLASSIFICATION OF MODERN NORTH AMERICAN LYCOPODIACEAE[1]

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ABSTRACT

Generic classification of North American Lycopodiaceae is analyzed in terms of the general factors that govern the recognition of the rank of genus, the character states that determine affinities, the hypothetical common ancestral groundplan, a tree based on these data, and a translation of this information into a classification scheme. The genera segregated here are based primarily on numerous characters of anatomy, chromosomes, spores, and gametophytes. Those groups that are recognized as genera have many distinguishing features, strong gaps separating them from other groups, monophylesis, uniquely derived states, inability to hybridize, and a level of segregation consistent and comparable with generic division in other pteridophytes. The classification adopted is as follows: subfamily Huperzioideae (*Phlegmariurus, Huperzia*), subfamily Lycopodioideae (*Lycopodium, Diphasiastrum*), and subfamily Lycopodielloideae (*Pseudolycopodiella, Lycopodiella,* and *Palhinhaea*).

At the species level, the classification of North American clubmosses, all formerly placed in a single genus *Lycopodium*, has been altered radically since the eighth edition of *Gray's Manual* (Fernald, 1950). More rigorous definitions of species, and the inclusion of data from population biology, anatomical characters, cytogenetics, and interspecific hybridization, have been important factors in this change. Recently, a new question has arisen: What should be the classification at the generic level? The traditional classification has been challenged by such recent European workers as Pichi Sermolli (1977), Holub (1975, 1983), and Øllgaard (1987). The generic interpretation of Lycopodiaceae has also been influenced by researchers in North America including Beitel, Britton, Bruce, Hickey, F. Wagner, Whittier, and Wilce, who have contributed valuable new information on anatomy, spores, chromosomes, life cycles, habitats, and interspecific hybridization. In the following report we attempt to interpret this information.

We have asked the following questions: What criteria are used for recognition of genera in pteridophytes overall? What characters can be used to differentiate the groups of Lycopodiaceae in particular? What, if any, directionality can be deduced for each character trend? What were the character states of the probable ancestral source of modern Lycopodiaceae? How do the character changes fit into a tree of relationships? And how should this body of information be translated into an acceptable classification scheme?

For nearly 20 years pteridologists were under the impression that the different gametophytic types reported in Lycopodiaceae were merely results of environmental modifications, as proposed by Freeberg & Wetmore (1957). The gametophyte was therefore considered unreliable as an indicator of relationships. However, Bruce (1976b) and Whittier (1981) showed that this conclusion was based on experimental error. For the past decade and a half, the gametophytic differences between species groups of Lycopodiaceae have proved to be valuable taxonomic characters (Bruce, 1972, 1976a, b, 1979; Bruce & Beitel, 1979). Other characters such as spore sculpture (Wilce, 1972; Tryon & Lugardon, 1990) and chromosome numbers (see F. Wagner, 1992) became available only during the past several decades. Also, Bruce (1975) provided data on mucilage canals, and Øllgaard (1975, 1979) new insights into the structure of the sporangium wall. Altogether, we now have a substantial array of new comparative data to aid us in classification.

In North America there are nearly 50 recognized species. Remarkably, approximately two-fifths of these are nothospecies as opposed to orthospecies, i.e., taxa of reticulate origin as opposed to

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those of normal divergent origin. For such a small clubmoss flora, there is, nevertheless, profound diversity, and as will be seen below seven discrete groups can be readily distinguished. The largest number of species in this family is in the tropics, where the family is made up largely of species related to *Phlegmariurus phlegmaria.* Only one of these is in North America, where it is found locally in southern Florida.

GENERIC DELIMITATION IN PTERIDOPHYTES

For generic delimitation there are far more gross morphological characters that can be used in angiosperms than in pteridophytes. Perhaps for this reason, workers familiar primarily with flowering plants have tended to lump Lycopodiaceae into one catch-all genus, simply because they all seem to look alike. However, when the plants are examined in detail, including many micromorphological characters, we rapidly become aware of multiple and often striking differences between pteridophyte groups. There are far more demonstrable differences between the groups of living Lycopodiaceae than between such filicean genera as *Dryopteris, Rumohra, Arachniodes, Polystichum,* and *Phanerophlebia* (Kramer & Green, 1990). If workers with Dryopteridaceae deal with the species groups of clubmosses and firmosses at the same level of generic discrimination, to maintain consistency they should accept seven genera of Lycopodiaceae in North America.

The reasons why taxonomists separate and recognize plant genera are numerous, and there is no widespread agreement on how to go about it. We have used the most dependable and objective criteria that we can adopt in delimiting the genera of Lycopodiaceae. They include the following: (a) The characters used for generic separation should be numerous, not only one or several. (b) It is imperative that there be strong gaps in the character patterns. There should be no intermediate taxa, whether these intermediates are produced by gradation in ordinary phylogenetic divergence or intermediates produced by interspecific hybridization. (c) No genus should be recognized if it can be shown that that genus arose from two or more sources, i.e., is polyphyletic whether by convergence or some form of reticulation. A genus should be monophyletic, with strong evidence for an immediate common ancestry of its species. (d) Lines should be based on uniquely derived character states. Parallelisms, convergences, and reversals can be used to bolster generic validity so long as their patterns and incidence show them clearly to be separate, though similar, derived states. (e) More and more pteridologists regard the presence of "intergeneric" hybridization as evidence for not separating genera. If hybridization does occur between members of "different" genera, that is evidence for their taxonomic unity. In the case of Lycopodiaceae, there is no evidence of intergeneric hybridization, even though in some groups (e.g., *Diphasiastrum, Huperzia, Lycopodiella*) intrageneric hybridization is rampant. (f) Above all, good genera in one group of pteridophytes should be approximately equivalent to and comparable with genera in other groups. One family of pteridophytes should not be finely split and another be grossly lumped. The character states involved in generic separations in the Lycopodiaceae should be reasonably similar in number and kind to those used in other families of pteridophytes. For example, if we keep the following pairs separate, *Marattia* and *Angiopteris* (Marattiaceae), *Pellaea* and *Cheilanthes* (Adiantaceae), *Athyrium* and *Diplazium* (Dryopteridaceae), then, as will be mentioned below, we should certainly keep *Palhinhaea* separate from *Lycopodiella,* or *Diphasiastrum* from *Lycopodium.* There should be some consistency.

CHARACTERS USED FOR GENERIC PHYLOGENY AND CLASSIFICATION

In trying to develop a consistent taxonomy for Lycopodiaceae there are, of course, pitfalls. Dealing only with North American taxa could lead to erroneous conclusions because links in other parts of the world might be overlooked. However, we believe that the taxa elsewhere on the earth will either fit the generic system given here and can be easily accommodated within it, or new ones can be added to it (Holub, 1991; Øllgaard, 1987). Because of the gaps in the divergence patterns (Fig. 1), it is no problem to delimit the genera. Another potential pitfall in this, as in all, systematic syntheses, is incompleteness or lack of data. The fossil record, although perhaps rich in comparison with the majority of other plant orders, is still replete with vast lacunae. And the living record has not been completely examined, especially in the tropics and Southern Hemisphere. We recognize that future research may change our understandings and even our basic conclusions.

For determining character state polarities there is no single living genus or family that we can use for comparison outside of the Lycopodiaceae. The Lycopodiaceae as we know them are diverse modern survivors of an ancient lineage. We used for outgroup comparison mainly three of the well known

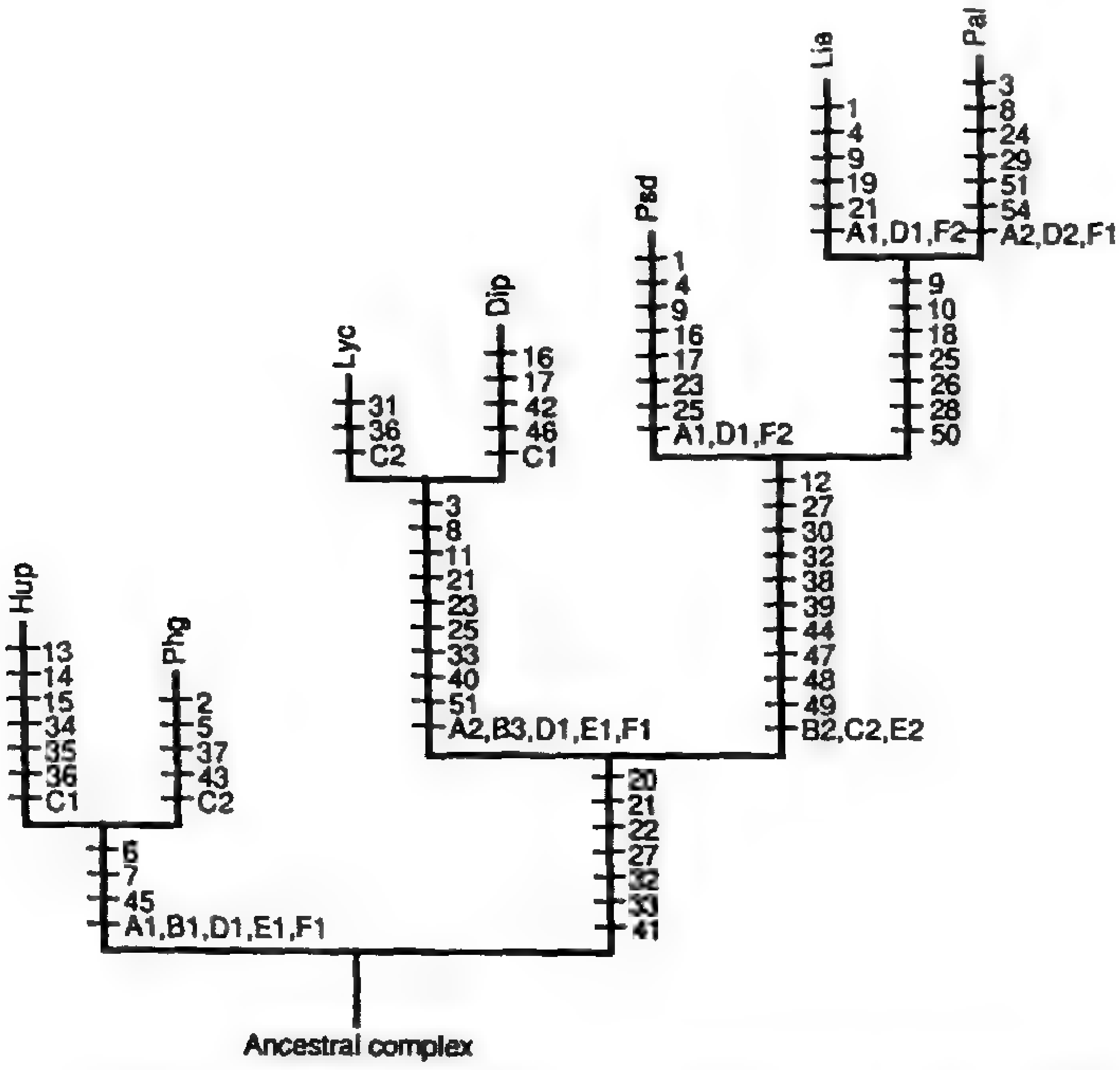

FIGURE 1. Wagner tree of characters in North American Lycopodiaceae. Abbreviations of taxa are as follows: Hup = *Huperzia*; Phg = *Phlegmariurus*; Lyc = *Lycopodium*; Dip = *Diphasiastrum*; Psd = *Pseudolycopodiella*; Lie = *Lycopodiella*; Pal = *Palhinhaea.*

early genera: *Asteroxylon, Drepanophycus*, and *Baragwanathia*, all from Lower to Middle Devonian strata. The ligulate, heterosporous lycopsids, Lepidodendrales, Selaginellales, Pleuromeiales, and Isoetales, apparently constitute separately derived assemblages of evolutionary lines that became established by the Carboniferous. The Devonian elements, commonly known as Protolepidodendrales, eligulate and homosporous, are more logical outside groups for comparison with the modern Lycopodiales and include the three genera listed. The original evolutionary progression probably began in the Upper Silurian: Rhyniopsids apparently gave rise to zosterophyllopsids, and these to lycopodiophytes, and the first two groups became extinct. The most primitive were the Protolepidodendrales, and they too became extinct, as did the ligulate orders Lepidodendrales and Pleuromeiales. These changes are discussed in numerous textbooks of paleobotany (e.g., Bierhorst, 1971; Taylor, 1981, Thomas & Spicer, 1987). Although there are disagreements on the details of the history of lycopsids, there is a fair consensus regarding the broad outlines. In addition to outside comparison, we examined trends within and between the subgroups of the present-day Lycopodiaceae. The highly complex and specialized propagative branches of the gemma firmosses, *Huperzia* sens. str., are uniquely derived and found only in this genus; comparisons within (and outside) the family support the conclusion that such bizarre shoots involving a number of character changes represent distinct and multiple advancements (cf. Stevenson, 1976, and references therein). So it is with such character states as cortical roots, plectosteles, ring meristems in gametophytes, napiform gametophyte thalli, nodular sporangial wall cells, unequal sporangial valves, and many of the other states summarized below. However, a number of obvious specializations found in North American Lycopodiaceae are useless at the generic level since they involve only individual species. These "peripheral" or "autapomorphic" states are obviously advanced within their phylads, but they cannot be used for delimitation of whole genera. They include such advancements as leaf margins toothed, leaf tips hair-tipped, stomates only on abaxial leaf surfaces, blade surfaces glaucescent with epicuticular wax, or rhizome subterranean.

At the generic level there are some striking alternative states for which we can assign no polarity at present. We have no basis for judgment either within or outside of the family. These include the patterns of the root base stele, sculpture of spores, extent of the triradiate groove on the proximal spore face, and the sculpture of the proximal face. A particular problem involves the chromosome base number: The chromosome numbers seem to concentrate around $x = 22$, 33, 55, 66, and 77, with various aneuploidal additions and subtractions (F. Wagner, 1992). Intuitively it might seem reasonable to say that lower ploidal levels are more primitive than higher ones and that fewer aneuploidal changes are more primitive than more, but we cannot be sure that this is so in any particular case. We have been forced, therefore, to use base numbers as they are, as a classificatory tool but without applying phylogenetic directionality. These unpolarized trends are summarized at the end of Table 1 and are represented by letters and numbers there and in the character tree, Figure 1.

POLARIZED CHARACTER TRENDS

The character polarizations we have deduced (numbered in Table 2 and Fig. 1, and in parentheses below) come primarily from comparisons with the members of the outside groups given above, supported by data presented by various authors (e.g., Bruce, 1975, 1976b; Holub, 1975, 1983, 1985; Øllgaard, 1975, 1979, 1987; Wilce, 1965, 1972), as well as by ourselves. The basis for determining directionality is outside comparison (Wagner, 1962, 1969, 1980). The terrestrial habitat is considered primitive. Two trends have occurred away from it: to semiaquatic, i.e., inundated for part of the growing season, (1) and to epiphytic

(2). The former is characteristic of *Lycopodiella* and *Pseudolycopodiella,* the latter the dominant condition of *Phlegmariurus,* some species of which have no doubt experienced reversal. Simple, dichotomous aerial branching is considered ancestral by outside comparison, and there are two different transformations: amplification to extremely complex dendroid habit of the aerial shoots (e.g., *Palhinhaea*) (3), and reduction to simple, unbranched aerial shoots (e.g., *Lycopodiella*) (4). The erect habit of terminal aerial branches is considered basic, and the pendent derived (5). The presence of a well-defined creeping rhizome is presumably the initial state, while the loss of a distinct rhizome is considered derived (6), as illustrated by *Huperzia* and *Phlegmariurus.* The emergence of roots close to their position of origin in the stem stele is the most probable ancestral condition, and the extensive basal migration of roots from the shoot apex downward through the cortex to the level of the substratum before emergence is specialized (7), as in the *Huperzia* group. The branching of the roots themselves was initially most likely isodichotomous and gave way to anisodichotomous (8), as is represented in *Palhinhaea.* In all Lycopodiaceae, evergreen condition of the vegetative aerial shoots is evidently the original one; deciduous components like the upright shoots of *Lycopodiella* are thus advanced (9). The lack of hairs and other emergences is the generalized primary condition, and their presence on stems and/or leaves is specialized and secondary (10). From the most likely original stele, the actinostele, there have been two major directions of change: to a meshed actinostele (like that of *Lycopodiella* and its nearest allies) (12), and to the peculiar and unique condition known as plectostele (like that of *Lycopodium* and *Diphasiastrum*) (11).

Highly evolved lateral branches that afford vegetative propagation are observed only in the genus *Huperzia.* They are complex and involve several, apparently de novo elements—the gemmiphore, the abscission layer, gemma axis, and dorsiventral, distinctively oriented, and modified leaves. The generalized condition for Lycopodiaceae and their outside sister groups is to lack such structures entirely, so that their presence alone is apomorphic (13). The gemma apparatus in *Huperzia* evolved *sui generis* a series of other advancements, namely from radial to bilateral (14) as well as others not used here. Aerial stem branching, judging from the fossil outgroups, was almost unarguably dichotomous in the ancestors, and became unequal (anisodichotomous) in the descendants (15). The ranks of leaves on the aerial shoots have undergone reduction in number from 6–12 to only 3–5 (16). The vegetative leaves of the aerial parts were originally monomorphic (e.g., *Lycopodium clavatum*), but became transformed in connection with major changes in overall shoot structure so as to be heteromorphic, as in most species of *Diphasiastrum* (17), in which the branches are cordlike and flattened like *Thuja.* (This trend refers only to adult shoots; the juvenile shoots have isophylly, as illustrated by *Diphasiastrum sitchense,* which is apparently neotenic, maintaining its juvenile condition into maturity.)

Presumably, mucilage canals are derived structures absent in the progenitors. The *Huperzia–Phlegmariurus* assemblage still lacks them, but the type of mucilage duct that is basal in the fertile leaf is present in all other genera (20). Veinal mucilage canals occur only in the vegetative leaves of *Lycopodiella* and *Pseudolycopodiella* (18). However, they are absent from the sporophylls in *Pseudolycopodiella,* being present there only in *Lycopodiella* (19). These different patterns, discovered by Bruce (1975), are treated here as separate trends rather than steps in a single trend, because it is not obvious how or even if the different conditions are sequenced.

Sporophylls in the primitive lycopsids were structurally mostly like trophophylls, as they are today in typical *Selaginella selaginoides* and all species of *Isoetes,* and in the Protolepidodendrales. This condition is retained to a large extent in the firmosses, *Huperzia* and many *Phlegmariurus* species. Nevertheless, differentiated sporophylls are found in all five genera of clubmosses (21). Those of *Lycopodiella* and *Palhinhaea* are only partially transformed. The independent development of distinct sporophylls on tassel-like strobiloids that differ from typical strobili in orientation and appendage structure in *Phlegmariurus* is considered a parallelism or convergence. The attachment of the sporangia is basal in Huperzioideae as in the Devonian outgroups, but becomes pseudopeltate to peltate in all of the other groups (22), and associated with this there is a change from unstalked to stalked (23), but this is found only in Lycopodioideae. Where a true strobilus has been formed, the erect orientation is surely the ancestral one, judging from the outside evidence: the peculiar nodding strobili as found in *Palhinhaea* are derived (24). Where strobili are pedunculate, the leafy condition of the stalk as seen in *Lycopodiella* and *Palhinhaea* is exchanged for the scaly to nearly naked condition seen in *Lycopodium* (certain species), *Diphasiastrum,* and *Pseudolycopodiella* (25). The sporangial valves are primitively equal

TABLE 1. Characters and character states used in this analysis.

Character	Primitive	Advanced	Hup	Phg	Lyc	Dip	Psd	Lie	Pal
1. Habitat	terrestrial	semiquatic	0	*	0	0	1	1	0
2. Habitat	terrestrial	epiphytic	0	1	0	0	*	*	*
3. Branching	simple-dichotomous	complex-dendritic	0	0	0–1	0–1	*	*	1
4. Branching	simple-dichotomous	reduced-unbranched	0	0	0	0	1	1	0
5. Habit	erect	pendent	0	1	0	0	0	0	0
6. Rhizome creeping	present	absent	1	1	0	0	0	0	0
7. Root emergence	immediate	cortícular	1	1	0	0	0	0	0
8. Root branching	isodichotomous	anisodichotomous	0	0	1	1	0	0	1
9. Aerial shoot	evergreen	deciduous	0	0	0	0	0	1	1
10. Indument	absent (glabrous)	absent to hairy	0	0	0	0	0	1	1
11. Stele	actinostele	plectostele	0	0	1	1	*	*	*
12. Stele	actinostele	meshed haplostele	0	0	*	*	1	1	1
13. Gemma occurrence	absent	present	1	0	0	0	0	0	0
14. Gemma shape	radial	bilateral	1	0	0	0	0	0	0
15. Branching	dichotomous	anisodichotomous	1	0	0	0	0	0	0
16. Ranks of leaves	6–12	3–5	0	0	0	1	1	0	0
17. Nature of leaves	monomorphic	heteromorphic	0	0	0	1	1	0	0
18. Veinal mucilage canal in trophophyll	absent	present	0	0	0	0	0	1	1
19. Veinal mucilage canal in sporophyll	absent	present	0	0	0	0	0	1	0
20. Basal mucilage canal in sporophyll	absent	present	0	0	1	1	1	1	1
21. Sporophyll	like trophophyll	reduced	0	0	1	1	1	0.5	1
22. Sporophyll attachment	basal	pseudopeltate-peltate	0	0	1	1	1	1	1
23. Strobilus attachment	unstalked	stalked	*	*	0–1	0–1	1	0	0
24. Strobilus orientation	erect	pendent	*	*	0	0	0	0	1
25. Peduncle appendages	leaflike	scalelike	*	*	1	1	1	0	0
26. Sporangial valves	equal	unequal	0	0	0	0	0	1	1
27. Sporangial valves	thick	thin	0	0	1	1	1	1	1
28. Sporangial shape	reniform	globose	0	0	0	0	0	1	1
29. Sporangial nature	non-enclosed	enclosed in cavity	0	0	0	0	0	0	1
30. Sporangium cell wall shape	sinuate	straight-walled	0	0	0	0	1	1	1
31. Sporangium cell wall shape	sinuate	sinuate w/invagination	0	0	1	0	*	*	*
32. Side wall thickenings	evenly thickened	nodular-semiannulate	0	0	*	*	1	1	1
33. Side wall thickenings	evenly thickened	not thickened	0	0	1	1	*	*	*
34. Spore sides	convex to straight	concave	1	0	0	0	0	0	0
35. Spore angles	rounded-pointed	truncate	1	0	0	0	0	0	0

TABLE 1. Continued.

Character	Primitive	Advanced	Hup	Phg	Lyc	Dip	Psd	Lie	Pal
36. Allohomoploid meiosis	normal	irregular	1	0	1	0	0	0	*
37. Nothospeciation	common	rare or absent	0	1	0	0	0	0	*
38. Gametophyte nutrition	holomycotrophic	hemimycotrophic	0	0	0	0	1	1	1
39. Gametophyte position	subterranean	surficial	0	0	0	0	1	1	1
40. Gametophyte meristem	central apex	subterminal, ring	0	0	1	1	0	0	0
41. Gametophyte symmetry	dorsiventral	radial	0	0	1	1	1	1	1
42. Gametophyte shape	buttonlike	rapiform	*	*	0	1	*	*	*
43. Gametophyte branching	unbranched	branched	0	1	0	0	0	0	0
44. Apical outgrowth	absent	photosynthetic lobes	0	0	0	0	1	1	1
45. Apical outgrowth	absent	paraphyses	1	1	0	0	0	0	0
46. Gametophyte pigment	white, gray-brown	orange-brown	0	0	0	1	*	*	*
47. Young sporophyte form	erect	horizontal	0	0	0	0	1	1	1
48. First leaves	microphylls	protophylls	0	0	0	0	1	1	1
49. Foot	large	small	0	0	0	0	1	1	1
50. Protocorm	absent	present	0	0	0	0	0	1	1
		Undirected characters							
A. Root base stele	A1. c-shaped; A2. plectostele		1	1	2	2	1	1	2
B. Spore sculpture	B1. foveolate-fossulate B2. rugulate; B3. reticulate		1	1	3	3	2	2	2
C. Proximal face	C1. sculptured; C2. not sculptured		1	2	[+2]	1	2	2	2
D. Triradiate groove	D1. reaching margin D2. not reaching margin		1	1	1	1	1	1	2
E. Margo	E1. absent; E2. present		1	1	1	1	2	2	2
F. Equatorial ridge	F1. absent; F2. present		1	1	1	1	2	2	1

Abbreviations of taxa are as follows: Hup = *Huperzia*; Phg = *Phlegmariurus*; Lyc = *Lycopodium*; Dip = *Diphasiastrum*; Psd = *Pseudolycopodiella*; Lie = *Lycopodiella*; Pal = *Palhinhaea*. * = Not applicable or unknown; scored as 0.

in size, but two of the genera have developed decidedly unequal valves (26). The valves of lycopsid ancestors were probably moderately thick as seen in Devonian fossils and modern Huperzioideae, but became thin in Lycopodioideae and Lycopodielloideae (27). The reniform sporangial type appeared in Lycopsida as early as the Devonian (even in the more primitive Zosterophyllopsida) and is still maintained in most modern lycopsids; however, the advanced globose type is found in two genera, *Lycopodiella* and *Palhinhaea* (28). The sporangia are free on the surface in most taxa, but in *Palhinhaea* they are enclosed in specialized cavities (29). In two of the major groups of lycopsids, the sporangial cell walls are characteristically sinuate, but in the third they have become straight-walled (30). The sinuate-walled condition has evolved a different complication, namely, distinctive invaginations, as in typical *Lycopodium* described by Øllgaard (1975) (31). The side walls of the sporangia are typically evenly thickened, but in the Lycopodielloideae, they have specialized nodular or semiannulate thickenings, which are undoubtedly advanced (32). Typical *Lycopodium* species have side wall cells that are not thickened at all, another apparent derivation (33).

The spores of Lycopodiaceae possess many characters, some of which (see above) cannot be polarized with our present knowledge. There are, however, likely initial states for certain features. For example, the equatorial sides of lycopsid spores were most likely convex to straight, as attested by the spores of most lycopsid fossils and even *Selaginella* and *Isoetes*. In one group of extant Lycopodiaceae, *Huperzia* sens. str., the equatorial walls are concave, certainly a specialization (34). Likewise, the spore condition of truncate rather than pointed corners is a derived condition (35). Both of these conditions separate the genus *Huperzia* from *Phlegmariurus*.

Hybridization between species would be expected on theoretical grounds to produce offspring still capable of undergoing normal meiosis. Only as the species accumulate specific incompatible genetic factors does the meiotic behavior become irregular, with progressive loss of pairing ability (36). This derived condition within members of a genus, the usual state in most pteridophytes, is notable in the genus *Huperzia*. However, three other genera, *Lycopodium* sens. str., *Diphasiastrum*, and *Lycopodiella*, are conspicuous because their members can still form apparently fertile hybrids with normal meiosis and spores, i.e., the theoretical primitive state. These genera have not yet lost pairing ability. Very little is known of hybridization in the remaining groups. There is a profound difference between the capability and results of hybrization within the groups that we do know, so we have used this as a character. If we are correct, the trend of the units within genera should be from interspecific nothospeciation with allohomoploid fertile hybrids, to interspecific nothospeciation with alloploid sterile hybrids, to very rare hybrids, to genera with no hybrids at all between their species. Thus, being able to form many hybrids between its component species (of any degree of fertility) is a more primitive condition within a genus than being able to form hybrids only rarely or never (37).

Some of the most prominent differentiations between present-day Lycopodiaceae pertain to the gametophyte generation. It has long been known that some groups have wholly subterranean gametophytes that are mycoparasitic, while others are surficial and have photosynthesis (38). The claims of Freeberg & Wetmore (1957) that these are environmentally determined conditions are no longer accepted, as stated above. We now regard photosynthetic gametophytes in Lycopodiaceae as probably specialized for the following reasons: (a) the species that show them are mainly aquatic, or semiaquatic; (b) the aquatic habitat is not suitable for the growth of subterranean gametophytes; and (c) the basal part of the photosynthetic gametophyte is fleshy and not similar to the ferns and most liverworts. The photosynthetic function is located in special dorsal projections (44). Typically, gametophytic meristems tend to be terminal or confined to a central position, but in two lycopsid genera the meristem forms a subterminal ring (39) as shown in *Lycopodium* and *Diphasiastrum* of the Lycopodioideae. The actual form of the gametophytes in these two genera, however, is otherwise very different. The buttonlike prothallus of the former is more like that of the outside groups than the peculiar carrot-shaped or rapiform type (42) present only in *Diphasiastrum*. Unbranched gametophytes are the widespread type in practically all pteridophytes (except the obviously specialized ones of certain schizaeas, filmy-ferns, and vittarioids). The tree inhabiting prothallia of the epiphytic *Phlegmariurus* species, where they are known, are branched (43). In this connection, the outgrowths or lobes of Lycopodielloideae, commented on above in connection with photosynthesis, are advanced (44), as they are not found elsewhere except in the (probably very remotely related) Equisetopsida. All other related groups apparently lack such outgrowths. The presence of specialized haploid trichomes or paraphyses among gametangia seems to be unique to the Huperzioideae (45).

The basic condition among Lycopodiaceae otherwise seems to be with the gametangial surfaces glabrous. The nonphotosynthetic gametophytes in the living state tend to be various shades of white, gray, and gray-brown. However, the carrotlike gametophytes of *Diphasiastrum* are usually pigmented orange or orange-brown (46).

Young sporophytes of most lycopsids and other pteridophytes tend to be erect, but in the Lycopodielloideae they are horizontal and creeping (47). In this subfamily, too, the first leaves are actually "protophylls" (48) rather than small versions of microphylls. In two of the genera of Lycopodielloideae, *Lycopodiella* and *Palhinhaea* (but not *Pseudolycopodiella*), there is a specialized structure, the protocorm (50), not found in any of the immediately related living or fossil outside groups (the tuber of *Phyllogossum* evidently not homologous (Bierhorst, 1971)). The foot of the young sporophyte is normally large in genera of Lycopodiaceae but is small (49) in the Lycopodielloideae.

ESTIMATED GROUNDPLAN OF THE ANCESTOR OF MODERN LYCOPODIACEAE

The specialized or advanced states of 50 characters are given above, as best they can be estimated, and each is given a number in parentheses. The primitive or plesiomorphous states may be used to conceptualize the hypothetical ancestral stock from which our present-day genera arose, and this is briefly summarized as follows: Habitat terrestrial; aerial stem branching simply dichotomous, upright; basal stem a horizontal rhizome; roots emerging next to their origin in stem stele, branching dichotomously, the type of root base stele unknown; aerial shoots evergreen, lacking hairs or other emergences; stem actinostelic; gemmae of any kind lacking; shoot branching dichotomous; leaves in 6–12 ranks, monomorphic. Lacking mucilage ducts of any kind. Except for presence of sporangia, sporophylls undifferentiated from trophophylls; sporangia basally attached; strobilus, if present, erect, and if pedunculate, invested by little-differentiated leaves; sporangia reniform, the valves equal, thick-walled, not enclosed in special cavities; sporangial cell walls sinuate and without invaginations, thickened evenly; spores with convex to straight sides and round-pointed angles, the type of sculpture and presence or absence of sculpture on proximal face or whether triradiate ridge reached margin unknown; hybridization between species within a genus common and chromosome pairing in hybrids normal; gametophyte holomycoparasitic, subterranean, the meristem central and terminal, the thallus ± dorsiventral, branching lacking; photosynthetic lobes absent; gametangial paraphyses absent; color whitish to gray-brown; young sporophyte erect, with small microphylls, foot large and protocorm absent.

TREE OF COMPARATIVE DATA

The tree shown in Figure 1 was constructed by assembling the data into what appeared to be the most parsimonious arrangement, using the manual groundplan-divergence principles of Wagner (1962, 1969, 1980), based on the operational idea that phylogeny (i.e., genetic history) is the amount, direction, and sequence of divergence from ancestral groundplans. For the initial layout, only those characters described above were used, and they are numbered on the tree to correspond with the numbers used there. These characters are believed, on the basis of outside evidence, to be uniquely derived or mostly so. Those distinctive character states that could not be assessed as to directionality were added to the tree, and are indicated by letters and numbers, as given in Table 2. The distances between the nodes of the tree are estimated on the basis of all characters, most of them polarized except for the few added later to indicate merely taxonomic differences. Thus, the tree can be used to present visually the broad picture of (systematic) relationships of all the North American Lycopodiaceae. New information can be added to the tree to embody tropical and subtropical genera, and new characters, and the polarities given here can be revised if necessary. If the number of data and taxa becomes very large, it will be necessary to resort to computer algorithms of the manual Wagner Tree.

DISCUSSION OF RESULTS

If the above arguments are valid, then we still must evaluate the traditional generic taxonomy of North American Lycopodiaceae. The application of categories is still arbitrary (Wagner, 1969). Progressively more segregated systems are shown in Table 3, starting with the classical single genus, *Lycopodium*. In order to maintain comparability and consistency of pteridophyte classification, we have kept in mind, for comparison, well-known pairs of sister genera in homosporous pteridophytes. Weak or dubious genera (cf. Table 2A) that are based upon one to few characters should probably be merged (cf. Kramer & Green, 1990): e.g., *Equisetum* and *Hippochaete* (stomates, chro-

TABLE 2. Some possible classifications for North American Lycopodiaceae. (For convenience, the same names are used for the same units, regardless of nomenclatural correctness.)

A.	Genus *Lycopodium*	E.	Genus *Huperzia*
B.	Genus *Huperzia*		Genus *Phlegmariurus*
	Genus *Lycopodium*		Genus *Lycopodium*
C.	Genus *Huperzia*		Genus *Diphasiastrum*
	Genus *Lycopodium*		Genus *Palhinhaea*
	Genus *Lycopodiella*		Genus *Pseudolycopodiella*
D.	Genus *Huperzia*		Genus *Lycopodiella*
	Subgenus *Huperzia*	F.	Subfamily Huperzioideae
	Subgenus *Phlegmariurus*		Genus *Huperzia*
	Genus *Lycopodium*		Genus *Phlegmariurus*
	Subgenus *Lycopodium*		Subfamily Lycopodioideae
	Subgenus *Diphasiastrum*		Genus *Lycopodium*
	Genus *Lycopodiella*		Genus *Diphasiastrum*
	Subgenus *Palhinhaea*		Subfamily Lycopodielloideae
	Subgenus *Pseudolycopodiella*		Genus *Palhinhaea*
	Subgenus *Lycopodiella*		Genus *Pseudolycopodiella*
			Genus *Lycopodiella*

mosome size), *Polypodium* and *Pleopeltis* (scales), *Pteris* and *Schizostege* (splitting of coenosori), *Jamesonia* and *Eriosorus* (no consistent states), *Polystichum* and *Cyrtomium* (reticulate veins), and *Asplenium* and *Camptosorus* (veins and sori). Some other, but still widely accepted, genera (Table 2B, C) are separated by only a moderate number of characters—in fact, considerably fewer than those used here in Lycopodiaceae: *Marattia* and *Angiopteris* (especially type of synangium); *Osmunda* and *Todea* (mainly sporangial arrangement); *Polypodium* and *Pyrrosia* (mainly soral arrangement); and *Dryopteris* and *Ctenitis* (especially trichomes). Few pteridologists would question their validity as genera, in spite of the relatively few characters that separate them, but most would be hesitant about dividing them into subfamilies, although they might set up subgenera (Table 2D) or separate genera (Table 2E). Further splitting is required of single or groups of genera that are so distinct from other singles or groups that they merit placement in distinct subfamilies (Table 2F). Examples from other homosporous pteridophytes are Ophioglossaceae: *Botrychium* and *Helminthostachys* (Botrychioideae) and *Ophioglossum* and *Cheiroglossa* (Ophioglossoideae); Gleicheniaceae: *Gleichenia* and *Dicranopteris* (Gleichenioideae) and *Stromatopteris* (Stromatopteridoideae); Cyatheaceae: *Dicksonia* and *Cibotium* (Dicksonioideae) and *Cyathea* and *Alsophila* (Cyatheoideae); and Dryopteridaceae: *Dryopteris*, *Davallia*, and *Tectaria* (Dryopteridoideae), and *Athyrium* and *Diplazium* (Woodsioideae). We conclude on the basis of these comparisons that the taxonomic division of modern North American Lycopodiaceae should correspond to Table 2F, i.e., seven genera placed in three subfamilies. The distinguishing characters are numerous, they are accompanied by large gaps and no transitions, they are monophyletic, they involve a number of uniquely derived characters, they do not hybridize with each other, and the segregation level is consistent with other homosporous pteridophytes. The genera fit readily into three subfamilies defined on the basis of their separate patterns of characters and trends.

The two current leaders in the systematics of Lycopodiaceae are Josef Holub and Benjamin Øllgaard, both of whom have made extensive contributions to our understanding of these plants. Their publications (see selected papers in Lit. Cited) contain an enormous amount of information, and they summarize our current knowledge. The classification accepted here for North America conforms, in general, to their concepts except for the assignment of certain ranks. Of the two systems, the ranks of Holub (1983), with all of the genera recognized, are closer to ours; Øllgaard's (1987) treatment has three genera (*Huperzia*, *Lycopodium*, and *Lycopodiella*) in Lycopodiaceae, but includes a number of subgeneric units. Our North American *Phlegmariurus* is in Øllgaard's *Huperzia squarrosa* group; our *Huperzia* is his *Huperzia selago* group; *Lycopodium* includes his *Lycopodium* sect. *Lycopodium*, *Lycopodium* sect. *Annotina*, and *Lycopodium* sect. *Obscura*; *Diphasiastrum*, *Lycopodium* sect. *Complanata*; *Pseudolycopodiella*, *Lycopodiella* sect. *Caroliniana*; *Lycopodiella*, *Lycopodiella* sect. *Lycopodiella*; and *Palhin-*

haea, Lycopodiella sect. *Campylostachys.* Holub's most recent treatment (Holub, 1991) of the firmosses recognizes two subgenera under *Huperzia* rather than two genera; his subgenus *Huperzia* equals our genus *Huperzia,* and his subgenus *Subselago* our *Phlegmariurus.* Both Holub and Øllgaard describe a number of tropical and Southern Hemisphere elements, at least some of which can be raised to generic or subgeneric status. However, we believe these non-North American elements will not modify the geographically circumscribed taxonomic treatment given here. This interpretation is summarized in the key that follows:

TECHNICAL KEY TO NORTH AMERICAN SUBFAMILIES AND GENERA

1a. Sporophylls like trophophylls, photosynthetic; plants epiphytic, epipetric, or terrestrial; roots running from the apex through cortex before emerging; leaves lacking mucilage canals; rhizome absent; paraphyses present among gametangia; spores foveolate-fossulate; chromosomes $x = 67$–68 ... Huperzioideae

2a. Plants epiphytic, mostly pendent at maturity; lacking gemmiphores and gemmae; gametophytes branched; spore angles pointed, spore sides straight or convex; proximal face unpitted, hanging firmosses ... *Phlegmariurus* Holub (1 orthospecies, 0 nothospecies in North America)

2b. Plants terrestrial or epipetric, mostly erect at maturity; producing specialized lateral gemmiphores among the leaves bearing flattened green gemmae; gametophytes unbranched; spore angles truncate, spore sides concave; proximal face pitted, gemma firmosses ... *Huperzia* Bernh. (6 orthospecies, 7 nothospecies)

1b. Sporophylls ± strongly modified, unlike trophophylls, nonphotosynthetic at maturity; plants terrestrial or semiaquatic; leaves with basal mucilage canals; roots emerging immediately, scattered along rhizome; rhizome present; paraphyses absent among gametangia; spores various but not foveolate-fossulate; chromosome x numbers various.

3a. Spore sculpture reticulate; capsule wall cells sinuate to invaginate; root stele like rhizome stele at base; gametophyte subterranean, nonphotosynthetic, growing by a ring meristem; archegonia long, persistent ... Lycopodioideae

4a. Shoots round-branched, the mature leaves monomorphic and separate, in 6–8 ranks; sporangial wall cells with invaginations and evaginations; gametophytes gray or brown, flat, buttonlike and convoluted when mature; chromosomes $x = 34$, common clubmosses ... *Lycopodium* L. (6 orthospecies, 0 nothospecies)

4b. Shoots flat-branched (with 1 exception), the leaves mostly dimorphic or trimorphic and overlapping and (or) imbricate, in 4–5 ranks (in *D. sitchense* leaves 5-ranked and morphologically as in juveniles); sporangial wall cells smoothly sinuate; gametophytes orange pigmented, narrowly top-shaped, nonconvoluted; chromosomes $x = 23$, flat-branched clubmosses ... *Diphasiastrum* Holub (5 orthospecies, 6 nothospecies)

3b. Spore sculpture rugulose; capsule walls straight; root stele various; gametophytes subsurficial, with photosynthetic lobes; archegonia short, ephemeral ... Lycopodielloideae

5a. Plants terrestrial; upright shoot complexly dendroidly branched; basal root stele like stem; spore laesura groove not reaching the margin; spore proximal faces not sculptured; chromosomes $x =$ ca. 55, tropical treelike clubmosses ... *Palhinhaea* Franco & Carv. (1 orthospecies, 0 nothospecies)

5b. Plants semiaquatic; upright shoot simple; basal root stele C-shaped in section; spore laesura groove reaching spore margin; spore proximal faces sculptured; chromosomes not $x =$ ca. 55.

6a. Peduncle leafy; sporophylls resembling trophophylls; horizontal shoot rounded, with uniform leaves ± spreading to erect; veinal mucilage canals present; $x = 78$, common bog clubmosses ... *Lycopodiella* Holub (6 orthospecies, 8 nothospecies)

6b. Peduncle mostly bare with scattered scalelike appendages; sporophylls much reduced, horizontal shoot flat, the leaves unequal, the larger ones in two rows and nearly flat on the substratum; veinal mucilage canals absent; $x = 35$, Carolina bog clubmosses ... *Pseudolycopodiella* Holub (1 orthospecies, 0 nothospecies)

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NEOTROPICAL LYCOPODIACEAE—AN OVERVIEW[1]

Benjamin Øllgaard[2]

ABSTRACT

Approximately 185 species of Lycopodiaceae are known to occur in the Neotropics: ca. 150 belong in the genus *Huperzia*, ca. 8 in *Lycopodium*, and ca. 25 in *Lycopodiella*. The species are enumerated according to assumed relationship, with information of the most important synonyms, a summary of their distribution, comments on their morphology and variability, and reference to selected illustrations. Species delimitation is problematic throughout the family. This is due to the simple morphology and the plasticity of the characters. Morphogenesis seems unstable in many species and may be strongly affected by environmental factors. Most characters are variable within a species, e.g., stem thickness, number of leaf orthostichies, leaf crowding, leaf direction, development of teeth on leaf margins, color, degree of heterophyllous differentiation. Often the diagnostic features of closely related species are without apparent adaptive significance. Hybridization is believed to occur rather freely, but the putative hybrids often have normally developed spores. Three new combinations, *Huperzia tubulosa* (Maxon) B. Øllg., *Huperzia watsoniana* (Maxon) B. Øllg., and *Lycopodiella torta* (L. Underw. & F. Lloyd) B. Øllg., are proposed.

The present paper attempts to survey the diversity and variation of the species of Lycopodiaceae sens. lat. in the area covered by *Flora Neotropica*, an area roughly defined as the parts of the Americas between the Tropics of Cancer and Capricorn. It presents preliminary results of studies prior to a monograph of the family for *Flora Neotropica*.

No earlier studies apply to the species in this area in its entirety, with the exception of an unsatisfactory worldwide synopsis by Nessel (1939). However, several recent regional treatments are available, e.g., for parts of Mexico (Mickel & Beitel, 1988; Smith, 1981); Guatemala (Øllgaard, 1983); Costa Rica to Colombian Chocó (Lellinger, 1989); Lesser Antilles, Jamaica, Puerto Rico, and the Virgin Islands (Proctor, 1977, 1985, 1989); Venezuela (Øllgaard, 1985b); Surinam (Kramer, 1978); Ecuador (Øllgaard, 1988); and Brazil (Øllgaard & Windisch, 1987). A paper by Rolleri (1980) treated *Lycopodium* [*Huperzia*] section *Crassistachys* Herter, a group of mainly neotropical distribution.

The total number of species contained in the family is uncertain, but is estimated to exceed 350. Approximately 185 species are known in the Neotropics, but several remain to be described, especially from the Andes, and several are expected to be discovered as a result of future exploration in the area. Detailed study of some of the complex and yet poorly understood species may add to the number of recognized species.

The special problems encountered in the family relate mainly to interpretation of morphological characters. The nomenclatural problems are relatively few and generally not very complex. This may be because relatively few botanists have been involved in the study of the family, and horticultural interest in the family has been sparse. The plants are generally small and easily collected, so the type material generally is of good quality. The most serious nomenclatural problems relate to the numerous taxa described in the years 1927–1940 by Hermann Nessel. Fortunately, Nessel's herbarium is preserved in Bonn, but numerous problems of typification of his names remain to be solved, due to poor or inane diagnoses, inconsistency of specimen citations with illustrations, and inaccurate, erroneous, or perhaps falsified label information.

The taxonomic characters and interpretations of their variation are discussed in the following, in

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the context of the genera and species groups where they are most relevant. The following features contribute to the problems of species delimitation in general: simple morphology, plasticity of characters in response to environmental factors, apparent lack of adaptive significance of several characters used for identification or recognition, and an apparently somewhat labile intrinsic control of morphogenetic processes. This means that species often are vaguely defined, based on common sense and experience rather than definite sets of characters. The ecology of species, e.g., the altitudinal range may yield important characters useful for identification.

ENUMERATION OF THE SPECIES

The following enumeration of the neotropical species follows the classification of Øllgaard (1987, 1989a). According to that classification three genera occur in the Neotropics, *Huperzia*, *Lycopodium*, and *Lycopodiella*. However, it should be noted that within each of the three genera as construed here there are groups, here treated as sections, which may well be treated as separate genera because the extent and number of differences between these groups exceeds that of widely accepted fern and seed-plant genera. Wagner & Beitel (1992) discuss this problem and call attention to the importance of comparability in generic definition.

Within each genus, as here construed and within the informal and formal groups, the species are arranged in so far as possible in a linear sequence according to assumed relationship.

After each accepted species name synonyms are given in parentheses. The descriptions of genera and sections include only the neotropical members of the groups. A summary of the distribution and ecology, and references to selected published illustrations conclude the entry when appropriate. For additional information on original publications, nomenclature, and types of the species, the reader is referred to the index by Øllgaard (1989a).

HUPERZIA BERNHARDI

Sporophytes terrestrial or epiphytic, isotomously branched throughout except in connection with bulbil formation (*H. selago* group), the branch portions between dichotomies being referred to as divisions. Growth habit pendent to recurved, erect, or ascending. Stele occupying a small proportion of the stem diameter, with radially arranged xylem groups. Branches are all similar, or in some terrestrial species differentiated (heteroblastic) into prostrate, sometimes subterranean (vs. erect) aerial branches. Roots penetrate the stem cortex longitudinally before emerging as one basal tuft. In some species with heteroblastic shoots, the roots may emerge more directly, at soil contact. Trophophylls and sporophylls conform, gradually dimorphic or in some species sharply dimorphic. Sporophylls lacking mucilage cavities, not ephemeral, remaining chlorophyllous and functioning like trophophylls long after the sporangium dehiscence, not specialized like the sporophylls in the other genera. Sporangia in species with constricted distal branches borne predominantly in these, but constricted branches not readily comparable with the strobili of the other genera, as often seen in the literature, both because of the unspecialized sporophylls and their being intermixed, often randomly, with conform trophophylls. Sporangia axillary, with a short slender stalk, isovalvate, with thickened, lignified, sinuate side walls in epidermal cells. Spores foveolate-fossulate. Gametophytes unknown in the area, but subterranean, mycoparasitic, elongate, cylindrical or with bilateral symmetry, with pluricellular, uniseriate hairs among the gametangia in related, extralimital species.

Virtually cosmopolitan, with perhaps 300 species, by far the largest of the three genera, with approximately 150 species in the Neotropics.

The species are diverse with respect to growth habit, size, leaf differentiation, and a variety of adaptations to protected or exposed growth conditions. Several striking types of growth habit and leaf differentiation are apparent in the genus. However, nearly all of these types are interconnected by intermediates, so that the species appear to form a virtually continuous morphological series. They were divided into 22 informal and vaguely defined groups by Øllgaard (1987). Twelve of these groups are represented in the Neotropics. The comments on relatives of the species of the groups often indicate that there are several points of uncertain group delimitation. Also, the occasional formation of hybrids between both ecologically and morphologically widely different species, e.g., *H. reflexa* × *H. linifolia* (Øllgaard, 1985a), indicates that some of these groups may be more closely related than their morphological characters suggest. Only one group of specialized species, including the type of the genus, *Huperzia selago* (L.) Mart. & Schrank, is so distinct that it may merit formal recognition.

These informal groups and their features of variation and distribution are presented below. The most important characters used for classification are the following: growth habit (e.g., erect, ascending, recurved, pendulous); stem thickness; shoot differentiation (homoblastic or heteroblastic); leaf differentiation (homophyllous, heterophyllous, or gradually heterophyllous); leaf arrangement (number of leaves in whorls, or of orthostichies in spirals), crowding (distance between whorls); leaf outline and solid shape (e.g., thickness, vein prominence, margin curvature), margin shape (e.g., teeth, rugulate, smooth), leaf dimensions, direction, color, texture, surface (smooth, papillate), stomate distribution, shape of epidermal cells; shape and color of decurrent leaf bases; sporangium shape and size; spore size.

The genus seems to be undergoing active evolution, especially in the Andes. Once the plants are adapted to the general environments at different levels of altitude, few selective forces seem to be operating on the morphological features that are used for recognition and identification. The species therefore are often difficult to define.

THE *HUPERZIA SELAGO* GROUP

With gemmiferous branchlets, and a distinct spore type with truncate corners and concave, pitted proximal faces.

Main distribution in northern and southern temperate regions, and in mountains of the Paleotropics. The group is represented in tropical America by a single species.

Huperzia serrata (Thunb. ex Murray) Trevisan (synonyms *H. catharinae* (Christ) Holub; *Lycopodium sargassifolium* Liebm.)

Leaves coarsely serrate; annual constrictions along the shoots arising in connection with the formation of whorls of bulbiferous branchlets. Mainly in the Paleotropics, rare in the Americas, with only a few stations in southern Mexico, in Cuba (Sierra Maestra), in Hispaniola, and a single enigmatic collection in Brazil (Santa Catarina). (Mickel & Beitel, 1988: fig. 5A–C).

The hybrid *H. serrata* × *lucidula* is reported from Hispaniola, where the second parent species is unknown (Mickel, 1984).

THE *HUPERZIA REFLEXA* GROUP

Leaves lanceolate to subulate, usually with denticulate margins, but sometimes entire. Most species with spreading, recurved or reflexed leaves. A few species, adapted to the more exposed habitats of the forest limit and just above it with ascending to appressed leaves, may be intermediate to the group of *H. saururus*.

Almost exclusively neotropical, with a single species (*H. dentata* (Herter) Holub) in the Azores and Réunion. The number of species is uncertain, perhaps higher than 20. It is a group of weakly differentiated, erect and homophyllous, terrestrial species growing in open habitats, especially pioneer vegetation, in the montane forest zone.

Huperzia reflexa (Lam.) Trevisan (*H. bifida* (Wild.) Holub; *H. densifolia* (Baker) Rolleri & Deferrari; *H. leptodon* (Herter) Rolleri & Deferrari; *H. parvifolia* (Nessel) Rolleri & Deferrari; *Lycopodium brutum* Herter; *L. reversum* C. Presl; *L. rigidum* Sw., *non* J. Gmelin; *L. squarrosum* Lam., *non* G. Forster, *nec* SW.; *L. squarrosum* Sw., *non* G. Forster, *nec* Lam.; *L. stellae-polaris* (Herter) C. Morton; *Urostachys jergii* Nessel)

The most common and widespread species of the group, polymorphic, both with respect to size and shape of leaves, presently poorly understood. Leaves denticulate, usually arranged in whorls of 6 or more. Tropical America.

The following names apply to *H. reflexa* in the broad sense: *Huperzia acifolia* (Rolleri) Rolleri & Deferrari (type from Peru), *H. mexiae* (Copel.) Rolleri & Deferrari (type from Peru), *H. pearcei* (Baker) Holub (type from Bolivia), *H. spongiosa* (Rolleri) Rolleri & Deferrari (type from Colombia), and *Huperzia rigida* (J. F. Gmelin) Holub (Hispaniola). Some of these names may represent valid taxa, but their delimitations and distributions are as yet uncertain.

Different morphological types of *H. reflexa*, as well as other closely related species, often occur together on large road banks or land slides, and here can be compared under uniform growth conditions. In such populations the individuals may exhibit subtle or obvious differences. Neighboring and more distant populations may exhibit similar variation and thus taxonomic recognition may be indicated. However, often the differences are not matched by other individuals, neither in the same nor in other populations, and therefore the plants have the character of individual aberrants. Some of these are intermediate between other forms and may be hybrids, without exhibiting hybrid features such as abortive spores or irregular meioses. The slight differences, for example, of leaf shape and direction, appear especially striking in the genus *Huperzia,* in which the features are repeated in hundreds of leaves on a stem, creating regular and recognizable patterns. At the same time these features, by which the individuals differ, appear to be without adaptive significance (Lellinger, 1989: fig. 36; Mickel & Beitel, 1988: fig. 1E, F; Øllgaard, 1988: fig. 4A).

Huperzia sintenisii (Herter) Holub

Tall and robust, very similar to *H. reflexa,* but with a thick stem and relatively broad leaves. West Indies.

Huperzia affinis Trevisan (*H. blepharodes* (Maxon) Holub; *Urostachys involutus* Nessel)

Leaves relatively large and wide, borne in alternating whorls of 5, with long, slender, hairlike teeth on the margins. Colombia to Peru. In upper montane forest (Øllgaard, 1988: fig. 4B).

Huperzia eversa (Poiret) B. Øllg. (*H. ecuadorica* (Herter) Holub; *Lycopodium polycarpum* (Sodiro) L. Underw. & F. Lloyd, *non* Kunze; *Urostachys ringshausenii* Nessel; *U. rolandii-principes* Nessel; *U. dingesianus* Nessel)

Forms amply branched individuals with narrow shoots, usually with distant whorls of 5 short, strongly recurved leaves. Central America, Colombia to Bolivia. On banks in upper montane forest (Øllgaard, 1988: fig. 4C).

Huperzia friburgensis (Nessel) B. Øllg. & Wind.

Resembling the common, small *H. reflexa* of Brazil, but taller, less branched, and with entire leaves. Southeastern Brazil.

Huperzia hemleri (Nessel) B. Øllg.

Superficially resembling *H. sellowiana* (*H. brongniartii* group) in size and growth habit, but with denticulate leaf margins. Its origin may involve this and a species in the H. reflexa group. The spores are normally developed. Southeastern Brazil. Presumably belongs in shaded high-altitude habitats in forest (Nessel, 1927, t. 9).

Huperzia hoffmannii (Maxon) Rolleri & Deferrari

A large and robust local high-altitude representative of the group, with broad, distant leaves. Costa Rica, Panama (Lellinger, 1989: fig. 28).

Huperzia austroecuadorica B. Øllg.

Approaching the growth habit of the *H. saururus* group, with ascending-appressed leaves on the fingerlike shoots. Southern Ecuador, low páramos (Øllgaard, 1988: fig. 13C).

Huperzia christii (Silveira) Holub (*Urostachys orgaosanus* Nessel)

Differing from *H. reflexa* mainly in the larger, abaxially convex, more coriaceous leaves. Southeastern Brazil, on banks at high altitudes.

Huperzia rostrifolia (Silveira) Holub

A poorly known high-altitude species, perhaps not distinct from the preceding one. Southeastern Brazil.

Huperzia riobambensis (Herter) B. Øllg. (*Lycopodium castoris* (Herter) C. Morton)

A large, robust representative of upper montane forests and low páramos with broad, coriaceous, reflexed, glossy leaves arranged in distant whorls of 5 or 6. Colombia.

Huperzia beitelii B. Øllg.

Coarse, erect or ascending to erect, to 1 m tall, sometimes with constricted distal divisions with reduced, appressed or ascending, somewhat clasping leaves, an unusual feature in the group. Venezuelan Guayana. Low scrub, low open forest of high altitudes (Øllgaard, 1989b: 152–155).

Huperzia sieberiana (Spring) Trevisan

A very robust high-altitude species, densely covered by narrow, coriaceous, subulate, entire leaves, arranged in whorls of 10 or more. Lesser Antilles.

Huperzia unguiculata B. Øllg.

A robust species of mid-altitudes, with coriaceous, nearly entire, usually strongly recurved leaves, arranged in whorls of 9–11, and recurved shoot apices. Colombia to Peru (Øllgaard, 1988: fig. 2B).

Huperzia intermedia Trevisan (*Urostachys commutatus* Herter)

A slender, often divaricately branching and scrambling rupestral species, occurring on sandstone; leaf margins entire. Guadeloupe, Venezuela, southeastern Brazil: Bahia, Minas Gerais, Espirito Santo. Perhaps as closely related to Brazilian species of the *H. brongniartii* group, especially *H. pungentifolia.*

Huperzia chamaeleon (Herter) B. Øllg.

With very narrow, recurved, linear, entire leaves without prominently decurrent leaf bases on the somewhat tumid stem. Costa Rica (Lellinger, 1989: fig. 18).

Huperzia firma (Mett.) Holub (*H. coriacea* (Rolleri) Rolleri & Deferrari, from Caldas, Colombia, is perhaps a synonym)

Resembling *Huperzia reflexa*, but more robust, and with more coriaceous leaves. This and the following species are distinct from other members of the group because of thick-walled, nearly isodiametric epidermal cells of the leaves. Andes of Venezuela and Colombia. Some Colombian plants usually referred to this species, which are larger in all parts and at least up to 1 m tall, may deserve recognition as a distinct species (Øllgaard, 1988: fig. 2D).

Huperzia urbanii (Herter) Holub

Closely related to the preceding species; differing by the smaller, sigmoid leaves, usually arranged in very close whorls of 11–14. Ecuador (Øllgaard, 1988: fig. 2C).

THE *HUPERZIA BRONGNIARTII* GROUP

Usually erect, weakly differentiated, terrestrial plants, many of them with a characteristically hygromorphic, bottle-brush-like growth habit, with sparsely branched stems, and long, perpendicular, monomorphic, linear and entire leaves; this aspect most apparent in *Huperzia hippuridea* and its closest relatives, viz, *H. arcuata*, *H. lechleri*, *H. nuda*, *H. recurvifolia*, and *H. mexicana*. Neotropical, approximately 22 species. Many species belonging in semishaded forest floor habitats in upper montane forest.

Huperzia hippuridea (Christ) Holub (*H. boliviana* (Rosenstock) Rolleri & Deferrari; *H. montana* (L. Underw. & F. Lloyd) Holub; *L. poseidonis* (Herter) C. Morton)

Growth habit bottle-brush-like, with sparsely branched stems, and long, perpendicular, monomorphic, linear and entire leaves. Variable with respect to stem thickness, direction and crowding of leaves. Widely distributed, occurring in Central America, the Greater Antilles, Venezuela, including Venezuelan Guayana, and south to Bolivia. Some local populations deviate more consistently from the aspect of the widespread, typical form of the species, e.g., in Ecuador. Here both typical populations occur, and populations with thick stems and relatively distant whorls of sharply reflexed leaves (Lellinger, 1989: fig. 27; Mickel & Beitel, 1988: fig. 2E; Øllgaard, 1988: figs. 1A, 2A).

Huperzia arcuata B. Øllg.

Deviating from the preceding species mainly by its basally twisted leaves and nodding shoot apices. Large epiphytic individuals may become entirely pendent, and thus resemble *Huperzia dichotoma*, but are ecologically distinct. Southern Colombia and Ecuador. Occurs sympatrically with the preceding species, but, in addition to the forest floor, also occurs in epiphytic habitats (Øllgaard, 1988: fig. 1D).

Huperzia lechleri (Hieron.) Holub (*Urostachys lehmannii* Herter)

Doubtfully distinct from *Huperzia hippuridea*, differing only by the narrower leaves, usually arranged in a greater number of orthostichies. Southern Peru, Bolivia. Overlaps the southern distribution of *H. hippuridea*.

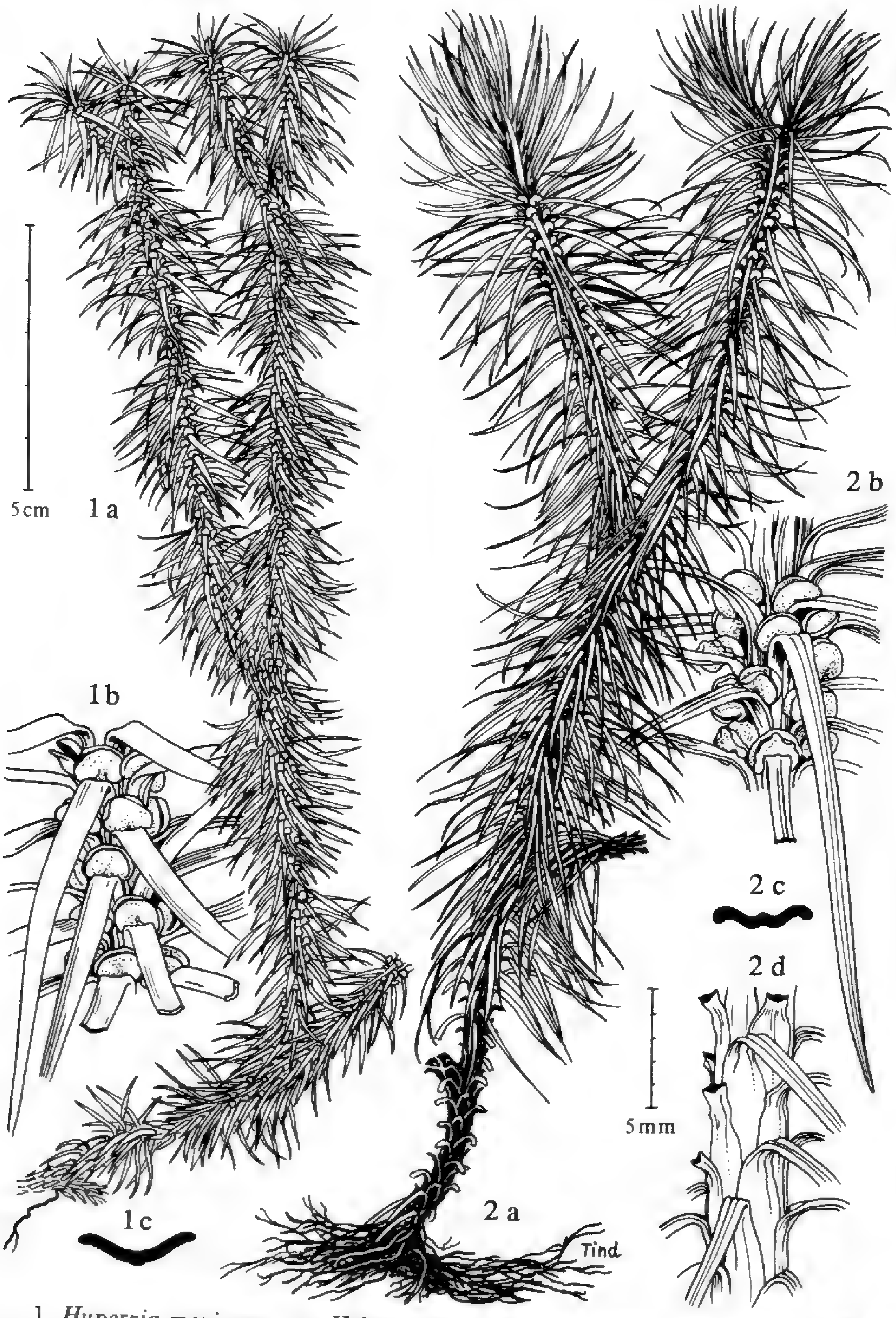
Huperzia nuda (Nessel) B. Øllg. & Wind. (*Urostachys nudiusculus* Herter)

Very similar to, but consistently smaller than, the preceding species. Brazil: Rio de Janeiro, São Paulo. Occurs in high-altitude cloud forests and is believed to have been derived from its Andean relatives (Nessel, 1927: t. 14).

Huperzia mexicana (Herter) Holub

Often difficult to distinguish from *H. hippuridea*, differing from this in being epiphytic, by the presence of seasonally induced variation in leaf length, appearing as constrictions along the shoots, by more coriaceous leaves, and by prominently decurrent, often reddish leaf bases. Leaf base characters approaching those of *H. pithyoides* (see below under the *H. dichotoma* group), to which the species may be equally closely related as with the present group.

The relatively xeromorphic features of this species may be correlated with the epiphytic habitat, which is more liable to desiccation during dry periods than are nearby terrestrial habitats, such as those of *H. hippuridea*. However, observations of the two species coexisting, confirming this correlation of the morphological differences with habitat, are missing. Northern Central America, Greater Antilles (Fig. 1).



FIGURES 1, 2. 1. *Huperzia mexicana.*—a. Habit.—b. Detail of sporangiate division.—c. Cross section of leaf. 2. *Huperzia pithyoides.*—a. Habit.—b. Detail of sporangiate division.—c. Cross section of leaf.—d. Detail of proximal division, with decurrent leaf bases.

Huperzia recurvifolia Rolleri

Deviates from *H. hippuridea* mainly in the softly recurving rather than sharply reflexed leaves, and by the finely protracted, twisted, pale or brownish leaf apices. Venezuela, Guyana, Brazil: Bahia. Mainly in open, rocky sandstone habitats of the Roraima formation (Rolleri, 1989: 209–215).

Huperzia huberi B. Øllg.

Closely related to the preceding species, and occurring in similar habitats. Differing by the wider leaves with acute, concolorous apices. Venezuelan Guayana (Øllgaard, 1989b).

Huperzia weddellii (Herter) Holub

A very robust species with thick stems and densely crowded, lanceolate, thick leaves, varying from reflexed to ascending-appressed position. Exhibiting highly variable morphological features, intermediate between those typical of the forest species mentioned above, and those typical of the páramo species mentioned under the *H. saururus* group. Ecuador to Bolivia. Habitats transitional between the upper montane forests (ceja andina), and páramo or jalca vegetation (Øllgaard, 1988: fig. 4D).

Huperzia loxensis B. Øllg.

Resembling *Huperzia hippuridea*, but more robust, with thicker stems and densely crowded, minutely denticulate leaves. Southern Ecuador. Like the preceding species in habitats transitional between the upper montane forests and low páramos in a restricted area on the mountain crests east of Loja (Øllgaard, 1988: fig. 3B).

Huperzia binervia (Herter) B. Øllg.

As in *H. weddellii*, exhibiting variable features intermediate between those of the forest and páramo species. In exposed habitats old individuals may exhibit the gradual transformation from the bottlebrush aspect of the proximal divisions, to fingerlike distal divisions with closely appressed leaves. Northernmost Peru. This narrowly endemic species occurs in habitats at or just above the forest limit (Øllgaard, 1988: fig. 5D).

The following seven species are endemic to southern and eastern Brazil. Most of them are rare and have very restricted distributions in rupestral habitats on isolated mountaintops.

Huperzia pungentifolia (Silveira) B. Øllg. (*Lycopodium ouropretanum* Christ; *Urostachys hennebergorum* Nessel)

Resembling *H. recurvifolia*, but with shorter, more coriaceous leaves, and often more divaricately branched and scrambling over the ground. Superficially very similar to *H. reflexa*, but with entire-margined, coriaceous leaves, and a more open branching pattern. Brazil: Minas Gerais, Rio de Janeiro. The most widespread and morphologically least specialized of the Brazilian species.

Huperzia regnellii (Maxon) B. Øllg. & Wind.

Very similar to the preceding species, but with reduced and appressed leaves in the distal divisions. Brazil: Minas Gerais. Very rare, no recent collections being known. (Maxon, 1914: t. 23).

Huperzia treitubensis (Silveira) B. Øllg. (*Lycopodium hoehnei* (Nessel) Rolleri; *L. inflexum* Silveira; *Urostachys capri* Herter)

Leaves of proximal divisions densely crowded, closely appressed, at the stem base often aggregated to a thickened bulblike shoot base. Brazil: Minas Gerais, a very local species (Fig. 3).

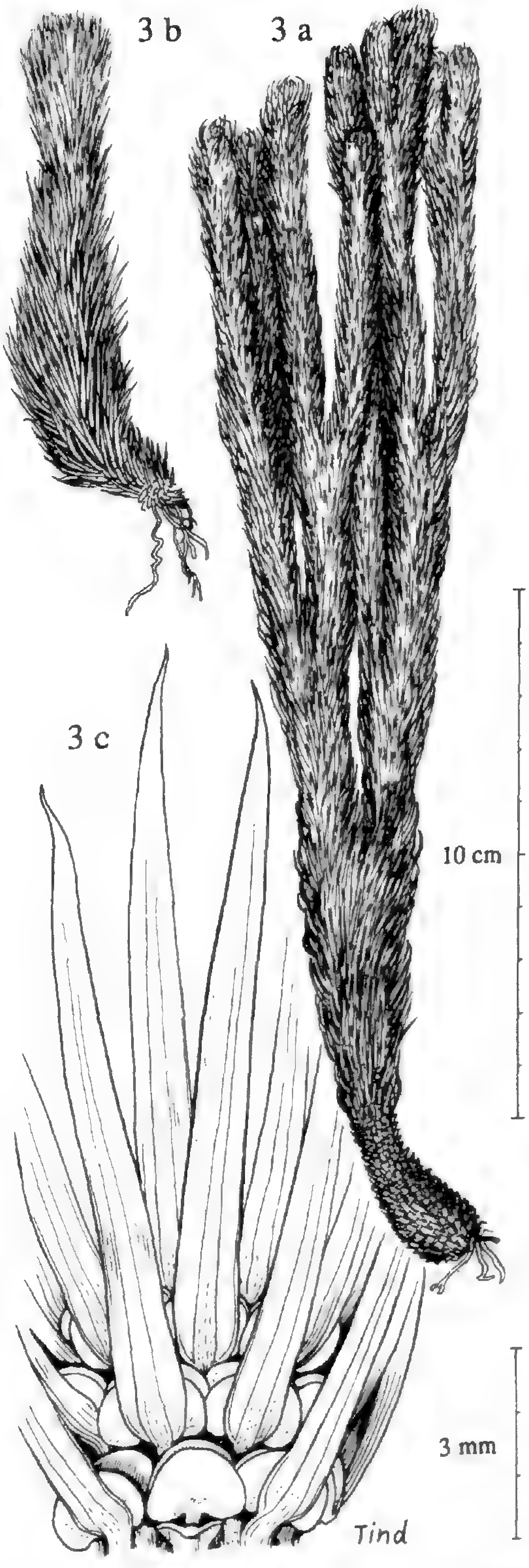


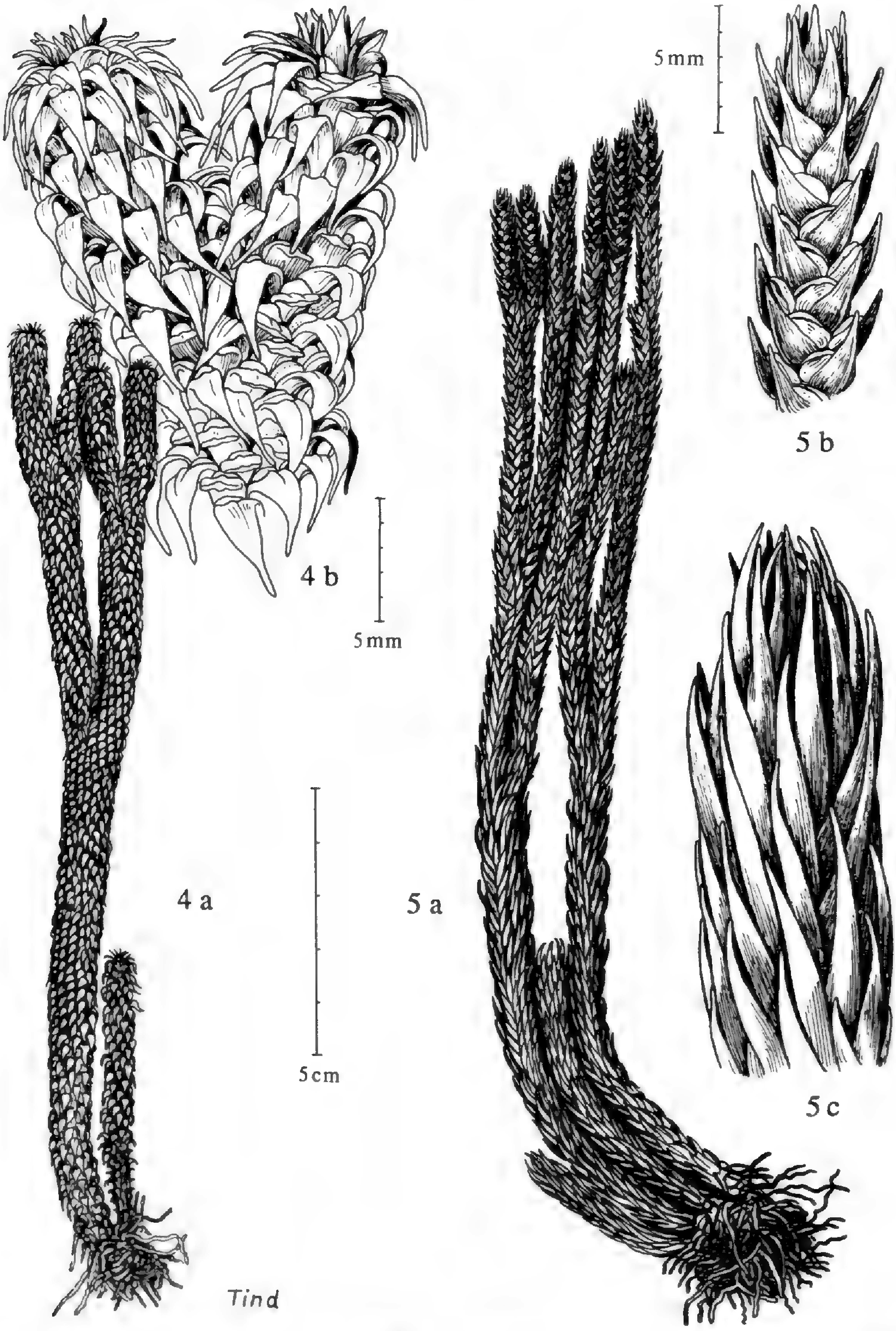
FIGURE 3. *Huperzia treitubensis.*—a. Habit.—b. Juvenile plant.—c. Detail of sporangiate division.

Huperzia deminuens (Herter) B. Øllg. (*Huperzia luederwaldtii* (Nessel) Holub)

With erect fingerlike distal divisions, in which the leaves are appressed, and strongly convex abaxially. Brazil: Minas Gerais, Rio de Janeiro. A rare rupestral species.

Huperzia itambensis B. Øllg. & Wind.

A highly specialized species with short, closely imbricate and abaxially somewhat carinate leaves



FIGURES 4, 5. 4. *Huperzia mooreana.*—a. Habit.—b. Detail of sporangiate division. 5. *Huperzia rubra.*—a. Habit.—b. Detail of sporangiate division.—c. Detail of proximal division.

on the stiffly erect stems. Brazil: Minas Gerais, known only from the type locality (Øllgaard & Windisch, 1987: fig. 1B).

Huperzia mooreana (Baker) Holub (*H. sydowiorum* (Herter) Rolleri & Deferrari; *Lycopodium luetzelburgii* Rosenstock)

The thick, stiffly erect stems densely covered by rigid, strongly and uniformly recurved, hooklike leaves. Brazil: Bahia. This narrow endemic is another highly specialized species of very distinctive appearance (Fig. 4).

Huperzia rubra (Cham.) Trevisan

Readily identified by its deep red stems and leaves. Brazil: Minas Gerais, Bahia?. Another highly distinctive high-altitude species (Fig. 5).

The following three species belong to upper montane forests in southern Central America, the Andes, and southeastern Brazil. They differ from the preceding species by their large, papery to subcoriaceous, lanceolate leaves and relatively narrow leaf bases. They appear to bridge the gap between the *H. brongniartii* group and species in the *H. taxifolia* group, especially to *H. rosenstockiana.* In the latter group the juvenile sporophytes of some species, e.g., *H. taxifolia,* may be initially erect and resemble plants of *H. brongniartii* and *H. sellowiana.*

Huperzia brongniartii (Spring) Trevisan

A heterogeneous species with slightly distinct populations in Ecuador–Colombia and Peru–Bolivia, the northern population often with finely denticulate margins of the leaf apices, as in *H. foliacea.* Colombia to Bolivia. The minutely rugulate leaf margins, characteristic of this species, occur also in *H. rosenstockiana* (*H. taxifolia* group) and may imply a close relationship (Øllgaard, 1988: fig. 3A).

Huperzia foliacea (Maxon) Holub

Smaller in all parts than the preceding species, with oblong-lanceolate to oblanceolate leaves. Costa Rica, Panama. A narrowly endemic, epiphytic species, probably closely related to the preceding species. The presence of red dots on the leaf bases may be evidence of relationship to species of the *H. dichotoma* group (Lellinger, 1989: fig. 24; Maxon, 1912: t. 1).

Huperzia sellowiana (Herter) B. Øllg. (*H. ulei* (Herter) Holub; *Lycopodium brasilianum* Herter)

Small differences of phyllotaxis and a more lax, decumbent to ascending growth habit separates this species from *H. brongniartii.* Southeastern Brazil.

THE *HUPERZIA DICHOTOMA* GROUP

Mainly epiphytes of low- and mid-altitude forests, several of them initially erect, with spreading to perpendicular, filiform or linear leaves, some with conspicuous red coloration of the leaf bases, especially *Huperzia pithyoides, H. mandiocana,* and *H. wilsonii.*

The group is here redefined, including the species of the *Huperzia mandiocana* group of Øllgaard (1987), but excluding *H. homocarpa,* which is thought to belong in the *H. taxifolia* group.

Huperzia dichotoma (Jacq.) Trevisan (*H. graminea* (Spring) Trevisan; *H. lindeneri* (Nessel) Holub; *H. mortonii* (Herter) Holub; *H. schlechtendalii* (Nessel) Holub; *Lycopodium barbatum* Christ, *non* Kaulf.; *L. chamaepeuce* Herter)

Plants usually rather short and recurved to pendulous, with linear, densely crowded, usually basally twisted, falcately ascending leaves. Florida, West Indies, Central America, northern South America, south to Ecuador with the Galápagos Islands, and Brazil (Acre, Mato Grosso, Ceará). The most widespread and variable species of the group. Closer study of the material referred to this species may show the presence of more than one taxon, especially in the northern part of the range, because there is considerable variation in the thickness of stems, leaf length and direction, and compactness of the plants. However, the correlation of the variation with growth conditions is unknown at this point (Lellinger, 1989: fig. 23; Øllgaard, 1988: fig. 19D).

Huperzia pithyoides (Schldl. & Cham.) Holub (*Lycopodium gigas* Herter)

One of the most impressive *Huperzia* species, with the aspect of a small pine tree, with thick, bright red stems due to the color of the prominent, decurrent leaf bases, and spreading, coriaceous, linear, bisulcate leaves, often up to 3.5 cm long. Old individuals may become pendulous, with falcately ascending leaves. Mexico to Costa Rica, Greater Antilles, Colombia: Huila, Venezuela: Falcón (Fig. 2; Lellinger, 1989: fig. 34; Mickel & Beitel, 1988: fig. 1C, D).

Huperzia mandiocana (Raddi) Trevisan (*Lycopodium pseudo-mandiocanum* Herter)

Like a diminutive replica of the preceding species, the characters being almost identical, except for the size. Brazil: Bahia and Minas Gerais to Rio Grande do Sul, Paraguay, northernmost Argentina (Øllgaard, 1988: fig. 1B).

Huperzia wilsonii (L. Underw. & F. Lloyd) B. Øllg. (*H. lindaviana* (Herter) Holub; *Lycopodium andinum* Herter, *non* Rosenstock; *L. arcanum* Maxon; *L. stamineum* Maxon; *L. trichodendron* Herter)

Usually an erect epiphyte, but like the preceding species, becoming pendulous when very large; often with bright red, but usually not prominent leaf bases; the capillary leaves canaliculate above. Central America, West Indies, Andean South America, south to Peru, Venezuelan Guayana, Brazil: Mato

Grosso (Lellinger, 1989: fig. 44; Mickel & Beitel, 1988: fig. 4B; Øllgaard, 1988: fig. 1C).

Huperzia polycarpos (Kunze) B. Øllg. (*Urostachys cuatrecasasii* Herter)

Like the preceding species, but usually pendulous, and smaller in all parts, with basally twisted, falcately ascending leaves. Costa Rica, Panama, Colombia to Peru (Lellinger, 1989: fig. 35; Øllgaard, 1988: fig. 19A).

Huperzia bradeorum (Christ) Holub (*H. brauseana* (Herter) Rolleri & Deferrari)

Erect epiphytes with patent, linear-lanceolate leaves with a slightly narrowed, petiolelike lamina base, and usually prominently decurrent leaf bases. Guatemala to Costa Rica, Venezuela: Isla Margarita, Ecuador. Probably related to the pendulous *H. orizabae* (*H. linifolia* group), which appears intermediate between *H. bradeorum* and *H. linifolia* (Lellinger, 1989: fig. 16; Øllgaard, 1988: fig. 19B).

THE *HUPERZIA TAXIFOLIA* GROUP

Pendulous or recurved, slender to very robust epiphytes or rupestral plants, with whorled, ascending to appressed, linear-lanceolate to lanceolate, more rarely linear to subulate, often subcoriaceous to coriaceous leaves. Some species entirely homophyllous, several gradually heterophyllous, showing at least potentially strong reduction and modification of the leaves of distal divisions. Neotropics, 10–14 species in lower to upper montane forests.

Under certain conditions abruptly dimorphic leaves may be induced. The modification usually depends on age and light conditions, juvenile and shaded plants often being entirely homophyllous. Leaf texture is variable according to exposure of the habitat within most of the species.

Huperzia hartwegiana (Spring) Trevisan (*H. caracasica* (Herter) Holub; *Lycopodium funckii* Herter; *Urostachys maxonii* Nessel)

The most robust species of the group, usually with strongly coriaceous, nitid leaves in alternating whorls of four. Northern Central America, Andes from Venezuela to northern Peru. Apparently adapted to a relatively drier range of habitats than the other species of the group, including dry rocky habitats. In Ecuador and Colombia it varies from a long, lax, epiphytic growth habit to initially erect and recurved in lava rocks. In the northern coastal ranges of Venezuela it usually remains short, compact, and nearly erect in terrestrial habitats (Øllgaard, 1988: fig. 14A).

Huperzia picardae (Krug) Holub

Perhaps representing a slender form of the preceding species, to which it corresponds rather closely. Greater Antilles. Seems connected to robust Antillean forms of *H. taxifolia* by intermediate forms. Status uncertain.

Huperzia cuernavacensis (L. Underw. & F. Lloyd) Holub

A very robust species, distinguished from *Huperzia hartwegiana* by the thick, homophyllous shoots, often exhibiting regular constrictions due to seasonally induced variation of leaf length, and linear-lanceolate leaves borne in alternating whorls of 5–6. Southern Mexico to Guatemala (Mickel & Beitel, 1988: fig. 3C).

Huperzia sotae (Rolleri) Holub

Resembling the preceding species closely, both with respect to stem thickness, leaf shape and arrangement, and the presence of regular constrictions, but a more delicate plant, with more soft-textured leaves. Northernmost Argentina. The names *Lycopodium buesii* (Herter) C. Morton (type from Peru) and *Huperzia aristei* (Nessel) Rolleri & Deferrari (type indicated as from Colombia, but possibly mislabeled, perhaps northern Argentina or Peru), appear to represent close allies of *H. sotae*, or perhaps are conspecific. They are only known from the type collections (Rolleri, 1970: fig. 1 (A–C), t. 2, t. 3(A)).

Huperzia taxifolia (Sw.) Trevisan (*H. costaricensis* (Herter) Holub; *H. cubana* (Herter) Holub; *H. haitensis* (Herter) Holub; *H. passerinoides* (Kunth) Trevisan; *H. subtubulosa* (Herter) Holub; *Lycopodium herminieri* Spring; *L. nitens* Schldl. & Cham.; *L. schwendeneri* Herter; *Urostachys bruelkei* Nessel; *U. rubiginosus* Nessel; *U. spongiosus* Herter)

The typical form with the leaves arranged in close whorls of three leaves, in the proximal divisions with ascending, subcoriaceous, lanceolate leaves, in the distal, fertile divisions, with short, appressed, apically involute leaves. Central America, West Indies, northern South America, south to Peru and Brazil; Paraná. This is the most widespread and variable of the species in the group, and its delimitation is problematic. Closer study may lead to the recognition of more than one taxon within the species. Some forms approach *H. linifolia* and *H. homocarpa*, with thin stems and flaccidly hanging, homophyllous shoots and relatively distant leaf whorls. Others approach *H. hartwegiana*, with thick, initially erect stems, and crowded 4-leaved whorls of coriaceous leaves. A large Costa Rican form has very large sporangia and spores. At present the basis for the variation is poorly understood (Lellinger, 1989: fig. 39; Mickel & Beitel, 1988: fig. 4A; Øllgaard, 1983: fig. 8b; Øllgaard, 1988: fig. 15A).

Huperzia tubulosa (Maxon) B. Øllg., comb. nov. Basionym: *Lycopodium tubulosum* Maxon, Contr. U. S. Natl. Herb. 17 (2): 178, t. 10 (1913)

Typical plants much smaller than the preceding species in all parts, and with more distant leaves. Costa Rica, Panama. This species is difficult to delimit from the *Huperzia taxifolia*, due to the presence of intermediate forms (Lellinger, 1989: fig. 41; Maxon, 1913: t. 10. 1913).

Huperzia killipii (Herter) B. Øllg.

A delicate species resembling the preceding species, but often completely homophyllous, with elliptic to oblanceolate, usually up to 10-mm-long proximal leaves. Venezuela, Colombia.

Huperzia homocarpa (Herter) Holub

Homophyllous, lax, pendulous, with rather distant whorls of relatively short, linear-lanceolate, usually basally twisted leaves. Greater Antilles, Costa Rica, Panama, Northern Andes, total distribution uncertain. Difficult to delimit in relation to *H. taxifolia*, *H. linifolia*, and *H. dichotoma* (Øllgaard, 1988: fig. 16A).

Huperzia lancifolia (Maxon) Holub

Resembling *H. tubulosa*, but with more acute, elliptic proximal leaves. Panama, known with certainty only from the type (Lellinger, 1989: fig. 29).

Huperzia lindenii (Spring) Trevisan (*H. sodiroana* (Herter) Holub; *H. stuebelii* (Herter) Holub; *H. wohlberedtii* (Nessel) Holub)

A distinct, flaccidly pendulous species, variable with respect to the degree of leaf dimorphism. Juvenile plants sometimes initially erect and recurved. Southern Colombia, Ecuador. Forest at the timberline, and often on solitary trees in the páramo. The closest relatives may be in similar habitats in New Guinea (Øllgaard, 1988: fig. 17C).

Huperzia rosenstockiana (Herter) Holub (*Lycopodium cassandrae* (Herter) C. Morton)

Usually a flaccidly pendulous epiphyte, but some populations in southern Ecuador terrestrial, erect, with nodding shoot tips. Leaves a deep translucent emerald to yellowish green, broadly lanceolate with minutely rugulose margins, a feature shared with *Huperzia brongniartii*, to which it may be related. Southern Colombia, Ecuador. In sheltered sites in very humid forest at the timberline (Øllgaard, 1988: fig. 14D).

Huperzia funiformis (Spring) Trevisan

A large, pendulous epiphyte with a distinctive, ropelike aspect, due to the very regularly appressed, coriaceous, strongly convex, subulate leaves. Southern Mexico to Panama, West Indies, Venezuela to Peru. It has no apparent close relatives and perhaps deserves recognition as an independent group (Lellinger, 1989: fig. 25; Øllgaard, 1988: fig. 17D).

THE *HUPERZIA HETEROCARPON* GROUP

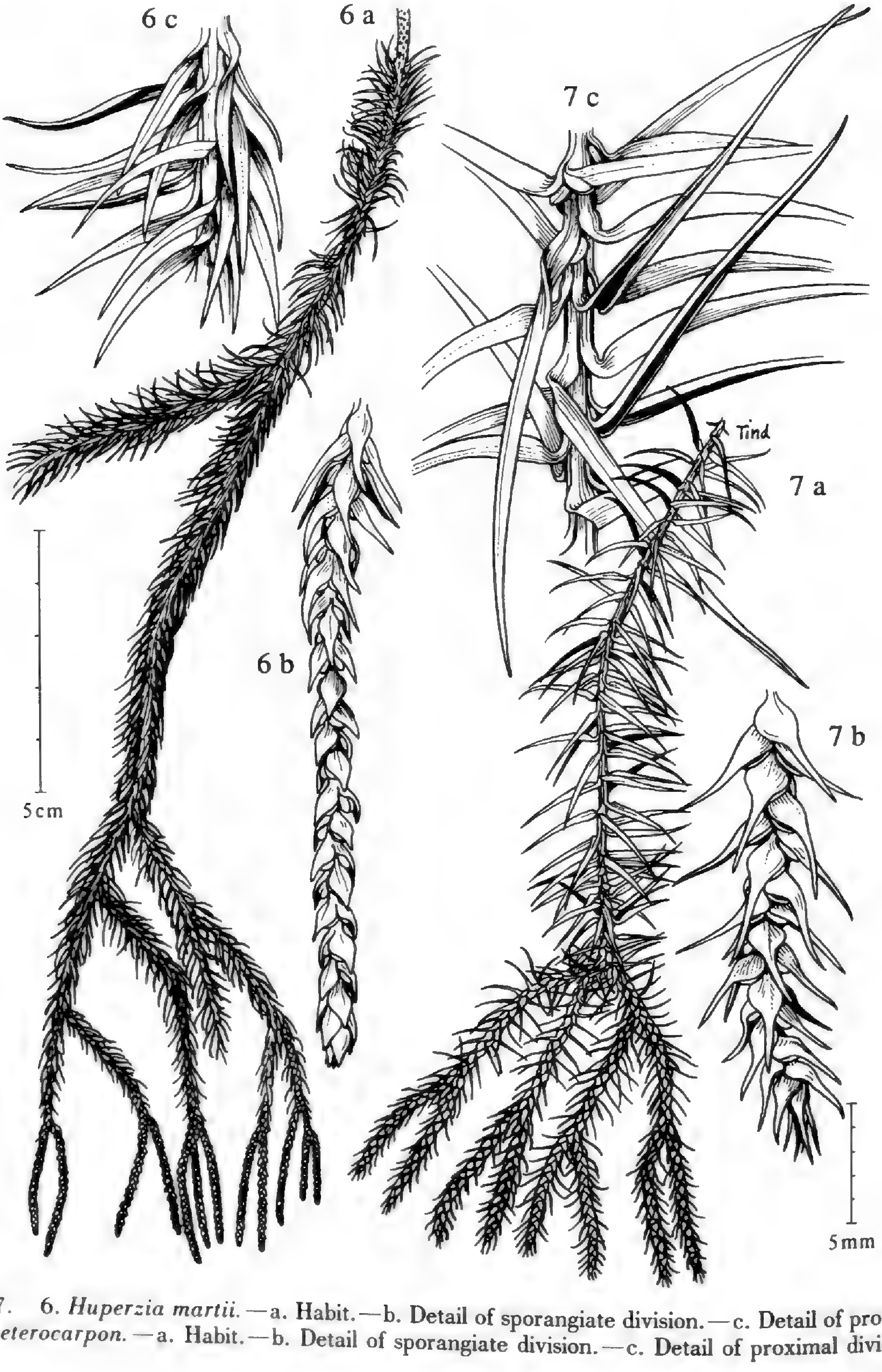
Resembling the preceding group, but differing in the clasping and usually twisted leaf bases, and the strong potential distal leaf reduction in most of the species. This is a mainly Brazilian group of pendulous epiphytes or rupestral plants, occurring in montane forests of the eastern and southern parts of the country.

Huperzia heterocarpon (Fée) Holub (*H. longearistata* (Christ) Holub; *Urostachys portoanus* Nessel; *U. spegazzinii* Nessel)

Leaves long, canaliculate, the sporophylls usually cuspidate, variable mainly in leaf length and degree of distal leaf reduction. Brazil: Minas Gerais and Rio de Janeiro to Rio Grande do Sul, Argentina: Missiones. The most common and widespread of the species (Fig. 7).

Huperzia loefgreniana (Silveira) B. Øllg. & Wind. (*Huperzia leitzii* (Nessel) Holub)

A somewhat heterogenous assemblage of plants, related to the preceding species, intermediate to, and possibly hybrids with members of the *H. quadrifariata* group, exhibiting strong reduction of the leaves in the squarish distal shoots, and short leaves



FIGURES 6, 7. 6. *Huperzia martii.*—a. Habit.—b. Detail of sporangiate division.—c. Detail of proximal division. 7. *Huperzia heterocarpon.*—a. Habit.—b. Detail of sporangiate division.—c. Detail of proximal division.

in the proximal divisions of the stems. Brazil: Minas Gerais and Rio de Janeiro to Santa Catarina.

Huperzia martii (Wawra) Holub (*Lycopodium cipoense* Damazio)

Distinguished by the densely crowded, rather short and narrow proximal leaves and the very strongly reduced leaves of the distal, fertile divisions. Brazil: Bahia, Espírito Santo, Minas Gerais, a rare species (Fig. 6).

Huperzia silveirae (Nessel) B. Øllg. & Wind.

With rather broad, and flattened, strongly twisted leaves, approaching *H. taxifolia.* Brazil: Minas Gerais and Rio de Janeiro to Santa Catarina.

THE *HUPERZIA LINIFOLIA* GROUP

Flaccidly hanging epiphytes, characterized by very slender stems, usually with leaves alternate, at least in the proximal divisions, not whorled or decussate, but occasionally paired. Leaves monomorphic, or gradually dimorphic, usually with a narrow, twisted, petiolelike lamina base, and often obliquely falcate-ascending. Neotropics, approximately 6 species. Lowland and lower montane forests.

Huperzia linifolia (L.) Trevisan (*H. jenmanii* (L. Underw. & F. Lloyd) Holub)

Central America, West Indies, northern South America, south to Bolivia and Amazonian Brazil. The most common and widespread of the species. Three varieties are recognized: Variety *linifolia* occurs in Central America, the West Indies, and along the Pacific slopes of the Andes south to Ecuador. Variety *tenuifolia* (Nessel) B. Øllg. occurs along the lower eastern slopes of the Andes, while variety *jenmanii* (Underw. & Lloyd) B. Øllg. occurs in the Amazonian lowlands, in the Guyanas, and along the northeastern Atlantic coast of Brazil (Lellinger, 1989: fig. 30; Mickel & Beitel, 1988: fig. 4C; Øllgaard, 1988: figs. 16B, C; 18A).

Huperzia flexibilis (Fée) B. Øllg.

Very similar to the preceding species, but with distinctly flexuous, zig-zag stems at the base of the plants, and broad proximal leaves. Brazil: Minas Gerais and Espírito Santo to Santa Catarina, restricted to lower montane forests of southeastern Brazil (Fée, 1872–1873: t. 105, fig. 3).

Huperzia pittieri (Christ) Holub

Resembling *Huperzia linifolia*, but with densely crowded, smaller, and very narrowly protracted, pale leaf apices. Cocos Island, a narrow endemic (Fig. 8).

Huperzia orizabae (L. Underw. & F. Lloyd) Holub

Appearing intermediate between *H. linifolia* and *H. bradeorum*, but with a rather compact growth habit, and relatively thick stems. Southern Mexico to Honduras (Mickel & Beitel, 1988: fig. 5D–F).

Huperzia tenuicaulis (L. Underw. & F. Lloyd) B. Øllg.

Very delicate, with distant, rather short, narrowly oblong leaves. West Indies.

Huperzia capillaris (Sodiro) Holub (*H. underwoodiana* (Maxon) Holub; *Lycopodium guatemalense* Maxon; *Urostachys rubescens* (Spring) Herter)

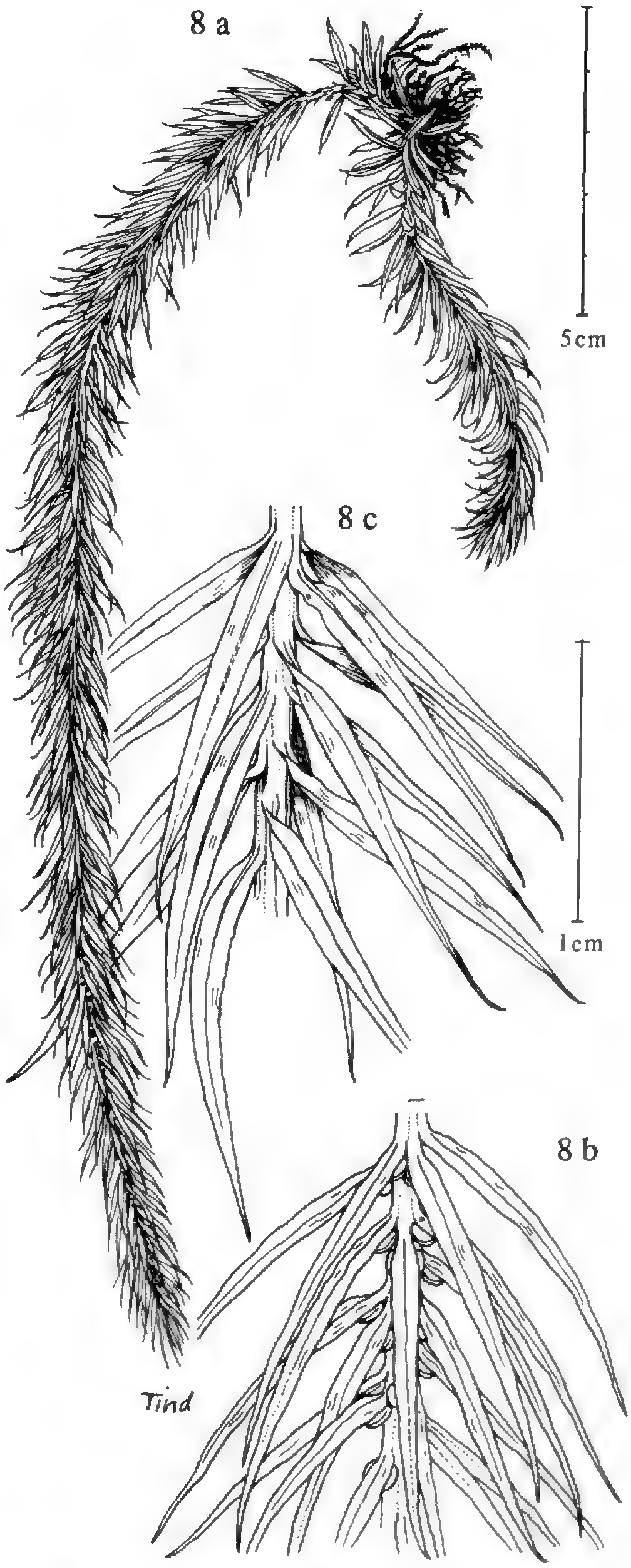


FIGURE 8. *Huperzia pittieri.*—a. Habit.—b. Detail of sporangiate division.—c. Detail of proximal division.

An extremely delicate epiphyte with very thin, often red stems, and distant, very narrow, falcately curved leaves. Stem coloration variable, apparently correlated with light conditions. Southern Mexico to Panama, Venezuela to Ecuador, Amazonian Brazil (Lellinger, 1989: fig. 17; Øllgaard, 1988: fig. 19C).

THE *HUPERZIA VERTICILLATA* GROUP

The most delicate of all the species groups, all species being thin, some stringy and tough, others very soft, pendulous epiphytes, homophyllous or gradually heterophyllous. Leaves of proximal divisions of the stems acicular, those of distal divisions often strongly modified. Throughout the Tropics, including perhaps 25 species of which approximately 11 species occur in the Neotropics; some of these poorly defined.

Size is highly variable in several species, as is the degree of heterophyllous differentiation and the size of the plants when differentiation begins. The most important taxonomic characters are in the texture, curvature, and direction of the proximal leaves, and the shape and direction of the distal leaves.

Huperzia acerosa (Sw.) Holub (*H. verticillata* auct., *non* (L.f.) Trevisan; *Lycopodium setaceum* auct., *non* Lam.)

Usually almost completely homophyllous, and with soft-textured leaves. Central America, West Indies, northern South America, south to Ecuador and southeastern Brazil. This is the most widespread and least specialized of the species. The name *Lycopodium portoricense* L. Underw. & F. Lloyd represents some West Indian, relatively coarse and vigorous, usually terrestrial plants, hanging over banks. They are closely related to, or perhaps conspecific with, *Huperzia acerosa* (Øllgaard, 1988: fig. 18C).

Huperzia brachiata (Maxon) Holub

Unspecialized in terms of leaf differentiation like the preceding species. The very few collections of the species rather small, very delicate plants with distant, very thin leaves, which are longer than in *H. acerosa*. Cocos Island.

Huperzia filiformis (Sw.) Holub (*H. polytrichoides* (Kaulf.) Trevisan; *H. tuerckheimii* (Maxon) Holub; *Lycopodium tortile* Christ)

Plants with slightly heterophyllous or homophyllous shoots, with densely crowded, usually closely appressed, rigid and coriaceous leaves in the proximal divisions, and more distant, usually omnilaterally arranged sporophylls in the distal divisions. Hawaiian Islands, Central America, Andes from Venezuela to Bolivia. Plants with more strongly reduced sporophylls have been referred to *Huperzia tuerckheimii*, but these are hardly distinct enough to merit species recognition. This species appears to be adapted to slightly drier growth conditions than the preceding species (Lellinger, 1989: fig. 40; Øllgaard, 1988: fig. 21A).

Huperzia pringlei (L. Underw. & F. Lloyd) Holub

Resembling the preceding species, also apparently adapted to relatively dry or exposed habitats, but larger and more robust, with thicker stems, and more distant, wider, and thicker leaves, and usually more strongly differentiated distal leaves. Southern Mexico to El Salvador.

Huperzia galapagensis (Hamann) Holub

Relatively robust and more compact than the previous specices, with broad and firm leaves throughout. Galápagos Islands (Hamann, 1974: fig. 1A, 2A).

Huperzia comans (Nessel) B. Øllg. & Wind.

More compact and shorter, but otherwise approximately twice as large in all parts as *H. acerosa* in the same area. Brazil: Minas Gerais, Rio de Janeiro, Paraná. Epiphytic and rupestral in high-altitude montane forest and in open vegetation.

Huperzia tenuis (Willd.) Trevisan

Proximal leaves somewhat secund, distal leaves patently diverging, ovate-cordate. Costa Rica, Panama, Andes from Venezuela to northern Peru, in upper montane forest. A highly variable species with respect to size, the Central American population being relatively large, the Andean ones consisting of both small and delicate, and extremely small and capillary plants (Øllgaard, 1988: fig. 20A, B).

Huperzia curvifolia (Kunze) Holub

Very delicate to extremely delicate, with omnilaterally arranged, uniformly falcately curved proximal leaves, and closely appressed narrow sterile distal leaves. Costa Rica, Colombia to Peru, low- to mid-altitude forests. Variable in size and compactness. The smallest forms represent the most extreme reduction of size in the family, with distal divisions often 0.3–0.5 mm thick including the leaves. The stronger individuals present problems of delimitation toward *Huperzia acerosa* and slender forms of *H. filiformis* (Øllgaard, 1988: fig. 20C).

Huperzia sarmentosa (Spring) Trevisan

Leaf whorls in the proximal divisions distant, leaves uniformly patent-ascending, linear or linear-subulate, with small auricles at the lamina bases.

Ecuador, Peru. This and the following closely related species stand apart from the preceding eight species and appear to connect the group to slender members of the *Huperzia taxifolia* group. They both occur in deep shade in cloud forest near the forest limit (Øllgaard, 1988: fig. 15C, D).

Huperzia watsoniana (Maxon) B. Øllg., comb. nov. Basionym: *Lycopodium watsonianum* Maxon, Smithsonian Misc. Collect. 56 (29): 3, t. 3. 1912

Closely resembling the preceding species, but smaller in all parts. Costa Rica, Panama (Lellinger, 1989: fig. 43; Maxon, 1912: t. 3).

Huperzia mollicoma (Spring) Holub (*H. flaccida* (Fée) Holub; *Lycopodium williamsii* L. Underw. & F. Lloyd)

Superficially resembling the two preceding species in size and growth habit, but differing by the more appressed, nonauriculate leaves and the prominent vein on the leaf undersides. ?Hispaniola, Costa Rica to Venezuela, central and southeastern Brazil, Ecuador, Bolivia, at low- and mid-altitudes (Lellinger, 1989: fig. 31; Øllgaard, 1988: fig. 18B).

THE *HUPERZIA PHLEGMARIA* GROUP

A large group of mainly epiphytic and pendulous species, characterized by rather sharply differentiated, dimorphic leaves. Constricted distal divisions usually with strongly reduced, decussate or subdecussate, imbricate leaves. Leaves of proximal divisions usually large and patent. The occurrence of sporangia commonly restricted to constricted divisions, and often to minor parts of these.

The majority of the species are paleotropic. In the Neotropics there are 12–16 species, representing four of the ten informal subgroups listed by Øllgaard (1987). None of these subgroups appear to be closely related to other neotropical groups.

The following four very distinct species do not form a group of closely interrelated species. They stand apart from the remaining species, being large and robust, high-altitude species.

Huperzia molongensis (Herter) Holub

Recognizable by the thick and sharply quadrangular constricted divisions. In some individuals the expanded leaves restricted to a few centimeters near the base of the plants, rendering the plants secondarily nearly homophyllous. Venezuela to northern Peru. Epiphyte in forests at the timberline. *Huperzia echinata* (Spring) Trevisan (type from Colombia) is only known from the lectotype collection. It is a larger plant than *H. molongensis* but may be conspecific. It deviates only by the terete constricted divisions, with leaves arranged in whorls of three, not decussate and sharply carinate as in *H. molongensis.* It may represent a single deviating giant individual of the latter species. In many other species individual size differences are correlated with changes in the number of orthostichies. Assuming that this is the situation in the present case, the addition of one leaf in each whorl represents a small, if any, genetic change, but a great change of the visual image by which the species is usually recognized. However, this assumption needs to be verified by field observations (Øllgaard, 1988: fig. 22C).

Huperzia campiana B. Øllg.

Smaller than the preceding, with very distinct expanded and constricted divisions, the constricted ones narrow and bluntly quadrangular. Ecuador, northern Peru. Epiphytic in forests at the timberline (Øllgaard, 1988: fig. 22B).

Huperzia pruinosa (Herter) Holub (*H. durissima* (Herter) Holub)

Probably an erect terrestrial plant with nodding shoot tips. Proximal divisions appearing woody, sparsely divided, with distant whorls of reflexed, coriaceous, expanded leaves. A rare and poorly known species from montane forest in northeastern Peru (Fig. 9).

Huperzia robusta (Klotzsch) Holub (*H. phelpsii* (Vareschi) Holub)

Epiphytic and recurved to pendent, or terrestrial and erect or recurved, with very long, usually revolute expanded leaves, often gradually heterophyllous. Venezuelan Guayana. Ravines or open sites on sandstone mesetas (Vareschi, 1966: fig. 2).

Subgroup of *Huperzia myrsinites*

Slender, lax, usually epiphytic species, usually with decussate or subdecussate, rather distant leaf pairs throughout, and often with bright red stems. Upper montane forest, near the forest limit.

Huperzia myrsinites (Lam.) Trevisan (*Lycopodium patens* Sprengel; *L. roraimense* L. Underw. & F. Lloyd; *L. skutchii* Maxon)

Usually with incompletely and heterogeneously differentiated constricted distal divisions, with highly variable, often intermediate leaf morphology,

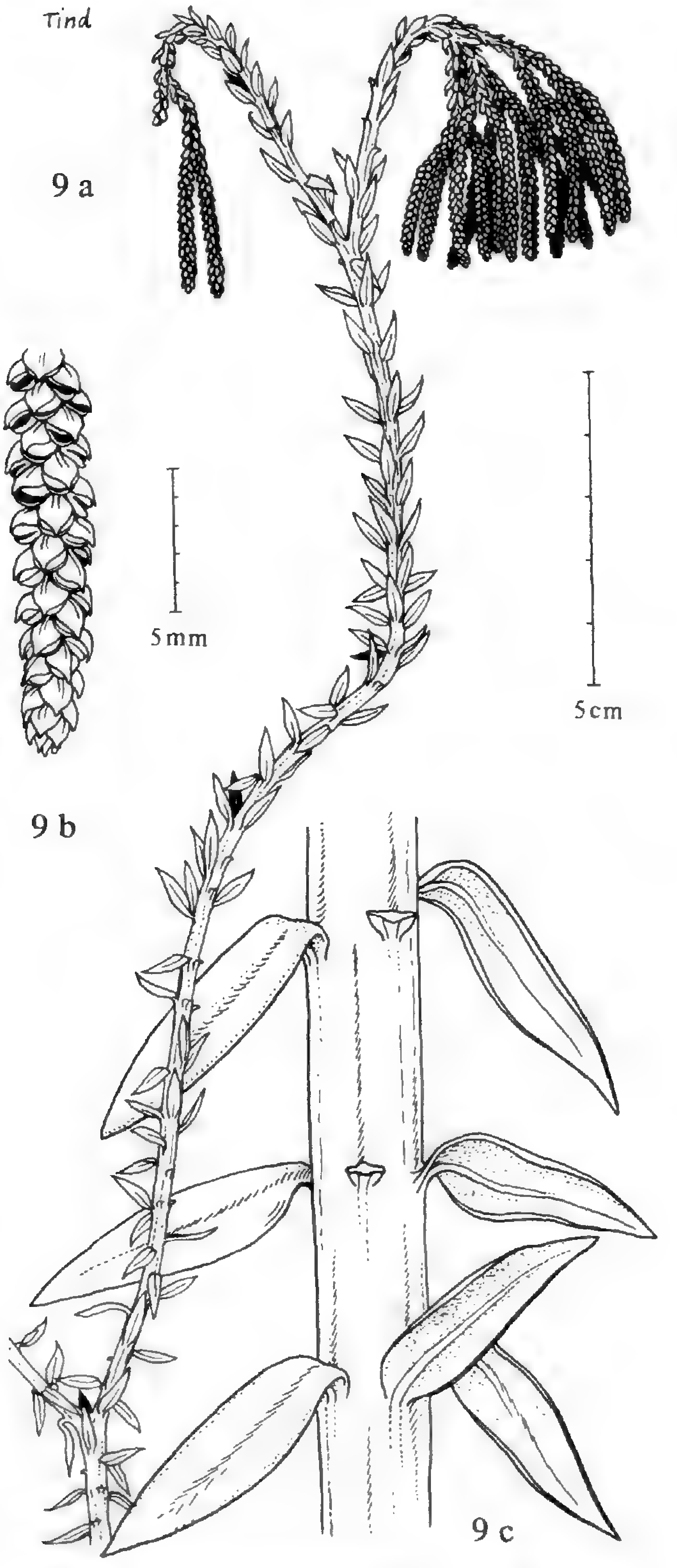


FIGURE 9. *Huperzia pruinosa.*—a. Habit.—b. Detail of sporangiate division.—c. Detail of proximal division.

and relatively broad expanded leaves. Central America, Greater Antilles, Venezuela to Ecuador (Lellinger, 1989: fig. 32; Mickel & Beitel, 1988: fig. 3A; Smith, 1981: fig. 82a, b).

Huperzia phylicifolia (Poiret) Holub (*Lycopodium congestifolium* Spring)

Andes, south to Peru, and possibly Bolivia, Galápagos Islands. The delimitation of this species in relation to the following three species is uncertain, because they are separated only by subtle differences in the shape of the expanded leaves and represent recognizable geographical populations, possibly of a single species (Øllgaard, 1988: figs. 15B, 17A).

Plants described as *Lycopodium nubigenum* Herzog, doubtfully distinct, and hence not as yet transferred to the genus *Huperzia.* With the expanded leaves broadest near the base, not at the middle as the preceding species. Peru, Bolivia, northernmost Argentina.

Huperzia biformis (Hook.) Holub

A soft-textured forest epiphyte with very slender constricted divisions, and expanded leaves almost as in the preceding species. Southeastern Brazil (Hooker, 1839: t. 228).

Huperzia erythrocaulon (Fée) Holub

Slightly more robust, more divaricately branched, slightly more coriaceous-leaved, more red-colored than the preceding species, of which it may represent merely a rupestral form of open habitats above the forest limit. Southeastern Brazil (Fée, 1872–1873: t. 106, fig. 2).

Huperzia subulata (Poiret) Holub (*Lycopodium ewanii* (Herter) C. Morton)

A very delicate species, with long, linear expanded leaves. Costa Rica, Colombia to Peru. It seems confined to the most humid forest, at the forest limit, where it usually occurs in deep shade, while *H. phylicifolia*, with which it has an overlapping distribution, occurs in a wider range of generally more exposed habitats (Lellinger, 1989: fig. 38 (var.); Øllgaard, 1988: fig. 17B).

Huperzia heteroclita (Poiret) Holub

Peculiar in the limited development of expanded leaves and the often very long, sharply quadrangular constricted divisions. Southern Ecuador, Peru (Øllgaard, 1988: fig. 22A).

Huperzia amentacea (B. Øllg.) Holub

With oblong expanded leaves and usually amply ramified, tassel-like constricted divisions. Guatemala, Venezuela, Colombia. This and the two following species are very closely related, but this is the largest. They are mainly separated on the basis of subtle differences in the shape and size of the expanded leaves (Øllgaard, 1982: 53).

Huperzia callitrichifolia (Mett.) Holub

Small, with short, oblong to broadly ovate or almost orbicular expanded leaves. Colombia to Ecuador (Øllgaard, 1988: fig. 23B).

Huperzia cuneifolia (Hieron.) Holub

The smallest of the species, with small to minute obovate to spathulate expanded leaves, sometimes only 3 mm long. Costa Rica, Panama, Venezuela, Colombia, Peru (Lellinger, 1989: fig. 21; Øllgaard, 1988: fig. 23A).

Subgroup of *Huperzia aqualupiana*

Slender, lax epiphytes without red color, with the expanded leaves usually very uniform in size, shape and direction, and arranged in straight longitudinal rows. Low- and mid-altitude montane forests.

Huperzia aqualupiana (Spring) Rothm.

With broad, ovate expanded leaves, usually arranged in whorls of 3, and long, sharply quadrangular constricted divisions with long-acuminate, imbricate leaves. West Indies, Venezuela, Colombia.

Huperzia dichaeoides (Maxon) Holub

Differs from the preceding species in the elliptic, usually decussate expanded leaves, and the short, less sharply angular constricted divisions with short-tipped imbricate leaves. Guatemala to Panama, Colombia, Ecuador. Replaces the preceding species in the western part of the area (Lellinger, 1989: fig. 22; Øllgaard, 1988: fig. 23C).

Huperzia ericifolia (C. Presl) Holub

With broadly lanceolate to oblong-lanceolate expanded leaves arranged in whorls of 3, and with constricted divisions as in *H. aqualupiana*. Ecuador to Bolivia. The southern representative of the subgroup (Øllgaard, 1988: fig. 23D).

Subgroup of *Huperzia quadrifariata*

Pendulous or recurved epiphytes, secondarily homophyllous, with complete suppression of the formation of expanded leaves in some of the individuals of all three species. Other individuals of the same species with few to many expanded leaves at the base, perhaps an indication of the relationship to the *H. phlegmaria* group. Only Brazil.

Huperzia hexasticha B. Øllg. & Wind.

Proximal divisions terete, rather thick, with alternating whorls of 3 scalelike, imbricate leaves, with decussate leaves in the bluntly quadrangular distal divisions. Expanded leaves, when present, narrowly oblong. Southeastern Brazil. The most common species (Øllgaard & Windisch, 1987: fig. 2).

Huperzia quadrifariata (Bory) Rothm. (*H. aschersonii* (Herter) Holub; *Lycopodium quadrangulare* Spring)

Relatively robust, like the preceding species, but with decussate, sharply carinate leaves throughout in the constricted divisions, the shoots sharply quadrangular. Expanded leaves, when present, are linear-oblong. Southeastern Brazil (Fig. 10).

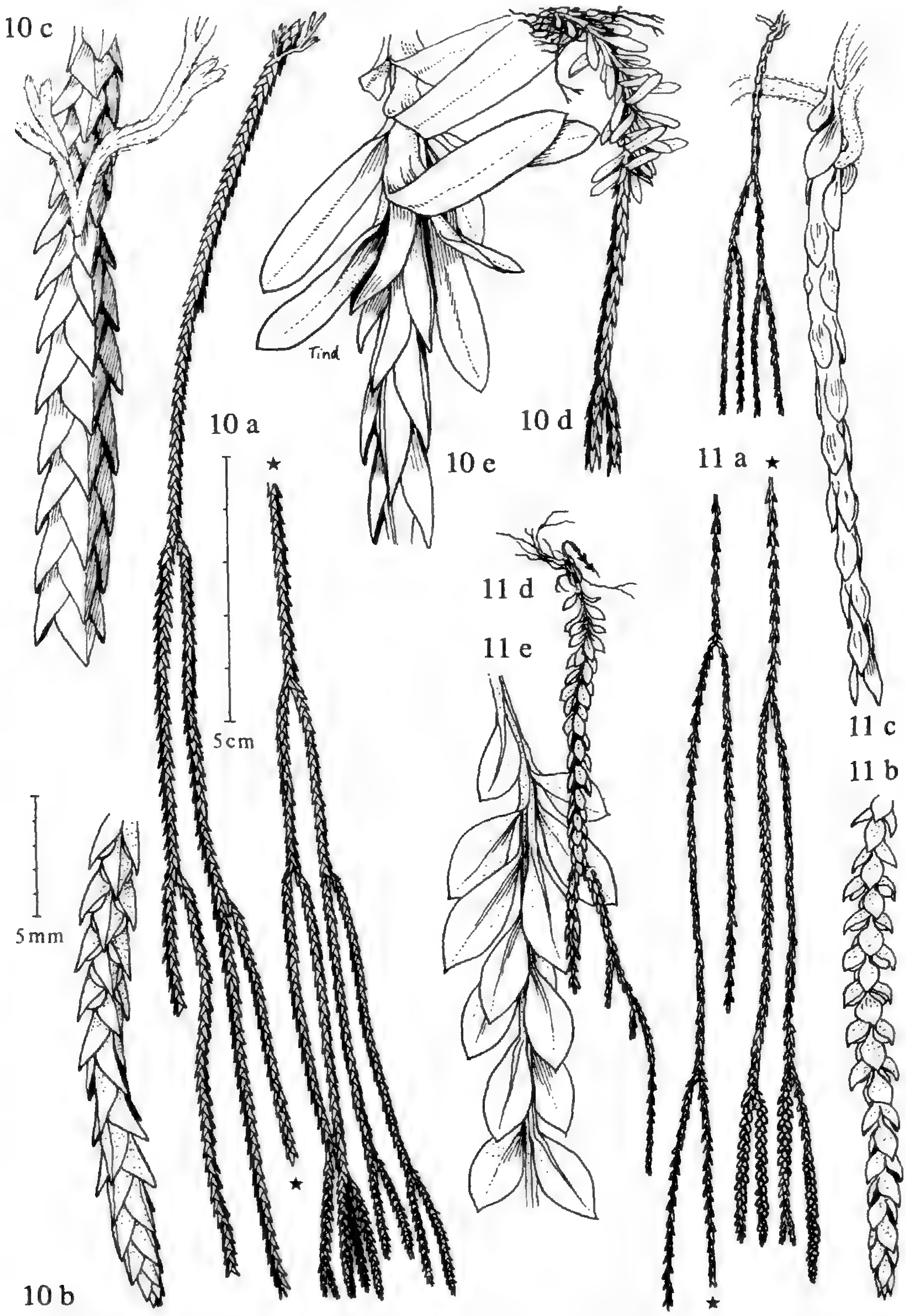
Huperzia fontinaloides (Spring) Trevisan (*H. gehrtii* (Nessel) Holub; *L. serpyllifolium* Fée)

A delicate species with thin, red stems, and small, decussate, dorsally rounded, imbricate leaves throughout in the wholly constricted individuals. Expanded leaves, which may occur in major parts of some individuals, closely situated and usually continuously overlapping, elliptic to obovate, oriented in one plane and forming a flattened shoot. Southeastern Brazil (Fig. 11).

THE *HUPERZIA SAURURUS* GROUP

Terrestrial, erect, often with characteristically fingerlike shoots. Leaves monomorphic or gradually slightly dimorphic, usually appressed, linear to lanceolate. In several species, especially those most closely related to *Huperzia crassa*, the leaves usually with a basal air cavity abaxially in the mesophyll, appearing as a bulge externally, and with shoots slightly to strongly heteroblastic, differentiated into erect sporangium-bearing shoots, and ascending to prostrate or subterranean and rhizomelike, rooting, juvenating shoots which continually give off erect shoots by equal dichotomies. Prostrate or subterranean shoots may considerably increase the diameter of individual plants, which ultimately may take the shape of a fairy ring, up to 1 m wide. Most of the species occur in open vegetation at or above the forest limit.

The number of species is uncertain, probably far exceeding the ca. 40 names listed below. Many



FIGURES 10, 11. 10. *Huperzia quadrifariata.*—a. Habit.—b. Detail of sporangiate division.—c. Detail of homophyllous proximal division.—d. Heterophyllous proximal division, habit.—e. Same, detail. 11. *Huperzia fontinaloides.*—a. Habit.—b. Detail of sporangiate division.—c. Detail of homophyllous proximal division.—d. Heterophyllous proximal division, habit.—e. Same, detail.

of the species are closely related. Species delimitation is highly problematic, because of variability of the same kind as mentioned above under *H. reflexa* and strong response to environmental factors. *Huperzia crassa* is perhaps the single most polymorphic species of the group, comprising several local, recognizable populations that may represent valid species or varieties. Many of these taxa are recognized on the basis of personal intuition rather than definite sets of characters.

The group undoubtedly arose as a consequence of the Andean uprise. It may be considered to represent a relatively modern, and continuing, evolutionary burst. Tolerance of frost is possibly the most important innovation achieved by the group, as this feature facilitated the occupation of new open habitats above the forest limit. This capacity is shared by very few other groups in the genus, mainly the *H. brevifolia* group, and a few species in the *H. brongniartii* group.

The greatest diversity is encountered in the northern Andes. The species of the Ecuadorian and Colombian páramos are especially numerous and poorly understood, particularly in Colombia. Many new species from this area may be added in the future. The group is further represented in the high mountains of Central America, Hispaniola, and southeastern Brazil. *Huperzia saururus* also occurs in temperate South America and in Africa, Madagascar, and the Mascarenes. This species, although it has a wide distribution, is both ecologically and morphologically specialized and rather uniform. It is not regarded as a likely ancestor of the group, as its wide distribution otherwise might suggest.

The first 12 species mentioned below are the least modified with regard to leaf and shoot differentiation. In these the development of air cavities in the leaf bases and heteroblastic shoots is weak or absent. They seem to be relatively close to species in the *H. brongniartii* group and may have been derived from predecessors with a labile morphology like that of *H. weddellii.*

Huperzia hystrix (Herter) Holub

Forming large and heavy individuals, with up to 2-cm-thick, densely foliose shoots, and thick, nearly solid, reddish-orange-tinged leaves, these commonly tapering into slender, whiplike, recurved tips. Southern Colombia, northern Ecuador. Banks, moss cushions, and other habitats with low competition (Øllgaard, 1988: fig. 5B).

Huperzia ulixis (Herter) Holub

A poorly known species resembling the preceding species, but with broader, less tapering leaf tips. Colombia.

Huperzia llanganatensis B. Øllg.

Apparently closely related to *H. hystrix,* but differing by the sparsely ramified, stiffly erect shoots, and by the much shorter, broader leaves. Senescent individuals of the species may form great numbers of lateral, easily detached brood shoots from old parts of the stems where the leaves have fallen off. Northern Ecuador (Øllgaard, 1988: fig. 13B).

Huperzia kuesteri (Nessel) B. Øllg.

Forming massively robust individuals up to 0.5 m diam., with up to 2.5-cm-thick, dark green or pruinous shoots, with leaves triangular-lanceolate, and usually borne in very regular rows. Southern Ecuador and northern Peru (Øllgaard, 1988: fig. 7B).

Huperzia hastata B. Øllg.

Resembling the preceding species in leaf characters, but much smaller, relatively slender, and sparsely branching. Basal auriclelike sinuses convey the hastate appearance of the leaves. Southern Ecuador (Øllgaard, 1988: fig. 6A).

Huperzia espinosana B. Øllg.

With denticulate leaves, often with a whitish hue. Southern Ecuador. A poorly known species of low páramos (Øllgaard, 1988: fig. 7A).

Huperzia weberbaueri (Nessel) Holub (*H. papillata* (Rolleri) Holub)

Unique because of its whitish waxlike cover and densely long-papillate leaves, strikingly contrasting with the surrounding vegetation. Southern Ecuador, northern Peru (Øllgaard, 1988: fig. 5C).

Huperzia polylepidetorum B. Øllg.

A very large species with arcuate-ascending, relatively broad, usually purely green leaves. Southern Ecuador, Peru. Its habitats are in *Polylepis* forest (Øllgaard, 1988: fig. 6B).

Huperzia capellae (Herter) Holub

Purely green, or yellowish green, with a more tender texture than usual for the páramo species. Leaves of exposed shoot tips often scorched by fire, or damaged or deformed by frost. Venezuelan Andes to Peru. In grass páramos, where it usually occurs in the shelter of bunch grasses (Øllgaard, 1988: fig. 8B).

Huperzia acuta (Rolleri) Rolleri & Deferrari

Known only from the type collection. Bolivia (Rolleri, 1980, t. 5A, C).

Huperzia ocanana (Herter) Holub (*H. arthurii* (Herter) Holub; *H. trachyloma* (Herter) Rolleri & Deferrari; ?*Lycopodium arcturii* (Herter) C. Morton; *L. nesselianum* Duek & Lellinger; *U. moritzii* Nessel; *U. orionis* Herter)

Relatively small, with relatively short and broad, ascending leaves. Venezuelan Andes, Colombia. An incompletely understood species or species complex, highly variable in size. Some of its features are intermediate between those of the present, and those of the *H. brevifolia* group.

Huperzia schlimii (Herter) B. Øllg.

With bright red, thick stems, and smooth, thin, appressed leaves. Leaves of proximal divisions tend to be very long and slightly revolute. Colombia: Sierra Santa Marta, a highly local and striking endemic. The species is placed in this group with doubt. It resembles the Brazilian *H. rubra* and may represent a parallel adaptation derived from elements in the *H. brongniartii* group.

In the following 15 species the development of air cavities and heteroblastic shoots, as mentioned above, is moderate to very distinct. They generally represent adaptations to habitat types at high altitudes with little or no shelter, generally higher and more exposed than the preceding 12 species.

Huperzia crassa (Willd.) Rothm. (*H. erythraea* (Spring) Trevisan; *H. pilgeriana* (Nessel) Holub; *H. springii* (Nessel) Holub); *H. nesselii* (Nessel) Rolleri & Deferrari; *Lycopodium bonae-voluntatis* (Herter) C. Morton)

With slender to very thick, fingerlike, erect shoots, with closely appressed, linear-lanceolate leaves. Epidermis of the abaxial leaf surface usually dull because of a waxlike layer, and uneven because of slightly protruding, blisterlike cells. Most populations with strong red coloration, but some, for example, the Costa Rican ones, green. Degree of heteroblastic differentiation may be influenced by the texture of the substrate. Central America, Hispaniola, the Andes south to Peru. This is the most polymorphic species of the group. Several local, recognizable populations of the species, often confined to single mountain massifs, may represent valid species or varieties. In some areas several varieties, or distinguishable populations, occur sympatrically. However, the differences between them are subtle, and the basis for the variation is not understood presently.

Huperzia crassa var. *manus-diaboli* B. Øllg., with slight heteroblastic differentiation, occurs on soft, boggy ground. Ecuador.

Variety *crassa*, with usually pronounced heteroblastic shoot differentiation usually inhabits drier and more solid ground. However, the latter variety may occur side by side with the former, and then usually is less distinctly heteroblastic. Throughout the range of the species (Lellinger, 1989: figs. 20, 37 (var.); Mickel & Beitel, 1988: fig. 1B; Øllgaard, 1988: figs. 8C, D, 10A).

Huperzia saururus (Lam.) Trevisan (*H. axillaris* (Roxb.) Rothm.; *H. sanctae-barbarae* (Rolleri) Rolleri & Deferrari; *Lycopodium elongatum* Sw.)

Usually distinguishable by the green, somewhat glossy leaves with a smooth epidermis and thickened margins, with the erect shoots so densely aggregated and pressed together that leaves at the stem bases lie flat to the stem, appearing etiolated. Peru to Argentina, Africa, Madagascar, Mascarenes. The preceding species often is confused with the present one.

Huperzia badiniana B. Øllg. & Wind.

Differing from *H. saururus* mainly in the more slender shoots and the loosely aggregated growth habit. Southeastern Brazil (Øllgaard & Windisch, 1987: fig. 1A).

Huperzia chiricana (Maxon) Holub

Resembling a small individual of *H. crassa*, but with denticulate leaf margins and a smooth epidermis, suggesting affinity to *H. hoffmannii* (group of *H. reflexa*). Panama, known only from the type collection (Lellinger, 1989: fig. 19; Maxon, 1913: t. 8).

Huperzia andina (Rosenstock) Holub

Resembling *H. saururus*, differing mainly in the somewhat distant, short, erect shoots and the reddish-tinged leaves. Peru, Bolivia.

Huperzia venezuelanica (Herter) Holub (*H. schneei* (Vareschi) Holub)

Resembling the preceding species, but entirely green and much smaller in all parts. Venezuelan Andes.

Huperzia ascendens (Nessel) Holub

With long, slender, surface-creeping and rooting shoots, bearing distant, slender, erect shoots, resembling *H. capellae*, or reddish-tinged as in *H. hypogaea*. Ecuador (Øllgaard, 1988: fig. 9C).

Huperzia cruenta (Spring) Rothm.

With surface-creeping shoots and slender, small, erect sporangium-bearing shoots of soft texture.

Colombia. A poorly understood, highly polymorphic species.

Huperzia catacachiensis (Nessel) B. Øllg.

With very slender shoots with short, semiterete, blunt-tipped, appressed leaves, resembling *H. cruenta*, but with the ascending shoots only slightly heteroblastic. Colombia. Apparently a species of soft, boggy substrates.

Huperzia cumingii (Nessel) Holub

Usually forming very large, rich-branched individuals of green, yellowish to orange-tinged, slightly glossy, relatively slender, and only slightly heteroblastic shoots. ?Colombia, Ecuador. Occurs in humid to wet grass páramos, often in partial shade of bunch grasses (Øllgaard, 1988: fig. 7C).

Huperzia macbridei (Herter) B. Øllg.

A relatively large species with prostrate-ascending rejuvenating shoots and stiffly erect shoots in the center of the individuals, up to 30 cm tall. Leaves yellowish green, linear-lanceolate, straight. Southern Ecuador, Peru (Øllgaard, 1988: fig. 9B).

Huperzia columnaris B. Øllg.

Resembling the preceding species in growth habit, differing in the broader, shorter, triangular-ovate-lanceolate leaves of fertile divisions, usually arranged in regular orthostichies. Southern Ecuador. Low páramos with little or no disturbance (Øllgaard, 1988: fig. 5A).

Huperzia talpiphila B. Øllg.

With thick, fleshy, subterranean, horizontal shoots with reduced leaves, and large, erect shoots with relatively flat, arcuately ascending leaves. Ecuador. Known only from the type (Øllgaard, 1988: fig. 9A).

Huperzia hypogaea B. Øllg.

With narrow, deeply subterranean, rooting horizontal shoots with colorless leaves, and distant, slender, erect aerial, red or reddish-tinged shoots. Southern Colombia to northern Peru. A species mainly of soft boggy habitats. On solid substrates the horizontal shoots become epigeous and creeping, with normal leaves (Øllgaard, 1988: fig. 8E).

Huperzia scabrida B. Øllg.

Closely related to the preceding species, but smaller in all parts, and with small, warty teeth on the leaf margins and a scabrous stem epidermis. Ecuador (Øllgaard, 1988: fig. 8A).

Huperzia attenuata (Spring) Trevisan (*Lycopodium tobarii* Sodiro)

Leaves arranged in alternating whorls of 3 or 4, shoots terete, tinged with red, with very convex to carinate leaf undersides, and fimbriate margins. Costa Rica, Ecuador. This and the following species seem very closely related and differ mainly in the number of orthostichies (Lellinger, 1989: fig. 15; Øllgaard, 1988: fig. 11D).

Huperzia tetragona (Hook. & Grev.) Trevisan (*Lycopodium catharticum* Hook.)

With slender, sharply quadrangular shoots with decussate, fimbriate leaves. In connection with branching anomaly, shoots with leaves arranged in alternating whorls of 3, and accordingly terete and virtually indistinguishable from those of the preceding species. The strong visual effect produced by the change in phyllotaxis, apparently does not reflect a great genetic difference. Colombia to Bolivia. Closely related to the preceding species (Øllgaard, 1988: fig. 11C).

The application of the following names, the types or protologs of which point to the present group of species, is not settled: *Huperzia polyclada* (Sodiro) Rolleri & Deferrari (type not seen, from Ecuador), *Huperzia rimbachii* (Sodiro) Holub (type unknown, from Ecuador), *Lycopodium crucis-australis* (Herter) C. Morton (Colombia), *L. innocentium* (Herter) C. Morton (Colombia), *Urostachys darwinianus* Nessel (probably Peru or Bolivia), *U. erectus* Nessel (?Venezuela), *U. eriksonii* Nessel (Colombia), *U. kupperi* Nessel (Colombia).

THE *HUPERZIA BREVIFOLIA* GROUP

Most species with broadly lanceolate to orbicular leaves, sometimes broader than long, and often patent to perpendicular or reflexed, often with air sacs in the leaf base mesophyll, and with a thick cuticle. Heteroblastic shoot differentiation rare.

This group is very closely related to the preceding group, and its delimitation from that group is somewhat arbitrarily based on differences of leaf shape. Some of the species, e.g., *Huperzia poly-*

dactyla, seem transitional, but most of them have broad, short leaves. This is believed to represent a further specialization and adaptation to the cold and windy habitats in páramo vegetation. Heteroblastic shoot differentiation occurs in *H. lignosa*.

Orientation of the leaves, appressed, ascending, spreading, perpendicular, recurved, or sharply reflexed, is highly variable in several of the species. In some of the species the leaf direction may vary from one extreme to the other in the same population, in the same individual, or even in different parts of the same shoot.

The group is mainly Andean, occurring from Venezuela to Bolivia with at least 16 species. Two species occur in Costa Rica.

Huperzia polydactyla B. Øllg.

Appearing intermediate between *H. sellifolia* and *H. cumingii* (*H. saururus* group), with lanceolate to broadly lanceolate leaves, but shows no other signs of hybridity. Ecuador (Øllgaard, 1988: fig. 11B).

Huperzia pflanzii (Nessel) Rolleri & Deferrari

Bolivia, Costa Rica. This species is placed in the present group with doubt. In size and leaf texture it seems equally close to the preceding group, but it has the broadly lanceolate to ovate leaves in common with the present group. The presence of nearly identical plants from Bolivia and Costa Rica may be due to parallel evolution. In both of these areas plants referred to this species are rare (Lellinger, 1989: fig. 33).

Huperzia dianae (Herter) B. Øllg.

With relatively large, long, and lax leaves and rather thin stems. Colombia. A local species of lower páramos of Depto. Antioquia.

Huperzia myrtuosa (Spring) Trevisan (*H. lellingeri* (Rolleri) Holub)

Exposed individuals approaching the aspect of *H. brevifolia*, with short, stiff, perpendicular leaves, shaded individuals approaching the aspect of a compact *H. brongniartii* (*H. brongniartii* group) with longer, softer and thin, recurved-arching leaves. Venezuelan Andes (Øllgaard, 1988: fig. 14B).

Huperzia engleri (Herter) B. Øllg.

Small plants, with somewhat distant, entirely green, broadly elliptic leaves, with a slender stem and very large, fully exposed sporangia that appear not to open. Peru. A poorly known species with features suggesting a sheltered habitat.

Huperzia eremorum (Rolleri) Holub

Resembling *H. rufescens* and *H. sellifolia*, but larger and less ramified than these, and with uniformly appressed, abaxially convex leaves. Colombia. A rare species (Rolleri, 1978: fig. 1).

Huperzia rufescens (Hook.) Trevisan

Closely related to *H. brevifolia* but smaller, with relatively thin stems, and forming small individuals with relatively few branches. Southern Colombia, Ecuador (Øllgaard, 1988: fig. 12D). *Lycopodium mirum* Vareschi from the Venezuelan Andes resembles the preceding species, differing in the mainly 6-ranked leaves, and doubtfully distinct from it. (Vareschi, 1958: figs. 2–3).

Huperzia sellifolia B. Øllg.

Resembling *H. rufescens*, but smaller in all parts, with narrower leaves, usually arranged in whorls of 5, not 4. Plants generally forming much larger clumps with numerous branches. Southern Colombia, Ecuador. Some plants from southern Ecuador and northern Peru, tentatively placed in this species, may belong to distinct taxa, but are presently insufficiently known (Øllgaard, 1988: fig. 12C).

Huperzia compacta (Hook.) Trevisan (*H. jamesonii* (Baker) Holub)

Resembling the preceding in size, usually less ramified, and with distinctly and irregularly toothed leaf margins. Ecuador (Øllgaard, 1988: fig. 12B).

Huperzia brevifolia (Grev. & Hook.) Holub (*H. serpentiformis* (Herter) Rolleri & Deferrari)

Stems relatively thick, with perpendicular to sharply reflexed, stiff and usually somewhat prickly, broad leaves, the broadest usually as broad as or broader than long. The largest plants usually forming heavy, massive clumps with numerous shoots often more than 25 cm tall. Costa Rica, Colombia to Peru. Polymorphic, consisting of several local, recognizable populations (Øllgaard, 1988: fig. 12A).

Huperzia schmidtchenii (Hieron.) Holub (*H. goudotii* (Herter) Holub)

Closely related to *H. brevifolia*, with thick stems and coriaceous, closely set, lanceolate leaves. Colombia (Lellinger, 1989: fig. 26).

Huperzia lignosa (Herter) Holub

The only species of the group with shoots distinctly differentiated into creeping and rooting, and erect and spore-producing shoots. The thick stems and very short leaves indicate close relationship to *H. brevifolia.* Northern Colombia.

Huperzia hohenackeri (Herter) Holub

Probably most closely related to *H. brevifolia,* with equally thick stems, but with larger, thinner, narrower, and usually ascending leaves. Colombia to Peru. A variable species, or perhaps better a species complex, poorly represented in collections (Øllgaard, 1988: fig. 13A, D).

Huperzia transilla (Baker) Holub

A giant species, with stems up to more than 1 cm thick, often bright red, up to more than 1 m long (to 60 cm tall). Leaves somewhat distant, emerald green, up to 11 × 8 mm, spreading. Colombia, Ecuador. Mainly in the lower parts of the páramos and subpáramos (Øllgaard, 1988: fig. 11A).

LYCOPODIUM LINNAEUS

Sporophytes terrestrial, anisotomously branched, with elongate, indeterminate, subterranean, creeping, or scandent main stems giving rise to usually determinate, ascending to erect, dendroid or spreading branchlet systems arising in a dorsolateral position on the main stems. Stele of main stems and major branches occupying a large proportion of the stem diameter (up to ½), with xylem in parallel bands; minor branches, peduncles, and strobili, usually with radially arranged xylem bands (in cross section). Roots emerge directly along the underside of main stems, with parallel-banded steles in the main roots. Branchlet leaves uniform or strongly anisophyllous. Sporophylls ephemeral, dying after sporangium dehiscence, gathered in specialized, compact strobili. Strobili erect, simple or forked, sessile or borne on simple or forked peduncles. Sporophylls peltate, or subpeltate with a thin, basal, decurrent wing, with or without a basal mucilage cavity. Sporangia attached to the sporophyll base, reniform, with a short thick stalk, isovalvate or slightly anisovalvate, their epidermis cells with thin, lignified, sinuate side walls, without partial thickenings, but in some species with distinct nodulelike in- and evaginations. Spores reticulate. Gametophytes unknown from the area, conic to convoluted disc-shaped, subterranean, mycoparasitic in extralimital representatives of the same sections (only neotropical members included).

A virtually cosmopolitan genus of approximately 40 species, with eight species in the Neotropics, representing four of the nine sections recognized by Øllgaard (1987). These sections are very distinct, sometimes recognized as distinct genera, exhibiting distinct types of anisophylly, sporophyll types, sporangium wall cell patterns, spore types, and chromosome numbers. None of them are connected by intermediate species or by intersectional hybrids.

In the Neotropics the *Lycopodium* species are restricted to relatively cool and cold montane regions. They generally seem to tolerate drier habitats than the *Huperzia* species, often occurring abundantly in sites where the latter genus is virtually absent.

Lycopodium sect. *Lycopodium*

Sporophytes with epigeous, creeping to subscandent main stems. Leaves isophyllous throughout, arranged in alternating whorls of 6–10, linear, terminating in a colorless hair tip or a membranous apex. Sporophylls subpeltate, with a basal mucilage cavity. Sporangium epidermis cells with numerous conspicuous in- and evaginations on the side walls. Spores reticulate on all faces. Gametophytes unknown from the area, convoluted disc-shaped in extralimital species of the section. Chromosome numbers based on $x = 34$. An Argentinean report of $n = 22$ for *Lycopodium clavatum* (Rolleri, 1982) is enigmatic, being close to the number that is prevalent in section *Complanata.*

The section is represented in all continents except Australia, by probably fewer than 10 species, but several additional species recently described from China may reflect a higher diversity than hitherto realized. Two species are present in the Neotropics.

Lycopodium clavatum L. (*L. aristatum* Willd.; *L. eriostachys* Fée; *L. piliferum* Raddi)

Typical plants usually amply branched, with diverging branches, well-differentiated, ramified peduncles, and hair-tipped leaves. Virtually cosmopolitan. A highly variable species. Morphologically recognizable tetraploids and triploids of this species, reported from Japan (Takamiya & Tanaka, 1982), indicate that some of the variation is genetically fixed. In the Neotropics interpopulation as well as intrapopulation variability suggests that the species may be genetically heterogeneous here also. However, this heterogeneity is not known to be linked to different chromosome numbers (Lellinger, 1989: fig. 3; Mickel & Beitel, 1988: fig. 2D; Øllgaard, 1983: fig. 7a; Øllgaard, 1988: fig. 24A).

High-altitude representatives from the Andes, Costa Rica, and Panama are recognized as *Lycopodium clavatum* L. subsp. *contiguum* (Klotzsch) B. Øllg. (*L. contiguum* Klotzsch; *L. herbaceum* (Spring) Hieron.; *L. mayoris* Rosenstock; *L. preslii* Grev. & Hook.; *L. serpens* C. Presl, *non* Poiret). They differ by the sparse ramification, parallel, stiffly erect branches, and epedunculate, or short-pedunculate strobili. Other similarly adapted ecotypes of this species, characterized by compact, less compound, monostachyous, and often epedunculate habit, occurring in exposed arctic and tropical alpine regions, have been recognized as species. In the present case the subspecies is connected to typical *L. clavatum* by numerous intermediates, the spores and meioses of which show no signs of hybridity (Lellinger, 1989: fig. 4; Øllgaard, 1988: fig. 24B).

Lycopodium vestitum Poiret (*Lycopodium albidum* Baker; *L. scariosum* Hook., *non* Forst.)

Growth habit closely resembling that of *L. clavatum* subsp. *contiguum*, differing by the striking, silvery appearance, due to the broadly membranous, whitish leaf apices. Southern Ecuador, northern Peru. The membranous leaves seem to be the only feature distinguishing the species, a feature of uncertain adaptive value. The apparent xeromorphy of the feature does not match the generally very humid páramo habitats of the species. Xeromorphic characters are sometimes associated with low-nutrient substrates, but this species often shares the habitats with *L. clavatum* subsp. *contiguum* and typical *L. clavatum*. The spores and meioses of intermediates between this species and both *L. clavatum* subsp. *contiguum* and typical *L. clavatum* show no signs of hybridity, so the species may be only vaguely distinct from that species (Øllgaard, 1988: fig. 24D).

Lycopodium sect. *Complanata* Victorin

Sporophytes with subterranean or creeping to subscandent main stems. Branchlets dorsiventral, strongly anisophyllous, with decussate, trimorphic leaves, one dorsal and one ventral rank of narrow leaves, and two lateral ranks of broad leaves. Branchlet leaves without colorless hair-tips. Strobili pedunculate or sessile. Sporophylls subpeltate, with a basal mucilage cavity. Sporangium epidermis cells with evenly sinuate side walls. Spores reticulate on all faces. Gametophytes not known from the area, narrowly conic in extralimital species of the section. Chromosome numbers based on $x = 23$.

This section is most diverse in northern temperate, arctic, and alpine regions. It is montane in the tropics, but absent from Australia. There are approximately 20 species, of which possibly two or more can be recognized in the Neotropics. However, these are as yet poorly understood. The section was monographed by Wilce (1965), who made no conclusive classification of the neotropical material.

Lycopodium fawcettii L. Underw. & F. Lloyd

Plants of the section *Complanata* from the Greater Antilles are fairly uniform and traditionally are maintained as a separate species. They are doubtfully distinct from the more variable and morphologically overlapping *L. thyoides*.

Lycopodium thyoides Willd. (*L. complanatum* auct.; *L. comptonioides* Desv.)

A highly variable species, or species complex (Wilce, 1965), the elements of which are as yet undefined. The morphology of these plants responds strongly to environmental factors (Lellinger, 1989: fig. 7; Mickel & Beitel, 1988: fig. 2A–C; Øllgaard, 1983: fig. 7b–d; Øllgaard, 1988: fig. 25A).

Lycopodium sect. *Diphasium* (Rothm.) B. Øllg.

Sporophytes with subterranean or creeping to subscandent main stems. Branchlets dorsiventral, anisophyllous, with dimorphic leaves arranged in two dorsolateral ranks of broad, entirely herbaceous, alternating leaves and two or three ventral ranks of narrow, scarious-tipped leaves. Strobili pedunculate or sessile. Sporophylls subpeltate, with a basal mucilage cavity. Sporangium epidermis cells with sinuate, finely curled side walls. Spores reticulate, with large meshes on the distal face and unornamented proximal faces. Gametophytes unknown in the area, broadly conic in an extralimital species of the section. Chromosome numbers not known with certainty: $n = 34$–36; and ca. 90 have been recorded.

Philippines to Tasmania and New Zealand, Juan Fernandez, Andes from Chile to Venezuela, Guyana Highlands, Mount Itatiaia (Brazil), Costa Rica, Jamaica. The section comprises perhaps four species, of which only the following occurs in the Neotropics.

Lycopodium jussiaei Poiret (*L. haenkei* C. Presl; *L. heterophyllum* Sprengel; *L. holtonii* L. Underw. & F. Lloyd; *L. lindseaceum* Spring)

Costa Rica, Jamaica, Venezuela to Bolivia, Guyana Highlands, Mount Itatiaia (Brazil). The considerable variability of the present species is believed to be due to response to environmental factors. The aerial shoots of plants growing in protected and moist scrub may attain a height of almost 1 m, while individuals of exposed mountain ridges may be only a few centimeters tall. Shoot compaction and leaf size and shape also seem correlated with growth conditions (Lellinger, 1989: fig. 5; Øllgaard, 1988: fig. 25B).

Lycopodium sect. *Magellanica* B. Øllg.

Sporophytes with subterranean main stems. Branchlets isophyllous, the leaves herbaceous throughout, without hair-tips. Strobili pedunculate or sessile. Sporophylls peltate, with a narrow, terete stalk lacking membranous wings, lacking mucilage cavities. Sporangium epidermis cells with thin, evenly sinuate side walls. Spores reticulate, with medium-sized, irregular meshes, unornamented on proximal faces. Gametophytes unknown in the area, broadly conic in an extralimital species of the section. Chromosome numbers based on $x = 31$.

The section comprises ca. five species mainly of austral distribution, occurring in Australia, Tasmania, New Zealand, Juan Fernandez, Costa Rica, Hispaniola, the Andes from Venezuela to Tierra del Fuego, southeastern Brazil, South Georgia, Kerguelen, Malvinas, and Mt. Aberdare (Africa). The greatest diversity of the group is in temperate South America, with four species, while the neotropical area has only two species.

Lycopodium magellanicum (P. Beauv.) Sw. (*L. pichinchense* Hook.; *L. spurium* Willd.)

Aerial shoot systems bushy and usually without a dominant, elongate main axis. Costa Rica, Hispaniola, the Andes from Venezuela to Tierra del Fuego, southeastern Brazil, South Georgia, Kerguelen, Malvinas. Restricted to high-altitude habitats, at or above the forest limit. The deeply subterranean main stems enable the species to tolerate páramo fires very well (Lellinger, 1989: fig. 6; Øllgaard, 1988: fig. 24C).

Lycopodium assurgens Fée (*L. schwackei* (Christ) Herter)

Deviates from the preceding species mainly by the treelike branching, with an elongate main axis in the aerial shoot systems, thereby closely resembling *L. erectum* Philippi (Chile, Argentina), and being doubtfully distinct from this. Southeastern Brazil (Fée, 1872–1873: t. 106, fig. 3).

LYCOPODIELLA HOLUB

Sporophyte growth habit diverse, with anisotomous branching throughout, either with prostrate, creeping vegetative shoots producing dorsally arising, erect, strobilus-bearing branches, or with arching-looping runner-shoots producing dorsally arising, highly ramified, usually treelike shoot systems that terminate in usually nodding branchlets with pendent strobili, a few species with a less clearly defined branching pattern. Stem steles with radially arranged, sometimes highly dissected xylem (sect. *Campylostachys*). Shoots isophyllous or anisophyllous. Leaves with or without veinal mucilage canals. Sporophylls subpeltate, with a median basiscopic wing, or with coalescent basal membranes which almost enclose the sporangia, with basal mucilage canals, with or without veinal mucilage canals. Sporangia on the sporophyll base, or axillary (sect. *Lycopodiella*), strongly anisovalvate, or isovalvate (sect. *Caroliniana*). Sporangium epidermis cells with thin, straight, nonlignified side walls, but with lignified, nodular, or semiannular thickenings. Spores rugate. Gametophytes unknown in the area, green, tuberous and lobed on the upper side, surface-living, hemisaprophytic in extralimital species of the genus.

This genus occurs in almost all moist temperate and tropical regions of the world. It comprises approximately 40 species, the majority of these in the Americas. Perhaps 25 species occur in the Neotropics, representing three of four sections recognized by Øllgaard (1987). These sections are very distinct, exhibiting distinct branching patterns, sporophyll types, sporangium shapes and sporangium wall cell patterns, spore types, and chromosome numbers. None of them are connected by intermediate species or intersectional hybrids. Although growth habit and morphological details are quite diverse, features of branching, sporangium anatomy, spores, and gametophytes indicate that *Lycopodiella* is a natural entity.

Lycopodiella sect. *Lycopodiella*

Sporophytes with prostrate or looping, rooting, indeterminate, isophyllous to slightly anisophyllous, horizontally branching shoots, and dorsally arising, erect, simple or up to twice-forked strobiliferous branches. Leaves of erect branches conform with leaves of prostrate shoots, or somewhat reduced.

Sporophylls arranged in alternating whorls of 5 or more, forming 10 or more longitudinal ranks, free, not enclosing the sporangia, subpeltate, with triangular cross section of the immature stalk, with veinal and basal mucilage canals. Sporangia axillary, subglobular, with a narrow stalk, strongly anisovalvate. Sporangium epidermis cells with semiannular thickenings. Chromosome numbers based on $x = 78$.

The type section occurs in northern temperate regions of America and Eurasia and in tropical America south to northern Argentina. Most of the species grow on moist or boggy, sandy soil. It comprises probably fewer than 10 poorly understood and freely hybridizing species. The hybrids may form normal spores when the parents have the same chromosome number. There are five or more species in the Neotropics.

Lycopodiella alopecuroides (L.) Cranfill

With high-looping indeterminate shoots. Vegetative leaves of the strobiliferous branch patent and nearly of the same length as the sporophylls. Leaves furnished with numerous irregular, partly hooked teeth. Temperate North America, Cuba. In the narrow sense this species is almost restricted to North America, but has been found once in Cuba. It occurs mainly in soft mossy bogs.

In the broad sense the name is applied to a heterogeneous assemblage of neotropical plants in the section, all different from the species sensu stricto, awaiting a detailed study and better understanding of the group. Undoubtedly the South American representatives are as complex as the North American ones (Bruce, 1976). The concept in the broad sense includes the types of *Lycopodium longipes* Grev. & Hook., and thus its synonym *Lycopodiella alopecuroides* var. *integerrima* (Spring) B. Øllg. & Wind. (Lellinger, 1989: fig. 8; Øllgaard & Windisch, 1987: fig. 4C), which represents the most widely occurring element in the group (almost throughout the neotropical range). The relation of this element, especially to the North American *Lycopodiella prostrata* (Harper) Cranfill, needs clarification. Other varieties, *L. alopecuroides* var. *dusenii* B. Øllg. & Wind. (Øllgaard & Windisch, 1987: fig. 4D) and variety *tupiana* B. Øllg. & Wind. (Øllgaard & Windisch, 1987: fig. 4B) (both southeastern Brazil) seem to represent equally distinct, but more local elements. This also applies to *Lycopodiella matthewsii* (Hook.) Holub (high altitudes in the northern Andes) (Øllgaard, 1988: fig. 26A) and to very slender plants from the lower, eastern Andean slopes from Ecuador to Bolivia (Øllgaard, 1988: fig. 26B). A narrowly endemic, dwarfed form from Hispaniola, with very short, erect, strobiliferous branches is as yet undescribed.

Lycopodiella appressa (F. Lloyd & L. Underw.) Cranfill

With flatly creeping indeterminate shoots and closely appressed leaves throughout the slender, erect strobiliferous branches. Temperate North America, Cuba. This species occurs almost exclusively in temperate North America, but has a few extant sites in Cuba.

Lycopodiella geometra B. Øllg. & Wind.

Remarkable because of its high-looping, indeterminate shoots, producing erect, fascicular, subisotomous, lateral branchlet systems. Erect strobiliferous branches often up to twice forked. Southeastern Brazil, Paraguay, northern Argentina (Øllgaard & Windisch, 1987: fig. 4A).

LYCOPODIELLA SECT. *CAROLINIANA* (BRUCE) B. ØLLG.

Sporophytes with prostrate, rooting, indeterminate, isophyllous to strongly anisophyllous, horizontally branching shoots and dorsally arising, erect, simple strobiliferous branches. Leaves of strobiliferous branches conform to leaves of prostrate shoots, or strongly reduced and distant. Sporophylls arranged in alternating whorls of 3–5, rarely decussate, forming 4–10 longitudinal ranks, free, not enclosing the sporangia, without veinal mucilage canals. Sporangia isovalvate, reniform, broadly attached to the sporophyll stalk. Sporangium epidermis cells with incompletely semiannular thickenings. Chromosome numbers based on $x = 35$.

This section is represented in most tropical and temperate regions, but is absent from Europe, western temperate Asia, and western temperate North America. Most of the species grow on moist or boggy, sandy soil. Some species are adapted to seasonal drought and may survive dry periods by means of subterranean, tuberous stem apices. There are 6–10 rather poorly understood species, with the highest diversity, including the primitive, isophyllous species in South America. At least four species occur in the Neotropics. A thick, spongy cortex in the prostrate shoots seems to have developed independently, possibly as an adaptation to growth in marshes or very shallow water, in species in southern Africa, Brazil, and the Guayana Highlands.

Lycopodiella contexta (C. Martius) Holub (*Lycopodium sprucei* Baker)

Isophyllous, with identical vegetative leaves on prostrate and strobiliferous branches. Vegetative leaves falcate from a perpendicular base, with subterete, acroscopically adnate leaf bases. Along the margins of the Amazon basin in Venezuela, Brazil, Peru, and Colombia (Fig. 13).

Lycopodiella iuliformis (L. Underw. & F. Lloyd) B. Øllg. (*Lycopodiella duidae* A. C. Smith; *L. tatei* A. C. Smith)

Isophyllous, differing from the preceding species by the flattened leaf bases and the more distant, appressed vegetative leaves of the strobiliferous branches. Guayana Highlands. Polymorphic, and in need of detailed study. The variation concerns especially size, number of orthostichies in the strobilus, and in correlation with this, shape of sporophylls. Some of the size variation appears genetically based. *Lycopodiella iuliformis* var. *tatei* (A. C. Smith) B. Øllg. has thick, spongy horizontal stems (Fig. 12).

Lycopodiella caroliniana (L.) Pichi-Serm. (*Lycopodium meridionale* L. Underw. & F. Lloyd; *Lycopodium paradoxum* C. Martius)

Distinctly anisophyllous. Temperate and tropical America, tropical Africa, tropical Asia. Polymorphic, exhibiting considerable variation in size and in the shape of the leaves of the prostrate shoots. A small and slender variety, with narrow lateral leaves on the prostrate shoots, closely resembling the type variety (temperate North America) occurs in Colombia.

Lycopodiella caroliniana var. *meridionalis* (L. Underw. & F. Lloyd) B. Øllg. & Wind. deviates from the type variety mainly through its larger size. It occurs throughout the neotropical range and is doubtfully distinct from part of the African material usually referred to *L. affinis* (Bory) Pichi-Serm. (Lellinger, 1989: fig. 9; Øllgaard, 1983: fig. 6a, b).

Lycopodiella caroliniana var. *paradoxa* (*Martius*) B. Øllg. & Wind. (southeastern Brazil, Paraguay, Venezuelan Guayana, ?Amazonian Colombia) is as small as or smaller than the type variety, but has very short and broad leaves.

Lycopodiella carnosa (Silveira) B. Øllg. (*Lycopodium goyazense* L. Underw. & F. Lloyd)

A large species with strongly anisophyllous, thick, spongy horizontal stems, with dorsal leaves strongly reduced. Southern and southeastern Brazil, Paraguay, Amazonian Bolivia (Fig. 14).

LYCOPODIELLA SECT. *CAMPYLOSTACHYS* (K. MUELLER) B. ØLLG.

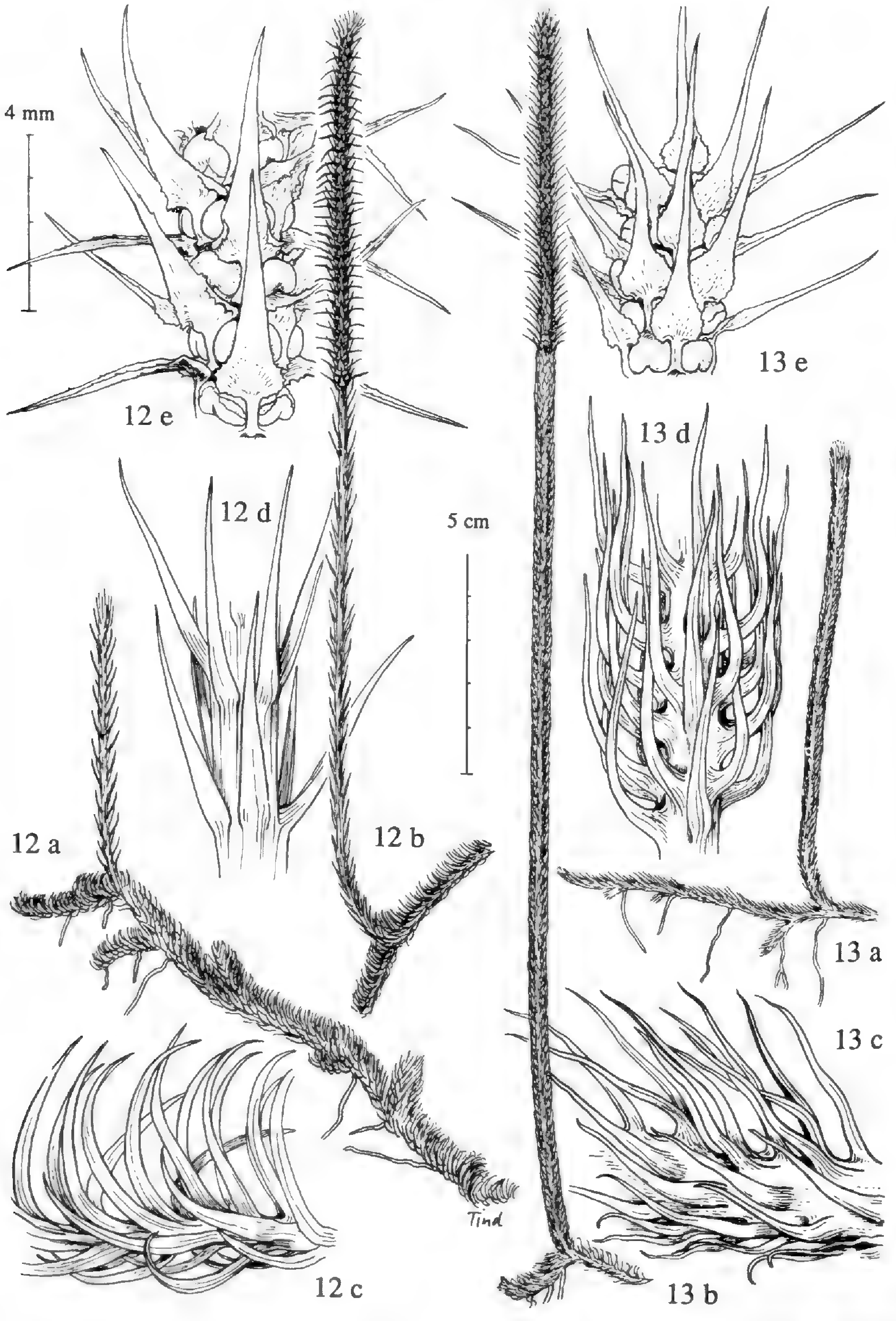
Sporophytes with trailing to arching or looping, rarely creeping, indeterminate shoots, rooting at usually long intervals, occasionally branching in the horizontal plane, giving off lateral, horizontal branchlet systems, and usually bearing one, dorsally arising, treelike, erect branch system on every loop. The erect branch bearing a series of subdecussately arranged, ascending to recurved or hanging, flabellate branchlet systems, which in turn may terminate in epedunculate, nodding to pendulous strobili; strobili sometimes also on the branchlets of the lateral branchlet systems of the indeterminate horizontal axes. Stem steles with highly dissected xylem. Leaves and stem surfaces often with short, usually unicellular hairs. Sporangia subglobular, anisovalvate, almost enclosed in cavities formed by the strobilar cortex and the coalescent basal membranes of adjacent sporophylls. Sporangium epidermis cells with nodular or buttresslike, lignified thickenings on the side walls. Chromosome counts problematic and varied, some of the published numbers possibly inaccurate: $n = 104, 108, 110, 136, 156$, ca. 165, 208.

The species of this section occur throughout moist regions of the tropics, commonly as pioneers on disturbed soil. *Lycopodiella cernua* is pantropical, while many other species have narrow distributions. Species diversity is especially high on tropical mountains. Most of the species have a treelike growth habit, but in some the branches corresponding to the treelike branch systems may become scandent and several meters long. *Lycopodiella steyermarkii* may occur as high-climbing epiphyte. *Lycopodiella bradei* is exceptional, being entirely creeping, with partly subterranean stems and erect strobili.

The total number of species in the section is uncertain, probably exceeding 20. Of these at least 13, but probably more, can be recognized in tropical America. The growth habit is important for species recognition, but at the same time is highly variable according to the size and luxuriance of plants, and as a response to light conditions. Hybridization between species seems to be common.

Lycopodiella cernua (L.) Pichi-Serm. (*L. capillaceum* (Spring) Hieron.)

With erect, treelike branches with lax, softly recurved lateral branchlet systems, with usually



FIGURES 12, 13. 12. *Lycopodiella iuliformis* var. *iuliformis*.—a, b. Habit.—c. Detail, prostrate shoot.—d. Detail, strobiliferous branch.—e. Detail, strobilus. 13. *Lycopodiella contexta*.—a, b. Habit.—c. Detail, prostrate shoot.—d. Detail, strobiliferous branch.—e. Detail, strobilus.

glabrous main axes with capillary, patent to reflexed or slightly ascending leaves, and small strobili. Pantropical. A common pioneer on disturbed soil in most tropical areas, especially in the lowlands (Lellinger, 1989: fig. 10; Mickel & Beitel, 1988: fig. 1A; Øllgaard, 1983: fig. 6c–e; Øllgaard, 1988: fig. 27A).

Lycopodiella camporum B. Øllg. & Wind.

Resembling *L. cernua* in most details, but with more densely foliose, stiffly ascending, not recurved, sterile branchlets. Treelike shoots often with the branchlet systems clustered in a fasciculate manner, and with sharply recurved strobili. Amazonian Venezuela and the Guianas, Colombia, Peru, and Bolivia, southern and southeastern Brazil. Ecologically this species is characterized by its affinity for savanna and campos vegetation, especially humid places along rivers, where the plants become temporarily flooded (Øllgaard & Windisch, 1987: fig. 3).

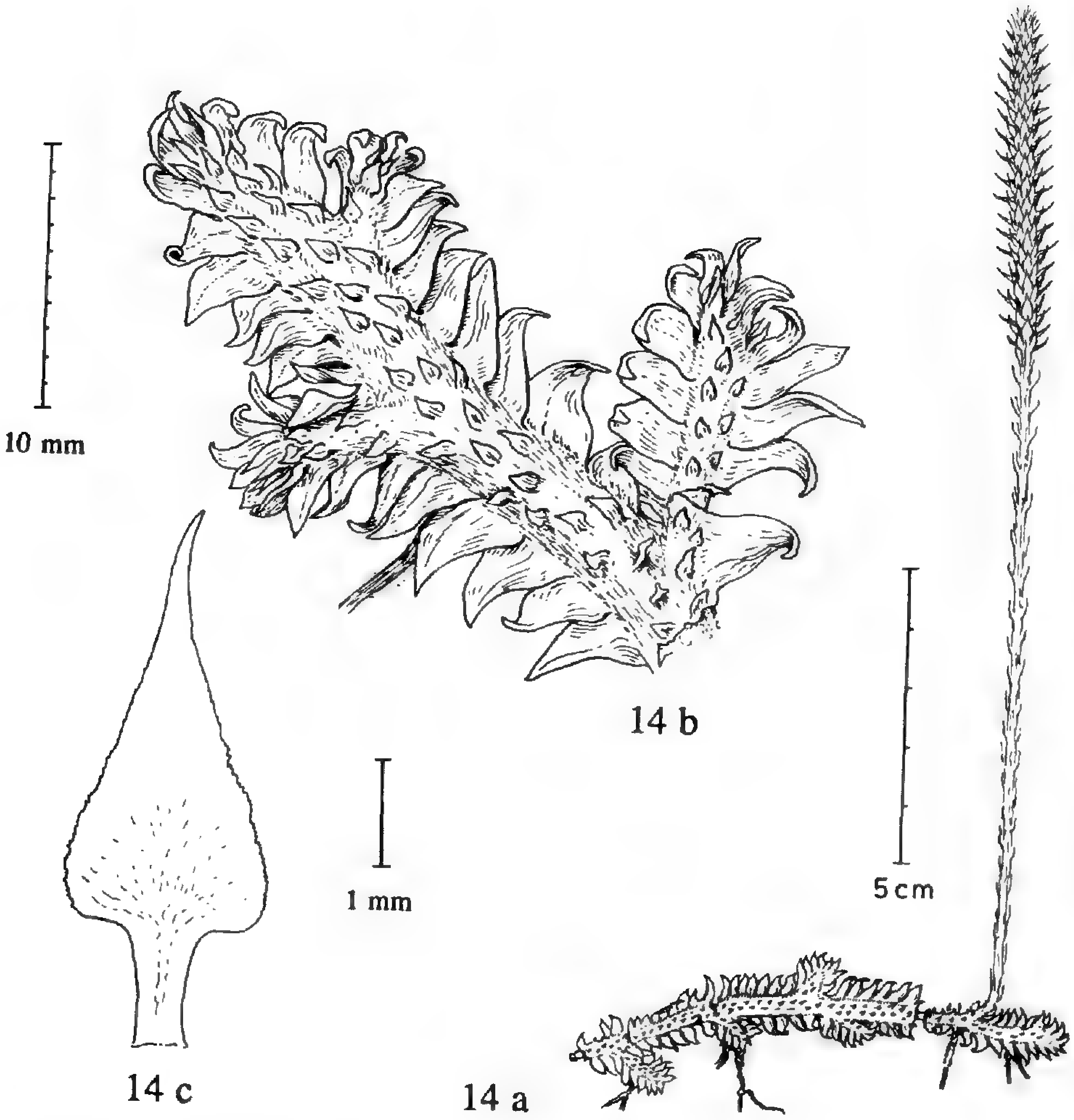


FIGURE 14. *Lycopodiella carnosa.*—a. Habit.—b. Detail, prostrate shoot, upper side.—c. Sporophyll.

Lycopodiella trianae (Hieron.) B. Øllg.

Vigorous plants, with self-supporting treelike shoots at least up to 2.5 m tall, and with hairy, appressed leaves on the main axes. Branchlets very thin, with small, appressed leaves with many stiff hairs, and with small strobili. Pacific coastal Colombia, northwestern Ecuador. The species is restricted to very humid areas on the western Andean foothills (Lellinger, 1989: fig. 14; Øllgaard, 1988: fig. 27C).

Lycopodiella descendens B. Øllg.

Closely related to *L. cernua*, but differing by the softly recurving treelike branches and by densely hairy main axes with appressed leaves. Eastern Andean slopes of Ecuador and Peru (Øllgaard, 1988: fig. 27A).

Lycopodiella glaucescens (C. Presl) B. Øllg.

A large and rather coarse, scandent species, with branches corresponding to the treelike branch systems often becoming scandent and several meters long. Leaves of main axes usually perpendicular or reflexed, sometimes curved upward like a hook, ca. 1 mm broad, and coriaceous. Strobilus size variable, but usually larger than in the species mentioned above. Costa Rica, Panama, Andes from Venezuela to Bolivia (Øllgaard, 1988: fig. 27C).

Lycopodiella lehmannii (Hieron.) B. Øllg.

With a growth habit resembling the preceding species, but with very slender, usually hairy axes and small strobili, doubtfully distinct from that species. Colombia, ?Ecuador (Øllgaard, 1988: 146, fig. 27B).

Lycopodiella pendulina (Hook.) B. Øllg. (*L. eichleri* (Fée) B. Øllg.)

Most closely related to *L. glaucescens*, but differing by the stiffly erect tree-like branches with thick, sparsely branched, weeping branchlet systems and thick strobili, with large sporophylls. Degree of branching, size and shape of the leaves of the main axes, and stem hairiness are variable. Costa Rica, Andes from Venezuela to Bolivia, southeastern Brazil. This heterogeneous species occurs in open, humid habitats at high altitudes (Lellinger, 1989: fig. 12; Øllgaard, 1988: fig. 26B).

The names *Lepidotis convoluta* P. Beauv., *Lycopodium cymosum* (Fée) Hieron., and *Lycopodium curvatum* Sw. may apply to one or more corresponding high-altitude species of the Antilles.

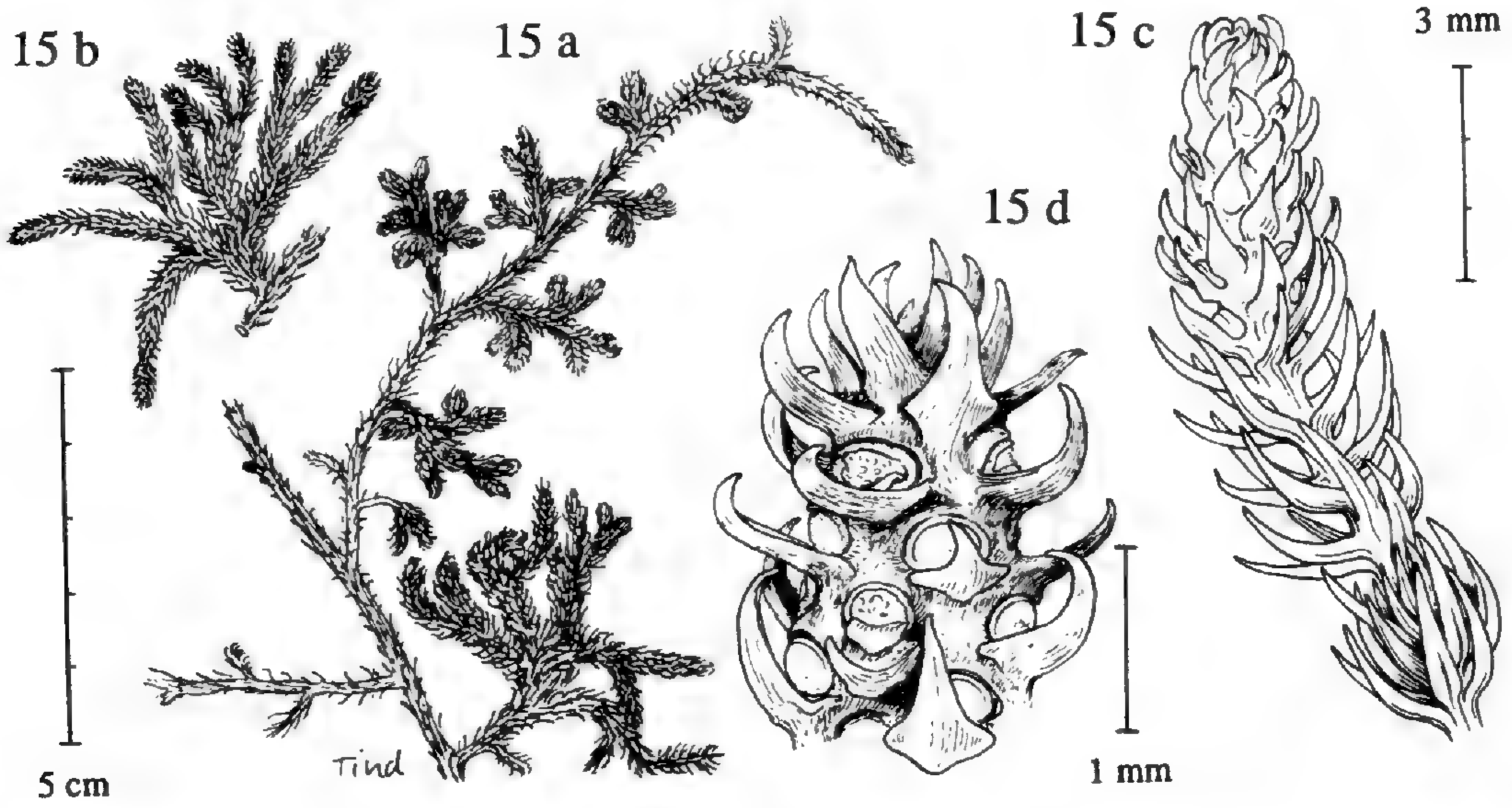


FIGURE 15. *Lycopodiella bradei.*—a. Habit.—b. Branchlet system with strobili.—c. Branchlet with strobilus.—d. Part of strobilus, showing coalesced sporophyll bases and deeply immersed sporangia.

However, I have not seen the types, and accordingly cannot apply the name with certainty,.

Lycopodiella torta (L. Underw. & F. Lloyd) B. Øllg., comb. nov. Basionym: *Lycopodium tortum* Sieber ex L. Underw. & F. Lloyd, Bull. Torrey Bot. Club 33: 118. 1906. (synonym: *Lycopodium cernuum* L. var. *dussii* Stehlé)

A very robust species with densely, and strongly, almost tangled, divaricately branched, treelike shoots, with thick and coriaceous leaves, and relatively small strobili. Lesser Antilles. Restricted to high volcanoes in its area.

Lycopodiella riofrioi (Sodiro) B. Øllg. (*L. pensum* Lellinger & Mickel in Lellinger)

Leaves imbricate, lanceolate, fimbriate, both on major and minor stems. Costa Rica, Colombia to northern Peru, Venezuela, and adjacent Brazil. A distinctive and easily recognized species (Lellinger, 1989: fig. 13; Øllgaard, 1988: fig. 26C).

Lycopodiella steyermarkii B. Øllg.

Unusual in the section by the apparent lack of typical erect, treelike shoots. Strobili produced on the lateral branchlet systems of the slender, glabrous, indeterminate horizontal shoots, unusually large, sometimes up to 9 cm long, with very long and narrow sporophylls. Venezuelan Guayana, Panama, Colombia, Ecuador. Some of the plants in the western part of the area are epiphytic, forming mats high up on tree trunks (Øllgaard, 1988: fig. 21B).

Lycopodiella bradei (Herter) B. Øllg.

Without erect, treelike aerial branch systems. The whole plant prostrate, forming a flabellate shoot system, with creeping, occasionally underground, main stems. Southeastern Brazil: Itatiaia and Caparaó. This is the most reduced and deviating of all the species of the section, with erect strobili and smooth sporophyll margins. However, its coalescent sporophyll bases, almost enclosing the sporangia, the cell structure of the sporangium wall, and the spore morphology clearly indicate its affinity to the section (Fig. 15).

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CYTOLOGICAL PROBLEMS IN *LYCOPODIUM* SENS. LAT.[1]

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ABSTRACT

Homosporous pteridophytes differ from seed plants most strikingly in their potential ability to produce completely homozygous offspring from a single haploid spore. The Lycopodiaceae share this characteristic with the ferns, but differ from them in the absence of apogamy and in the relatively high frequency of allohomoploid nothospeciation in certain genera. Determining chromosome numbers in this family is often difficult, and discrepancies are found in published accounts. Evidence in support of a base number of 11 is presented. Allohomoploid nothospeciation is described involving four species of *Diphasiastrum*. A table giving the published chromosome numbers in *Lycopodium* sens. lat. is included.

The lycopsids are spore-producing vascular plants that, along with *Psilotum* and *Equisetum*, are often referred to as "fern-allies." This is a designation badly in need of replacement. No apt substitute has been suggested. The category "homosporous pteridophytes" is inapplicable since that includes the ferns and excludes the heterosporous groups, *Selaginella, Isoetes*, and the heterosporous "water ferns."

However, for the purposes of this paper, which deals with cytology, homosporous pteridophytes is a useful classification supported by traits that contrast with the angiosperms, such as the relatively large size and high numbers of pteridophyte chromosomes, and the absence or paucity of multivalent formation in polyploid meioses. A guide to the nomenclature of the Lycopodiaceae is given in Øllgaard (1987, 1989).

The most important distinction between homosporous pteridophytes and seed plants (as well as heterosporous pteridophytes) has to do with fertilization. The gametes involved in "selfing" in seed plants arise from two different recombinant products of meiosis, and, therefore, selfing does not often produce homozygous offspring. All homosporous pteridophytes, on the other hand, have the capacity to produce completely homozygous offspring since a gametophyte and its gametes are produced from a single haploid spore. This is referred to as *intra*gametophytic selfing (Klekowski, 1970) as opposed to *inter*gametophytic mating, which results from fusion of gametes from the gametophytes of two spores.

The Lycopodiaceae as homosporous pteridophytes share these characteristics, but they differ from ferns in two notable respects: (1) apogamy, a specialized nonsexual life cycle that accounts for as much as 10% of fern species (Walker, 1979, 1985) but has never been reported in *Lycopodium* sens. lat.; and (2) allohomoploid nothospeciation, which is the production of fertile sporophytes with no change of ploidal level. Though rarely found in most pteridophytes, it is relatively common in Lycopodiaceae (Bruce, 1975; Hersey & Britton, 1981; F. Wagner, 1980). In contrast, allopolyploidy as a pathway to establishing nothospecies is well known in ferns (Wagner & Wagner, 1980), and in at least two genera of the Lycopodiaceae (Bruce, 1975; Wagner et al., 1985), but is rare in *Diphasiastrum* and *Lycopodium* sens. str.

THE CHROMOSOMES OF *LYCOPODIUM* SENS. LAT.

Determining the chromosome numbers of species in the traditional genus *Lycopodium* sens. lat. has not been popular with cytologists, and justifiably so because of the difficulties frequently encountered. *Lycopodium* spore mother cells, in general, have very thick walls. Indeed, at first glance, they look like young spores and may be full of cytoplasmic granules and oil droplets. Also, the chromosomes, unlike those of most ferns, are commonly of different sizes. Figure 1 illustrates a recent study I made of *Huperzia selago* with $n = 134$ (a tetraploid) and demonstrates some of the technical problems. *Huperzia selago* chromosomes were once categorized by Manton (1950) as the worst cytological object she had ever encountered. One figure she illustrated has lagging univalents, often

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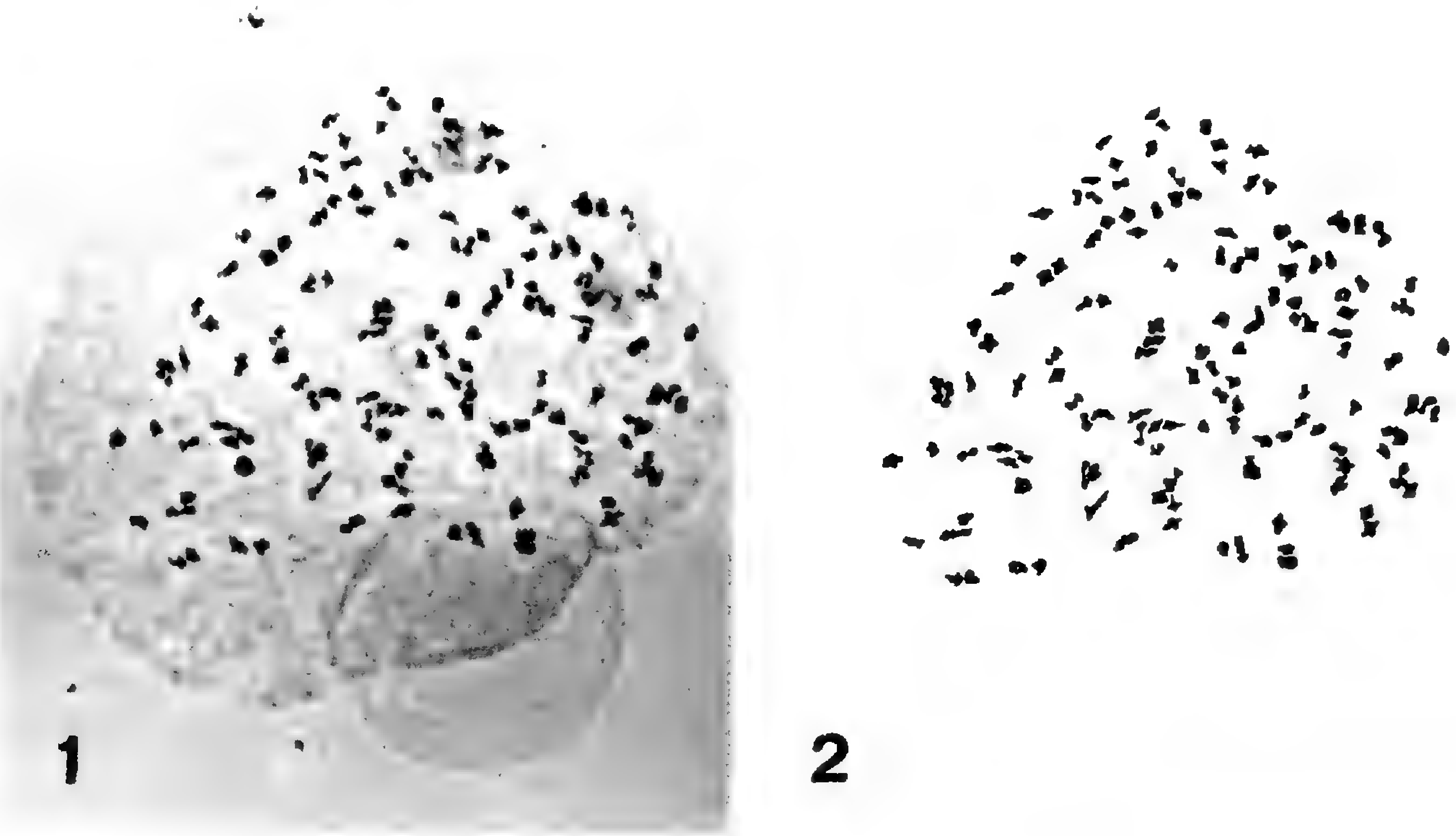

FIGURES 1, 2. Meiotic chromosomes of *Huperzia selago.*—1. Photomicrograph at diakinesis, with 134 pairs.—2. Explanatory diagram. Material from Michigan, Mackinac Co., Carp River.

an indication of hybridity, and approximately 113 pairs, 37 univalents. Chromosome numbers of 132 and 136 have also been reported for this species (see Table 2). *Huperzia lucidula*, a related species, has 67 pairs of chromosomes at meiosis (Beitel & F. Wagner, 1982). The diploid number 68 and the tetraploid count 136 are numbers found frequently in *Huperzia* species in Japan (Takamiya & Kurita, 1983). The technical difficulties mentioned above, and the fact that *Lycopodium* chromosome pairs often show precocious disjunction, contrive to make differing counts possible. Do counts that differ in only one pair, for related species, truly reflect aneuploid changes, or mere prejudice in interpretation? Not all species of *Lycopodium* exhibit these pitfalls; chromosome figures in *Diphasiastrum*, almost all counts of which are $n = 23$, are usually cytological models. But, considering the more than 500 species in traditional broadly construed *Lycopodium*, we have very few dependable counts (see Table 2).

THE BASE CHROMOSOME NUMBER IN *LYCOPODIUM* SENS. LAT.

The average number of chromosomes in *Lycopodium* sens. lat. is around 80 pairs. This number in the angiosperms would indicate high polyploidy. Recent research, however (e.g., Haufler, 1987; see also Pichersky et al., 1990), suggests that pteridophytes, in spite of their high numbers, are genetically diploid, having essentially the same number of alleles as diploid angiosperms. One explanation for the genetic diploidy suggests a history of repeated allopolyploidization followed by gene silencing. Repeated polyploidization of originally low numbers is also supported by outside evidence (Wagner & Wagner, 1980). Not only do the heterosporous lycopsid pteridophytes, such as *Selaginella* and *Isoetes*, have low numbers (Klekowski & Baker, 1966; Löve et al., 1977; Wagner & Wagner, 1980), but heterosporous pteropsid ferns, such as *Marsilea* and *Azolla*, do also. In fact, all vascular plants probably have original base numbers of 7 to 13 (Wagner & Wagner, 1980).

The contrary hypothesis, that ancestral homosporous pteridophytes as well as contemporary species have had high base chromosome numbers from the beginning, is advanced as an alternative to the above by several biologists (see Duncan & Smith, 1978; Wagner & Wagner, 1980; Soltis & Soltis, 1988a).

If we can assume, however, that the high chromosome numbers of the homosporous pteridophytes (including the Lycopodiaceae) represent repeated polyploidization of ancestral low numbers, we can attempt to estimate what the base numbers are in the family.

Table 1 portrays a scheme with a base number of 11. *Lycopodium* sens. lat. is here divided into four genera (and three possible additional genera; the issue of how many genera are actually represented in the traditional *Lycopodium* sens. lat. is dealt with elsewhere in this symposium by Wagner

TABLE 1. Chromosome numbers in *Lycopodium* sens. lat. based on 11.

Genus[1]	Base number 11	Common denominator	Numbers reported[2]	Anomalous numbers reported in genus[2]
Huperzia	6 × 11	66	132	
		67	67	
			134	
		68	68	
			136	
			204 (3×)	
Phlegmariurus (*Huperzia*)	6 × 11	66	132	ca. 128 *H. reflexa*
		68	136	
			ca. 275 (4 × 68?)	
Lycopodium	3 × 11	34	34	22 *L. clavatum*
			31	90–92 *L. jussiaei*
			68	
			102 (3 × 34)	
Diphasiastrum	2 × 11	23	23	48 *L. wightianum*
Lycopodiella	7 × 11	78	78	
			156	
Pseudolycopodiella (*Lycopodiella*)	6 × 11	35	35	
		68	68	
		70	70	
Palhinhaea (*Lycopodiella*)	5 × 11	52	104	136 *L. cernua*
			156 (3 × 52)	
		54	108	
		55	110	
			ca. 165 (3 × 55)	

[1] For a discussion of the classification used here see Wagner & Beitel (1992).

[2] For references to these numbers see Table 2. Chromosome numbers in *Lycopodium* sens. lat.

& Beitel, 1992). Aneuploid changes account for the common denominators shown here, and polyploidy results in further changes shown in the actual numbers reported.

The anomalous numbers listed in the last column of Table 1 can be interpreted in several ways. *Lycopodium clavatum* with $n = 22$ from Bolivia is most likely a taxon different from the worldwide species of that name that has $n = 34$. *Diphasiastrum wightianum* with $n = 48$ was counted by Ninan (1958), who wrote, "The bivalents at diakinesis exhibit very peculiar shapes and are of different sizes, presenting difficulties in interpretation." One is tempted to think that *D. wightianum* is a tetraploid based on $n = 23$, the only number in the genus, in which case *D. wightianum* would be the only tetraploid in *Diphasiastrum*.

Ecuadoran *Lycopodium jussiaei* was found by Øllgaard (1987) to have 90–92 pairs (Table 1). This number is difficult to relate to other numbers in the genus except perhaps *L. magellanicum* with $n = 31$. The two species, however, are placed in different groups by Øllgaard (1987).

The 128 pairs of chromosomes in *Huperzia reflexa* (Table 1) is an approximate count made by Walker (1966), who suggested that it is of the same order of magnitude as a count of $n = 132$, which is a number reported in other huperzias.

The photograph of a figure substantiating the count of 136 pairs in *Lycopodiella cernua* (Kuriachen, 1965) is difficult to interpret. When dealing with *Lycopodium* chromosomes in numbers of this size, a drawing in addition to a photograph is often needed to assist interpretation. With regard to the hypothesis that the base number for *Lycopodium* sens. lat. is 11, it is not unreasonable to assume that many aneuploid and polyploid changes could have accumulated during the long history of the genus. Such changes would be based on 11—for to assume a number other than 11, e.g., 7 or 17, would require an even greater number of alterations. Earlier studies have attempted to require the existence of exact multiples of a hypothesized base number as a criterion, e.g., 34 in *Lycopodium* sens. str., 68 and 136 in *Huperzia*, which are all exact multiples of 17 (e.g., Takamiya

TABLE 2. Chromosome numbers in *Lycopodium* sens. lat.

Species	Locality	Chromosome number	Photo or drawing	Reference*
Huperzia				
chinensis (Christ) Ching	Japan	$n = 68$	Photo	Takamiya & Kurita (1983)
herterana (Kumm) Sen & Sen[1]	India	$n = 132$	Drawing	Mehra & Verma (1957)
herterana[1]	India	$2n =$ ca. 405 (180 II + 45 I)	Photo, Drawing	Ninan (1958)
lucidula (Michx.) Trevisan	Canada	$2n = 264$		Löve & Löve (1958)
lucidula	U.S.A.	$n = 67$	Photo, Drawing	Beitel & F. Wagner (1982)
miyoshiana (Makino) Ching	U.S.A.	$n = 134$		Soltis & Soltis (1988a)
occidentalis (Clute) Beitel & Mickel	U.S.A.	$n =$ ca. 134		Soltis & Soltis (1988a)
selago (L.) C. Martius & Schrank	Canada	$2n = 264$		Löve & Löve (1958)
selago	Finland	$2n =$ ca. 90 $n =$ ca. 45		Sorsa (1962) Sorsa (1963b)
selago	Great Britain	ca. 113 II, 37 I	Photo, Drawing	Manton (1950)
selago	Iceland	$2n = 264$		Löve & Löve (1958)
selago	U.S.A.	$2n = 264$		Löve & Löve (1966)
selago	U.S.A.	$n = 134$	Photo, Drawing	F. Wagner (this paper)
selago var. *acuminatum* Sugimoto	Japan	$n = 136$		Tak & Kur in Mitui (1980)
serrata (Thunb. ex Murray) Trevisan	India	$n = 264$	Photo, Drawing	Ghatak (1965)
serrata	Japan	$n = 68$ $n = 136$	Photo Photo	Takamiya & Kurita (1983)
serrata	Japan	$2n = 204$	Photo	Takamiya (1984)
vernicosa (Grev. & Hook.) Trevisan	India	$n = 136$	Photo, Drawing	Ninan (1958)
Huperzia (*Phlegmariurus*)				
cryptomerina (Maxim.) Dixit	Japan	$n = 136$	Photo, Drawing	Takamiya & Kurita (1983)
dichotoma (Jacq.) Trevisan	Puerto Rico	$n =$ ca. 132		Sorsa in Fabbri (1965)
fordii (Baker) Dixit	Japan	136	Photo, Drawing	Takamiya & Kurita (1983)
hamiltonii (Spreng.) Trevisan	India	$n = 136$	Photo, Drawing	Ninan (1958)
linifolia (L.) Trevisan	Puerto Rico	$n =$ ca. 130–140		Sorsa in Fabbri (1965)
macrostachys (Spring) Holub[2]	India	$n = 136$	Photo, Drawing	Ninan (1958)
phlegmaria (L.) Rothm.	India	$n = 136$	Photo, Drawing	Ninan (1958)
phlegmaria	Japan	$n =$ ca. 275	Photo, Drawing	Takamiya & Kurita (1983)
phyllantha (Hook. & Arn.) Holub	India	$n = 170$	Photo, Drawing	Ghatak (1965)
phyllantha[2]	India	$n = 136$	Photo, Drawing	Ninan (1958)
pulcherrima (Hook. & Grev.) Pichi-Serm[3]	India	$n = 136$	Photo, Drawing	Ninan (1958)

TABLE 2. Continued.

Species	Locality	Chromosome number	Photo or drawing	Reference*
pulcherrima[3]	India	$2n = 330\text{–}340$		Mehra & Verma (1957)
reflexa (Lam.) Trevisan	Jamaica	$n =$ ca. 128		Walker (1966)
saururus (Lam.) Trevisan	Bolivia	$n = 132$	Drawing	Rolleri (1982b)
sieboldii (Miq.) Holub	Japan	$n = 136$	Photo, Drawing	Takamiya & Kurita (1983)
squarrosa (G. Forster) Trevisan	India	$n = 136$	Photo	Ninan (1958)
		$n = 138$	Drawing	
Lycopodium				
annotinum L.	Canada	$2n = 68$		Löve & Löve (1958)
annotinum	Finland	$n = 34$	Drawing	Sorsa (1958)
		$2n = 68$		Sorsa (1963b)
annotinum	Japan	$n = 34$	Photo	Takamiya & Kurita (1983)
annotinum	Sweden	$2n =$ ca. 58		Ehrenberg (1945)
annotinum	Sweden	$n = 34$	Photo, Drawing	Manton (1950)
annotinum	U.S.A.	$2n =$ ca. 50		Dunlop (1949)
annotinum var. *acrifolium* Fern.	Japan	$n = 34$	Photo	Takamiya & Kurita (1983)
annotinum subsp. *alpestre* Löve & Löve	Iceland	$2n = 68$		Löve & Löve (1958)
casuarinoides Spring	Japan	$2n = 68$	Photo	Takamiya & Tanaka (1983)
clavatum L.	Bolivia	$n = 22$		Rolleri (1982a)
clavatum	Canada	$2n = 68$		Löve & Löve (1958); Löve (1976)
clavatum	Ecuador	$n = 34$		Øllgaard (1987)
clavatum	Finland	$n = 34$	Drawing	Sorsa (1958)
		$2n = 68$		Sorsa (1963b)
clavatum	India	$n = 34$	Drawing	Mehra & Verma (1957)
clavatum sens. lat.	India	$n = 68$	Drawing	Ghatak (1965)
clavatum	Great Britain	$n = 34$	Photo, Drawing	Manton (1950)
clavatum	Jamaica	$n = 34$	Photo	Walker (1966)
clavatum	Japan	$2n = 68$	Photo	Tanaka & Takamiya (1981)
		$2n = 102$	Photo	Takamiya & Tanaka (1982)
		$2n = 136$	Photo	Takamiya (1989)
clavatum	Sweden	$2n =$ ca. 66		Ehrenberg (1945)
clavatum	Taiwan	$n = 34$	Photo	Tsai & Shieh (1983)
clavatum	U.S.S.R.	$n = 14$	Drawing	Baranov (1925)
clavatum × *vestitum*	Ecuador	$n = 34$		Øllgaard (1987)
clavatum var.?.	U.S.A.	$2n =$ ca. 60		Dunlop (1949)
clavatum subsp. *megastachyon* (Fern. & Biss.) Löve & Löve	Canada	$2n = 68$		Löve & Löve (1958)
clavatum var. *nipponicum* Nakai	Japan	$n = 34$	Photo	Takamiya & Kurita (1983)
contiguum Klotzsch	Ecuador	$n = 34$		Øllgaard (1987)
dendroideum Michx.	Canada	$2n = 68$		Löve (1976)

TABLE 2. Continued.

Species	Locality	Chromosome number	Photo or drawing	Reference*
jussiaei Desv. in Poiret	Ecuador	$n = 90$–92	Photo, Drawing	Øllgaard (1987)
jussiaei		$n = 34$–36		Wilce (1972)
lagopus (Læst. ex Hartm.) I. Zinzerl. ex Kuzen.-Proch[4]		$2n = 68$		Löve & Löve (1958)
magellanicum (Beauv.) Sw.	Ecuador	$n = 31$		Øllgaard (1987)
magellanicum	Argentina	$n = 31$	Photo	Øllgaard (1987)
obscurum L.	Canada	$2n = 68$		Löve & Löve (1958)
obscurum	Japan	$n = 34$	Photo	Takamiya & Kurita (1983)
obscurum	U.S.A.	$n = 34$	Photo, Drawing	Wagner & Wagner (1966)
obscurum	U.S.A.	$2n =$ ca. 50		Dunlop (1949)
vestitum Poiret	Ecuador	$n = 34$		Øllgaard (1987)
Diphasiastrum				
alpinum (L.) Holub	Canada	$2n = 48$		Löve & Löve (1958)
alpinum	Finland	$n = 22$–24 $2n = 44$	Drawing	Sorsa (1963a, b)
alpinum	Great Britain	$n = 24$–25	Photo, Drawing	Manton (1950)
alpinum	Scandinavia & Canada	$2n = 46$		Löve & Löve (1961)
complanatum (L.) Holub	Canada	$2n = 46$		Hersey & Britton (1981)
complanatum	Canada & Scandinavia	$2n =$ ca 48 $2n = 46$		Löve & Löve (1958, 1961)
complanatum	Finland	$n = 22$–24	Drawing	Sorsa (1963a)
complanatum	Finland	$n =$ ca. 24		Kukkonen (1967)
complanatum	Japan	$n = 23$		Tak & Kur in Mitui (1980)
complanatum	Labrador	$n = 23$	Drawing	Wilce (1965)
complanatum × *tristachyum?*	Canada	$2n = 46$	Photo	Hersey & Britton (1981)
complanatum var. *elongatum*	U.S.A.	$n = 40$	Drawing	Dunlop (1949)
digitatum (A. Braun) Holub	Canada	$2n = 46$		Hersey & Britton (1981)
digitatum[5]	Canada	$2n =$ ca. 48		Löve & Löve (1958)
digitatum	Canada	$2n = 46$		Löve (1976)
digitatum	U.S.A.	$2n = 46$	Drawing	Wilce (1965)
fawcettii (Lloyd & Underwood) Holub	Jamaica	$n = 23$	Photo	Walker (1966)
×*habereri* (House) Holub	Canada	$2n = 46$	Photo	Hersey & Britton (1981)
×*habereri*	U.S.A.	$n = 23$		F. Wagner (1980)
×*issleri* (Rouy) Holub	Germany	$2n = 46$	Drawing	Damboldt (1962)
×*sabinifolium* (Willd.) Holub	Canada	$2n = 46$		Löve (1976)
×*sabinifolium*	Canada	$n = 23$		F. Wagner (1980)
sitchense (Rupr.) Holub	Canada	$2n = 46$		Löve (1976)
sitchense	Labrador	$n = 23$		Wilce (1965)
sitchense	U.S.A.	$2n = 46$		Löve & Löve (1966)

TABLE 2. Continued.

Species	Locality	Chromosome number	Photo or drawing	Reference*
sitchense subsp. *nikoënse* L. & L.	Japan	$2n = 46$		Löve (1976)
sitchense var. *nikoense* Takeda	Japan	$n = 23$	Photo	Takamiya & Kurita (1983)
thyoides (Willd.) Holub	Ecuador	$n = 23$		Øllgaard (1987)
tristachyum (Pursh) Holub	Canada	$2n = 46$	Photo	Hersey & Britton (1981)
tristachyum	Canada	$2n =$ ca. 48		Löve & Löve (1958)
tristachyum	Canada	$2n = 46$		Löve (1976)
tristachyum	U.S.A.	$n = 23$	Drawing	Wilce (1965)
veitchii (Christ) Holub	Taiwan	$n = 68$	Photo	Tsai & Shieh (1983)
wightianum (Grev. & Hook.) Holub	India	$n = 48$	Photo, Drawing	Ninan (1958)
× *zeilleri* (Rouy) Holub	Germany	$2n = 46$	Drawing	Damboldt (1962)
× *zeilleri*	U.S.A.	$n = 23$		F. Wagner (1980)
Lycopodiella				
alopecuroides (L.) Cran.	U.S.A.	$n = 78$	Photo, Drawing	Bruce (1975)
alopecuroides × *appressa*	U.S.A.	$n = 78$	Photo, Drawing	Bruce (1975)
alopecuroides × *prostrata*	U.S.A.	$n = 78$	Photo, Drawing	Bruce (1975)
appressa (Chapman) Cranfill	U.S.A.	$n = 78$	Photo, Drawing	Bruce (1975)
appressa × *prostrata*	U.S.A.	$n = 78$	Photo, Drawing	Bruce (1975)
inundata (L.) Holub	Canada	$2n = 156$		Löve & Löve (1958)
inundata	Canada	$2n = 156$		Löve (1976)
inundata	Finland	$n = 78$	Drawing	Sorsa (1961)
inundata	Great Britain	$n = 78$	Photo, Drawing	Manton (1950)
inundata	U.S.A.	$n = 78$	Photo, Drawing	Bruce (1975)
margueritae Bruce, Wagner & Beitel[7]	U.S.A.	$n = 156$	Photo, Drawing	Bruce (1975)
prostrata (Harper) Cranf.	U.S.A.	$n = 78$	Photo, Drawing	Bruce (1975)
subappressa Bruce, Wagner & Beitel[6]	U.S.A.	$n = 156$	Photo, Drawing	Bruce (1975)
Pseudolycopodiella (*Lycopodiella*)				
caroliniana (L.) Holub	Japan	$n = 68$	Photo	Takamiya & Kurita (1983)
caroliniana	Japan	$n = 68$	Photo	Takamiya & Kurita (1983)
caroliniana	U.S.A.	$n = 35$ $n = 70$ $2n = 115$[8]	Photo, Drawing	Bruce (1976)
meridionalis (L. Underw. & F. Lloyd) Holub	Jamaica	$n =$ ca. 69		Walker (1966)
Palhinhaea (*Lycopodiella*)				
cernua (L.) Carv. Vasc. & Franco	Japan	$n = 108$	Photo	Takamiya & Kurita (1983)
cernua	India	$n = 104$	Photo, Drawing	Ninan (1958)

TABLE 2. Continued.

Species	Locality	Chromosome number	Photo or drawing	Reference*
cernua	India	$n = 104$ $n = 156$ $n = 208$	Photos Drawings	Ghatak (1965)
cernua	India	$n = 104$ $n = 110$ $n = 136$ $n =$ ca. 160II, 20I	Photo	Kuriachen (1965)
cernua	Jamaica Trinidad	$n =$ ca. 165 $n =$ ca. 165	Photo, Drawing	Walker (1966)
cernua	Taiwan	$n = 102$	Photo	Tsai & Shieh (1983)

[*] For references, see Literature Cited. The following references were not seen and therefore not included in this table: Hadac, E. & V. Haskova. 1956. Taxonomické poznámky o tatranskych rostlinách ve vztahu k jejích Bratislava/cytologii. Biológia Brat. 11: 717–723. Löve A. & D. Löve. 1948. Chromosome numbers of northern plant species. Icel. Univ. Inst. Appl. Sci., Dept. Agric. Rep. B. 3: 1–131.

[1] As *Lycopodium lucidulum.*

[2] *macrostachys* and *phyllantha* are treated as synonyms by Ninan.

[3] As *Lycopodium setaceum.*

[4] As *clavatum* subsp. *monostachyum* (Grev. & Hook.) Selander.

[5] As *complanatum* var. *flabelliforme.*

[6] As "northern appressa" See Bruce et al. (1991).

[7] As "appressed inundata" See Bruce et al. (1991).

[8] Somatic count of a presumed triploid hybrid—possibly 105?

& Kurita, 1983). Such suggestions do not take aneuploidy into consideration.

ALLOHOMOPLOID NOTHOSPECIATION IN *LYCOPODIUM* SENS. LAT.

Even though the potential for self-fertilization exists, in *Lycopodium* sens. lat. as in all the homosporous pteridophytes with gametes of both sexes produced in the same gametophyte, evidence for high frequencies of intergametophytic matings has been found. Soltis & Soltis (1988b) studied a total of 22 widely scattered populations of *L. clavatum*, *L. annotinum*, and *Huperzia miyoshiana*, and, using electrophoretic analyses of polymorphic loci, calculated low estimates of intragametophytic self-fertilization. They concluded, therefore, that these species predominantly cross-fertilize. Because *Lycopodium* sens. lat., with the exception of *Lycopodiella* sens. lat., has entirely underground gametophytes, it had been presumed in the past that sperms would have difficulty swimming underground through the soil, with the result that selfing would be the rule and hybridization would be difficult. On the contrary, intergametophytic mating and interspecific hybridization have turned out to be common in the Lycopodiaceae (Wagner et al., 1985).

Typically in plants, nothospeciation (hybridization) involves two steps: (1) AA × BB → AB, which is formation of a sterile diploid, and (2) AB → [AABB], which is formation of a fertile allopolyploid through endomitosis or chromosome doubling. In *Lycopodium* sens. lat., another pattern is found in which a fertile sexual nothospecies is formed without doubling, and parents and hybrid are homoploid, i.e., of the same ploidal level, AA × BB → [AB], which is formation of a fertile homoploid. (The use of brackets here and below to indicate a reproductively competent hybrid, is proposed by Werth & Wagner (1990).)

In Figure 3 three species of *Diphasiastrum*—*digitatum*, *complanatum*, and *sitchense*—are shown with *D. tristachyum*, a species that hybridizes with all three. The hybrids resulting from these crosses, *D.* [×] *habereri*, [×] *zeilleri*, and [×] *sabinifolium* (all of which have been found in the wild), are fertile to the extent that their genomes show complete pairing of chromosomes, and their spores are apparently normal (Figs. 4, 5). The number of chromosome pairs in the hybrids ($n = 23$) is the same as that for all the parents involved (F. Wagner, 1980; Hersey & Britton, 1981).

Unfortunately, germination of *Lycopodium* spores can only be carried out with difficulty (see Whittier, 1977, 1981; Whittier & Webster, 1986). Tests of the germinability of these morphologically normal spores have yet to be made. Some indication of their fertility, however, is attested to by the fact that we find isolated populations of *D.* ×*habereri*,

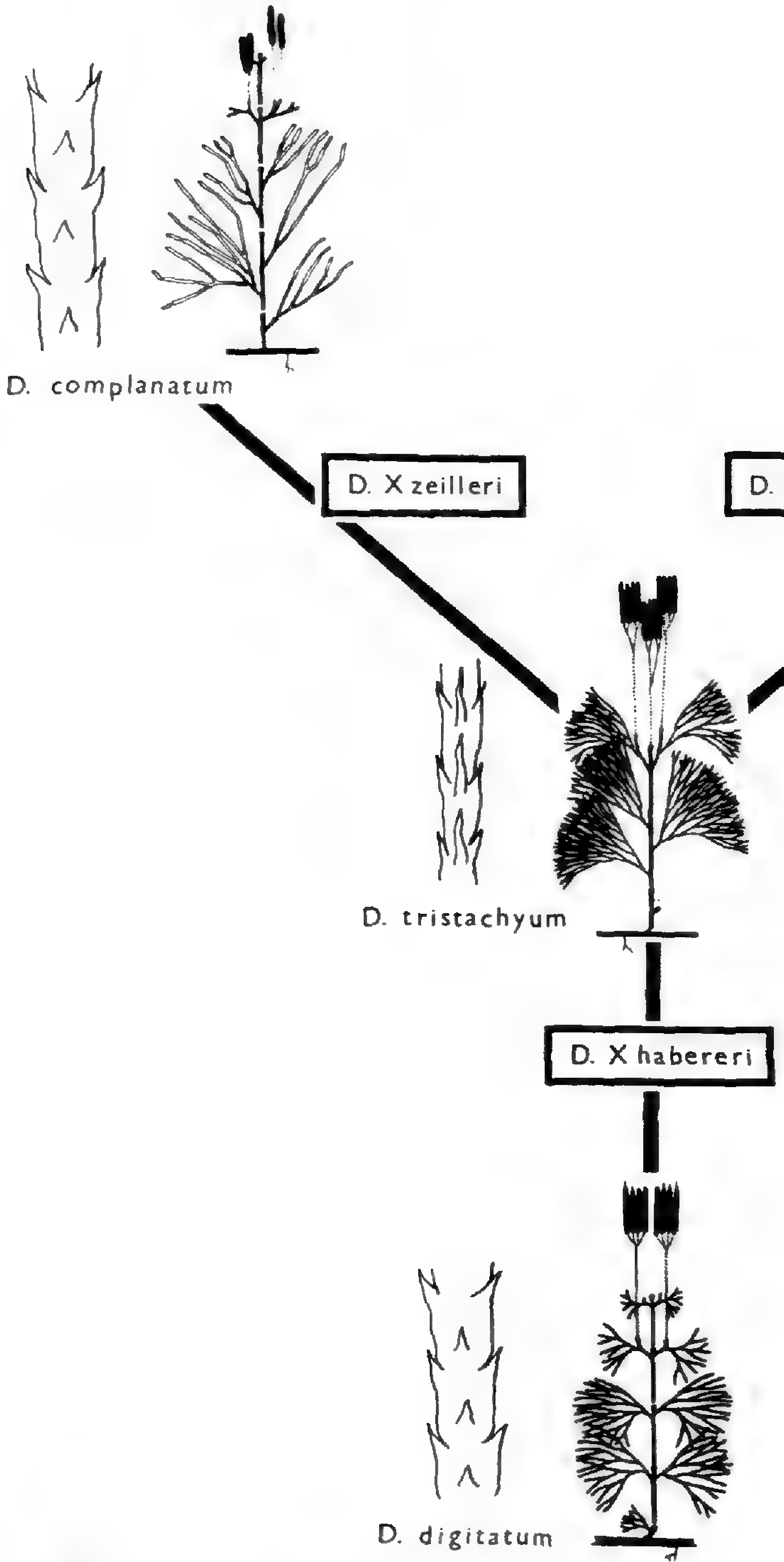

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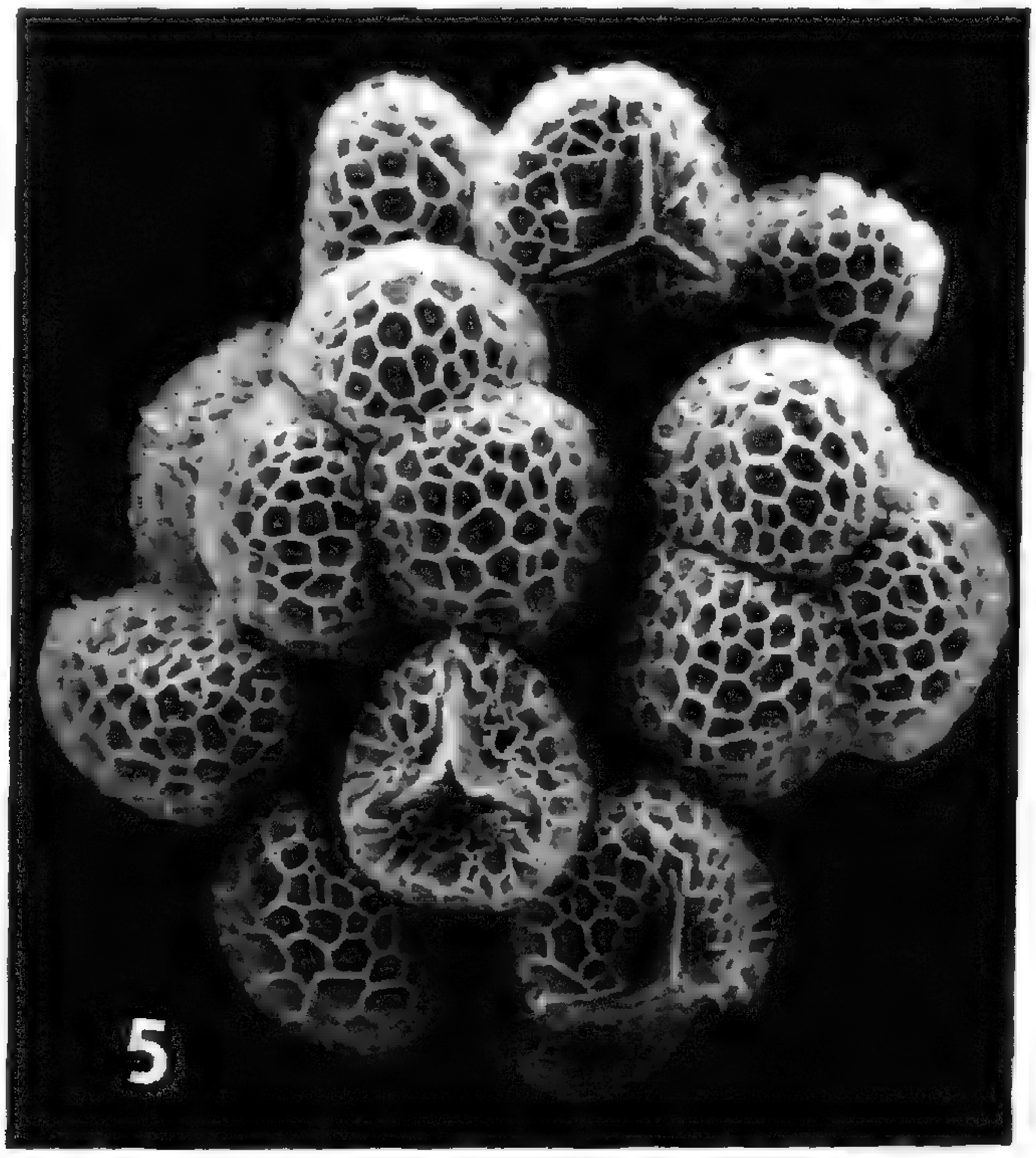
FIGURE 3. *Diphasiastrum.* Diagram showing hybridization of *D. tristachyum* with *D. complanatum* to form *D.* × *zeilleri*; with *D. sitchense* to form *D.* × *sabinifolium*; and with *D. digitatum* to form *D.* × *habereri.* All taxa have $n = 23$ pairs of chromosomes. Branchlet drawings show relative sizes of leaves. Habit drawings are from Wilce (1965).

for example, presumably initiated by a single fertile spore with no parental species or only one parent in the area (Wagner & Wagner, unpublished).

Homoploid nothospecies in *Lycopodium* sens. lat. have not been confined to *Diphasiastrum*, although most reported examples are in that genus. Bruce (1975) found hybrids in *Lycopodiella* between *L. alopecuroides* and *L. appressa*, and between *L. alopecuroides* and *L. prostrata*, with pairing of genomes, the same chromosome number as the parents, and morphologically normal spores. Øllgaard (1987) has reported a homoploid nothospecies, *L. clavatum* × *vestitum*, in the genus *Lycopodium* sens. str.

Fertile homoploid nothospeciation in pteridophytes was first reported in a classic study by Trevor Walker (1958) in the fern genus *Pteris.* Two species, *P. multiaurita* and *P. quadriaurita* in Ceylon, formed a hybrid swarm of intermediates occupying an ecotone between the parents. The hybrids were fertile but without chromosome doubling; all had the same chromosome number as the parental species.

Homoploid hybrids of *Ceratopteris* have also



FIGURES 4, 5. 4. Photomicrograph of chromosomes of *Diphasiastrum* ×*sabinifolium* at diakinesis with 23 pairs of chromosomes.—5. Scanning electron photomicrograph of spores of *D.* ×*habereri*.

been produced in culture by Hickok & Klekowski (1974), and homoploid hybrids in the Cyatheaceae, first reported by Conant & Cooper-Driver (1980), are found in Puerto Rico. The cyatheoid hybrids backcross and form hybrid swarms, but recombinant second generation hybrids may become stabilized and maintain their genetic integrity by means of autogamy, i.e., intragametophytic selfing.

In the North American *Lycopodium* sens. lat., the morphological variation seen in the *Diphasiastrum* hybrids seems clearly to be environmentally produced, i.e., sun and shade forms (Beitel, 1979a, b; Beitel et al., 1982). However, although we have searched for years, we have not found backcrosses in these hybrids. This seems surprising since *Diphasiastrum* species have been found to be primarily outcrossers (see above and Soltis & Soltis, 1988b). Hybridization produces the original hybrid and if such hybrids retain this capacity, then continued outcrossing should ultimately lead to backcrossing, introgression, and hybrid swarms. Apparently this is not happening in *Diphasiastrum*, and it may be that rarity is a factor; there may not be enough individuals of associated parental species to cross with. Related perhaps, is the fact that species of *Lycopodium* sens. lat. are great clone formers and rely heavily on vegetative reproduction. It may be that there is in reality very little sexual reproduction.

Unlike *Diphasiastrum* and *Lycopodiella*, hybridization in *Huperzia* follows a course more familiar in the ferns resulting in either sterile allodiploids or fertile allopolyploids (Beitel, 1986, 1988). No allohomoploid hybrids have been reported in the genus.

DISCUSSION

A number of generalizations can now be made regarding the cytology of Lycopodiaceae. The basic chromosome numbers are high, the lowest being $x = 23$. In this respect the clubmosses are like other homosporous pteridophytes and unlike the heterosporous Selaginellaceae and Isoetaceae, which have x numbers like seed plants. Also, like other homosporous pteridophytes, Lycopodiaceae bear both sex organs on the same gametophyte and potentially can undergo intragametophytic mating. The Lycopodiaceae differ from homosporous ferns in the apparent absence of apogamy and in a greater tendency for allohomoploidy, as illustrated primarily by *Diphasiastrum*.

To explain the curious "step-wise" increases now known in *Lycopodium* chromosome base numbers, i.e., 23, 31–34, 52–55, 66–70, and 78, I can offer only a hypothesis that we are dealing here with a polyploid series, involving some aneuploid changes as a minor element, i.e., 2 × 11, 3 × 11, 5 × 11, 6 × 11, and 7 × 11. The graded nature of the base numbers tends to negate the possibility that the original clubmosses had high chromosome numbers. Also, the fact that the heterosporous lycopsids have low numbers as do the seed plants supports the idea that paleopolyploidy accounts for the genome sizes known today in the Lycopodiaceae. Neopolyploidy probably occurs in all genera of Lycopodiaceae, but seems to be rare in certain groups, notably *Diphasiastrum* and *Lycopodium* sens. str., in comparison to *Huperzia*, where neopolyploidy is common.

The chromosomes of these plants are, for various reasons, often difficult to study, especially those of the polyploid fir mosses, *Huperzia*. The great diversity of numbers already known in the Lycopodiaceae indicates that further work will be informative, but care must be taken to find precise and thoroughly documented numbers.

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THE YOUNG GAMETOPHYTE OF *PHYLLOGLOSSUM* (LYCOPODIACEAE)[1]

Dean P. Whittier[2] *and John E. Braggins*[3]

ABSTRACT

Any similarities between *Phylloglossum* and specific subgenera of *Lycopodium* sens. lat. have been difficult to determine, because the reduced sporophyte of *Phylloglossum* has few characters for comparison. Gametophytes can provide useful characters, but it is difficult to find *Phylloglossum* gametophytes in nature. These gametophytes have been grown in axenic culture for study. Spores of *Phylloglossum* germinate in the dark on a nutrient medium containing minerals and glucose. No germination occurs in the light. In early development, a globular gametophyte forms that later becomes cylindrical. The cylindrical gametophytes are negatively gravitropic and grow vertically away from the surface of the nutrient medium. As long as the gametophytes are cultured in the dark they remain cylindrical and nonphotosynthetic. Moving the gametophytes into light initiates chlorophyll development and brings about a new growth habit that is oriented more or less horizontally rather than vertically. Growth in the light is elongated but deltoid in cross section. Sexually mature, photosynthetic gametophytes have not yet been grown. Information from axenic culture helps to explain the habit of these gametophytes described from nature. It would appear that the spores have to be covered with soil before they germinate. The young gametophyte, which is mycorrhizal, becomes cylindrical and grows to the surface of the soil. Once exposed to light the mature habit develops. Germination in the dark, mycorrhizal young gametophytes, and other characters suggest that *Phylloglossum* is not as similar to the subgenus of *Lycopodium* (*Lepidotis*) having photosynthetic gametophytes as once thought.

The extant Lycopodiaceae are often regarded as being composed of two genera, *Phylloglossum* (one species) and *Lycopodium* sens. lat. (more than 200 species). *Lycopodium* is complex, comprising discrete groups of species recognized as subgenera (Wilce, 1972), genera (Øllgaard, 1987) or even higher categories (see Wagner & Beitel, 1992).

Phylloglossum is a small, homosporous member of the Lycopodiaceae of shrubland areas from New Zealand and Australia. Its shortened, erect, underground stem bears a pseudowhorl of up to 10 quill-like microphylls at the soil surface. Even reproductively mature plants rarely exceed 5 cm in height. A few roots are produced from the side of the stem. The plant bears reniform sporangia on the adaxial surface of sporophylls in a small, stalked strobilus.

Phylloglossum is a tuberous perennial. Each growing season (winter) the stem branches and sends a new tuber down in the soil. The tuber apex, which is the shoot apex for the next year's plant, is not external or terminal but rather is internal (marsupial) and oriented toward the soil surface and away from the tip of the downwardly growing tuber. The tuber is fleshy and contains storage materials. At the beginning of the next growing season, the tuber apex grows upward, producing the new stem with leaves, roots, and cone.

The relationship of *Phylloglossum* to *Lycopodium* has been discussed by a number of workers (Bower, 1886; Thomas, 1901; Holloway, 1935; Hackney, 1950; Breckon & Falk, 1974). However, the extremely reduced structure of the *Phylloglossum* sporophyte makes comparisons with *Lycopodium* difficult.

For the purposes of this paper we follow Wilce (1972) in recognizing the following subgenera of *Lycopodium*:

> *Urostachys*, with stems isodichotomous; sporophylls usually little differentiated from leaves, persistent, and not subpeltate; walls of sporangial epidermal cells sinuate and lignified; spores foveolate-fossulate; mature gametophytes mycorrhizal, cylindrical, branched or unbranched with radial or bilateral symmetry.
>
> *Lepidotis*, with stems anisodichotomous, main stems with indefinite growth; lateral, usually determinate, branchlet systems; sporophylls modified, ephemeral, and subpeltate; walls of spo-

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rangial epidermal cells straight and nonlignified; spores rugulate; mature gametophytes photosynthetic, tuberous with dorsal lobes.

Lycopodium, as for *Lepidotis* but walls of the sporangial epidermal cells sinuate and lignified throughout; spores baculate or saccate; mature gametophytes mycorrhizal, carrot- or disc-shaped.

The morphology of *Lycopodium* gametophytes is variable and has been considered of taxonomic value (Bruchmann, 1898; Rothmaler, 1944; Boivin, 1950; Bruce, 1976b). Comparisons between the gametophytes of *Lycopodium* and *Phylloglossum* could be of value in determining relationships between the two genera. Although little is known about *Phylloglossum* gametophytes, they do not appear to have a reduced morphology. Of the three studies carried out in the 1900s (Thomas, 1901; Sampson, 1916b; Holloway, 1935), only Thomas based his report on observations of more than one gametophyte. The gametophytes are described as being photosynthetic, but Thomas (1901) noted that their basal portions can be white.

No twentieth-century worker has been successful in germinating the spores of *Phylloglossum*. However, Crié (1883) reported that the spores germinated to form gametophytes similar to those of the Ophioglossaceae. Crié's very brief report has generally been ignored in the recent literature on *Phylloglossum* and will be considered later in this report.

The present study employed axenic culture techniques to germinate the spores and grow the gametophytes of *Phylloglossum* in order to gain more information on their structure and physiology that might be useful in determining affinities *Phylloglossum* may have with subgenera of *Lycopodium*. These techniques are useful in germinating the spores and growing gametophytes of various pteridophytes that have proven difficult to find in nature or grow in culture (Whittier, 1972, 1981).

MATERIALS AND METHODS

Strobili of *Phylloglossum drummondii* Kunze collected at Lake Ohia and Ahipara, New Zealand, provided spores for this study. Vouchers of sporophytes are deposited at the Vanderbilt University Herbarium (VDB). Strobili were removed from the plants and dried to release the spores that fit the description for *Phylloglossum* spores (Knox, 1950; Harris, 1955; Breckon & Falk, 1974). They were trilete and had an average diameter of 40.5 μm (measured fresh in water). The proximal face of the spore was essentially smooth (Fig. 1); however, the hemispherical distal face of the spore had dense regular foveolate ornamentation.

Often spores obtained from pteridophytes that bear their sporangia close to the soil give high rates of bacterial and fungal contamination when inoculated in axenic culture. To reduce the possibility of contamination, the spores were wetted with a 2% Tween 80 solution, rinsed in several changes of water, and then soaked in the final water rinse overnight. The following day the spores were surface sterilized with 20% Clorox for 2 minutes. The sterilized spores were collected by filtration and washed on the filter paper with several changes of sterile distilled water. They were finally suspended in sterile distilled water and pipetted into culture tubes.

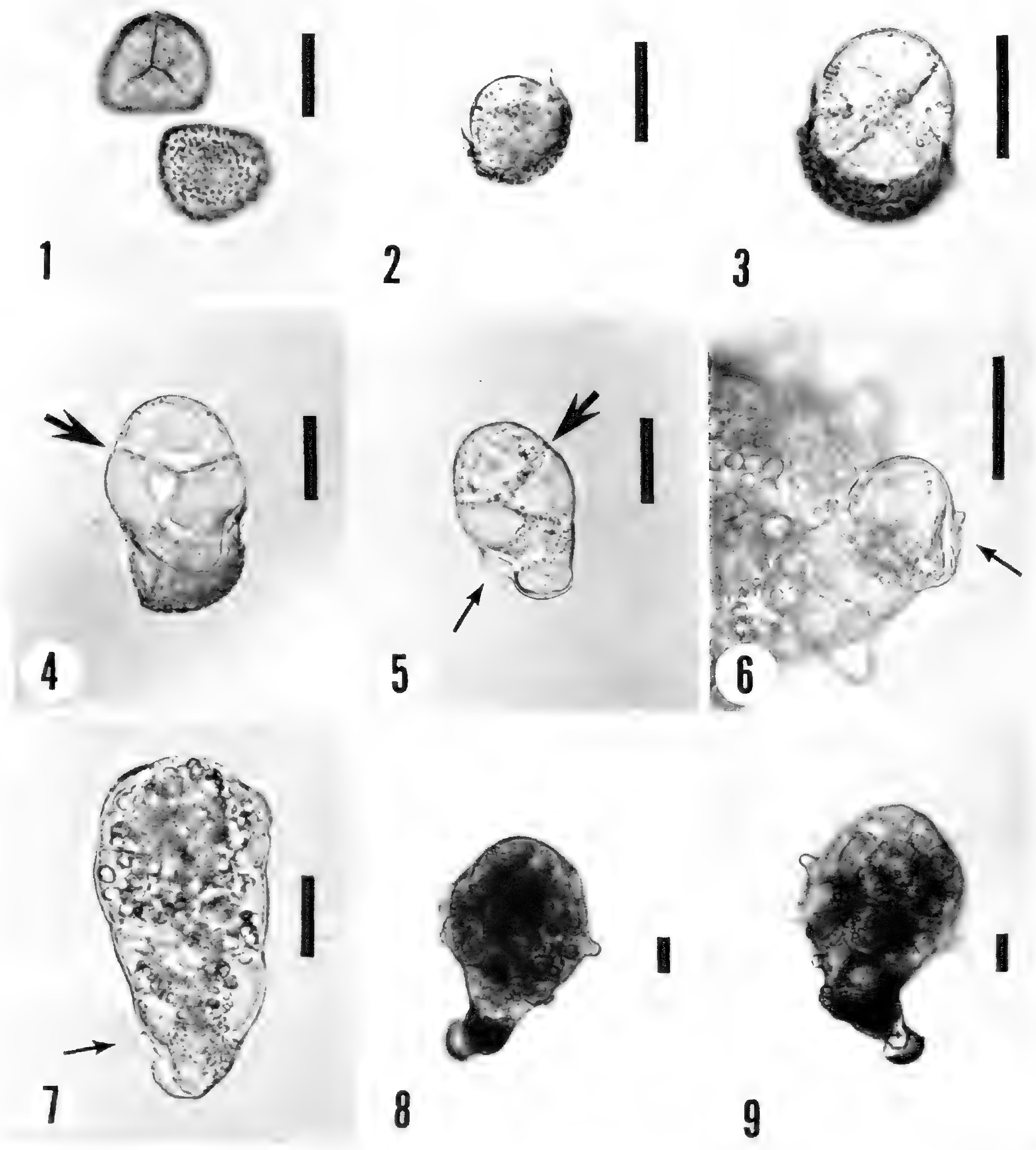
The spores were inoculated onto 15 ml of nutrient medium in 20 × 125 mm culture tubes with screw caps, which were tightened after inoculation. A liter of nutrient medium contained 100 mg $Mg_2SO_4 \cdot 7H_2O$, 100 mg NH_4NO_3, 40 mg $CaCl_2$, and 100 mg K_2HPO_4. The medium was completed with 0.25 ml of a minor element solution (Whittier & Steeves, 1960), 8.5 ml of a FeEDTA solution (Sheat et al., 1959), and 0.1% glucose. It was adjusted to pH 5.0 and solidified with 0.8% agar. The cultures were maintained at 24 ± 1°C in light for 12 of every 24 hours or in darkness. The irradiance level was 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ from Gro-lux fluorescent lamps.

RESULTS

Twenty percent of the spores germinated after three months in dark culture. Since 3- and 4-celled gametophytes were found at this time, the earliest germination was initiated prior to three months. No germination occurred in illuminated cultures after one year. Because spores cultured in the light for one year germinate if moved into the dark for three months, it may be assumed that light inhibited germination.

Germination occurs as the cell expands and ruptures the triradiate ridge of the spore coat (Fig. 2). Shortly after the cell bulges out of the spore coat, the first cell division takes place (Fig. 3). This division, which produces the 2-celled gametophyte, is oblique to the polar axis of the spore. However, it forms more or less proximal (toward the triradiate ridge) and distal (away from the triradiate ridge) cells. A portion of the distal cell remains inside the spore coat while the proximal cell becomes free of it.

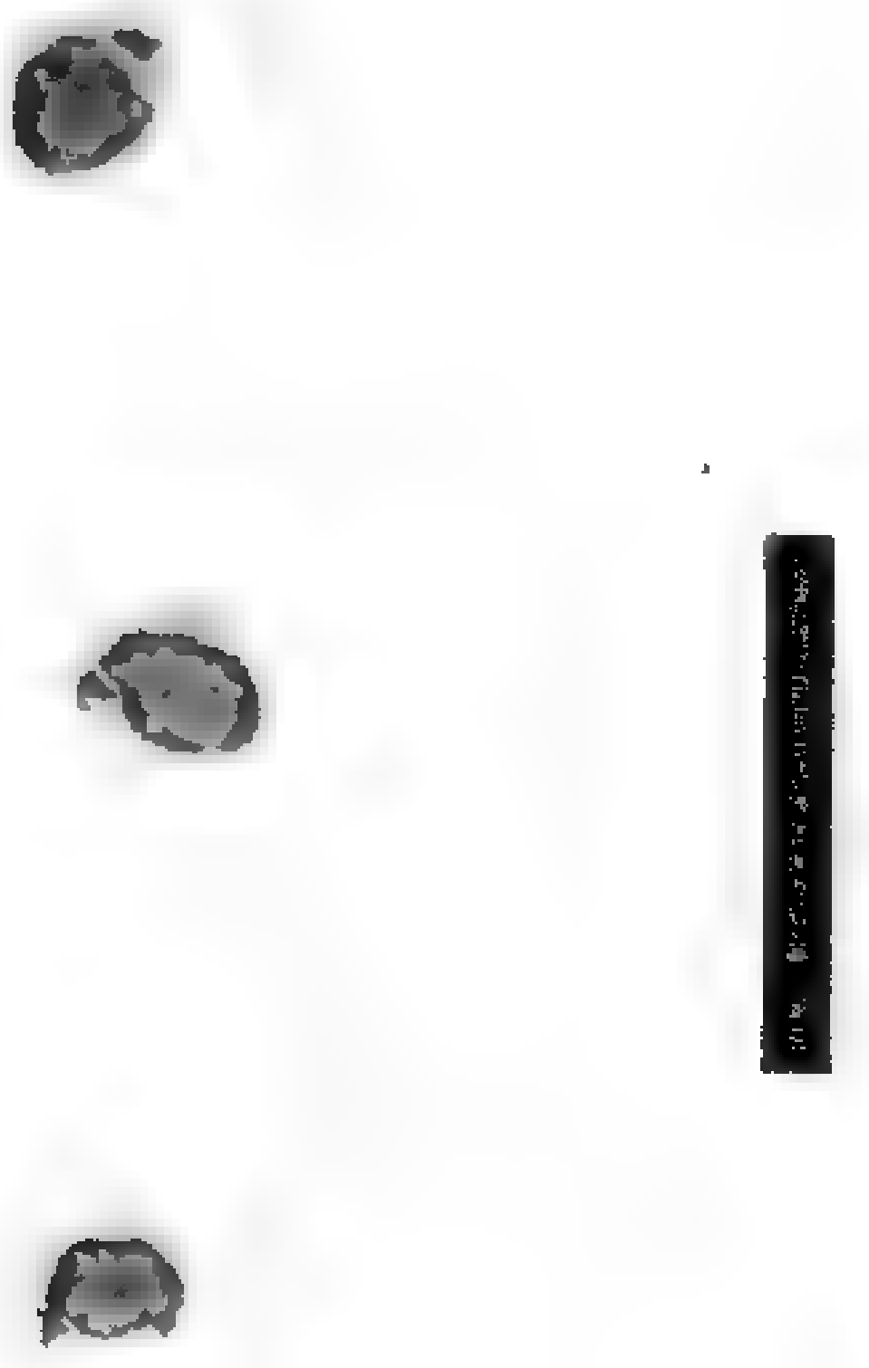
The second cell division occurs in the proximal cell to produce a 3-celled gametophyte (large ar-



FIGURES 1–9. Spores and gametophytes of *Phylloglossum drummondii*.—1. Spores.—2. Germinating spore.—3. Two-celled gametophyte formed by oblique wall. Most of the distal cell and less of the proximal cell are in the spore coat.—4. Three-celled gametophyte with spore coat attached to distal cell. Arrow indicates the wall formed by second cell division of the gametophyte, which occurred in the proximal cell.—5. Three-celled gametophyte without spore coat. Note cytoplasm accumulated in base of distal cell. Small arrow indicates mucilage on surface of partially thickened wall of distal cell. Large arrow indicates cell wall formed by second cell division of gametophyte.—6. Distal end of multicellular gametophyte. Arrow indicates mucilage secretion by thickened portion of the wall of distal cell.—7. Small multicellular gametophyte. Arrow indicates mucilage and thickened wall of distal cell.—8, 9. Young globular gametophytes with young rhizoids and attached spore coats. All scale bars = 30 μm.

rows indicate new walls in Figs. 4, 5). The new wall produced by this division initially is almost perpendicular to the original wall formed by the first division. The distal cell does not undergo any more divisions (Figs. 6, 7).

Wall differentiation of the distal cell becomes apparent at the 3-celled stage (Fig. 5). The distal portion of this wall thickens (Figs. 5–7). Usually in association with the wall thickening, either on it or adjacent to it, there is a secretion of muci-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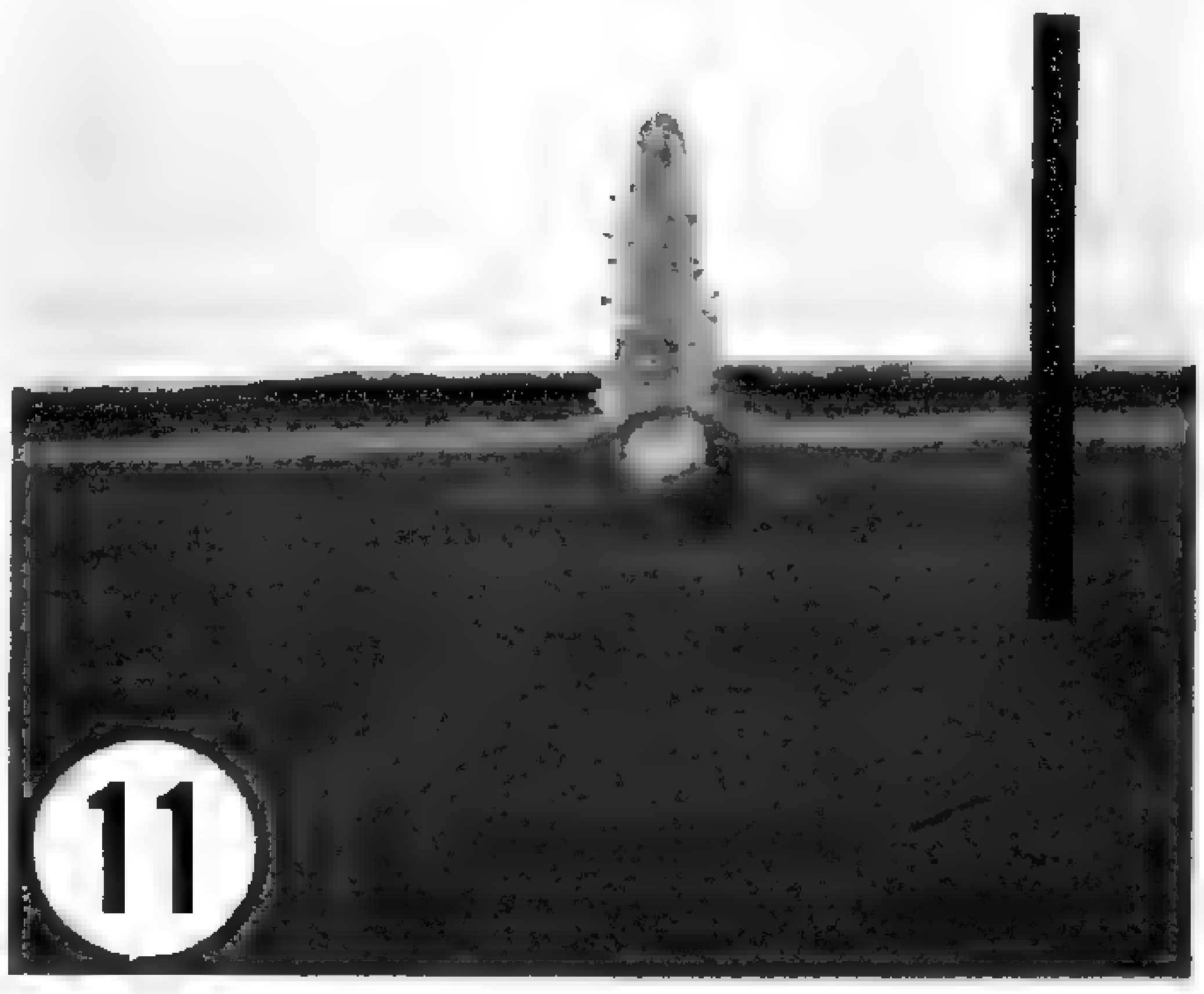
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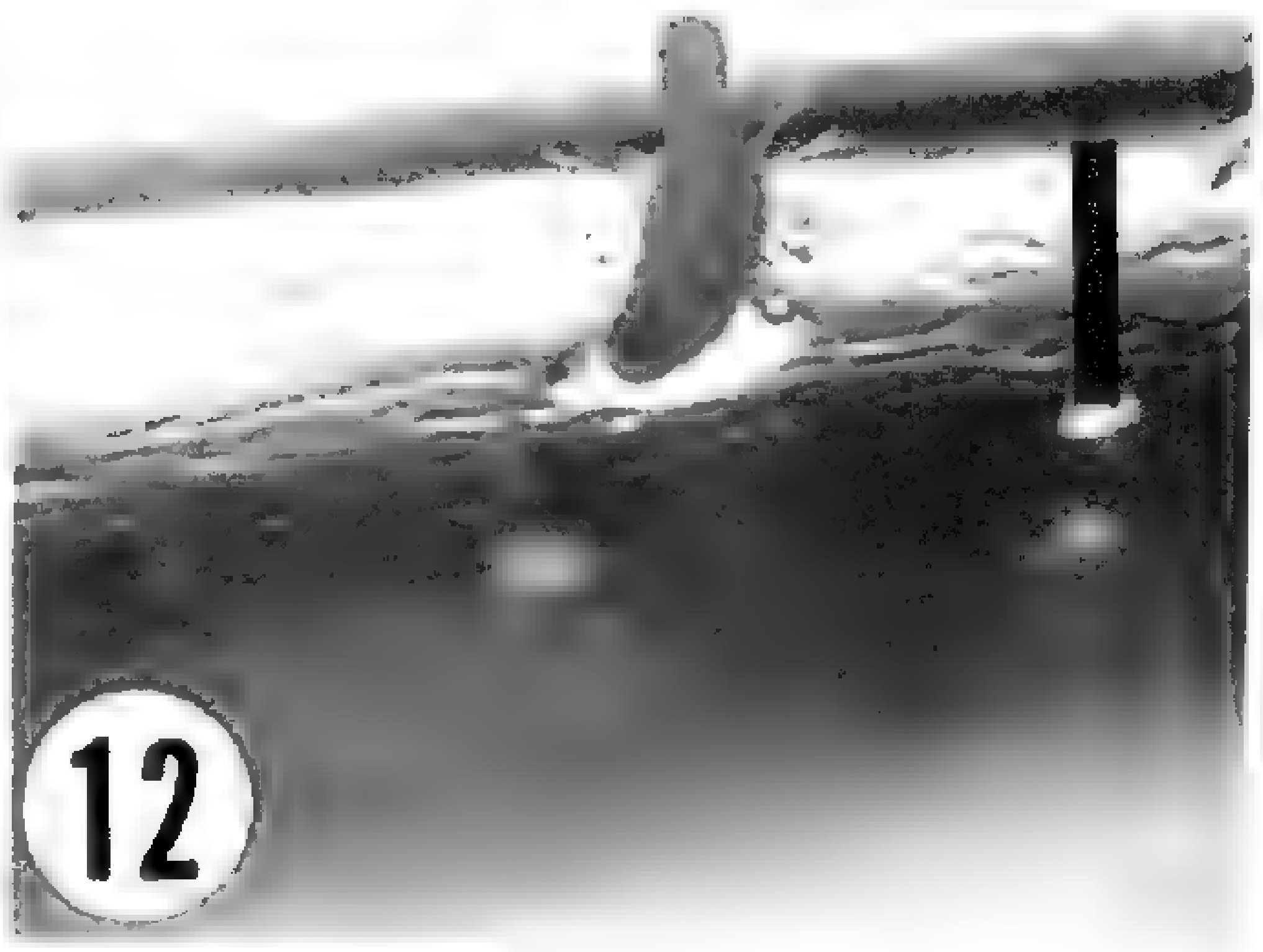
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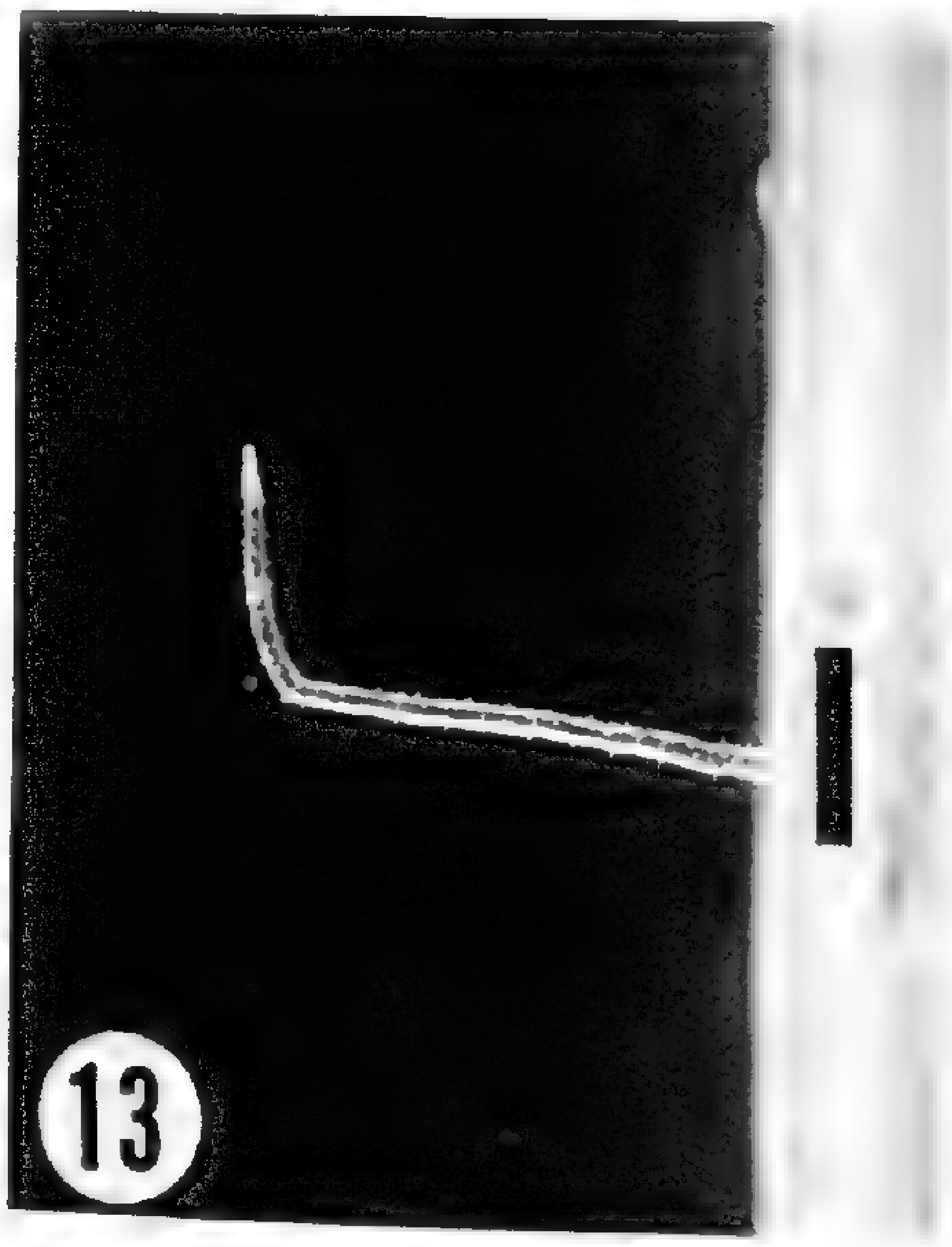
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FIGURES 10–18. Gametophytes of *Phylloglossum drummondii.* — 10. Globular gametophytes. — 11. Small vertically oriented cylindrical gametophyte with young rhizoids. — 12. Gametophyte with globular base and apical cylindrical growth. — 13. Cylindrical gametophyte with bend. New apical growth parallel to surface of nutrient medium (near scale bar) that was oriented vertically in the horizontal culture tube. New growth away from gravity. — 14. Cylindrical gametophyte taken from reorientation experiment showing bending of gametophyte and new growth away from source of gravity. — 15. Young photosynthetic gametophyte. Arrow indicates area at base of cylindrical portion without chlorophyll. — 16. Young photosynthetic gametophyte. New tissue formed in light having a rough surface. Arrow indicates region at base of cylindrical portion without chlorophyll. — 17, 18. Young photosynthetic gametophytes with horizontal orientation of the noncylindrical, new growth. All scale bars = 1 mm.

laginous material (Figs. 5–7; small arrows indicate mucilage). The mucilage stains with alcian blue at pH 2.6 (0.1% alcian blue in 3% acetic acid), which demonstrates that it contains an acid mucopolysaccharide.

The spore coat often remains attached to the distal cell until the gametophyte has attained a macroscopic size (Figs. 8, 9). It usually gets caught on the enlarging distal cell and deforms the surface of this cell. The deformity appears as a notch or indentation in the wall where one edge of the spore coat is or was attached (Figs. 4–7).

Derivatives of the proximal cell undergo additional divisions to give rise to a small multicellular gametophyte (Fig. 7). The young gametophytes become globular with more divisions and cell growth (Figs. 8–10). At this stage rhizoids begin to develop.

If the gametophytes continue to grow in the dark, they become variously sized globular gametophytes. However, they eventually develop into cylindrical gametophytes (Figs. 11, 12), which grow up and away from the surface of the nutrient medium. The diameter of the cylindrical gametophytes appears to be related to the size of the globular gametophyte from which they develop because larger globular gametophytes give rise to thicker cylindrical gametophytes. The diameter of the globular gametophyte can be larger than the diameter of the cylindrical growth (Fig. 12). As long as the cylindrical gametophytes grow in the dark, they continue to grow vertically. The gametophytes tend to decrease in diameter as the apices get further from the nutrient medium. With some very long and narrow gametophytes the apical growth appears to be very slow or to stop. This appears related to the distances that carbohydrate has to move from the nutrient medium through the gametophytes to the apical growing points.

The growth of all the cylindrical gametophytes vertically and away from the surface of the nutrient medium suggested a negatively gravitropic response. To test this, cultures with gametophytes growing vertically were laid on their sides (horizontally) and maintained in the dark for five months. The apices of these gametophytes responded to the positional change by bending at right angles and growing away from the source of gravity (Figs. 13, 14). The gametophyte in Figure 13 was photographed in the culture tube at the end of the experiment. The direction of the new growth was parallel to the surface of the nutrient medium which had a vertical orientation in the horizontal culture tube (Fig. 13). The gametophyte in Figure 14, which shows the same reorientation to gravity, was removed from the culture tube to be photographed. Gametophytes in the reorientation test changed their direction of growth and became cylindrical gametophytes with right angle bends. These gametophytes demonstrate that the cylindrical gametophytes growing in the dark are negatively gravitropic.

Mature gametophytes of *Phylloglossum* are described as being green and photosynthetic (Thomas, 1901). However, the gametophytes in axenic culture maintain their white, cylindrical habit and do not produce gametangia in the dark. Cylindrical gametophytes were moved into the light to determine whether photosynthetic gametophytes can be raised in culture and whether they will become sexually mature.

The cylindrical gametophytes moved into the light become green (Figs. 15, 16). New growth from the apical region develops chlorophyll first, and this region is often darker green than older portions of the gametophyte. Chlorophyll development in the original cylindrical portions of these gametophytes is often slower. Sometimes the basal regions of these gametophytes never turn green (Figs. 15, 16; arrows indicate nongreen basal region).

New growth of the gametophytes in light is not cylindrical (Figs. 15–18) or vertical. A broader apical meristem replaces the conical apex of the cylindrical gametophyte. This broad apex forms a green, thickened gametophyte that grows more or less horizontally (i.e., perpendicular to the incident light). Besides the growth in length, the subapical regions of the green gametophyte widen and thicken (Fig. 16). The thickest part is the median dorsal region, making these areas hemispherical in cross section. The surface of the new growth is rough compared to the smooth surface of the white cylindrical gametophytes. Although these gametophytes are about one and a half years old, they are still immature and do not bear gametangia. Even though the gametophytes grow slowly in axenic culture, at this time they exhibit a shift toward their mature morphology.

DISCUSSION

The best description of *Phylloglossum* gametophytes is by Thomas (1901). He described the gametophytes as having a primary tubercle, an upright cylindrical shaft, and an irregularly shaped photosynthetic crown bearing gametangia. The youngest gametophyte he described had a primary tubercle and an upright cylindrical shaft; the crown had not developed. He noted that the length of the shaft varied on mature gametophytes and that these shafts could be green near the crown; however, the ends near and including the primary tubercle were without chlorophyll. These gametophytes had a mycorrhizal fungus that was best developed in their lower portions. Finally, Thomas suggested that *Phylloglossum* gametophytes "may begin life as a saprophyte dependent on an endophytic fungus."

This description of gametophyte development in axenic culture is the first account of germination

TABLE 1. Character comparisons of *Phylloglossum* and subgenus *Lepidotis* of *Lycopodium*.

Character	*Phylloglossum*	*Lepidotis*
Basal mucilage duct in sporophyll	absent	present
Epidermal walls of sporangium	sinuate lignified	straight unlignified
Spore ornamentation	foveolate	rugulate
Spore germination	dark	light
Nutrition of young gametophyte	mycorrhizal	photosynthetic
Position of mature gametophyte	surficial	surficial
Nutrition of mature gametophyte	photosynthetic	photosynthetic
Photosynthetic lobes on gametophyte	absent	present
Multicellular uniseriate hairs on gametophyte	absent	absent
Embryo type	large foot	small foot

and early gametophyte growth for *Phylloglossum*. Prior to this report, the youngest gametophytes described were those with a primary tubercle and cylindrical shaft (Thomas, 1901). Bertrand (1885), Sampson (1916b), and Holloway (1935) failed to germinate the spores of *Phylloglossum*. An earlier and very brief report by Crié (1883) reported the germination of these spores but did not describe the early stages of gametophyte development. He did report mature, white, bulbous gametophytes that he considered to be similar to those of the Ophioglossaceae. Because the gametophytes he described do not fit the descriptions of gametophytes from nature (Thomas, 1901; Sampson, 1916b; Holloway, 1935) or from axenic culture, we choose to disregard the Crié report.

The 2-celled gametophyte of *Phylloglossum* consists of a proximal and distal cell. The distal cell undergoes no cell division. The most distal region of its cell wall thickens and secretes mucilage. At maturity the distal cell of these gametophytes is very similar to the proximal cell of young *Botrychium* gametophytes, which has a mucilage-coated, thick wall (Melan & Whittier, 1989). The proximal cell of the young *Phylloglossum* gametophyte with its thin wall remains meristematic. Through divisions of the proximal cell, the multicellular gametophyte is formed.

The globular gametophyte forms early in the development of *Phylloglossum* gametophytes in the dark. In axenic culture it usually does not become large before the initiation of the cylindrical gametophyte. However, in some cases the globular gametophytes are larger than the diameter of the cylindrical growths that arise from them. In these cases the gametophytes fit the description of a primary tubercle and cylindrical shaft described by Thomas (1901). Gametophytes moved to illuminated cultures appear to be initiating the gametophyte crown as described by Thomas (1901). Thus, morphological changes to the gametophytes in the light occur in both the soil and axenic culture.

The development of these gametophytes in culture is similar to that for gametophytes from nature. Growth of the gametophytes up through the soil to the light has to be simulated in culture by moving the gametophytes from the dark to the light. Also gametophytes in culture are dependent on sugar in the nutrient medium for their development and not on the mycorrhizal fungus necessary for gametophyte growth in nature.

Observations on the growth and development of *Phylloglossum* gametophytes in axenic culture can help to explain how they grow in nature. *Phylloglossum* spores germinate only in the dark, and the white cylindrical stage of these gametophytes is negatively gravitropic. It would appear that the spores in nature germinate only after being covered by soil or percolating into the soil. The early development of the white gametophyte requires a mycorrhizal fungus for its organic nutrition. Because the white cylindrical portion is negatively gravitropic, it grows up through the soil until it reaches the soil surface. Once the apex of the cylindrical gametophyte is exposed to the light, its developmental pattern changes and the photosynthetic, gametangia-bearing crown forms. Only at this stage is there any possibility for sexual reproduction.

The photosynthetic gametophytes and confusion about the tuber of *Phylloglossum* (Bower, 1886), led many to consider *Phylloglossum* as having affinities with *Lycopodium cernuum* or other members of subgenus *Lepidotis*. Also, Thomas (1901) described the embryo of *Phylloglossum* as being similar to that of *L. cernuum*. Although recognition that the tuber of *Phylloglossum* was not equivalent to the protocorm of *L. cernuum* (Sampson, 1916a; Osborn, 1919) has reduced the number of proposed similarities between *Phylloglossum* and subgenus

Lepidotis, Phylloglossum is generally considered to have affinities with subgenus *Lepidotis* (Holloway, 1935; Hackney, 1950; Bruce, 1976a).

In an effort to examine more closely any possible similarities between *Phylloglossum* and subgenus *Lepidotis*, a list of sporophytic and gametophytic characters are presented in Table 1. The sporophytic characters, which are few, do not include those used to classify *Phylloglossum* in the Lycopodiaceae or those altered by the reduced habit of *Phylloglossum*. Although a more exhaustive comparison awaits a complete description of the mature gametophyte of *Phylloglossum*, it appears that *Phylloglossum* and subgenus *Lepidotis* have few similarities (Table 1). The number of differences between *Phylloglossum* and subgenus *Lepidotis* suggests that a reexamination of past proposals of affinities between them is in order.

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SYSTEMATICS OF THE *GUADUA ANGUSTIFOLIA* COMPLEX (POACEAE: BAMBUSOIDEAE)[1]

Stephen M. Young[2] *and Walter S. Judd*[3]

ABSTRACT

Guadua angustifolia Kunth is the largest and most economically important bamboo in the Western Hemisphere. It is the primary source of building material for urban and rural dwellings in many areas within its geographical range, especially in Colombia and Ecuador. *Guadua aculeata* Rupr. ex Fourn. from Central America and *Bambusa* (*Guadua*) *chacoensis* N. Rojas from Argentina and Paraguay are two closely related taxa that were often confused with or identified as *G. angustifolia*. These three taxa comprise the *Guadua angustifolia* complex. A detailed morphological analysis was performed on all three species using traditional taxonomic methods as well as principal components analysis. The *Guadua angustifolia* complex was also compared with other sympatric species of the genus. The results indicate that *G. angustifolia* should be regarded as one polymorphic species consisting of two subspecies, subspecies *angustifolia* and subspecies *chacoensis*, which are differentiated by a mosaic of vegetative and reproductive characters. Subspecies *angustifolia* consists of populations from Central America (formally *G. aculeata*) and northwestern South America that exhibit variability in certain vegetative and reproductive characters.

The woody bamboos of the grass subfamily Bambusoideae are widespread throughout the tropics, and bamboos of the genus *Guadua* Kunth commony occur in the hot lowland regions of Latin America. The genus contains approximately 30 species that vary from slender, thornless plants with scandent culms to large, thorny plants with erect culms.

The largest and one of the most beautiful of these bamboos is *Guadua angustifolia*. It was first

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[1] This study is dedicated to the memory of Thomas R. Soderstrom, whose encouragement, support, and enthusiasm for the study of bamboos made this work possible. We thank our friends and the staff of the University of Florida herbarium (FLAS) and the Department of Botany for help in completing the research. Additional thanks go to the Herbarium Services Unit of the United States National Herbarium (US) for help in obtaining specimens and information. We thank the curators of the following herbaria for allowing access to material under their care: B, COL, CTES, ENCB, F, G, LE, MEXU, MO, NY, P, S, UC, US, and VEN. Special thanks to Lynn Clark of Iowa State University, Camilo Quarín of Argentina, and Ximena Londoño and Oscar Hidalgo of Colombia for providing much useful information. Photos were taken by the first author except where otherwise indicated.

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discovered by Humboldt and Bonpland during their expedition to South America and was formally described by them in 1806. Its distribution ranges from southern Mexico to northern Argentina, and its economic importance is unsurpassed by any other native bamboo in the Western Hemisphere. Where temperature ranges are high enough and rainfall or water supply is adequate, these large bamboos provide the raw material for a nearly endless array of products. It is in Colombia and Ecuador that the uses of plants in the genus *Guadua*, especially *Guadua angustifolia*, reach their greatest development. Here *G. angustifolia* can be seen in large stands consisting of hundreds of culms up to 30 m tall and 20 cm diam. Its form of growth, strength, and ease of transport, cutting, and working make *G. angustifolia* the preferred source of construction material wherever it occurs. Many of the houses of these areas are built entirely of the culms of *G. angustifolia* (Fig. 1). Even though its tremendous size, beauty, economic importance, and broad geographic distribution are outstanding among the Latin American bamboos, its taxonomy and natural history have not been studied in detail. The last taxonomic treatment of the group was written by William Munro in 1868, and many new species have been discovered since then.

The *Guadua angustifolia* complex includes *G. angustifolia* and two closely related species, *G. aculeata* and *Bambusa chacoensis*, often confused with or identified as *G. angustifolia*. In order to delimit taxa within the complex, a detailed analysis of the morphological variability of the complex was undertaken. During this study the characters that separate the *G. angustifolia* complex from other species in the genus *Guadua* also were defined. The paucity of complete herbarium specimens and lack of recent revisionary studies have led to a poor understanding of species delimitation within the genus and frequent misidentification of many specimens, including those of *G. angustifolia*.

The patterns of variation in over 150 vegetative and reproductive characters from throughout the geographic range of *Guadua angustifolia*, *Bambusa chacoensis*, and *G. aculeata* were studied using traditional taxonomic methods (including herbarium and field studies) and principal components analyses. The results of these methods led to the conclusion that the complex is best treated as a single variable (polymorphic) species consisting of two subspecies (i.e., subsp. *angustifolia* and *chacoensis*), with the former showing several slightly divergent geographic races.

Guadua angustifolia subsp. *chacoensis* is found along rivers in northeastern Argentina and eastern Paraguay and is geographically isolated from *G. angustifolia* subsp. *angustifolia*, which is found from northern Peru, through Ecuador, Colombia, and central America to southern Mexico, often occurring along water courses. The two subspecies can be separated using a combination of vegetative and reproductive characters, but since the morphological gap separating them is smaller than that separating most species in the genus, the taxa are considered here to be only subspecifically distinct.

TAXONOMIC HISTORY

THE GENUS *GUADUA*

A great deal of controversy has centered around the separation of the genus *Guadua* Kunth from *Bambusa* Schreber. When Humboldt and Bonpland described *Bambusa guadua* and *B. latifolia* (1806), the first species of large bamboos collected in South America, they included them in *Bambusa*. At that time the genus consisted of six Asian species, and the use of *Bambusa* Schreber rather than *Bambos* Retz., both published in 1789, was still controversial. A history of this problem and recommendations for conserving *Bambusa* Schreber can be found in McClure (1946) and Holttum (1956). Humboldt & Bonpland (1806) chose *Bambusa*, which they thought had been more commonly used and was more pleasing to the ear. The New World species of *Bambusa* are very similar to the Asian species in such features as stature, branch complements, thorniness, and spikelet structure, and it was understandable that Humboldt and Bonpland would place them in the same genus.

A short time later their specimens were closely studied by Carl S. Kunth after he was employed by Humboldt to help publish the information gathered on Humboldt and Bonpland's journey to the New World (Stearn, 1956). Kunth (1822a, b) decided to place the two New World species in a new genus that he called *Guadua*, but he failed to state what characters separated it from *Bambusa*. Later, Munro (1868) described a number of characteristics that previous authors had used to distinguish

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FIGURE 1. House construction using *Guadua angustifolia*, Ecuador.—a. House construction, Cayapas River, Esmeraldas.—b. Cayapas Indian house, Cayapas River, Esmeraldas.—c. House in Muisne.—d. Experimental housing project in Huaquillas.


a
b
c
d

the genus. These included the presence of alate palea keels, nondistichous inflorescences, three-parted styles, sterile lower florets, and a well-defined geographical distribution. However, these morphological characteristics are not completely consistent because they are known to appear in species from both hemispheres. This led Hackel (1887) to include *Guadua* as a subgenus of *Bambusa*. Munro's (1868) monograph was influential in the acceptance of *Guadua* as a genus, even though he expressed doubts as to its validity. After 1868, the group was generally treated as *Guadua* until McClure (1973), uncertain of its generic separation, reduced it to a subgenus of *Bambusa*.

In their study of the genera of American bamboos with pseudospikelets, Soderstrom & Londoño (1987) restored *Guadua* to generic status based on a number of distinctive features, i.e., a triangular culm leaf in which the margins of the sheath and blade are contiguous or almost so, presence of thorns on the culms and branches, a distinctive band of short white hairs both above and below the nodal line, and a palea of firm texture with prominent wings emanating from the keels.

We are following this most recent treatment of the group and use the name *Guadua*. Monographic studies of the genus and related groups will be needed to further clarify generic limits.

GUADUA ANGUSTIFOLIA KUNTH

Humboldt & Bonpland (1806) described *Bambusa guadua* and *B. latifolia* based on specimens made during their 1799–1804 South American voyage. These were the first of the more than 30 species of New World bamboos of the genus *Guadua* to be described. In addition to Latin and French descriptions, illustrations and observations on local uses and ecology were provided for both species. The specific epithet *guadua* came from the common name used by the people of Colombia. This name is still in use and is usually pronounced guá-du-a in Colombia and gua-dú-a in Ecuador. Poiret (1808), using Humboldt's information, also published an extensive description of *B. guadua* and discussed its economic uses.

When Kunth (1822a) transferred *Bambusa guadua* and *B. latifolia* to his new genus *Guadua*, he failed to specify which species was to be the type. McClure later selected *B. guadua* as the type, citing, "The internal evidence as to which species he [Kunth] probably had principally in mind consists of the extensive documentation by Humboldt and Bonpland (l.c. 63 et seq) of *B. guadua* (basis of *Guadua angustifolia*) in relation to the local economy and to the flora of the type locality" (McClure, 1957: 203). Kunth avoided the use of a tautonym by changing *B. guadua* to *G. angustifolia*, referring to the narrow branch leaves that distinguish it from *G. latifolia*. This narrow-leaved characteristic has subsequently been found in many species of the subgenus, and its use as a diagnostic feature is limited. *Guadua angustifolia* is the name most often found in the literature and has been used in recent years (Burkart, 1969; Rosengurtt et al., 1970; Purseglove, 1972; Azevedo Correa et al., 1977; Azzini et al., 1977a, b; Soderstrom & Londoño, 1987), although *B. guadua* has frequently appeared (Hidalgo López, 1974; Turpe, 1975; Rincón Sepúlveda, 1977; Hidalgo López, 1978; Smith et al., 1981; Maecha Vega & Echeverri Restrepo, 1983; Soderholm, 1984).

GUADUA ACULEATA RUPR. EX FOURN.

Ruprecht first used the name *Bambusa aculeata* (meaning thorny) after examining and annotating specimens from the 1841–1842 Mexican journey of the little-known German collector Wilhelm von Karwin (Karwinsky). Fournier (1877), after seeing Karwinsky's specimens, used the name *Guadua aculeata* in a discussion of polygamy in pseudospikelets, but no formal description appeared until the publication of Fournier's *Mexicanas Plantas* (1886). Seven specimens were listed as syntypes, five from Colipa, Veracruz, and two from unknown Mexican localities.

Fournier also described another of Ruprecht's "herbarium species" with the name *Guadua intermedia*. The name probably referred to the position of the branch leaves, which are intermingled with the spikelets. Leaves are also in this position in *G. aculeata* and *G. angustifolia*. The only difference between the original descriptions of *G. intermedia* and *G. aculeata* is the length of the spikelets, described as short in *G. aculeata* and more than 5.1 cm long in *G. intermedia*. The few spikelets seen from the type collection are about 2.5 cm long and are indistinguishable from those of *G. aculeata*. *Guadua intermedia* appears two more times in the literature without further elaboration of Fournier's description (Hemsley, 1885; Camus, 1913). McClure (1973) included it as a synonym of *B. aculeata*.

Another species that McClure synonymized under *Bambusa aculeata* is *Guadua inermis* (meaning thornless), which he was not able to distinguish from *B. aculeata* on the basis of inflorescences in their respective type collections (McClure, 1973). The only differences between these presumed species, upon reading the original descriptions, are their thorniness and spikelet size (i.e., *B. aculeata* with seven florets per spikelet and thorns, and *G. inermis* with eight to nine florets per spikelet and thornless). A thornless form of the similar species, *G. amplexifolia* Presl, also occurs sympatrically with *G. aculeata* in southern Mexico and further confuses assessment of taxonomic affinities of *G. inermis*. (This problem is discussed in more detail under interspecific relationships.) Unfortunately, culm leaves were neither collected, illustrated, nor described for these species when they were first collected and thus cannot be used to clarify the taxonomic disposition of these names. Hitchcock (1913) transferred *G. aculeata* to *Bambusa* and included it in his listing of the Mexican grasses in the U.S. National Herbarium. He mistakenly gave credit to Ruprecht for describing the species, an error that was carried over to McClure's (1973) work. The correct citation in the genus *Bambusa* is *B. aculeata* (Rupr. ex Fourn.) Hitchcock.

BAMBUSA CHACOENSIS N. ROJAS

The large bamboos of the subtropical regions of Argentina and Paraguay have rarely been described in the literature. Nicolas Rojas Acosta, an Argentine botanist known for his unorthodox methods and fragmentary descriptions, described these bamboos under the name *Bambusa chacoensis* (Rojas Acosta, 1918). His description was so vague as to encompass many of the species now included in the genus, but his locality data and the common name he used, "tacuara," distinguish it from the other bamboos that grow in its range (i.e., *Guadua paraguayana* Doell ex Mart. and *G. paniculata* Munro, "la picanilla"; and *G. trinii* (Nees) Rupr. and *G. tagoara* (Nees) Kunth, "tacuarazú"). Unfortunately, he regarded nature itself as his herbarium and generally did not collect specimens (Krapovickas, 1970). Consequently, he did not collect a specimen of this bamboo nor did he designate a type specimen.

In 1931 this species appeared in a key as *Bambusa guadua* (Anonymous, 1931). The similarity of these bamboos to *Guadua angustifolia* led Parodi (1936) to identify them as *G. angustifolia*. Whether Parodi knew of Rojas Acosta's description and disregarded its validity is not known, but in all subsequent literature these bamboos have been identified as *G. angustifolia* (Lombardo, 1943; Parodi, 1943; Ragonese, 1943; Young, 1946; Burkart, 1969; Rosengurtt et al., 1970) or *B. guadua* (Roseveare, 1948; Turpe, 1975). McClure (1973) included *B. chacoensis* as an unresolved specific taxon, and only recently Quarín (1977), Soderstrom (1981), Nicora & Rúgolo de Agrasar (1987) and Londoño & Peterson (1992) chose to resurrect the name *B. chacoensis*. Only two published photographs, both long-distance views, are known to exist of *B. chacoensis* (Short, 1975).

PAST COMPARISONS

These three groups of bamboos have never been satisfactorily separated in a key or adequately compared. *Guadua angustifolia* has been separated from *G. aculeata* only once, by Camus (1913), but the distinction was based on the presence (*G. aculeata*) or absence (*G. angustifolia*) of thorns. It is now known that these two bamboos show various degrees of thorn development.

McClure (1955) included detailed descriptions of *Guadua aculeata* and *G. angustifolia* in the *Flora of Guatemala*, but failed to separate the two in the same key. He included two forms of *G. angustifolia* in a separate key to introduced bamboos, but none of the characteristics coincided with those included in the key to native species containing *G. aculeata*.

Bambusa chacoensis has rarely been considered different from *Guadua angustifolia*, and therefore has never been separated from it in a key. Rojas Acosta did not seem to be aware of *G. angustifolia* and made no attempt to compare *B. chacoensis* with this species. Londoño & Peterson (1992) compare *G. angustifolia*, *G. trinii* and *G. chacoensis* in a table and conclude that *G. chacoensis* is a separate species more closely related to *G. trinii* than *G. angustifolia*. However, they do not include information from the entire range of *G. angustifolia* and exclude important characters such as size ratio of culm leaf blade to the entire culm leaf.

MATERIALS AND METHODS

This investigation involved field studies, traditional taxonomic methods utilizing herbarium specimens, and multivariate statistical analyses of the *Guadua angustifolia* complex.

HERBARIUM STUDIES

A Wild dissecting microscope was used to examine 105 herbarium specimens for vegetative features and 51 specimens for reproductive features. Measurements were taken with an ocular micrometer and calibrated using a stage microm-

TABLE 1. Foliage leaf characters used in principal components analysis. * = omitted from analysis of culm and foliage leaf data.

1. Leaves per complement
2. Position on sheath of hairs sized ≥ 0.1 mm
3. Position on sheath of hairs sized ≤ 0.09 mm*
4. Density on sheath of hairs sized ≥ 0.1 mm
5. Degree of stramineous coloration in sheath
6. Degree of brown coloration in sheath
7. Degree of purple coloration in sheath*
8. Degree of green coloration in sheath
9. Number of oral setae
10. Length of oral setae
11. Degree of stramineous coloration in oral setae
12. Degree of white coloration in oral setae
13. Degree of brown coloration in oral setae
14. Degree of purple coloration in oral setae
15. Sheath auricle length
16. Leaf auricle width
17. Collar length
18. Collar flaring
19. Ligule height
20. Position on ligule of hairs sized ≤ 0.09 mm*
21. Position on ligule of hairs sized ≥ 0.1 mm
22. Pulvinus height
23. Degree of stramineous coloration on pulvinus
24. Degree of brown coloration on pulvinus
25. Degree of green coloration on pulvinus*
26. Degree of purple coloration on pulvinus*
27. Pulvinus vesture
28. Position on adaxial petiole of hairs sized ≤ 0.09 mm
29. Position on adaxial petiole of hairs sized ≥ 0.1 mm
30. Density of adaxial petiole hairs sized ≤ 0.09 mm
31. Density of adaxial petiole hairs sized ≥ 0.1 mm
32. Position on abaxial petiole of hairs sized ≤ 0.09 mm
33. Position on abaxial petiole of hairs sized ≥ 0.1 mm*
34. Density of abaxial petiole hairs sized ≤ 0.09 mm
35. Density of abaxial petiole hairs sized ≥ 0.1 mm*
36. Blade width
37. Blade length
38. Blade width to length ratio*
39. Blade adaxial hair distribution
40. Blade adaxial hair density
41. Blade abaxial hair distribution
42. Blade abaxial hair density

TABLE 2. Foliage and culm leaf characters included in second PCA with foliage leaf characters.

1. Thorn development
2. Culm leaf sheath length
3. Culm leaf sheath base width
4. Culm leaf sheath ligule width
5. Culm leaf blade length
6. Culm leaf blade to culm leaf ratio
7. Culm leaf sheath vesture
8. Culm leaf blade vesture
9. Contact of ligule with culm leaf margin
10. Density of culm leaf ligule cilia
11. Length of culm leaf ligule cilia

eter. Each specimen usually consisted of several sheets.

NUMERICAL TECHNIQUES

The fragmentary and incomplete nature of bamboo herbarium specimens prevented the simultaneous gathering of detailed vegetative and reproductive data from all but a few herbarium specimens. In order to include as many specimens as possible, data (consisting of continuously varying or "count" characters) are analyzed in four separate categories, two vegetative and two reproductive.

The first vegetative data set includes 42 characters measured from the foliage leaves of 105 specimens. These characters are listed in Table 1. The second vegetative data set includes selected branch leaf data plus 11 additional characters from culm leaves and branches of 65 specimens. These additional characters are listed in Table 2. Another 24 vegetative characters were measured but omitted from the analyses because of inadequate herbarium material, distortion in pressed material, or their extreme variability.

The first reproductive data set includes 33 characters measured by examining the external features of inflorescences and spikelets of 49 specimens. These characters are listed in Table 3. The second reproductive category includes all external features plus seven internal characters from dissected spikelets of 30 specimens. These additional characters are listed in Table 4. Another 33 characters were measured and omitted from the analyses because they proved to be too variable.

A total of 152 vegetative and reproductive characters were measured during the course of study. The absence of any previous detailed studies of this group necessitated the use of a large number of characters in order to understand adequately the pattern of variation of the group.

The data were analyzed by Principal Components Analysis (PCA) using the program CLUSTAN (Wishart, 1975); see discussion of this ordination technique in Wiley (1981). Results are presented in the taxonomic treatment section of this paper.

SPECIES CONCEPT

In the Bambusoideae the challenge of delimiting and ranking taxa is complicated by the absence of complete herbarium specimens. A reproductive system that produces flowers only after many years

TABLE 3. External reproductive characters used in principal components analysis.

1. Number of lateral leaves in inflorescence
2. Number of terminal leaves in inflorescence
3. Spikelets per cluster
4. Spikelet length
5. Spikelet width
6. Spikelet stature (erect to arcuate)
7. Number of gemmiparous bracts
8. Uppermost gemmiparous bract length
9. Uppermost gemmiparous bract width
10. Degree of stramineous coloration in bract
11. Degree of brown coloration in bract
12. Degree of purple coloration in bract
13. Degree of green coloration in bract
14. Number of veins on bract
15. Density of hairs at base of bract
16. Density of hairs at center of bract
17. Density of hairs at apex of bract
18. Density of hairs on edges of bract
19. Number of florets
20. Lowermost lemma length
21. Lowermost lemma width
22. Lowermost lemma mucro length
23. Degree of stramineous coloration on lemma
24. Degree of brown coloration on lemma
25. Degree of purple coloration on lemma
26. Degree of green coloration on lemma
27. Number of veins on lemma
28. Density of short hairs at base of lemma
29. Density of short hairs at center of lemma
30. Density of short hairs at apex of lemma
31. Density of short hairs on edges of lemma
32. Density of long hairs at base of lemma
33. Density of long hairs at center of lemma

TABLE 4. Interior spikelet characters used in principal components analysis.

1. Lowest rachilla section length
2. Lowest rachilla section width
3. Lowermost palea length
4. Lowermost palea width between keels
5. Style length
6. Style width
7. Style hair length

of vegetative growth drastically reduces the opportunity to observe, collect, and experiment with reproductive structures, a situation McClure (1973) likened to the system of "Fungi Imperfecti" developed by mycologists. These problems have limited our knowledge of the processes involved in bamboo speciation and have kept bamboo taxonomy from advancing much beyond the alpha stage.

Past bamboo classifications have been based strictly upon overall similarity and the presence of gaps in observed morphological patterns rather than hypothesized evolutionary changes or biological interactions. While this system is not ideal, constraints of time and the problems referred to above have limited the present study to a similar approach.

Species will be delimited here on the basis of consistent morphological gaps in a number of vegetative and/or reproductive characters. The category of subspecies will be considered synonymous with that of variety as proposed by Raven (1974). Both categories have been used sparingly by bamboo taxonomists (Munro, 1868; Camus, 1913; Holttum, 1958; McClure, 1973), but in this study subspecies will be used to delimit populations that are geographically isolated and exhibit variation, which results in slight morphological gaps of a few vegetative and/or reproductive characters. Populations that vary in a few vegetative and/or reproductive characters and show some geographic continuity but no consistent morphological gaps are referred to as "incipient geographic races."

INTERSPECIFIC RELATIONSHIPS AND DEFINITION OF THE *GUADUA ANGUSTIFOLIA* COMPLEX

The genus *Guadua* is in need of revision, since many of the species have been inadequately described and collected. However, the species of the *G. angustifolia* complex are clearly separable from the remaining taxa. The combination of characters that define the *G. angustifolia* complex are as follows: culms of large stature (i.e., (7–)10–20(–30) m tall), erect with arched tops; internode walls of medium thickness; culm leaves large, abaxially pubescent, and usually without auricles; foliage leaf sheath glabrous or pubescent toward midrib of lower half, sometimes approaching the apex but never present there; foliage leaf blade about 10–25 cm long and 1–4 cm wide, surfaces glabrous or only sparsely pubescent, petioles glabrous along midrib of abaxial surface. Synflorescence consisting of 2–5 multiflowered pseudospikelets on delicate, branching twigs; main florescence 2–9 cm long and 3–8 mm wide; florets 3–14; surface of bracts and lemmas glabrous or with sparse hyaline hairs at base, center, and edges, rarely densely pubescent at base and center, margins glabrous; palea keels with pubescent margins exserted beyond the lemmas; lodicules 3.

Most plants in the genus do not grow taller than 10 m, while plants of *Guadua angustifolia* usually grow to between 10 and 20 m and are often taller, sometimes reaching 30 m. The other large species of the genus are few and are easily separated from *G. angustifolia* by several vegetative and reproductive characters. In Tables 5 and 6, a detailed comparison is made among the species that are sympatric with *Guadua angustifolia.*

Although the species sympatric with *Guadua angustifolia* are easily separated from this species on vegetative and floral characters, the scarcity of *G. angustifolia* subsp. *angustifolia* in Mexico and Central America (formerly known as *G. aculeata*) has caused problems in the past. Two forms of *G. amplexifolia* are more common than *G. angustifolia* in Mexico and Central America. As a result, *G. amplexifolia* has often been misidentified as *G. aculeata.* This problem developed because of the lack of detailed vegetative descriptions and a vegetative key separating the two species. Both *G. amplexifolia* and *G. angustifolia* are very thorny, and early collections were given the name *G. aculeata.* Once these collections were misidentified the error was carried over to the determinations of later specimens. Another problem concerns the thornless forms of *G. amplexifolia* and *G. angustifolia.* The thornless form of *G. angustifolia* in Mexico, originally named *G. inermis,* was described from flowering material from Colipa, Veracruz. The culms were described as 16 m tall and unarmed, and the branch leaf sheaths and petioles were described as glabrous, all characteristics of *G. angustifolia.* There are some clumps of *G. angustifolia* in other parts of its range (mainly in the province of Esmeraldas, Ecuador) that have few or no thorns on the upper branches. When branches on the lower third of the culm, which are thorny, fail to develop, the culm could be considered thornless. *Guadua inermis* likely has this same growth form. Unfortunately, there is no complete vegetative specimen of *G. inermis* from Mexico and, because its occurrence is so restricted, no living plants may remain.

The thornless form of *Guadua amplexifolia,* which occurs in many areas of Central America, has not been described in the literature and thus has often been misidentified as *G. inermis.* It is readily distinguishable from *G. angustifolia* on the basis of size, culm spacing, wall thickness, culm leaves, and foliage leaves (see Table 5). These plants (which have been collected in Mexico by the first author) can be separated from the thorny and solid-culm form of *G. amplexifolia* by their hollow but thick-walled culms. Thus, we have chosen to call this form "hollow culm." While "hollow culm" almost always lacks thorns, they may be present in reduced numbers. More study is needed to determine the precise taxonomic relationship of the "hollow culm" form to typical *G. amplexifolia.*

PHYTOGEOGRAPHY

Guadua angustifolia has the widest geographic range of any species in *Guadua.* Its northernmost localities are found in the state of Veracruz, Mexico, and its southernmost localities are found in northeastern Argentina and southeastern Paraguay. *Guadua angustifolia* is one of only three species that are known from both Central and South America; the others are *G. paniculata* and *G. amplexifolia.*

Speculation on the factors resulting in such extensive distributions is difficult because of the paucity of information on the mechanisms of dispersal of these large bamboos. Discontinuities in flowering periods can be very long, up to 35 years, and no studies have been made to ascertain the vectors responsible for seed dispersal or seed-dispersal distances of these bamboos. Vegetative dispersal must certainly be a factor in increasing their range; studies have been done that show the ease with which culms root when planted (McClure, 1966). These large bamboos frequently grow along riverbanks, and floods could serve as an efficient means of vegetative dispersal, especially downstream.

Long-distance dispersal between continents or islands could possibly occur when culm sections are carried by ocean currents. No studies have tested the viability of culms after prolonged exposure to seawater, but the first author has observed clumps growing within a kilometer of the ocean and on islands within tidal bays. Raven & Axelrod (1974) suggested that bamboos found north of Panama probably arrived in Neogene times or even more recently from South America. It is interesting that only three species of *Guadua* have a bicontinental distribution, and even more intriguing is the fact that no large bamboos are native to the islands of the West Indies (except Trinidad, which is geologically part of South America). This suggests that oceanic transport is not a common means of dispersal.

Even though *Guadua angustifolia* is found from Mexico to Argentina, there are large gaps in its distribution (Figs. 2–4). Throughout Central America it is not very common and, as McClure (1955) suggested, it may have been extirpated from much of its former range by selective cutting of its superior culms. In his personal notes he wrote, "According to the late Dr. Ross E. Moore, who spoke from personal experience covering many years as

TABLE 5. A morphological comparison of *Guadua angustifolia* subsp. *angustifolia* and other sympatric species of *Guadua*.

	Guadua angustifolia subsp. *angustifolia*	*Guadua amplexifolia* "solid culm"	*Guadua amplexifolia* "hollow culm"	*Guadua longifolia*	*Guadua paniculata*
Culms	erect; 10–30 m tall, 10–20 m diam.; medium wall thickness	erect; 8–10 m tall, 6–10 cm diam.; solid with pithy center	erect; 8–10 m tall, 6–10 cm diam.; thick-walled	clambering; to 15 m long, to 5 cm diam.; thick-walled	weakly erect; 8–9 m tall, 5–7 cm diam.; thick-walled
Culm leaves	brown pubescent; deciduous; blade about ¼ or less as long as leaf, persistent; auricles absent	brown pubescent; tardily deciduous to persistent and rotting; blade ⅓ to ½ as long as leaf, persistent; auricles present to absent	brown pubescent; tardily deciduous to persistent and rotting; blade ⅓ to ½ as long as leaf, persistent; large auricles present	slightly white pubescent; promptly deciduous; blade about ⅓ as long as leaf, base much lower on one side; auricles absent	yellow-green with purple horizontal stripes, pubescent; sheath tardily deciduous; blade ½ to ⅓ as long as leaf, caducous from sheath; auricles absent
Thorns	present to rarely absent; 1–5 at the node; short to long	present; 1–5 at node; short to long	absent to very sparse; few at node if present; short	present; 1 or rarely 2 at node, pointing downward	present; usually 3 at node; fairly long, slender and very sharp
Branch leaves	blades medium width; sheaths glabrous or pubescent along midrib of lower half; abaxial petiole glabrous; auricles absent to rarely present	blades medium to wide; sheaths glabrous to totally pubescent, usually on edges of lower or upper half; abaxial petiole glabrous; auricles absent to present	blades wide; sheaths usually glabrous; abaxial petiole glabrous; auricles present	blades very narrow; sheaths glabrous to rarely pubescent; abaxial petiole glabrous to pubescent; auricles present to absent	blades narrow, pendant; sheaths pubescent; abaxial petiole pubescent; auricles absent
Spikelets	short to long, narrow, flattened; 1–3 per cluster; glabrous to slightly pubescent	long and wide, rarely short, round; usually 3 or more per cluster; glabrous to rarely pubescent	same as "solid culm"	very long and narrow, round; 1–3 per cluster; glabrous	short and narrow, flattened; usually 3 or more per cluster; pubescent

TABLE 6. A morphological comparison of *Guadua angustifolia* subsp. *chacoensis* and other sympatric species of *Guadua*.

	Guadua angustifolia subsp. *chacoensis*	*Guadua paraguayana*	*Guadua trinii*	*Guadua tagoara*	*Guadua paniculata*
Culms	10–15 m tall, 8–10 cm diam.	8–10 m tall, 2–4 cm diam.	8–10 m tall, 3–5 cm diam.	8–10 m tall, 6–8 cm diam.	8–9 m tall, 5–7 cm diam.
Culm leaves	brown pubescent; blade ¼ or less as long as leaf, persistent; auricles absent	brown pubescent; blade ⅓ as long as leaf, persistent; auricles present	brown pubescent; blade ½ as long as leaf, persistent; auricles absent	brown pubescent; blades ⅙ as long as leaf, much wider than long, persistent; auricles absent	yellow-green with purple horizontal stripes, pubescent; blade ½ to ⅓ as long as leaf, caducous from sheath; auricles absent
Branch leaves	blades medium to narrow; sheaths glabrous; abaxial petiole glabrous	blades medium to narrow; sheath with hairs on one or both sides of apex; abaxial petiole pubescent on one or both sides	blades medium to narrow; sheaths glabrous to pubescent at apex; abaxial petiole glabrous to pubescent	blades wide; sheaths pubescent on one side of apex; abaxial petiole glabrous	blades narrow, pendant; sheaths pubescent; abaxial petiole pubescent
Spikelets	long and wide, glabrous to slightly scabrous; palea wings exserted, ciliate	long to short and narrow, pubescent; palea wings usually not exserted, ciliate	short and narrow, glabrous; palea wings broadly exserted, glabrous to minutely ciliate	short and narrow, glabrous; palea wings broadly exserted, not ciliate	short and narrow, pubescent; palea wings not exserted, ciliate

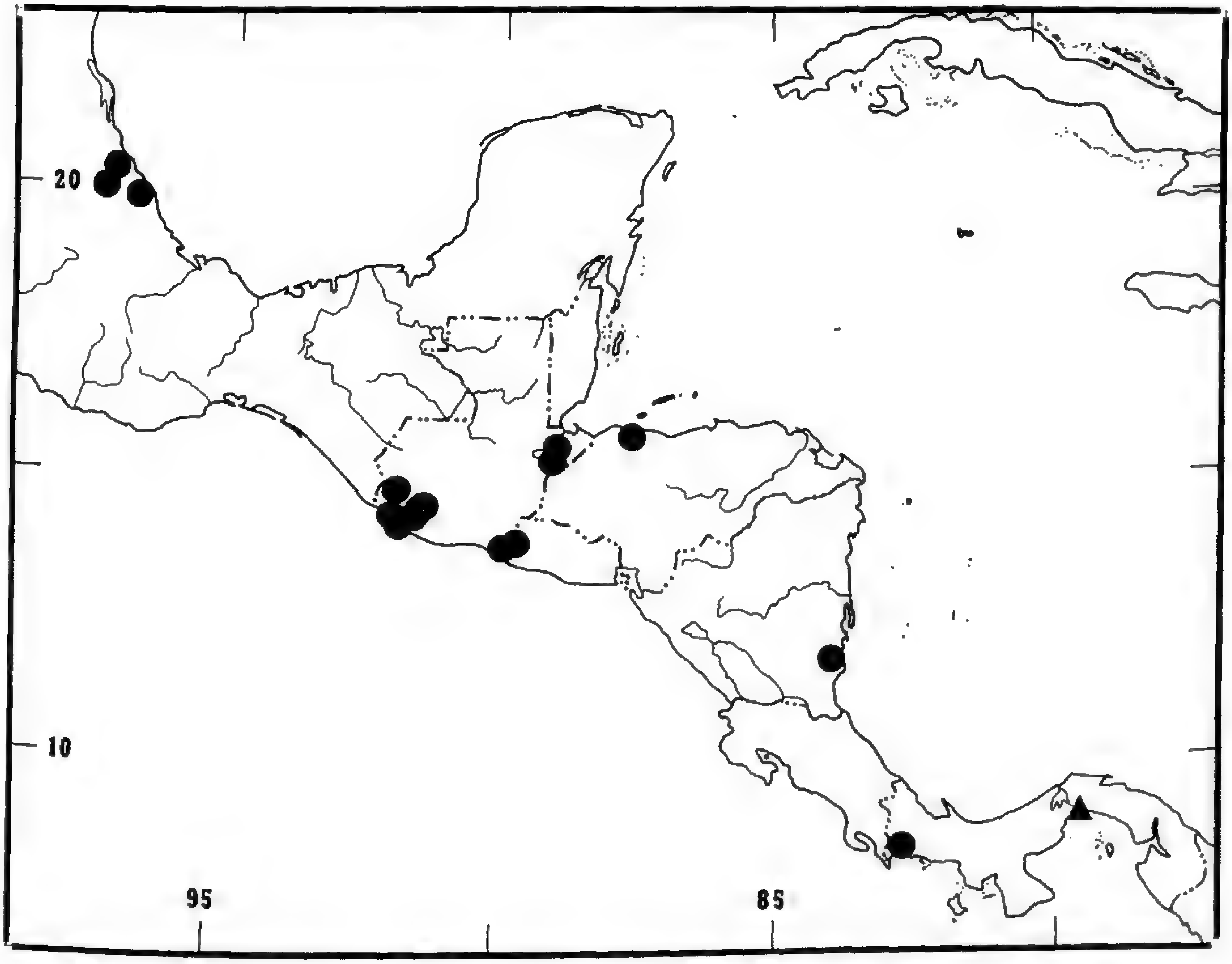

FIGURE 2. Distribution of the northern populations of *Guadua angustifolia* subsp. *angustifolia*. Dots = native plants; triangle = possible cultivated plant.

a consultant on land utilization in several countries of Central America, thousands of acres of land originally occupied by more or less pure stands of bamboo [*G. amplexifolia* and *G. aculeata*] have been cleared in recent decades for agricultural purposes." Unfortunately, bamboo stands were synonymous with "good banana land."

Past climatic changes may have decreased the distribution of the habitats available, as Toledo (1982) described in the changes undergone by the tropical forest in Mexico. Within the last 10,000 years there were times when the extent of the tropical forest must have decreased considerably, and bamboo habitats in southern Central America, where there are very few collections, may have been eliminated altogether. *Guadua angustifolia* is conspicuously absent in most of Nicaragua and in all of Costa Rica, and even though it occurs in North and South America, there are no collections from eastern Panama or lands bordering Panama in western Colombia. In contrast, *G. angustifolia* of Colombia and Ecuador has a broad ecological amplitude and can be found in lowland rainforest, lower montane rainforest, semideciduous forest, deciduous forest, and savanna (Harling, 1979) as long as water is plentiful, and edaphic conditions are satisfactory. This ecological amplitude may have made the species more resistant to past climatic changes. Many areas of Central America where it could possibly occur have yet to be explored botanically, especially the Caribbean lowlands, and the species may thus be more common than maps would suggest. Standley (1931) described it as one of the conspicuous features of the landscape in the coastal regions of Guatemala and Honduras, being abundant in swamps and along rivers at low elevations, often forming extensive groves.

Another large disjunction occurs between eastern Colombia and the few specimens of southern Venezuela and Guyana. Its distribution in the Amazon basin remains very poorly known. The eastern populations can be found along many of the large rivers of the Ecuadorian Oriente, but just how far they continue into Peru and Brazil is unknown.

Guadua angustifolia is divided here into two subspecies separated by morphological differences (see taxonomic section) and occurring in widely separated geographic ranges (Figs. 2–4). Subspe-

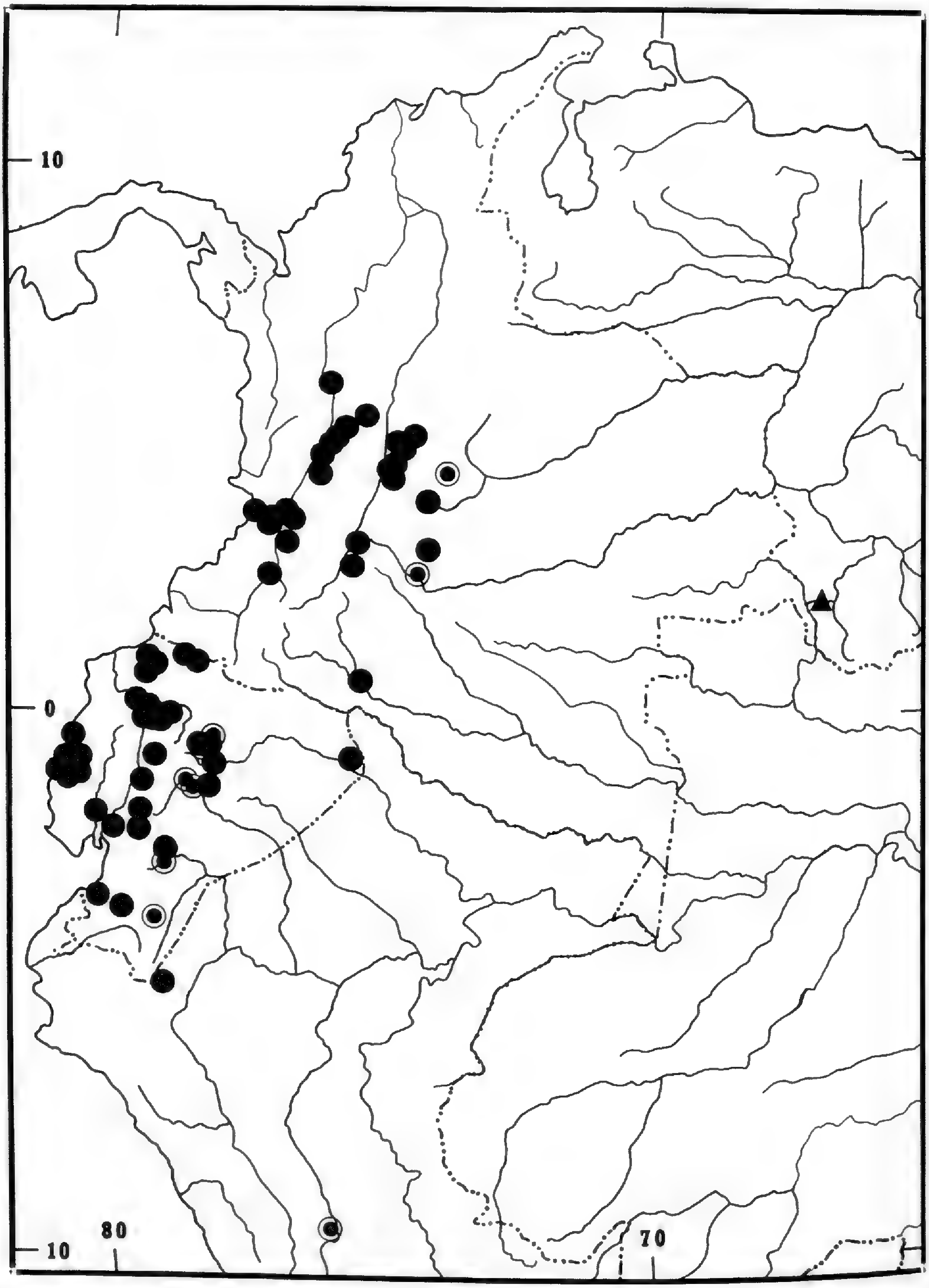

FIGURE 3. Distribution of western (dots) and eastern (dots in circles) populations of *Guadua angustifolia* subsp. *angustifolia*. Triangle = possible cultivated plant.

cies *angustifolia* extends into the northern Amazon basin of Peru, and subspecies *chacoensis* has its northernmost distribution in eastern Paraguay. Most of the specimens of *G. angustifolia* subsp. *chacoensis* have been collected along the Paraná and Paraguay rivers, but it is not known if the subspecies extends up these rivers into Brazil and if so how far. In a study of bamboo-dwelling birds in southeastern Peru, Parker (1982: 483) reported, "It is interesting to note that close relatives of *Hemitriccus flammulatus*, the Flammulated Pygmy-Tyrant and *Sporophila shistacea*, the Slate-colored Seedeater (i.e., *Drymophila ochropyga*, Drab-breasted Pygmy-Tyrant and *Sporophila fal-*

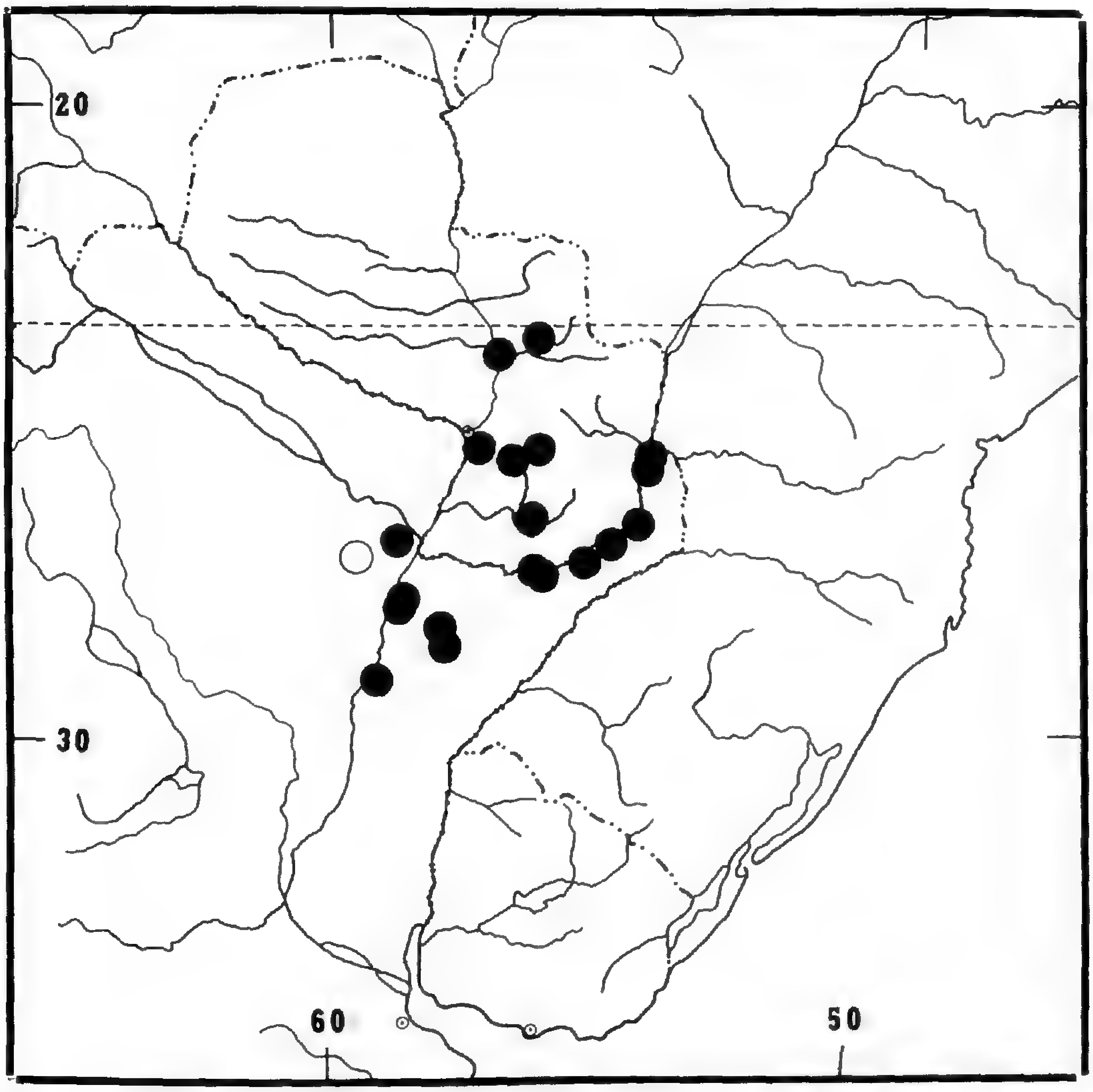

FIGURE 4. Distribution of *Guadua angustifolia* subsp. *chacoensis*. Open circle = unspecified locality in Chaco Province.

cirostris, Temminck's Seedeater) are found in bamboo in montane or subtropical areas from SE. Brazil to NE. Argentina. This suggests that certain bamboos were an important floristic element in a relatively cool, humid forest that may have once extended from the Andes to the Atlantic south of Amazonia proper." He listed eight other birds that are associated with bamboo and show similar disjunct distributions across the South American continent. Past climatic changes described by Prance (1982) lend credence to the setting up of a climatic barrier between the two regions. Future bamboo exploration in areas such as the Beni region of Bolivia or the southwestern regions of Brazil, and study of bamboo-animal associations, may yet reveal a former or even a present connection between the two subspecies.

Another unresolved problem is the role human cultivation has played in transporting these bamboos. The economic importance of *Guadua angustifolia* in pre-Columbian times is obscure although when the Spanish arrived in Colombia, they observed the native inhabitants using it in construction and wearing it as protective garb against arrows (Farrelly, 1984). *Guadua angustifolia* has been and is being cultivated in many botanical gardens and agricultural experiment stations throughout Latin America. Some of the plants collected as wild have been suspiciously close to experiment stations and may be merely escapes; *G. angustifolia* plantings are known from southern Brazil to southern Florida.

TAXONOMIC CRITERIA

Collecting difficulties have always hindered the detailed study of large woody bamboos. Most of the plant parts, aside from foliage leaves and spikelets, are too large to be easily gathered, pressed, or transported. The combination of a hot tropical climate, elephantine plant size, and masses of thorny branches is usually enough to deter even the most intrepid botanist from collecting these woody grasses unless the plants are flowering. Complete collections that include many of the vegetative parts of a bamboo have proven just as valuable in identification as specimens with floral parts (McClure, 1966; Soderstrom & Young, 1983). Unfortunately, herbarium specimens containing only foliage leaves far outnumber those containing culms, culm leaves, and branches. Rhizomes are almost never collected.

The taxonomic usefulness and variation within the characters of the *Guadua angustifolia* complex are discussed below.

RHIZOMES

Guadua angustifolia possesses pachymorph rhizomes (McClure, 1966). These rhizomes are composed of two parts—the neck, a narrow portion where internodes do not possess buds (Fig. 5a), and the rhizome proper, a thick part where buds are present at the nodes. In *G. angustifolia,* the neck is elongated and positively geotropic so it first grows down from the rhizome proper to form prop-like structures before giving rise to another short, swollen, fusiform rhizome. The shape of the rhizome and accompanying necks has been likened to an alligator, and the rhizomes are often called *caimán* by locals (Fig. 6a).

CULM INTERNODES

The culm internodes of *Guadua angustifolia* differ from all other species of the genus *Guadua* mainly in diameter, length, and wall thickness. Culms of *G. angustifolia* have the largest diameters of any of the species (Fig. 6b), and the wall is of medium thickness (Fig. 6c) with the basal internodes being the shortest and the most thick-walled. The length of the internode and its variation in length and diameter from base to apex is rarely measured. Internode length at the basal 2 m of the culm usually does not exceed 30 cm. The lumen is often filled with potable water and sometimes contains insects or insect larvae (Fig. 7a). The sulcus above the branch bud usually does not extend beyond mid-internode, although it may be perceptible along the entire length.

Hairs cover the surface in varying densities. They are usually sparse and do not obscure the surface (Fig. 5b), or they may be entirely absent. These hairs are deciduous and leave distinct impressions in the culm surface.

During the first two years of growth the internodes are dark green but then become gradually lighter green and covered with lichens (Fig. 5d). As in most bamboos, when the culms die they turn from green to tan. No studies have been done on the life span of individual culms.

CULM NODES

The culm nodes of *Guadua angustifolia* do not differ significantly from many other species in *Guadua*. Most species have a characteristic band of white hairs extending from the nodal ridge to the nodal line and below the nodal line for 1–3 cm. In *G. angustifolia* this band of hairs is very prominent on young culms (Fig. 5c), but may be partially worn off or obscured with age. The nodal ridge is often difficult to observe, but its presence can be felt with the hand. This prominence varies within *G. angustifolia* from easily seen to absent. The interior nodal wall may be convex or horizontal and varies in different diameter culms (Londoño & Prieto, 1983).

CULM LEAVES

Culm leaves are one of the most useful vegetative characters in separating taxa and are used here in separating subspecies. Because the culms of *Guadua angustifolia* are large, the culm leaves are also large (Fig. 7b) and often must be folded over to fit into a plant press. They surround and protect the newly developing culm and, like the internodes they cover, vary in size and shape from the base to the apex of the culm (Fig. 9a). At the base they are usually as long as they are wide, and toward the apex the leaves become progressively longer and more narrow, and the blade makes up a larger percentage of the whole leaf.

The shape of the ligule in *Guadua angustifolia* subsp. *angustifolia* varies within the same plant but is most often convex in the center. The ligules almost always turn up and end a few millimeters

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FIGURE 5. Vegetative morphologyy of *Guadua angustifolia* subsp. *angustifolia.*—a. Long rhizome necks extending down from rhizome.—b. Stiff hairs on internodes.—c. Nodal region and bud.—d. Lichen-covered culm.

FIGURE 6 (p. 752). Vegetative morphology of *Guadua angustifolia* subsp. *angustifolia.*—a. Pachymorph rhizomes.—b. Cutting a large diameter culm from Chocolá, Guatemala (photo F. A. McClure).—c. *Guadua* culms showing medium wall thickness and lumen.—d. Culms with no basal branches, Chinchiná River, Colombia (photo F. A. McClure).

FIGURE 7 (p. 753). Vegetative morphology of *Guadua angustifolia* subsp. *angustifolia.*—a. Larvae of microlepidopterous insect found inhabiting the internode of a culm, Chocolá, Guatemala (photo F. A. McClure).—b. Large culm leaf from Chuchumbleza, Zamora-Chinchipe, Ecuador.—c. Upper branches developing in young culm.—d. Lower branches developing from culms, Coatepeque, Guatemala (photo F. A. McClure).

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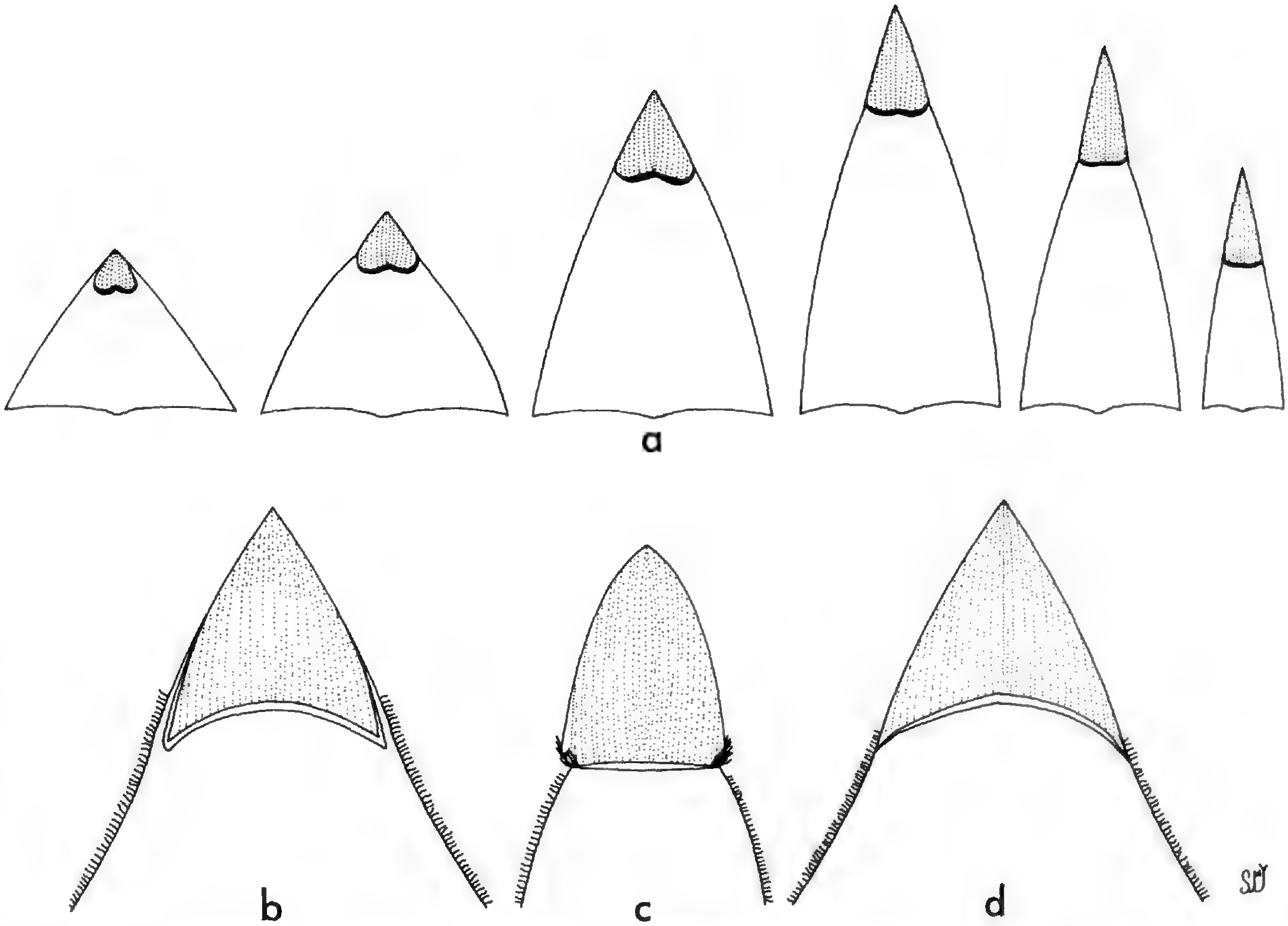

FIGURE 9. Culm leaves of *Guadua angustifolia.*—a. Culm leaf variation within the same culm (left to right = base to apex of culm).—b. Ligule of lower culm leaf of *Guadua angustifolia* subsp. *angustifolia*; *McClure 21401-21403.*—c. Ligule of culm leaf near apex of culm of *G. angustifolia* subsp. *angustifolia*; *McClure 21737.*—d. Ligule of culm leaf of *G. angustifolia* subsp. *chacoensis*; *Krapovickas et al. 25470.*

before the margins (Fig. 9b). Apical culm leaves may have ligules that are continuous to the margin and have groups of oral setae present there (Fig. 9c). *Guadua angustifolia* subsp. *chacoensis* is distinguished by having ligules that are often continuous to one or both margins in the lower culm leaves, but no oral setae are present as in *G. angustifolia* subsp. *angustifolia* (Fig. 9d). The hairs on the margin of the ligule are also less dense and longer in subspecies *chacoensis* than in subspecies *angustifolia.* Auricles are not present in *Guadua angustifolia*, and the blade comprises only a small percentage, usually less than 20%, of the total leaf length.

Hairs covering the abaxial side of the leaf vary from dense to sparse, and their position on the leaf also varies a great deal. These hairs are long and straight to short and contorted and vary from black or brown to golden in the longer hairs and to white in the shorter hairs. The longest hairs are stiff, sometimes branched, and sharp-pointed. They are readily detached.

The culm leaves are caducous and usually can be found within the clump in good condition for pressing. The blade is erect and stays firmly attached to the sheath. Leaves at the base of the culm remain attached for a longer period of time than those from farther up the culm and may disintegrate in place.

BRANCHES

Branching patterns do not vary significantly within *Guadua angustifolia*, although the position

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FIGURE 8. Vegetative morphology of *Guadua angustifolia* subsp. *angustifolia.*—a. Branching from middle portion of culm, Chocolá, Guatemala (photo F. A. McClure).—b. Branch from lower culm developing as a large thorn, Río Palenque Biological Station, Ecuador.—c. Culms along Cayapas River, Esmeraldas, Ecuador.—d. Culms with no basal branches, Escondido River, Nicaragua.

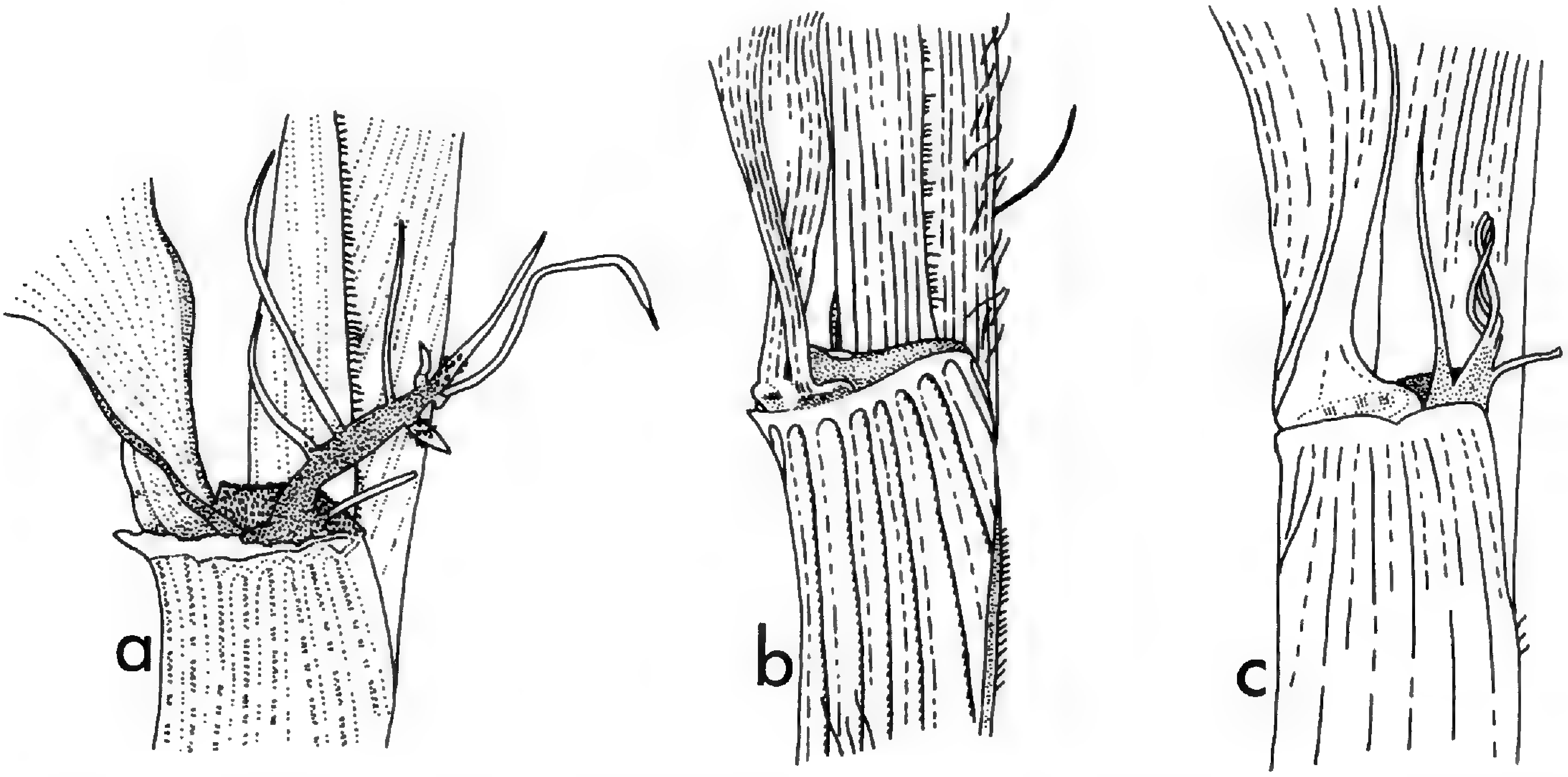

FIGURE 10. Foliage leaves of *Guadua angustifolia.*—a. "Eastern race" of subspecies *angustifolia*; *Young 92.*—b. "Western and northern race" of subspecies *angustifolia*; *Young 117.*—c. Subspecies *chacoensis*; *Krapovickas et al. 25470.*

along the culm where branches develop does show variation. One main branch develops from a single bud at the node (Fig. 5d), and while branches from the upper one-third of the culm always develop (Fig. 7c), the development of the lower branches varies. The development of branches in the lower third of the culm is common (Fig. 7d), but in certain areas within its geographic range most of the culms of *G. angustifolia* do not possess lower branches (Figs. 6d, 8d). Most of the culms observed by the first author in the province of Esmeraldas, Ecuador (Fig. 8c), were devoid of lower branches until a culm was cut. Then, one of the lower buds broke dormancy to produce a very thorny lateral branch. This characteristic will remain of doubtful taxonomic significance until additional studies are made.

The closely set nodes at the base of the branches contain buds that remain dormant or produce one or two secondary branches which may again branch (Fig. 8a). These higher-order branches may develop as thorns or elongate into normal vegetative branches. While the upper branches may be thorny or thornless, the lower branches, when they develop, always possess thorns. The main branch may develop only slightly and produce one large thorn (Fig. 8b) or it may rebranch and develop one to four additional thorns at its base. There do not seem to be consistent differences in thorn development within *Guadua angustifolia*, and the taxonomic usefulness of this character is negligible.

Branch internodes and nodes are covered with hairs similar to the culm internodes but their caducous nature makes them of little taxonomic use.

FOLIAGE LEAVES

The variation in structures that comprise foliage leaves is often used in distinguishing species. Within *Guadua angustifolia* there is significant variation in foliage leaves as well as culm leaves, and care must be taken in selecting average leaves when comparing taxa. Within one plant, for example, leaf size may vary considerably since the first leaves to appear on a branch (juvenile leaves) are longer and wider and have slightly different indumentum than subsequent leaves. When these juvenile leaves are the most abundant and most accessible leaves on the culm they are sometimes the only ones included in a collection. New leaves may also develop to a smaller size when flowering takes place because they gradually decrease in size toward the spikelets. Leaves closest to the spikelets fail to develop their blades altogether and become the gemmiparous bracts of the pseudospikelet.

Particular characters of the leaf that are taxonomically useful are leaf size, leaf sheath indumentum, oral setae number, presence of auricles, outer ligule size, inner ligule size and indumentum, pulvinus size, and blade and petiole indumentum (Fig. 10). All of these vary somewhat between primary and subsequent leaves.

Hairs and the marginal rows of prickle-hairs were examined on the blade. The number of rows of prickle-hairs varied a great deal within *Guadua angustifolia*, but their presence may prove useful in separating this species from others within the genus. Petiole length also varies more between species than within *G. angustifolia*, as does the length of sheath margin hairs.

INFLORESCENCE

The structure of pseudospikelets has been problematic in this group of bamboos because the inflorescence branching differs from the typical grass spikelet. McClure (1934) was the first to discuss the structure of pseudospikelets and later (1966) called this type of inflorescence indeterminate. Holttum (1958), Soderstrom (1981), and Soderstrom & Londoño (1988) have also provided explanations of the structure of pseudospikelets that seem to be clearer and easier to understand than those of McClure. Morphological analysis of the synflorescence of *Guadua angustifolia* (and of pseudospikelets in general) is given below and follows the description developed by Soderstrom & Londoño (1988).

A pseudospikelet is simply a shortened vegetative axis or branch that terminates in a single spike of florets. If we look first at the growth form of the entire bamboo culm, it originates underground as a rhizome branch from another rhizome. It then eventually turns up and grows erect out of the ground and is called a culm. From the main culm an alternate, monopodial pattern of branches develops from the nodes with each successive branch becoming smaller until the sequence stops at the smallest twigs. Each branch is subtended by a leaf or bract and begins with a double-keeled leaf called a prophyll. The prophyll and subtending bract for the main culm (a branch from a rhizome) is underground where it branches from another rhizome (Fig. 11a).

When flowering occurs, the vegetative twigs elongate to varying lengths beyond the foliage leaves and terminate in a series of one to four short vegetative internodes followed by a single spikelet, the main florescence. Additional flowering branches or paracladia may also arise from vegetative buds farther down the branch (Fig. 11b, c).

The short uppermost internodes of these flowering branches are vegetative and contain one to several vegetative buds. These buds are subtended by modified leaves called gemmiparous bracts, which resemble the lemmas, making that part of the branch appear as part of the spikelet. The vegetative branch segments bearing the gemmiparous bracts and the spikelet proper are together called the pseudospikelet (Fig. 12a).

When flowering begins, the pseudospikelets that develop at the apex of branches have the same prophylls and subtending bracts as the branches from which they develop (Fig. 12a). Therefore, if a pseudospikelet develops at the apex of the main culm axis, its prophyll and subtending leaf will be underground at the junction of the rhizomes. Pseudospikelets that develop from the nodes of branches begin with a prophyll and are subtended by a leaf or bract at the base of the branch.

As flowering continues, each bud within a gemmiparous bract may develop into another shortened vegetative axis, a paracladium, terminating in a spikelet or coflorescence. This sequence may proceed to form a ball of pseudospikelets, but in *Guadua angustifolia* usually only two or three shortened branches develop close together to form a synflorescence, or the buds may not develop at all (Fig. 12b). The pseudospikelet that gives rise to this synflorescence is here called the main florescence. The main florescence is usually the largest one and is used for comparison among taxa since pseudospikelets of further coflorescences gradually diminish in size. The length of branches and distance between internodes varies in each complement of branches, and it is often difficult to delimit a "cluster" in a nonarbitrary fashion. If pseudospikelets were separated by an internode of less than 1 cm, they were considered part of the same cluster, containing a main florescence and associated coflorescences. If two pseudospikelets were separated by an internode of more than 1 cm, they were considered to be two distinct synflorescences. The above distribution is made arbitrarily and only for convenience, since all spikelets are terminal to a vegetative branch.

When the vegetative portion of the branch becomes reproductive, buds along the axis, now called the rachilla, develop into florets consisting of a short axis beginning with a prophyll called the palea. The axis terminates in a flower consisting of three lodicules, six stamens, an ovary, style, and three stigmas. The axis is subtended by a bract called the lemma.

We found no budless bracts (glumes) between the gemmiparous bracts and the lemmas, although they have been observed in other species. Sometimes there were no gemmiparous bracts at all on the branch, especially in coflorescences, and florets began immediately distal to the prophyll. The prophyll may subtend a bud but is almost always empty. Once a bud develops at a node, the subtending bract is quickly deciduous and is almost never found.

The short axis (here called the peduncle) between the vegetative portion of the branch and the floral portion does not branch before it becomes part of the spikelet (Fig. 12).

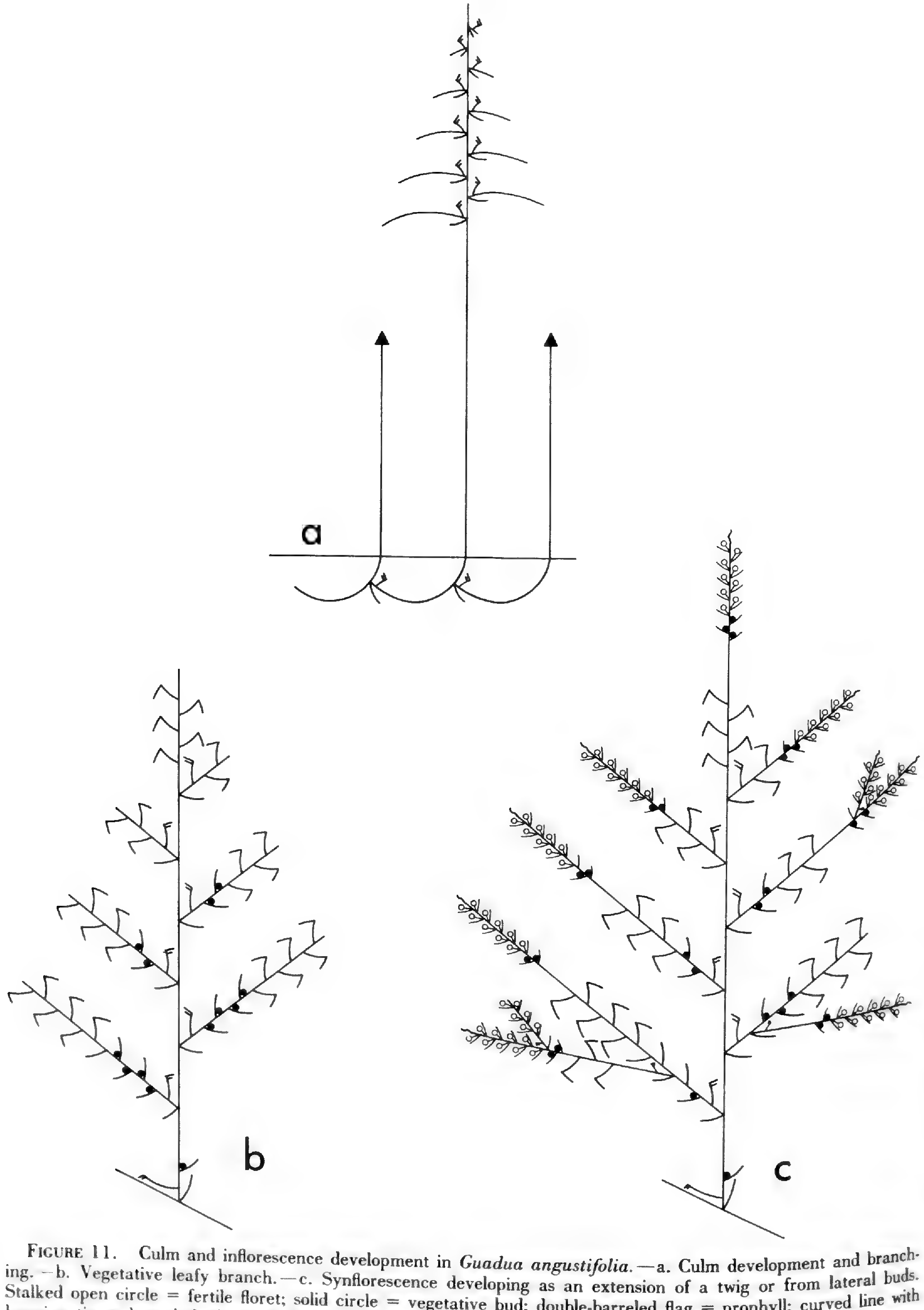

FIGURE 11. Culm and inflorescence development in *Guadua angustifolia.*—a. Culm development and branching.—b. Vegetative leafy branch.—c. Synflorescence developing as an extension of a twig or from lateral buds. Stalked open circle = fertile floret; solid circle = vegetative bud; double-barreled flag = prophyll; curved line with hanging tip = branch leaf sheath and blade, respectively; curved line alone = subtending branch leaf or bract, gemmiparous bract, lemma, or glume; wiggly line = terminal aborted part of axis.

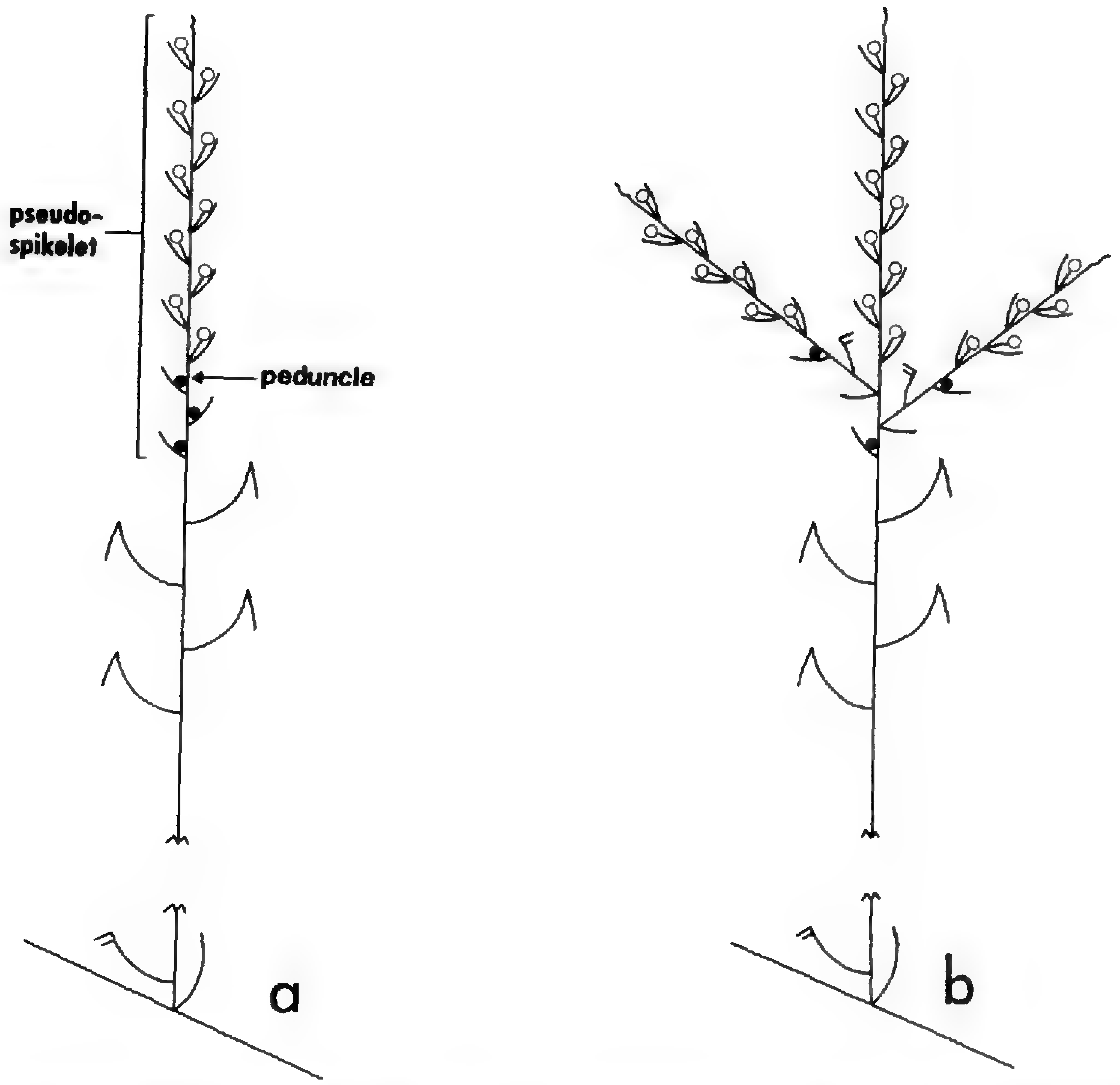

FIGURE 12. Pseudospikelet morphology in *Guadua angustifolia.*—a. Main florescence.—b. Branching of vegetative buds of main florescence to form a synflorescence of one main florescence and two coflorescences. Stalked open circle = fertile floret; solid circle = vegetative bud; double-barreled flag = prophyll; curved line with hanging tip = branch leaf sheath and blade, respectively; curved line alone = subtending branch leaf or bract, gemmiparous bract or lemma; wiggly line = terminal aborted part of axis.

In order to standardize measurements, the first author measured the characteristics of the uppermost gemmiparous bract and lowermost floret of terminal pseudospikelets, and the first rachilla segment between the lowermost floret and the one distal to it. The vegetative axis was measured between the uppermost gemmiparous bract and the one below it and was called the "uppermost vegetative internode."

The gemmiparous bracts often differed slightly in indumentum characteristics and color from the lemmas. They were sometimes more pubescent and lighter in color.

The lowermost florets develop first, and those formed subsequently gradually become smaller toward the apex as in a typical racemose inflorescence. The size of the ovary decreases between the proximal and distal florets within a spikelet, and the uppermost two or three florets possess only rudimentary stamens.

Many spikelets examined had already undergone anthesis, and the anthers had become detached from the filaments. This gave the impression that the lowermost florets were carpellate, especially since the filaments are very delicate and difficult to observe.

External inflorescence characters are more useful than characters from dissected pseudospikelets when comparing populations within *Guadua angustifolia.* The physical dimensions of the pseudospikelets (i.e., length, width, stature) and the number of florets per spikelet are the most useful external characteristics. The presence of leafy branches intermingled with the pseudospikelets is not consistent in Central America but tends to be a more reliable distinction between the subspecies in South America. Indumentum characteristics of the pseudospikelets are important in distinguishing *G. angustifolia* from other species of the genus, but they are less valuable within the species itself. However, a few internal inflorescence characters, i.e., palea length, style length, and style hair length, proved helpful in distinguishing populations.

CHROMOSOMES

Quarín (1977) reported a somatic chromosome number of $2n = 46$ for *Guadua angustifolia* subsp.

chacoensis. This number has been found in two additional species of *Guadua* (*G. capitata* Munro and *G. paraguayana*), but no counts have been taken from any plants in *G. angustifolia* subsp. *angustifolia*.

TAXONOMIC TREATMENT

Guadua angustifolia Kunth, Synopsis Plantarum 1: 253. 1822.

Clump caespitose to open caespitose, variable in extent from 5 to many meters diam., culms arising 0.5–2 m apart. *Rhizomes* pachymorph, necks elongated to form props. *Culms* 7–25(–30) m tall and 7–15(–20) cm diam., erect with arched tops; indumentum of unicellular, terete, pointed, hollow, unbranched or rarely branched hairs or prickle-hairs. *Internodes* dark green when young, turning green to light green when mature, but some forms with irregular, narrow, vertical yellow or white stripes, sulcate to slightly sulcate above buds and branches; walls 1.5–2.5 cm thick; glabrous to rarely densely covered with stiff, dark brown to black, occasionally white, antrorsely or retrorsely oriented hairs, 0.1–2.5 mm long, often deciduous and leaving imprints, and usually increasing in density toward apex of culm. *Nodes* solitary; surface densely covered with white, cream, or golden brown, variously oriented hairs 0.1–2 mm long and extending 1.5–2.5 cm below node, loosely attached, and sometimes lacking on older culms; nodal line prominent; nodal ridge inconspicuous to absent. *Culm leaves* deciduous but usually persistent at lower nodes, sheath and blade falling together, size varying with position on culm, (18–)20–70(–78) cm long and (9–)10–50(–55) cm wide at sheath base, average leaf 36 cm tall and 32 cm wide; *sheath* stiff, dark to light brown, adaxially densely to sparsely covered with white to light brown, twisted hairs 0.1–0.4 mm long, and densely covered to lacking, light to dark brown or black, straight, stiff, rarely once-branched, deciduous hairs 0.5–2.3 mm long, the larger hairs usually prostrate and antrorsely oriented, the margins entire with scattered, stramineous to brown hairs measuring 0.5–4.0 mm long, the auricles lacking, the oral setae sometimes present at junction of sheath and blade margins in culm leaves from upper culm, the ligule commonly convex at center, sometimes straight, ends usually curved up before reaching leaf margin, sometimes continuous to one or both margins, with entire margin fringed with hairs measuring 0.1–0.5 mm long; *blade* stiff, triangular, erect, persistent, dark to light brown or grayish brown, (1.5–)2–14.5(–15.5) cm long, average length 7.2 cm, the blade length as a ratio to the total culm leaf length 0.07–0.23 : 1, the base continuous with sheath to slightly cordate, the margins entire with marginal hairs usually scattered toward base or absent, the abaxial surface covered with or lacking both types of sheath hairs, but large hairs usually only present at base or along margins. *Branches* not developing from buds along center ⅓ or lower ⅔ of culm or rarely developing from buds at all nodes, buds rarely absent from center ⅓ of culm; main branch one, developing intravaginally at nodal line or remaining as a thorn; higher-order branches typically 0–4 at base of other branches, sometimes remaining as 1–4 thorns; thorns 1–5 at node, almost always present on branches from lower ⅓ of culm, upper branches thorny or thornless; branch internodes thick-walled to solid, the surface sparsely covered with or lacking dark brown to white deciduous hairs, 0.1–2.5 mm long; branch nodes in close succession at base of branches, otherwise solitary, the surface glabrous to covered with white to golden brown hairs to 0.2 mm long, and that may extend to 5 mm below nodal line. *Foliage leaves* 2–8(–12) per complement; *sheaths* stramineous to light brown, rarely marked with purple along margins or at apex, the veins conspicuous at apex to inconspicuous toward base, entirely glabrous or sparsely to densely covered toward midrib of lower half by light brown to hyaline, prostrate, antrorsely oriented hairs to 1.5 mm long, rarely approaching along midrib to within a few millimeters of apex, the margins glabrous or sparsely to completely lined with hyaline hairs, 0.1–0.5(–0.8) mm long, the auricles usually absent, if present mainly on juvenile leaves (those first produced by twigs), 0.5–4.5 mm long and 0.1–1 mm wide at base, purple, with 2–20 cilia along margins, the oral setae absent or numbering up to 15(–20), most abundant on juvenile leaves, 1–20 mm long on juvenile leaves, 1–10 mm long on higher-order leaves, entirely white or white to stramineous above and stramineous, brown or purple at base, scabrous to glabrous at base, the outer ligule absent or to 0.6 mm long, flaring to prostrate, rarely fringed with short hairs, the inner ligule 0.1–0.5(–1) mm long, densely to sparsely covered with hyaline erect hairs, 0.02–0.2 mm long; *blades* green to dark green; variable in size according to sequence of growth (juvenile leaves with blades usually longer and wider than higher-order leaves), (0.6–)1–3.5(–5) cm wide and (7.8–)9.8–24(–25.6) cm long, narrowly oblong, blades on flowering branches gradually smaller and narrowly ovate toward spikelets, abaxially glabrous to sparsely covered with hyaline hairs

0.2–1.5 mm long, adaxially glabrous to sparsely covered with hyaline hairs (0.1–)0.5–1.5 mm long, one edge with 0–5 rows of prickle-hairs, the margins scabrous, the apex acuminate, base obtuse, narrowing into a pseudopetiole, the pseudopetiole abaxially usually glabrous to sparsely pubescent, adaxially glabrous to densely pubescent, a pulvinus present on each side of pseudopetiole base, rarely absent, stramineous, brown, green, or purple, usually glabrous but sometimes sparsely pubescent. *Synflorescence* borne on leafy or leafless, delicate, branching twigs. *Pseudospikelets* 2–5(–8) per synflorescence or solitary, narrowly ovate, erect to arcuate, elliptic in cross section, disarticulating between the florets. *Main florescence* (1.5–)2.2–9(–10) mm long and 3–8 mm wide; uppermost vegetative internode 0.5–3.6(–9) mm long and 0.5–2 mm wide at apex, sparsely to densely covered on distal half with hyaline hairs 0.1–0.2 mm long, ventral half glabrous to sparsely covered with hyaline hairs to 0.1 mm long; gemmiparous bracts 0–3, stiff, stramineous to light brown, occasionally mixed with light green and/or marked with purple along margins; uppermost gemmiparous bract 7–14 mm long, 4–7 mm wide, ovate, the apex acute with mucro 0.2–1.4 mm long, the margins glabrous, the surface glabrous throughout or sparsely to densely pubescent, the nerves 11–17; empty bracts absent; lowest rachilla segment (1.7–)2.6–7(–8.5) mm long, 1–2.3 mm wide at apex, the surface similar to rachis. *Florets* 3–14(–18), upper 2 or 3 underdeveloped; *lemma* stiff, similar in color to bracts but usually somewhat darker, 10–17 mm long, 6–10 mm wide, ovate, the apex acute with mucro 0.1–1 mm long, the margins glabrous, the surface glabrous or sparsely to rarely densely pubescent, becoming sparse to absent toward edges and apex, the nerves 11–17; *palea* papery, stramineous, occasionally marked with purple on margins of keels, usually with winged keels exserted beyond margins of lemma, 7–14 mm long, 2–3 mm wide between keels, elliptic to obovate, the apex acute, the margins densely ciliate, the surface between keels pubescent on distal ⅔ to ½, other surfaces glabrous; *lodicules* 3, filmy, transparent and colorless to translucent and entirely stramineous, sometimes orange-red at base, the surface and margins sparsely ciliate, the anterior pair 2–5.2 mm long, 1–2.5 mm wide, ovate to elliptic to obovate with apex acute to obtuse to truncate, rarely acuminate, the posterior one 2–5.2 mm long, 0.8–1.8 mm wide, ovate to elliptic to obovate with apex acute to acuminate; *stamens* 6, filaments hyaline, very delicate, anthers stramineous, rarely marked with purple, 5–8 mm long, the base sagittate, apex rarely minutely penicillate; *ovary* brown, rectangular (in longitudinal section), 0.3–1.5 mm wide, glabrous; *style* yellow, ovate, 1.3–2.5 mm long, 0.3–1.3 mm wide at base, the base truncate, the apex acuminate, the surface densely pubescent; *stigmas* 3, hyaline to light purple, surface pubescence similar to style; *fruit* a dry caryopsis, 5 mm long, sulcate.

Ecology. Principally near rivers, streams, and wet places, or other openings in forest canopy in well-drained to wet soils, on flat or sloping terrain, from sea level to 1,800 m; also cultivated in urban areas, on farms, and along roadsides.

Key to the Subspecies of *Guadua angustifolia*

1a. Culm leaf ligule continuous to one or both margins, occasionally curved up before reaching both margins; foliage leaf sheath glabrous; outer ligule 0–0.3 mm high, not flaring to slightly flaring; abaxial foliage leaf blade usually glabrous; synflorescence borne on leafless to rarely leafy twigs; pseudospikelets erect to rarely slightly arcuate; main florescence (4–)5–7(–8) mm wide .... subspecies *chacoensis*

1b. Culm leaf ligule nearly always curved up before reaching margin, rarely continuous to one or both margins; foliage leaf sheath glabrous to pubescent toward midrib of lower half, rarely along midrib of upper half; outer ligule 0.1–0.9 mm high, slightly flaring to clearly flaring; abaxial foliage leaf blade commonly with scattered hairs, occasionally glabrous; synflorescence borne on leafy or occasionally leafless twigs; pseudospikelets erect and arcuate or entirely erect; main florescence (2–)3–6(–7) mm wide, but if synflorescence contains only erect pseudospikelets, these less than 5 mm wide .... subspecies *angustifolia*

a. **Guadua angustifolia** Kunth subsp. **angustifolia**. Figures 1, 6–10.

Bambusa guadua Humb. & Bonpl. Plantae Aequinoctiales 1: 63, pl. 20. 1806. *Guadua angustifolia* Kunth, Synopsis Plantarum 1: 252, 253. 1822. *Nastus guadua* (Humb. & Bonpl.) Sprengel, Caroli Linnaei . . . Vegetabilium 2: 113. 1825. TYPE: Nov. Granada [Colombia], *Bonpland 2003* (lectotype, here designated, P not seen, photo and fragment, US; isolectotypes, B not seen (and possibly destroyed), fragment, US; possible additional isolectotype, P).

Guadua aculeata Rupr. ex Fourn. Mexicanas Plantas . . . Pars secunda Gramineae, p. 130. 1886. *Bambusa aculeata* (Rupr. ex Fourn.) Hitchcock, Contr. U.S. Natl. Herbarium 17: 387. 1913 [as *Bambos*]. TYPE: Mexico. Veracruz: Colipa, 1841, *Karwinsky 944* (lectotype, here designated, LE, fragment, US).

Guadua inermis Rupr. ex Fourn. Mexicanas Plantas . . . Pars secunda Gramineae, p. 129. 1886. TYPE: Mexico. Veracruz: Papantla, 1841–1842, *Karwinsky 946b* (lectotype, here designated, LE, fragment, US).

Guadua intermedia Rupr. ex Fourn. Mexicanas Plantas

. . . Pars secunda Gramineae, p. 130. 1886. TYPE: Mexico. Veracruz: Papantla, *Karwinsky 1464* (holotype, LE, fragment, US).

Guadua aculeata Rupr. ex Fourn. var. *liebmanniana* Camus, Les Bambusées, p. 112. 1913. TYPE: Mexico. Veracruz: Colipa, Mar. 1841, *Liebmann 136* (lectotype, here designated, US).

Guadua angustifolia Kunth var. *bicolor* Londoño, Rev. Acad. Colomb. Cienc. 17: 379. 1989. TYPE: Colombia. Cundinamarca: vía Honda–Guaduas, "Km 119," 930 m, 29 Jan. 1987, *Londoño & Quintero 70* (holotype, COL not seen; isotypes, COL not seen, TULV not seen, US not seen).

Culms 7–25 m tall, 7–15 cm diam., exceptional culms to 30 m tall and 20 cm diam. *Culm leaf ligule* almost always curved up before reaching leaf margin, rarely continuous to one or both margins. *Foliage leaf sheath* entirely glabrous to covered toward midrib of lower half, rarely along midrib of upper half, with light brown to hyaline, prostrate, antrorsely oriented macrohairs, 0.05–1.5 mm long, the collar 0.1–0.9 mm long, slightly flaring to clearly flaring, the oral setae 0–13(–20), the auricles absent to present, the ligule 0.1–0.9(–1.2) mm long, pubescent. *Foliage leaf blade* (7.5–)10–20(–23) cm long, 0.9–3.2(–5) cm wide, glabrous to commonly with scattered hyaline hairs. *Synflorescence* borne on leafy or occasionally leafless twigs. *Pseudospikelets* erect to arcuate, 1.5–9(–10) cm long, (2–)3–6(–7) mm wide, containing (4–)5–17(–18) florets.

Distribution. Occurring sporadically from Veracruz and Puebla, Mexico, south through Guatemala, Honduras, El Salvador, Nicaragua, and Panama; common in Colombia in middle to upper watersheds of Cauca and Magdalena rivers and east into southern llanos and Amazon basin; common in Ecuador west of Andes and along rivers of Amazon basin; sporadic in northern Amazon basin of Peru; also collected from a few localities in southern Venezuela (possibly cultivated) and Guyana (Figs. 2, 3).

Common names. Tarro, Otate (Central America); Guadua, Caña brava, Caña mansa, Garipa (Colombia and Ecuador); Marona, Ipa (Peru); Juajua, Puru puru (Venezuela).

Additional specimens examined. MEXICO. VERACRUZ: District of Papantla, Tajín, 26 Mar. 1948, *Kelly 180* (US); Colipa, Mar. 1841, *Liebmann 137* (LE, US); San Sebastian, *Liebmann 135* (US); Colipa River valley 3 km W of Vega de Alatorre, *Young 205* (FLAS, US, XAL). PUEBLA: Cuauhtapanaloyán, Cuetzalán, 4 Apr. 1981, *Basurto et al. 409* (MEXU). GUATEMALA. SAN MARCOS: Finca Ona near El Quetzal, *McClure 21562* (US). IZABAL: Boca Ancha, 5 July 1948, *McClure 21675* (US); vicinity of Quiriguá, *Standley 24035* (NY, US); between Virginia and Lago Izabal, Montaña del Mico, *Steyermark 38762* (F); Quiriguá, *Weatherwax 39* (US). RETALHULEU: N of San Luis, 29 Jan. 1948, *McClure 21572* (US); between Nueva Linda and Champerico, *Standley 87743* (F). SUCHITEPEQUEZ: Hacienda Chocolá along Chocolá River, *McClure 21488* (US); Puente ICAM at 21 km from Chocolá on the road to Quezaltenango via Mazatenango and San Francisco Zapotitlán, 30 Jan. 1948, *McClure 21573* (US); El Pito, experiment gardens of the Instituto Agropecuario Nacional (from Honduras), 13 Feb. 1948, *McClure 21591* (US); near Pueblo Nuevo, *Standley 66933* (F, US). SOLOLA: Finca Monte de Oro, *Popenoe 976* (US). HONDURAS. ATLANTIDA: Tela, Lancetilla Experiment Station, a native species, *McClure 21673* (US); Lancetilla Valley near Tela, *Standley 53166* (F). EL SALVADOR. AHUACHAPAN: road from San Salvador to Ahuachapán, 20 km W of Santa Ana, *McClure 21608* (US); nursery "Las Actuales Circunstancias" near Ahuachapán, 8 Apr. 1948, *McClure 21615* (US). NICARAGUA. ZELAYA: El Recreo, agricultural experiment station, wild along Chiwawa Creek at farthest rice test plot, *McClure 21477* (US). PANAMA. CHIRIQUI: Boquerón, 2 Apr. 1937, *Allen 300* (US). CANAL ZONE: near property shed at the experiment gardens, Summit, 15 May 1945, *McClure 21339* (US). GUYANA. Banks of rivers, Dec. 1892, *Jenman 6370* (US); Aruka River, *Jenman 7274* (US). VENEZUELA. AMAZONAS: Río Casiquiare, base of Piedra Guanare, *Wurdack & Adderley 43186* (P, US, VEN). COLOMBIA. META: Reserva Nacional La Macarena, frente a la desembocadura del Río Sansa, Apr. 1957, *Idrobo 2600* (COL); Puerto López, *Little & Little 8333* (COL); margen izquierda del Río Guayabero, raudal de la Macarena (Angostura #1), *Pinto & Bischler 314* (COL, P, US); municipio de San Martín, vereda Bajo Humadea, margen derecha del Río Humadea, Finca la Isla, *Pinto & Bernal 1675* (COL, P, VEN). CAQUETA: Solano on Río Caquetá, 12 Mar. 1945, *Little & Little 9779* (COL, US). ANTIOQUIA: Granja de Las Mercedes, en Venecia, *Gutiérrez & Barkley 17C609* (COL, US). CUNDINAMARCA: Nocaima, Hacienda Tobia, 15–20 Jan. 1942, *García-Barriga 10685* (COL); La Vega, camino a Nocaima, 27 Jan. 1942, *García-Barriga 10648* (COL, US); La Esperanza a San Javier, camino de herradura y línea del ferrocarril a Girardot, 15 Jan. 1947, *García-Barriga 12202* (COL, US); carretera de Pacho a Talauta, 1 Nov. 1940, *Jaramillo-Mejía 25* (COL); La Esperanza, *Obregon 108* (COL); Tocaima, *Pérez-Arbeláez 2416* (COL); La Mesa, Tena, *Triana s.n.*, Dec. 1854 (US). CALDAS: Chinchiná, *McClure s.n.*, 31 Dec. 1949 (US). RISARALDA: Pereira, en la vereda de Mundo Nuevo, *Rodríguez 001* (COL). QUINDIO: municipio de Pijáo, Hacienda Paraguaycito (FEDECAFE), *Ramírez s.n.*, 4 Nov. 1976 (COL). HUILA: 1 km SW of San Antonio Fortelecillas, 20 km E of Neiva, 25 Jan. 1943, *Fosberg 19831* (US); along Río Neiva, Juntas, near Algeciras, *Little & Little 7805* (COL, US). VALLE: Cordillera Occidental, vertiente occidental, hoya del Río Anchicaya, El Paso, *Cuatrecasas 14858* (US); cerros cerca de Alcalá, 15 Nov. 1946, *Cuatrecasas 22874* (COL, F, P, S, US); Bitaco, 14 Aug. 1949, *García-Barriga 8005* (COL, US); La Cumbre, *Killip 5998* (US); Hacienda Miranda near Palmira, *McClure 21233* (US); Palmira, wild on campus of the agriculture school, *McClure 21737* (US). CAUCA: near Popayán, *Alston 8566* (COL, US); Popayán, Cauca Valley, *Lehmann 7639* (US); Hacienda García, Corinto, between Miranda and Padilla, *McClure 21232* (US). NARIÑO: Tumaco, right bank of Rosario River, 5 km above Caserío de Santa María, *Romero Castañeda 5197* (COL). ECUADOR. NAPO: Arajuno, flood plain of Arajuno River, 72 mi. NE of Shell-Mera, *McClure 21360* (US); S shore Aguarico River near Zancudo Lake, *Young 25* (FLAS, QCA, US); across Napo River from Misahuallí, *Young 66* (FLAS, QCA, US); 48 km N of Tena on road to Baeza, *Young 84* (FLAS, QCA, US); 4 km W of Borja on road to Baeza, *Young 95* (FLAS, QCA, US); 6 km W of Coca Falls on road to El Charco, *Young 99* (FLAS, QCA, US). CARCHI: environs of Chical, 12 km below Maldonado on Río San Juan, *Madison et al. 4671* (F, US); River San Juan bridge crossing near Maldonado, *Young 140* (FLAS, QCA, US). ESMERALDAS: Concepción, up Río Santiago to Selva Alegre, near village of Timbura, *Little 6390* (F, UC, US); Playa de Oro, *Little 6409* (F, UC, US); Río Guayabamba, 10 km E of Quinindé, *Little & Dixon 21251* (F, US); Río Bravo, 0.5 km S of Cayapas River, *Young 67* (FLAS, QCA, US); junction of San Miguel and Cayapas rivers, *Young 68* (FLAS, QCA, US). PICHINCHA: between Santo Domingo and Quinindé, *Acosta-Solís 14013* (US); Nanegalito, N of Tandayapa, *Acosta-Solís 17157* (US); Quito–Santo Domingo road, *McClure 21400* (US); outskirts of Santo Domingo, *McClure 21401* (US); Rancho Ronald, km 28 on Santo Domingo–Chone road, *Young 117* (FLAS, QCA, US). MANABI: Mount Monte Cristi, near Colorado, SE of Manta, *McClure 21375* (US); Cerro de Balsamo, *McClure 21376* (US); Chagualu, 7–8 mi. N of Chone on the Quito road, *McClure 21377* (US); Cerro Plácido, hillside above San Plácido, *McClure 21378* (US); San Antonio on Chone River, *McClure 21380* (US); edge of Porto Viejo, *McClure 21382* (US); Salima, 3 km SE of Jama, *Young 65* (QCA, US). TUNGURAHUA: trail up to Hacienda La Gloria from Río Negro bridge on way across the Río Pastaza, *McClure 21361* (US); between San Francisco and Machay along road in valley of Pastaza River, 13 July 1945, *McClure 21364* (US); 11 km E of Baños on road to Puyo, *Young 53* (FLAS, QCA, US). COTOPAXI: Tenefuerte, Río Pilaló, km 52–53, Quevedo–Latacunga, *Dodson & Gentry 12252* (MO). BOLIVAR: Charquiyacu, descenso inferior externo de la Cordillera Occidental, *Acosta-Solís 6127* (F). LOS RIOS: Estación Biológica Pedro Franco Dávila at Jauneche on road from Mocachi to Palenque on Estero Peñafiel, *Dodson & Gentry 12689* (US); Pichilingüe Experiment Station, *Little 6437* (F, UC, US); Hacienda Camarones, 30 mi. N of Quevedo, *McClure 21347* (US); near Pichilingüe on Quevedo River flood plain, *McClure 21354* (US); Hacienda Pichilingüe, *McClure 21384* (US). GUAYAS: Teresita, 3 km W of Bucay, *Hitchcock 20415* (US); Panigón Plantation, 8 mi. S of Milagro, *Hitchcock 20585* (US); Daule on Daule River, *McClure 21383* (US). MORONA–SANTIAGO: along the path El Descanso near the Yungaza River N of Limón on the Cuenca–Macas road, *Young 32* (QCA, US); 17 km S of the junction of the Negro and Paute rivers on the Cuenca–Sucúa road, *Young 33* (QCA, US). ZAMORA–CHINCHIPE: 3 km E of Zumbi towards the Nangaritza River, 1 June 1980, *Young 151* (FLAS, QCA, US). EL ORO: between El Carmen and El Blanco, 23 Nov.–15 Dec. 1987, *Albert de Escobar 983* (MO); El Tablón, 6 km E of Portovelo, *Fosberg & Giler 23013* (US). PERU. LORETO: km 174 from Huánuco on the Tingo María–Pucallpa road, *McClure 21437* (US). AMAZONAS: confluence of Icikiti and Cenepa, *Berlin 626* (MO, US).

b. **Guadua angustifolia** Kunth subsp. **chacoensis** (N. Rojas) S. Young & W. Judd, comb. et stat. nov. *Bambusa chacoensis* N. Rojas, Bull. Acad. Int. Geogr. Bot. 26(4): 157. 1918. TYPE: Argentina. Chaco: Depto. Bermejo, General Vedia, riberas del Río de Oro, 23 July 1974, *C. Quarín et al. 2384* (neotype, here designated, CTES; isoneotypes, F, G, US). Figures 9, 10.

Culms 12–20 m tall, 10–15 cm diam. *Culm leaf ligule* continuous to one or both margins or occasionally curved up before reaching margin. *Foliage leaf sheath* glabrous, the collar (0–)0.1–0.2(–0.3) mm long, not flaring to slightly flaring, the oral setae (0–)1–5(–7), the auricles absent, the ligule 0.1–0.3(–0.4) mm long, pubescent. *Foliage leaf blade* (6.5–)9.2–15.6(–25.6) cm long, (0.5–)0.7–1.7(–2.8) cm wide, glabrous or with only a few scattered hairs. *Synflorescence* borne on leafless to rarely leafy twigs. *Pseudospikelets* erect to rarely slightly arcuate. *Main florescence* (2.8–)3.2–5.6(–6) cm long, (4–)5–7(–8) mm wide, containing (5–)6–10(–11) florets.

Distribution. Paraguay and Paraná river watersheds of eastern Paraguay, northeastern Argentina, and southeastern Brazil; also possibly along Uruguay River in northeastern Argentina and northwestern Uruguay (Fig. 4).

Common names. Tacuara, Tacuaruzú.

Specimens examined. BRAZIL. PARANA: just outside of Foz do Iguaçú on the border between Brazil and Paraguay, along the Rio Paraná on the Brazilian side, *Davidse et al. 11233* (F, NY). ARGENTINA. MISIONES: Depto. San Ignacio, Peñon Reina Victoria, *Krapovickas & Cristóbal 28759* (US); vicinity of Puerto Aguirre, *Curran 676* (US); Puerto León, *Curran 677* (F, US); Eldorado, *Meyer 5.567* (UC); Iguazú Falls, *Rodriguez 486* (MO, US). CORRIENTES: Depto. Concepción, Rincón de San Pedro, *Burkart et al. 30.687* (US); vicinity of Goya, *Curran 313* (US); Depto. Ituzaingó, Isla Apipé Grande, Puerto San Antonio, *Krapovickas et al. 23851* (CTES, G, MO, US); Depto. Ituzaingó, Rincón Ombú Chico, *Krapovickas et al. 25470* (CTES, ENCB, G, MO, US); Depto. Capital, Riachuelo y Ruta 12, borde be bosque de Urunday, *Maruñak 635* (CTES, US); Isla San Martín, frente a Ituzaingó, *Meyer 6284* (UC); Depto. Capital, Arroyo Riachuelo y Ruta 12, *Quarín et al. 1859* (CTES, US); Depto. Concepción, Paso Aguirre, Rincón de San Pedro, *Quarín 2870* (CTES, US); Depto. Mercedes, 75 km N of Mercedes, Laguna Trin, Culantrillar, *Quarín 3182* (CTES, US); Depto. Capital, puente Pesoa, Arroyo Riachuelo, *Schinini et al. 6819* (CTES, US). CHACO: Depto. Bermejo, General Vedia, riberas del Río de Oro, *Quarín et al. 2384* (CTES, F, G, US); Casa Lata, *Rojas 11719* (S). PARAGUAY. SAN PEDRO: Colonia Nueva Germania, *Rojas 2311-10492* (US); Alto Paraguay, Primavera, *Woolston G112* (UC, US). CAAGUAZU: entre Coronel Oviedo y Colonia Independencia, orillas Arroyo Tebicuary, *Burkart 18741* (US). CAAZAPA: Salitre Cué, barranca selvática del Río Tebicuary-guazú, *Pavetti & Rojas 10959a* (US). CENTRAL: Ruta 2 y Arroyo Mboiy, *Schinini 10956* (US). PARAGUARI: forest near Sapucay, *Hassler 1730* (G); Sapucai, près de Paraguari, *Balansa 4346* (US).

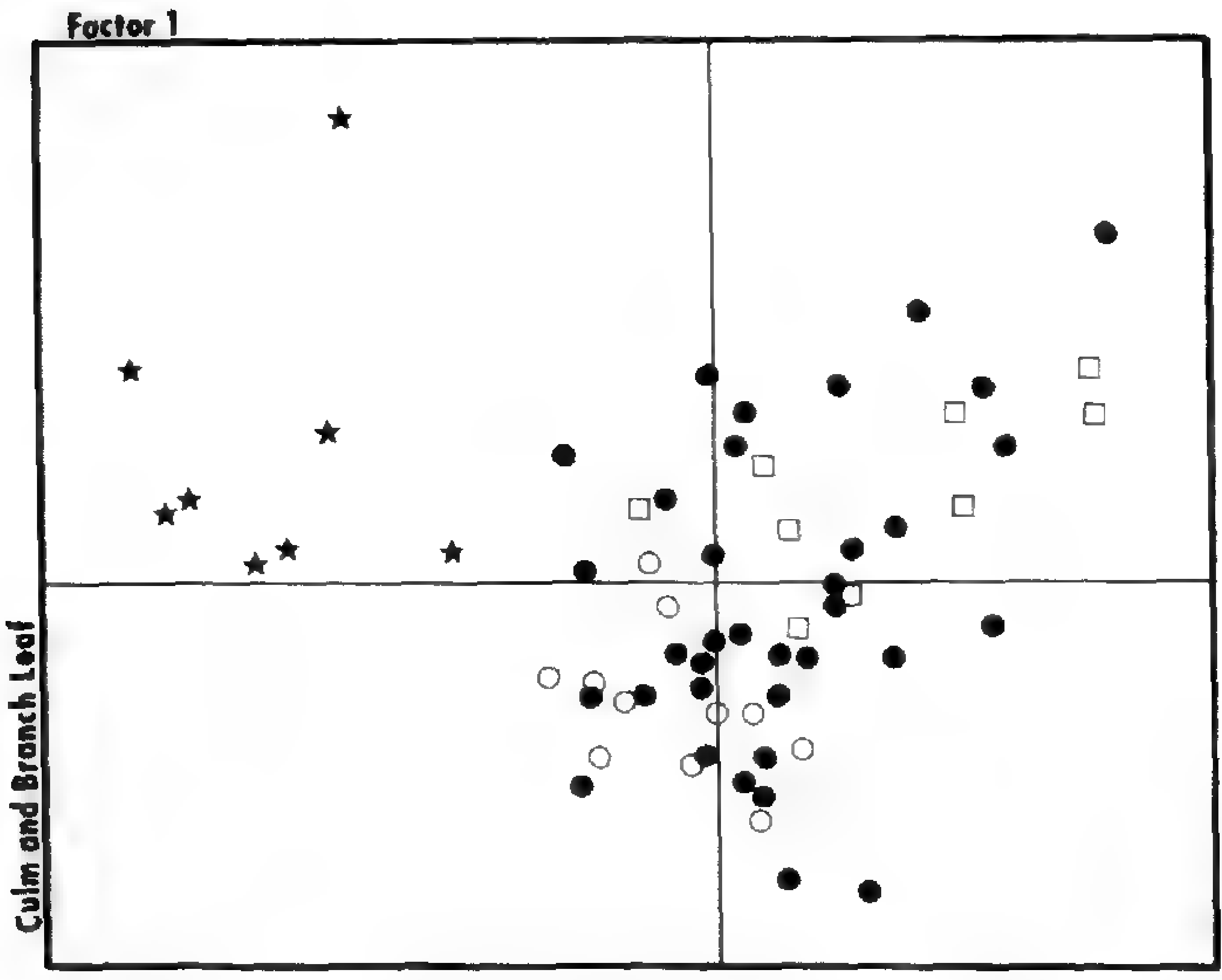

FIGURE 13. Principal components analysis of culm and foliage leaf data; the first two components account for 23.5% of the variation. Stars = subspecies *chacoensis*; dots = subspecies *angustifolia* "western populations"; open circles = subspecies *angustifolia* "northern populations"; squares = subspecies *angustifolia* "eastern populations."

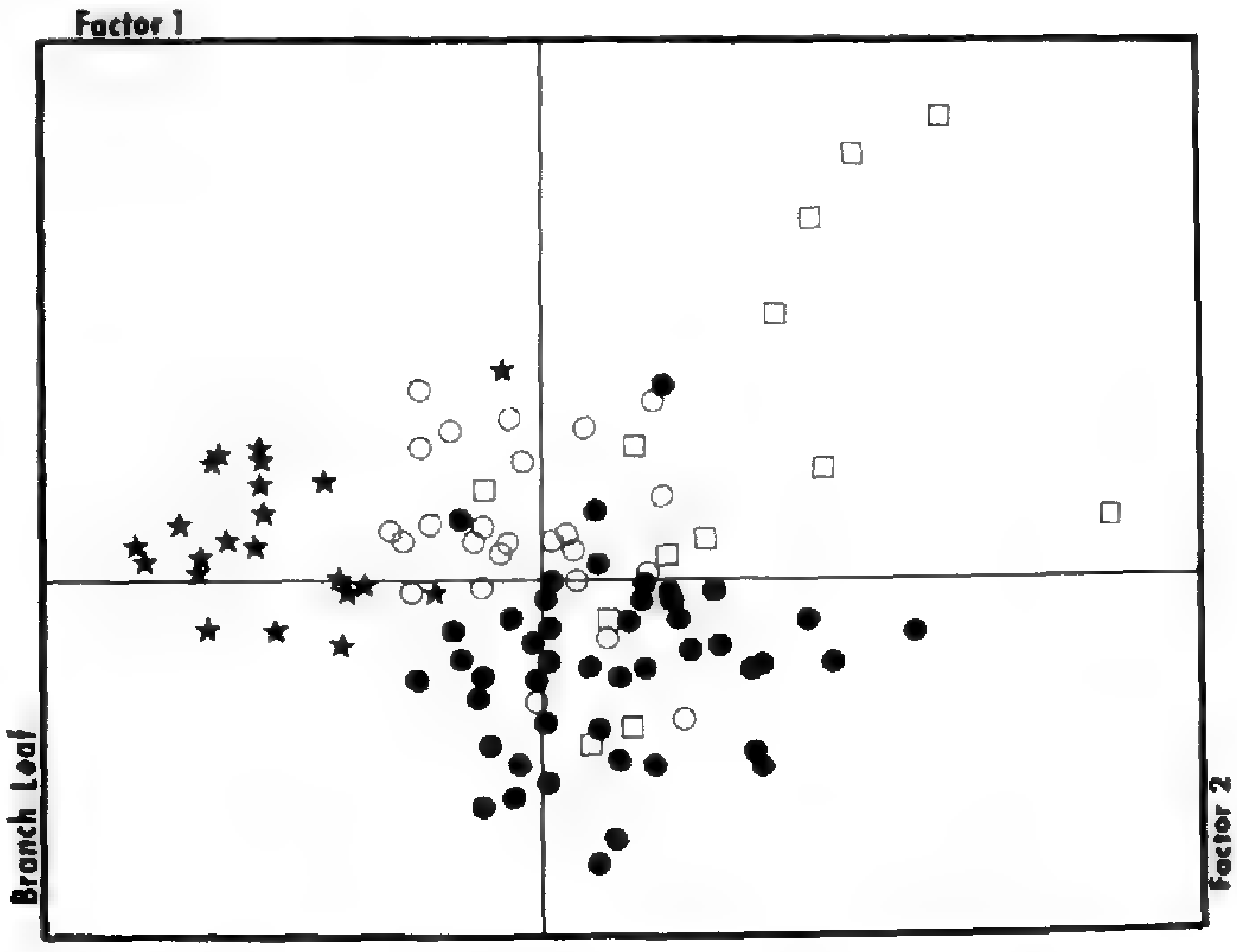

FIGURE 14. Principal components analysis of foliage leaf data; the first two components account for 25.1% of the variation. Stars = subspecies *chacoensis*; dots = subspecies *angustifolia* "western populations"; open circles = subspecies *angustifolia* "northern populations"; squares = subspecies *angustifolia* "eastern populations."

The range of *Guadua angustifolia* is extraordinarily broad in comparison to most bamboos. Most plant and animal species with extensive ranges show some infraspecific variation, but until now there have been no detailed studies of the variation within any of the species in the genus *Guadua*. The geographical barriers between populations of *G. angustifolia* are wide enough to have favored some degree of local divergence. The variation is relatively complex, with vegetative and floral characters showing differing and mosaic patterns of variation. Thus, populations (and taxa) may be separated only by using sets of correlated characters.

The populations that make up *Guadua angustifolia* subsp. *angustifolia* are more similar in both vegetative and floral features to each other than they are to the southern populations here recognized as *G. angustifolia* subsp. *chacoensis*. These populations of *G. angustifolia* subsp. *angustifolia* can be divided into three main groups: the Mexican and Central American populations (i.e., "northern race," formerly called *G. aculeata*); the western Colombian and western Ecuadorian populations (i.e., "western race") including the few specimens from Venezuela (possibly introduced) and Guyana; and the Amazon basin populations (i.e., "eastern race") from Colombia, Ecuador, and Peru.

Vegetatively, these three population groups or "incipient geographical races" are very similar. Principal components analysis of culm and branch leaves shows the variation of the eastern and northern populations to be contained wholly within that of the western populations (Fig. 13). A similar overlapping pattern of variation in these populations is seen when only branch leaves are considered (Fig. 14). The northern populations tend to have foliage leaf sheaths that are glabrous, whereas the sheaths of the eastern and western populations usually possess macrohairs. In the eastern populations some specimens possess distinct auricles on the foliage leaves and tend to have longer ligules and larger pulvini, especially on the juvenile leaves (Fig. 10b). These characteristics do not appear anywhere else within the range of the species, and their influence is evident on the PCA diagram based upon branch leaf characters (Fig. 14). Some of the specimens (i.e., those with auricles) are placed well away from the "central cluster," but other eastern specimens (those lacking auricles) are not separated. This character does not seem to be constant within the eastern populations, and its taxonomic value is in doubt. We conclude here that these eastern populations do not warrant formal taxonomic recognition. The first author noted the general trend toward smaller culms in the Oriente of Ecuador (Young, 1981), but no systematic study of culm size has been carried out, due to the lack of adequate collections.

Inflorescence characteristics are also variable among these three "incipient geographic races" of *Guadua angustifolia* subsp. *angustifolia*, but no large gaps are present. The "western race" possesses the largest spikelets, i.e., (3.1–)3.5–9(–10) cm long, which have a tendency to arch. The "northern race" seems to show a cline in spikelet length, with the spikelets becoming shorter from Panama northward. They are (1.5–)2–5.3(–7) cm long and erect or rarely slightly arching (Fig. 17b,

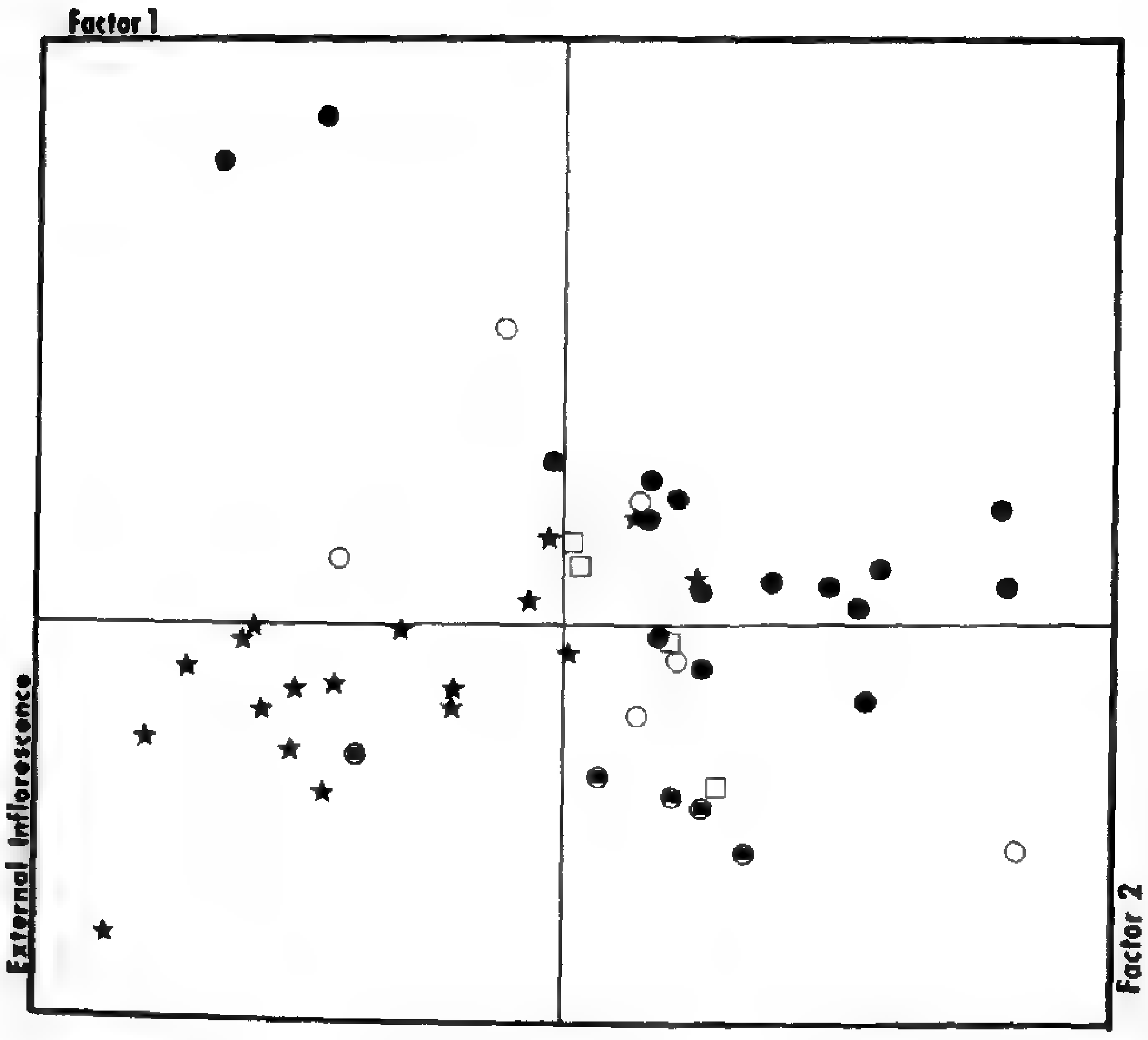

FIGURE 15. Principal components analysis of external inflorescence data set; the first two components account for 27.8% of the variation. Stars = subspecies *chacoensis*; dots = subspecies *angustifolia* "western populations"; open circles = subspecies *guadua* "northern populations" from Central America; circles with letter "m" = subspecies *angustifolia* "northern populations" from Mexico; squares = subspecies *angustifolia* "eastern populations."

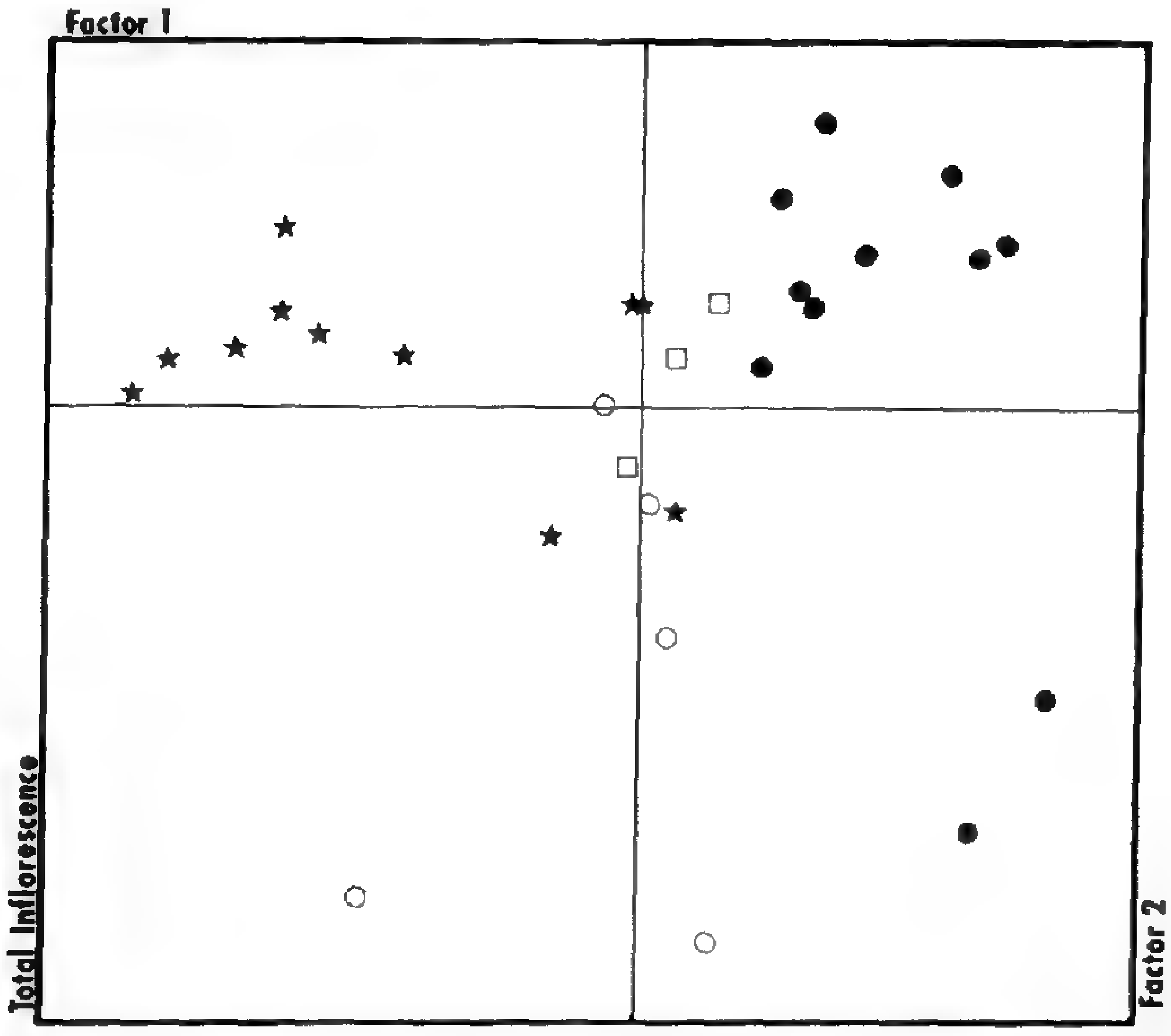

FIGURE 16. Principal components analysis of total inflorescence data set; the first two components account for 31.2% of the variation. Stars = subspecies *chacoensis*; dots = subspecies *angustifolia* "western populations"; open circles = subspecies *angustifolia* "northern populations"; squares = subspecies *angustifolia* "eastern populations."

d). Principal components analysis of external inflorescence characters shows the Mexican specimens to be most different from the western populations, with other Central American plants bridging the "gap" between these areas (Fig. 15). When the PCA of data from dissected spikelets is examined (Fig. 16), an analysis involving a greater number of characters (and showing the influence of internal structures such as palea and style length and style hairs on the principal component loadings), there is a small gap between these "races" of subspecies *angustifolia*. The "northern race" tends to have longer styles and style hairs than either the "eastern race" or "western race," and their paleas are slightly longer. This analysis should be interpreted with caution, however, since the sample size is very small. In McClure's (1955) detailed descriptions of *B. guadua* and *B. aculeata* in the *Flora of Guatemala*, there are only four significant differences between the two, and they all involve floral characters. These include gemmiparous bract length, spikelet length, floret number per spikelet, spikelet cross section, and anther connective extension. The present study shows more overlap in these same characters when more specimens are taken into account than were available to McClure (see descriptions).

The "eastern race" also tends to have short pseudospikelets that are not arched (Fig. 17c), but some plants from this region have pseudospikelets comparable to those of western plants. For example, Figure 17a depicts the pseudospikelets from a clump growing in the southern Amazonian region of Ecuador. They are longer and more arched than is typical for plants in the eastern region and are comparable to many from the "western race" of subspecies *angustifolia*. This illustrates the need for more material from this region before any formal taxonomic decision concerning the status of these "incipient geographical races" can be made.

In contrast to the situation involving the "incipient geographic races" within *Guadua angustifolia* subsp. *angustifolia*, *G. angustifolia* subsp. *chacoensis* shows a number of vegetative and floral characters that allow these southern populations to be consistently distinguished from any other populations of the species. The degree of vegetative difference is shown in PCA of both branch and culm and branch leaf characters (Figs. 13, 14) where there is a clear, although not large, gap between *G. angustifolia* subsp. *chacoensis* and the remaining populations of *G. angustifolia*.

In subspecies *chacoensis* the ligule of the culm leaf is often continuous to the leaf margin (Fig. 9d). In other respects it is similar to the culm leaf of subspecies *angustifolia*. The foliage leaves are the most distinctive vegetative feature of this subspecies. The sheaths are always glabrous. The collar is shorter and less flared, the ligule possesses longer hairs, and the pulvini are smaller than those of subspecies *angustifolia*. The blades are almost always glabrous abaxially and rarely possess any macrohairs adaxially. Subspecies *angustifolia* of-

FIGURE 17. Spikelet variation in *Guadua angustifolia* subsp. *angustifolia*. —a. Long spikelets of "eastern race"; *Young 151*. —b. Long spikelets of "northern race"; *McClure 21573*. —c. Short spikelets of "eastern race"; *McClure 21364*. —d. Short spikelets of "northern race"; *Karwinski 944*.

ten has macrohairs on one or both surfaces except on primary leaves. Blade widths also tend to be narrower in subspecies *chacoensis*, but there is a fair amount of overlap in this character.

Culm characteristics of the two subspecies were not compared because of the lack of material of subspecies *chacoensis*. From label data and photos the culms do not appear to be significantly different, although subspecies *chacoensis* does not attain the height of some culms of subspecies *angustifolia*.

Some degree of separation is also shown in PCA of floral characters. *Guadua angustifolia* subsp. *chacoensis* tends to have shorter and more erect pseudospikelets than the western populations of *Guadua angustifolia* subsp. *angustifolia*, and therefore shows some overlap with the eastern northern populations in PCA based upon these characters (Figs. 15, 16). However, subspecies *chacoensis* almost always has wider pseudospikelets than the eastern and northern populations of subspecies *angustifolia*, and therefore is easily distinguished (see key). It shows more of an overlap in pseudospikelet width with the western populations of subspecies *angustifolia*. The synflorescences of subspecies *chacoensis* are almost always borne on leafless twigs, whereas those of subspecies *angustifolia* often are intermixed with leafy twigs or have leaves on the same twigs. However, there are some specimens of subspecies *angustifolia* that have pseudospikelets borne only on leafless twigs. The color of pseudospikelets is difficult to determine because of developmental changes, but those of subspecies *chacoensis* tend to be brownish (vs. more or less stramineous in subsp. *angustifolia*). Again, this difference is not absolutely consistent, but is only a general trend. Paleas tend to be longer and wider in subspecies *chacoensis*. The lengths of the style and style hairs are longer in subspecies *chacoensis* than in the western and eastern "races" of subspecies *angustifolia*, but are similar to the "northern race."

The flowering cycle for *Guadua angustifolia* has not been accurately determined, but it appears to be close to 30 or 35 years. In 1976, extensive flowering was observed in clumps of subspecies *angustifolia* in Colombia and subspecies *chacoensis* in Argentina. This may provide evidence that the two taxa are conspecific. In addition, the overall similarity of the two subspecies (especially when compared to other sympatric species of the genus *Guadua*) indicates that they are best treated as one polymorphic species.

In past descriptions of *Guadua angustifolia* from Colombia and Ecuador (McClure, 1955, 1966; Hidalgo, 1978; Maecha Vega & Echeverri Restrepo, 1983), various growth forms have been described. Local people who work with "guadua" on a daily basis distinguish among three forms known as "guadua macana" or "caña brava," "guadua cebolla" or "caña mansa," and "guadua rayada." Guadua rayada is recognized as variety *bicolor* by Londoño (1989). Guadua macana is distinguished from guadua cebolla by having a smaller diameter, more basal branches that are thorny and hinder entrance to the clump, and stronger wood with more resistance to decay. Guadua macana is used for all kinds of heavy construction, whereas guadua cebolla is usually split longitudinally and used as bamboo boards called "esterilla" in Colombia and "picada" in Ecuador. Guadua rayada possesses vertical yellow or white stripes between the nodes and is stronger than guadua cebolla but not as strong as guadua macana. Londoño & Prieto (1983) described guadua macana as by far the most common form in the Cauca Valley of Colombia, with the other forms being found scattered within clumps of macana. These forms are not separated geographically or ecologically and are probably due to slight genetic differences or even environmental and/or competitive effects. However, further study is needed (e.g., breeding studies, common garden experiments) in order to clarify their status.

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A REVISION OF *PANICUM* SUBGENUS *PHANOPYRUM* SECTION *LAXA* (POACEAE: PANICOIDEAE: PANICEAE)[1]

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ABSTRACT

Panicum subg. *Phanopyrum* sect. *Laxa* is revised. Twelve American and one Asian species are treated in this work, in which exomorphological and anatomical characters are considered. Section *Laxa* is defined mainly as perennial plants of humid places, with membranous ligules, spikelets unilaterally disposed on the inflorescences, upper anthecia membranous to indurate, with silica bodies and simple papillae, a basic chromosome number of $x = 10$, and conspicuous fusoid cells in the leaves. Possible relationships of *Laxa* to other sections of subgenus *Phanopyrum* and subgenus *Steinchisma,* as well as with other genera of the Paniceae such as *Homolepis* and *Hymenachne,* are discussed. A key to the species as well as an anatomical description of the section and photomicrographs of six species, morphological descriptions of the species, and distribution maps are presented. The taxonomic position of *Panicum scabridum* and *Panicum grande* are also discussed.

The group Laxa was informally established within *Panicum* by Hitchcock & Chase (1910); these authors initially included seven species in the group: *Panicum polygonatum* Schrader, *P. longum* A. Hitchc. & Chase, *P. pilosum* Sw., *P. laxum* Sw., *P. cupreum* A. Hitchc. & Chase, *P. hians* Elliott, and *P. exiguiflorum* Griseb. In 1915, Hitchcock & Chase validly published the group, adding to Laxa *P. stevensianum* A. Hitchc. & Chase and *P. milleflorum* A. Hitchc. & Chase, defining the group mainly by the inflorescence type, with spikelets unilaterally disposed on short pedicels. Hitchcock & Chase (1915) also described *P. stagnatile* and *P. grande,* not grouping these species within *Panicum.*

Pilger (1931) raised the Laxa group to sectional level and in 1940 characterized the section by the inflorescence type, considering approximately 20 species as belonging to the section. Examples are *P. grumosum* Nees, *P. pernambucense* (Sprengel) Mez ex Pilger, and *P. gynerioides* (Griseb.) Pilger (= *P. prionitis* Nees).

Hsu (1965) differentiated *Laxa* as having 3-nerved lodicules, membranous ligules, papillose upper anthecium, and a basic chromosome number of $x = 10$. Hsu noted relationships between *Laxa* and sections *Tenera* and *Verrucosa* and stated that *Laxa* should be excluded from subgenus *Panicum* and included in subgenus *Megathyrsus,* because of the ornamentation of the upper anthecium.

The classification of *Panicum* has undergone many changes in recent years, due mainly to the study of the Kranz syndrome (Brown, 1977). These new anatomical and physiological characters showed that section *Laxa* sensu lato included species differing markedly in exomorphological and photosynthetic characteristics. Brown & Brown (1975) cited *P. milioides* Nees ex Trin. (= *P. hians*) as a species with physiological characters intermediate between Kranz and non-Kranz species, as is the case in other species such as *P. spathellosum* Doell and *P. decipiens* Nees ex Trin. (Ku et al., 1976; Ku & Edwards, 1978; Morgan & Brown, 1979; Morgan et al., 1980). Brown (1977) placed these three species in a separate genus *Steinchisma* Raf., with intermediate C_3/C_4 photosynthesis, spikelets not unilaterally disposed on the inflorescences, upper anthecium entirely papillose, and lower palea expanded at spikelet maturity. Brown (1977) included eight species of the Laxa group within subgenus *Sarmentosum,* whereas he placed others in the Grandia group. The Grandia group in the sense of Brown is a complex of Kranz species, i.e., *P. petersonii* A. Hitchc. & E. Ekman and *P. prionitis,* and non-Kranz species, such as *P. grumosum, P. pernambucense,* and *P. stagnatile.*

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Zuloaga (1987) defined section *Laxa* by the inflorescence type, nervation of the spikelet, and upper anthecia ornamentation. He included approximately 15 species in the section, which he placed in the non-Kranz subgenus *Phanopyrum* of *Panicum*. *Panicum prionitis* and *P. petersonii* were excluded and placed in section *Prionitia* of subgenus *Agrostoides*, and *P. grande* was ungrouped within subgenus *Phanopyrum*. *Steinchisma* was considered as a separate subgenus of *Panicum*.

In the present treatment, section *Laxa* is defined and diagnosed by its exomorphological and anatomical characters. In addition, the systematic position of *P. scabridum* Doell, *P. condensatum* Bertol., *P. auritum* J. S. Presl ex Nees, and *P. grande* is discussed in relation to this definition of section *Laxa*.

MATERIALS AND METHODS

Procedures of classical taxonomy were used in this study. Specimens were examined from the following herbaria: B, BAA, BAF, BLA, CEN, CEPEC, COL, F, G, GH, HB, IAN, IBGE, K, LE, LIL, M, MO, MY, NY, P, PORT, R, RB, SI, SP, UB, US, VEN, W. Field methods included collection and drying of specimens for herbaria, preserving leaves, spikelets, and other structures in FAA (formalin-ethanol-acetic acid) and transferring them to 70% ethanol in the laboratory.

Laboratory studies were made using a Wild M5 dissecting microscope. For the scanning electron microscope (SEM), anthecia were removed from herbarium specimens, secured on stubs, carbon coated in a vacuum evaporator, and coated with a gold-palladium alloy. These specimens were then viewed in a Cambridge S4-10 or Cambridge Stereoscan 259 Mk2 scanning electron microscope operating at 10–20 kV.

Transverse sections of leaf blade material, 10 μm thick, were sectioned after desilicification in 30% hydrofluoric acid, dehydration in a methyl cellosolve series and infiltration and embedding in Tissue Prep (Fisher Scientific). The sections were stained in safranin and fast green. For abaxial epidermis scrapes, the mesophyll and vascular tissue was removed with a scalpel and camel's hair paintbrush. These were stained in safranin.

The standardized terminology of Ellis (1976, 1979) was used for the anatomical descriptions. The following abbreviations are used: vb/s—vascular bundles; 1'vb/s—first order vascular bundle/s; 3'vb/s—third order vascular bundle/s; ibs—inner bundle sheath; mestome sheath; obs—outer bundle sheath; parenchyma sheath.

Freshly fixed material of the following taxa was studied: *Panicum grumosum* (3 accessions), *P. hylaeicum* (4 accessions), *P. laxum* (13 accessions), *P. pernambucense* (6 accessions), *P. pilosum* (9 accessions), *P. polygonatum* (7 accessions), and the sectional anatomical description is based on this material. This sample was augmented by herbarium material of *P. auritum* (2 accessions), *P. bresolinii* (1 accession), *P. condensatum* (2 accessions), *P. leptachne* (2 accessions), *P. stagnatile* (2 accessions), *P. stevensianum* (6 accessions), *P. grande* (3 accessions), *P. scabridum* (6 accessions) and *P. longum* (1 accession), but anatomical detail was difficult to ascertain in much of this material.

Vouchers for this study are marked with an asterisk (*) in the specimens examined section of the taxonomic treatment.

EXOMORPHOLOGICAL CHARACTERS

Species of section *Laxa* grow in humid places, either along the borders of woods or forming dense colonies on the banks of streams and rivers. Examples are *Panicum pernambucense*, *P. grumosum*, and *P. stagnatile*. *Panicum laxum* and *P. pilosum*, on the other hand, are pioneer species and usually invade modified habitats.

The plants are short-rhizomatous or stoloniferous, decumbent and rooting and branching at the lower nodes, with hollow internodes and leaf blades flat, linear to ovate-lanceolate. The ligules are membranous, shortly laciniate or occasionally ciliate at the apex, commonly absent in *P. pilosum*.

INFLORESCENCE

The inflorescence type is one of the most distinguishing characters of this section, the spikelets being arranged unilaterally on first- or second-order racemose branches. All included species possess this feature.

First-order branches are alternate, subopposite, or whorled toward the base, diverging in all directions in relation to the main axis. A small membranous bract is usually present at the first node of the panicle. This bract has pilose margins or sometimes is reduced to a small arc of papillose hairs.

There is a gradient in the degree of ramification of the inflorescence. Paired spikelets are present on the ventral side of first-order branches in species such as *P. pilosum*, *P. leptachne* Doell, *P. condensatum*, and *P. longum*. In the other species spikelets are paired on second-order branches, with these branches unilaterally disposed in relation to the first-order ones; the second-order branches are appressed or divergent from the axis of first-order branches, and there is variation in the length of the second-order branches, which gives the inflorescence a more or less lax appearance.

SPIKELET

The spikelet in section *Laxa* has the typical structure of the Paniceae, with two glumes and two anthecia, the lower one with a lemma and with or without a palea, the flower present or absent, being male when present; the upper anthecium is hermaphrodite, with a lemma and palea enclosing it. Internodes of the rachilla are inconspicuous between glumes, lower and upper flower.

The spikelets are biconvex, the lower glume reaching ⅓ to ¾ the length of the spikelet, 1–3-nerved; the upper glume and lower lemma are subequal, or the upper glume is slightly shorter and not covering the apex of the upper anthecium, 5(–7)-nerved; the lower palea may be conspicuous and either the same length as the lower lemma, or reduced to completely absent; the lower flower is occasionally present, with two lodicules and three stamens, but is usually absent; the upper anthecium encloses a perfect flower, with two cuneiform, conduplicate lodicules, which embrace the lower borders of the palea; the caryopsis has a punctiform to oblong hilum, with the embryo reaching ⅓ to ½ the length of the caryopsis.

The lower lemma is commonly membranous but occasionally indurate at maturity in specimens of *P. polygonatum*, e.g., *Idrobo & Cuatrecasas 2665*, and *P. laxum*, e.g., *Cuatrecasas & Llanos 24054*. Bisexual flowers occur in the lower anthecium of specimens of *P. stevensianum*, with two lodicules, three stamens and a conspicuous gynoecium, with two styles and a plumose stigma; in this case there is no variation in the consistency of the lower lemma, it being similar to the upper glume; no caryopsis was found in these bisexual lower flowers. The presence of bisexual flowers in the lower anthecium of *Panicum* was previously reported by Palacios (1968), Pohl (1980), and Zuloaga & Sendulsky (1988).

Three-flowered spikelets were occasionally observed in specimens of *P. grumosum*, e.g., *Quarín et al. 2745* and *Millán 568*, with anthecium I neuter, while anthecium II and upper anthecium were bisexual, the two latter with the lemma and palea indurate.

UPPER ANTHECIUM TEXTURE AND ORNAMENTATION (FIG. 1)

The epidermis of the lemma and palea has rectangular long cells arranged in longitudinal rows, with longitudinal and transverse anticlinal walls strongly undulated. Stomata, simple papillae, prickle hairs, and silica bodies are present in species of this section.

The presence of stomata is variable among the different species, being located, when present, toward the apex of the lemma and palea.

Simple papillae are regularly distributed in longitudinal rows. They are associated with the periclinal, external wall of the long cells, eccentric, and near the anticlinal transversal distal wall.

Prickle hairs are frequent toward the apex of the lemma and palea, being retrorse in *P. bresolinii*, *P. polygonatum*, and *P. pilosum*, antrorse in *P. stagnatile*, *P. longum*, *P. laxum*, and *P. hylaeicum* Mez, or with both dispositions in *P. grumosum*, *P. stevensianum*, and *P. leptachne*.

Silica bodies are exfoliate, more or less cross-shaped to nodular.

The upper anthecium varies from membranous at maturity, in such species as *P. grumosum*, *P. pernambucense*, *P. bresolinii* L. B. Smith & Wasshausen, *P. leptachne*, *P. longum*, *P. condensatum*, *P. stevensianum*, and *P. stagnatile*, to more or less indurate in *P. polygonatum*, *P. laxum*, *P. hylaeicum*, and *P. pilosum*.

Anthecial ornamentation varies in relation to the texture of the anthecium, with simple papillae, prickle hairs, and silica bodies abundant in species with membranous anthecia. In the rest of the species with indurate upper anthecia, such as *P. polygonatum*, *P. pilosum*, *P. hylaeicum*, and *P. laxum*, stomata, simple papillae, and prickle hairs are only present toward the apex, and silica bodies are occasionally present at the tip of the lemma.

Verrucose papillae, similar to the ones found in

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FIGURE 1. Scanning electron photomicrographs of female florets of species of *Panicum*.—A. *Panicum longum*, ×100 (from type specimen).—B. *Panicum grumosum*, ×500 (*Smith & Klein 15723*). C, D. *Panicum auritum*.—C. Upper portion, ×50.—D. Tip of the lemma, ×250 (*Merrill 101*). E, F. *Panicum grande*.—E. Dorsal side, ×100.—F. Upper portion of the lemma, ×250 (*Black 15352*). G, H. *Panicum scabridum*.—G. Dorsal side, ×100.—H. Ventral side, ×100 (*Wurdack & Adderley 42986*).

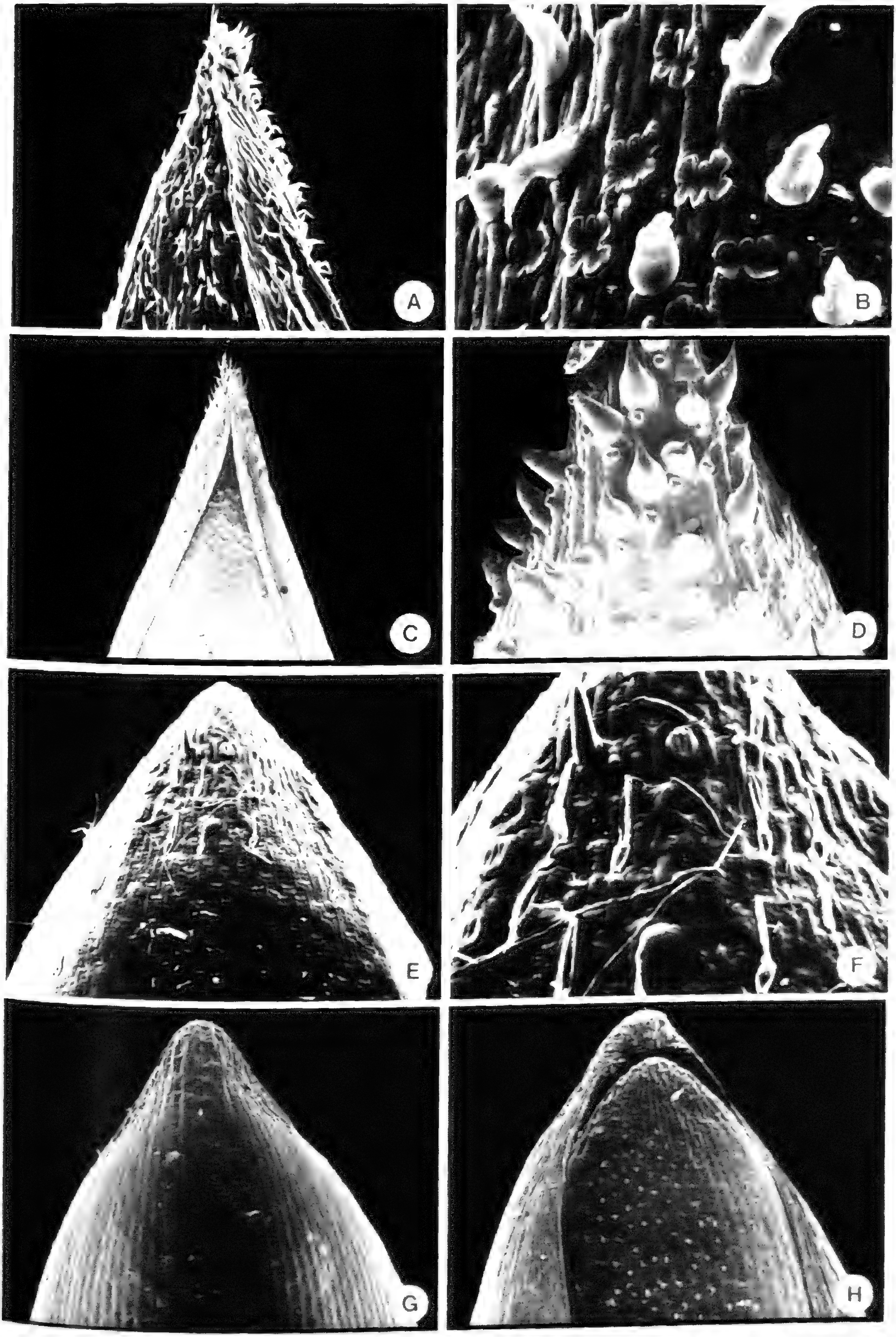
A
B
C
D
E
F
G
H

FIGURE 2. Distribution of *Panicum bresolinii*, *P. longum*, and *P. pilosum*.

species of subgenus *Steinchisma*, are sometimes present in specimens of *P. laxum*.

CHROMOSOME NUMBERS

There are few karyological studies on taxa belonging to section *Laxa*, with data of the cytology of only six species being available. A basic chromosome number of $x = 10$ characterizes the section. *Panicum auritum:* $n = 15$ (Mehra, 1982); $2n = 30$ (Christopher & Abraham, 1976; Mehra & Chaudhary, 1981; Mehra, 1982); $2n = 36$ (Mehra & Chaudhary, 1976, 1981). *Panicum grumosum:* $2n = 40$ (Núñez, 1952). *Panicum hylaeicum:* $2n = 40$ (Bouton et al., 1981). *Panicum laxum:* $n = 20$ (Davidse & Pohl, 1972b, 1974, 1978); $2n = 36$ (Gould & Soderstrom, 1967; Tateoka, 1962); $2n = 40$ (Pohl & Davidse, 1971; Gould & Soderstrom, 1967). *Panicum pilosum:* $n = 10$ (Davidse & Pohl, 1972a, 1974, 1978); $2n = 20$ (Pohl & Davidse, 1971, under *P. milleflorum*). *Panicum pernambucense:* $2n = 40$ (Bouton et al., 1981, under *P. rivulare*). *Pan-*

FIGURE 3. Distribution of *P. grumosum*, *P. hylaeicum*, and *P. polygonatum*.

icum polygonatum: $2n = 40$ (Pohl & Davidse, 1971, under *P. boliviense* Hackel; Pohl & Davidse, 1971).

LEAF ANATOMY (FIGS. 6–17)

The section *Laxa*, as constituted here, exhibits variable leaf blade anatomy, and two slightly different species groupings are evident. These two groups intergrade in their leaf anatomy, and the taxonomic significance of the differences between them will only become apparent once additional species of section *Laxa* are collected and fixed in the field. The anatomical description of the section will, nevertheless, only be based on the following species: *Panicum hylaeicum*, *P. laxum*, *P. pilosum*, *P. bresolinii*, *P. longum*, *P. leptachne*, *P. stagnatile*, *P. stevensianum*, *P. auritum*, *P. condensatum*, and *P. polygonatum*. These species constitute a homogeneous anatomical group in which the leaf anatomy is remarkably uniform, as illustrated in Figures 8–11, 13–16. For convenience,

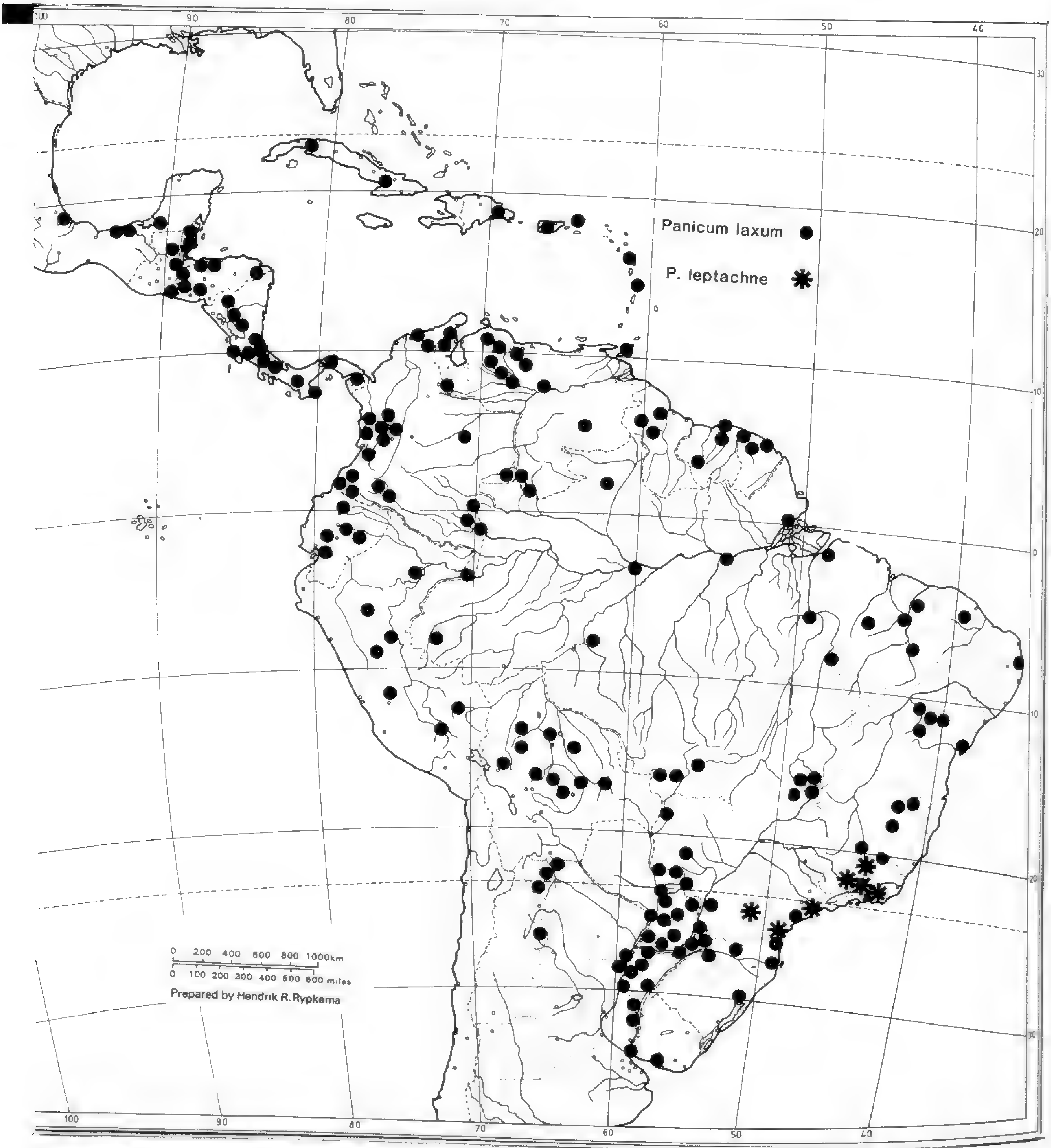

FIGURE 4. Distribution of *P. laxum* and *P. leptachne.*

this will be called the Laxa species group. The anatomy of *P. grumosum* and *P. pernambucense* will be treated separately, as their anatomy differs somewhat from that of the Laxa group (Figs. 7, 12). This will be informally called the Grumosum species group.

LEAF BLADE IN TRANSVERSE SECTION

Outline: expanded, either flat or very broadly V-shaped; the arms of the lamina either straight or outwardly bowed; the two halves often not symmetrical on either side of the median vb, with one half being slightly wider, with more vbs; this asymmetry not pronounced being due to an extra 1′vb with an additional 3′vb between successive 1′vbs in one half of lamina; this can result in a maximum of an extra 20 vbs in one half out of a total of 52 (up to 99 in some specimens of *P. hylaeicum*) in the entire section. Thickness at mid-lamina 150–230 μm. *Ribs and furrows:* rounded adaxial ribs always present over all vbs; all ribs of similar size and shape; size of ribs differs between specimens; adjacent ribs separated by wide, open furrows; depth

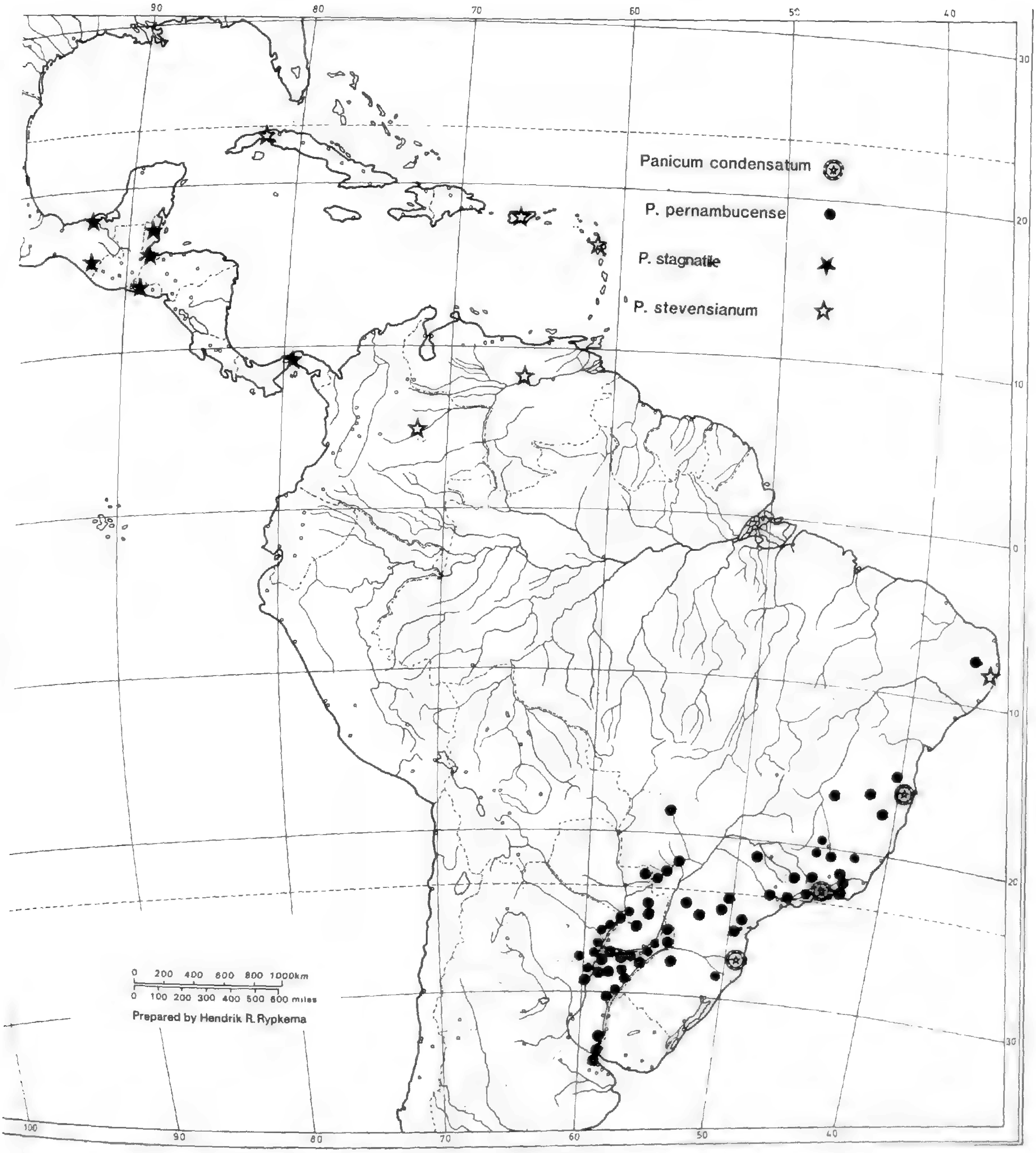

FIGURE 5. Distribution of *P. pernambucense*, *P. stagnatile*, *P. stevensianum*, and *P. condensatum*.

varies from very shallow to medium furrows on different specimens of all species. Slight abaxial ribs usually distinguishable; vary from slight undulations associated with the vbs to ribs the same size as the adaxial ribs, resulting in a ± moniliform outline. *Keel:* always present, but size and amount of associated colorless parenchyma variable; varies from a simple median vb with small amount of adaxial colorless parenchyma to well-developed V-shaped keel incorporating 5 vbs, including 3 1′vbs; the vbs all abaxially located; no lacunae; this structure abruptly separated from the lamina by bulliform cell groups; this type of keel differs considerably from that present in the Grumosum group of this section, where the keel intergrades with the lamina. *Vascular bundle arrangement:* (8–)9–13(–18) 1′vbs in entire blade, usually with an additional 1′vb in one half of lamina; 3, 4, 5, or 6 3′vbs between consecutive 1′vbs; this number differs by one in each half of the lamina; no 2′vbs. All vbs centrally located in the blade thickness, although 3′vbs may be slightly abaxially displaced. *Vascular bundle description:* 3′vbs angular with xylem and phloem distinguishable, 1′vbs circular

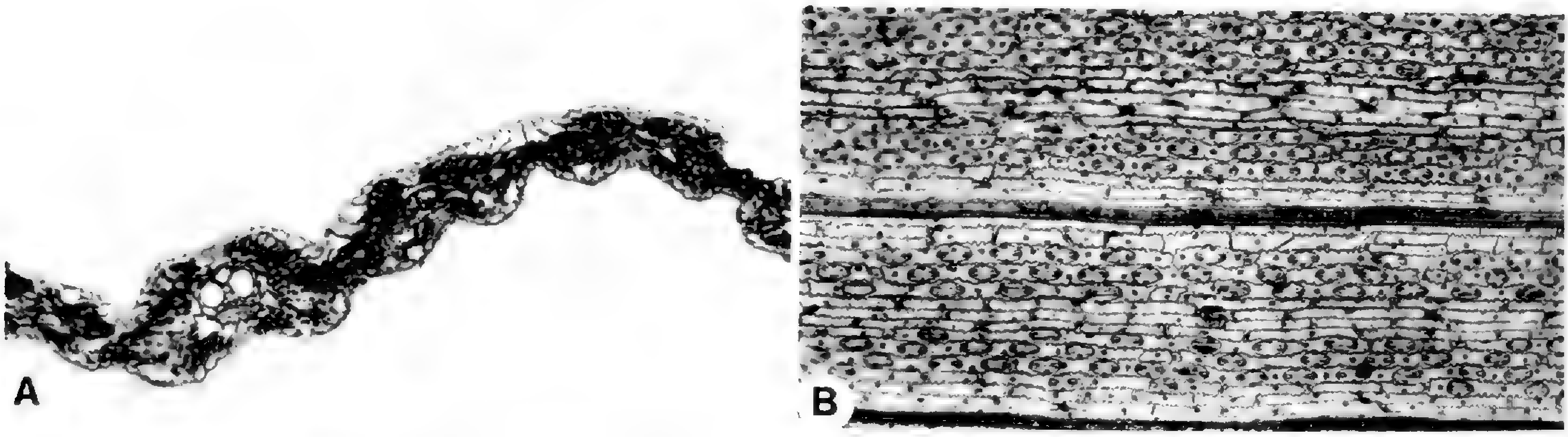

FIGURE 6. Leaf blade anatomy of *P. condensatum.*—A. Transverse section of poorly reconstituted herbarium specimen; fusoid cells and pallisadelike adaxial chlorenchyma are present.—B. Abaxial epidermis with narrow costal zones with dumbbell silica bodies and the intercostal zones clearly divided into lateral stomatal bands, and central files without stomata but with microhairs; epidermal cells nucleate (×250, based on *Davidse et al. 11494*).

to slightly elliptical in outline; phloem adjoins the ibs; lysigenous cavities and protoxylem present; circular metaxylem vessels narrower than the obs cells as seen in section. *Vascular bundle sheaths:* obs of 3′vbs conspicuous, entire, round, without extensions, although an additional adaxial cell is sometimes evident, consisting of 5 or 6 inflated, rounded cells, but up to 8 in some specimens of *P. hylaeicum, P. auritum, P. stevensianum, P. stagnatile,* and *P. bresolinii,* especially toward the midnerve; adaxial cells tend to be largest; chloroplast presence and type variable: either absent, or rarely, relatively small, centripetal specialized chloroplasts occur with few, small plastids; ibs absent. Obs of 1′vbs round or slightly elliptical, with slight abaxial interruption, without extensions, comprised of 8–11 cells; cells smaller than those of 3′vbs, inflated, rounded, usually all similar in shape, but extreme abaxial cells tend to be smallest. Chloroplasts as in obs of 3′vbs. Ibs present, complete, of small cells with uniformly thickened walls. *Sclerenchyma:* minute, inconspicuous adaxial and abaxial girders associated with all vbs; fibers lignified, secondary thickening variable. Small sclerenchyma cap in margin. *Mesophyll:* chlorenchyma not radiate but adaxial cells tend to a pallisade-type of arrangement; these cells tabular whereas the abaxially located chlorenchyma cells are very irregular in shape; more than 8 chlorenchyma cells between consecutive vbs; the cells, particularly those located abaxially, with definite invaginations of the walls, resembling arm cells very closely. Fusoid cells present in mesophyll: elongate, narrow, and inclined downward and present on either side of each vb. Very little reduction evident except near the margin where the lateral fusoid cells may be absent. No colorless cells. *Adaxial epidermal cells:* bulliform cells present in adaxial furrows between all vbs; in restricted groups, generally with a large, fan-shaped, inflated central cell or cells; occupy up to ½ leaf thickness. Epidermal cells small, regular in size, with a distinct continuous cuticle; no macrohairs, prickles, or papillae. *Abaxial epidermal cells:* no bulliform cells; thickened cuticle, no epidermal projections.

ABAXIAL EPIDERMIS IN SURFACE VIEW

Intercostal long cells: elongated, up to 3× longer than wide; parallel side walls; vertical or angled end walls; unthickened, moderately undulating anticlinal walls; this sinuosity conspicuous. Cell shape consistent across intercostal zones except that interstomatal long cells are shorter, long cells in a file either adjoin one another or are separated by short cells—either a single tall and narrow cell or cork-silica cell pairs. Conspicuous nuclei usually present in intercostal long and short cells. *Stomata:* low dome-shaped or ovoid but may tend to low triangular; subsidiary cells with conspicuous nucleus often contained within a slight evagination at the apex. Common with 6–10 files of stomata per intercostal zone, with only the 3–6 central long cell files without stomata—these cells more elongate than the interstomatals and may stain less intensely. Stomatal rows in adjoining files of cells; usually one interstomatal cell between successive stomata in a file but this arrangement variable. Stomata files separated from the costal files by 1–2 intercostal files without stomata. *Intercostal short cells:* either absent, on solitary and tall and narrow or paired with both cork and silica cells and tall and narrow. Distribution irregular, but most common in central files of intercostal zones. *Papillae:* absent except in single specimen of *P. stevensianum* (*Chase 6616*). *Prickle hairs:* absent except for small intercostal hooks on one specimen of *P. pilosum* (*Davidse 21866*). Small angular prickles with short barbs present on the leaf margin. *Microhairs:* elongated, fingerlike, with distal and basal

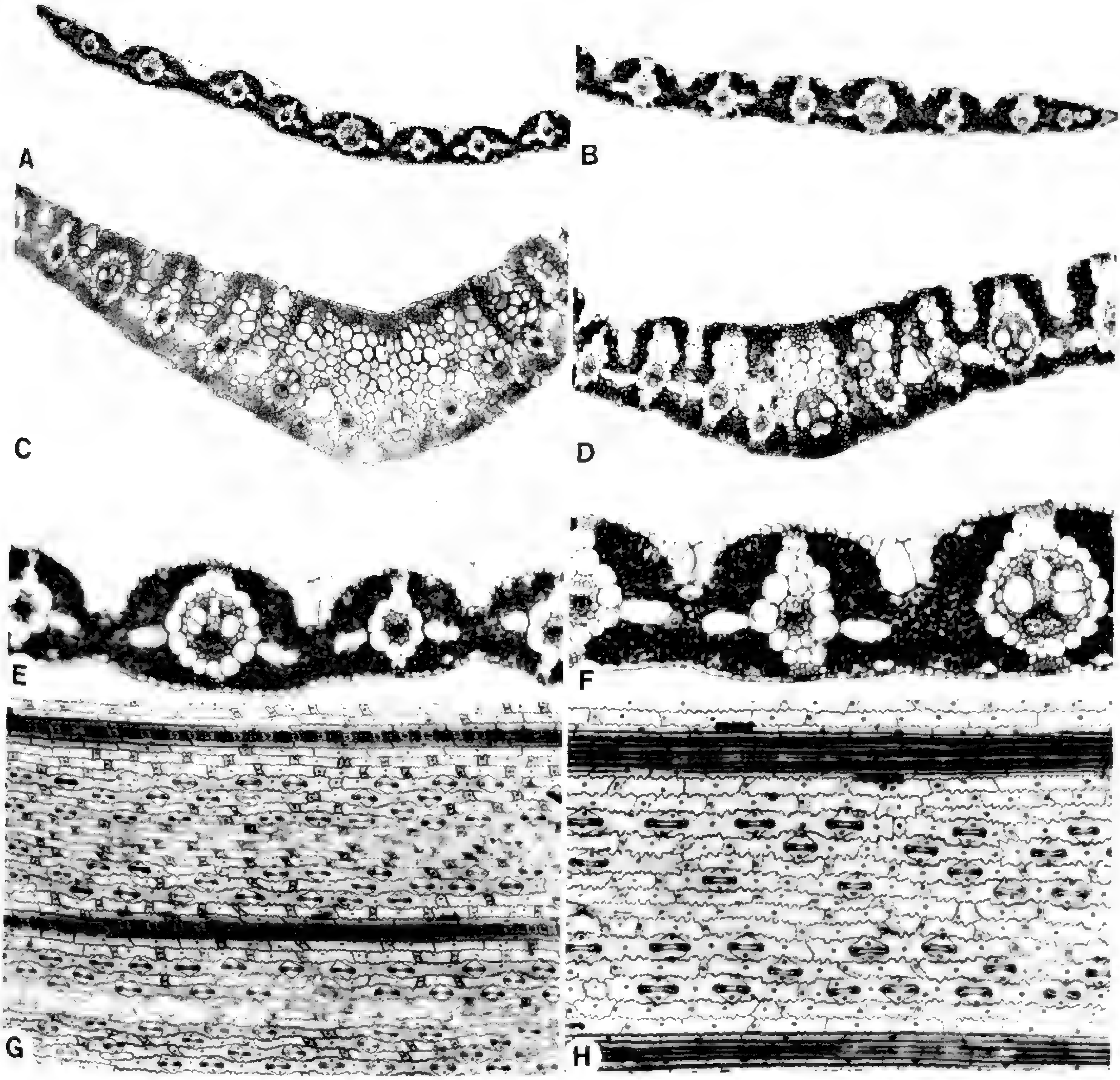

FIGURE 7. Leaf blade anatomy of *Panicum grumosum*. A–F, transectional anatomy.—A. Gently tapering leaf blade margin; note rather irregular occurrence of fusoid cells near margin.—B. Slightly acute margin with small sclerenchyma cap; fusoid not associated with three most lateral bundles and presence irregular, with other bundles situated near the margin.—C. Keel consisting of many vascular bundles (more than 12), all with adaxial bundle sheath extensions and gradually intergrading into the lamina; fusoid cavities in this region of the leaf resemble lacunae, as only a single cavity is present in the mesophyll between successive bundles.—D. Specimen in which keel is less developed but incorporates at least seven bundles; note lacunae intergrading laterally into typical fusoid cavities.—E. Detail of mesophyll at mid-lamina; note regular occurrence of fusoids and much shorter bundle sheath extensions than nearer the center of the blade.—F. Irregular occurrence of fusoid cells and extension of the outer bundle sheaths of the third-order vascular bundles in particular. G, H. Abaxial epidermal structure.—G. Nucleate intercostal long and short cells and narrow costal zones with irregularly dumbbell-shaped silica bodies; central files in intercostal zones without stomata.—H. Detail of nucleate intercostal long, short, and triangular subsidiary cells (A, E, based on *Zuloaga 3087*; B, D, F, H, *Zuloaga s.n.*; C, G, *Zuloaga 3073*; A–D ×50; E–G ×125; H ×200).

cells of equal length; distal cell deciduous with very thin walls; common in the center of the intercostal zones. *Macro-hairs:* absent except for new cushion-based hairs on single specimen of *P. pilosum* (*Davidse 21866*). *Silica bodies:* vertically elongated dumbbell- or cross-shaped, or equidimensional dumbbell-shaped to elongated nodular (more rarely and only overlying the 3′vbs). Alternate regularly with similar shaped or shorter costal short cells along central costal file; only 3 (rarely 5) files of cells per costal zone. Each costal zone therefore only has a single file of cells with silica bodies bounded on either side by a file of costal long cells.

This description is based only on the anatomy

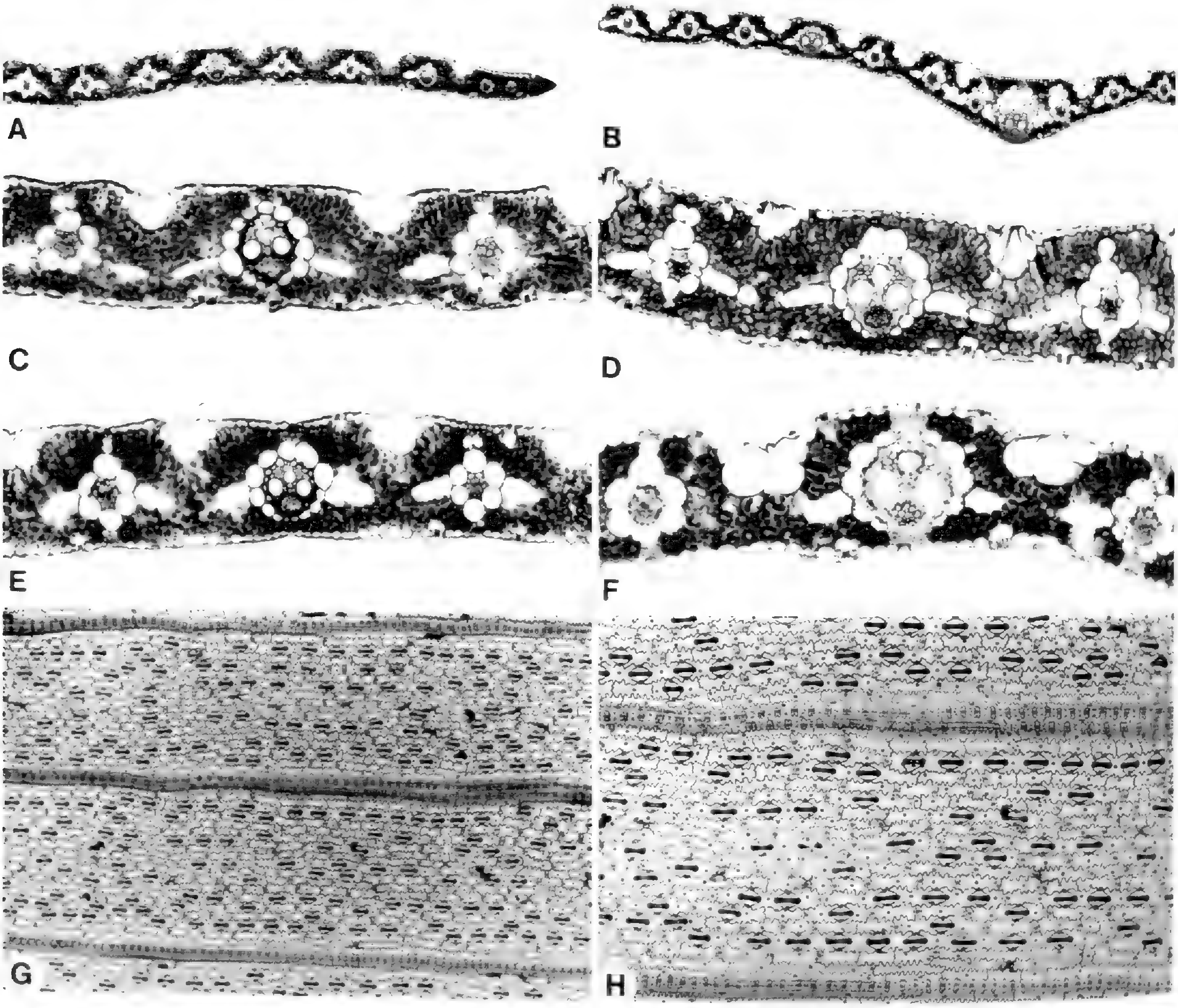

FIGURE 8. Leaf blade anatomy of *Panicum hylaeicum*. A–F, transectional anatomy.—A. Lateral part of lamina showing tapering margin with small cap of sclerenchyma; note regular presence of fusoid cells associated with all vascular bundles except for penultimate and ultimate lateral bundles in the margin.—B. Restricted keel comprising three vascular bundles; adaxial parenchyma developed in association with median first-order vascular bundle and adjacent third-order bundle on either side with bundle sheath extensions; regular fusoid cells not associated with these bundles.—C. Outer bundle sheath cells without chloroplasts, fusoids narrow and inclined toward the abaxial surface, adaxial chlorenchyma with pallisade arrangement.—D. Detail of arm cell-like chlorenchyma cells, particularly those located abaxially and adjacent to the fusoid cells; note the fusoid cavities appear to be bounded by the thin walls of the fusoid cells.—E. Regular occurrence of a fusoid cell on either side of most vascular bundles.—F. Specimen with small, unspecialized chloroplasts in the outer bundle sheath cells. G, H. Abaxial epidermis.—G. Narrow costal zones (3–5 files wide) and wide intercostal zones (16–19 files wide).—H. Low triangular stomata in files throughout intercostal zones, in all horizontal cell files, but tend to be less concentrated in the central files of the zones; subsidiary and intercostal long cells with characteristic persistent nuclei; note irregular dumbbell-shaped costal silica bodies alternating with similar shaped cork cells along costal cells files (A, B, E, F, *Zuloaga et al. 2293*; C, *Zuloaga 2218*; D, G, H, *Zuloaga 3197*; A, B × 50; G ×80; C–F, H ×125).

of the Laxa species group, *P. hylaeicum*, *P. laxum*, *P. pilosum*, and *P. polygonatum*, as well as *P. leptachne*, *P. longum*, *P. condensatum*, *P. auritum*, *P. stagnatile*, *P. stevensianum*, and *P. bresolinii*. The Grumosum group, *P. grumosum* and *P. pernambucense*, differs in several respects: *lamina width* generally wider, although *P. hylaeicum*, *P. stagnatile*, and *P. leptachne* sometimes have blades as wide as those of *P. grumosum*, a maximum of 105 vbs versus 52 in the Laxa group (although up to 99 can occur in *P. hylaeicum*); asymmetry less marked (48 versus 57 vbs); *thickness* at mid-lamina generally greater; *keel* well developed, incorporating 7–12 vbs (1–5 in Laxa group), wide and expanded and intergrading into the lamina (not abrupt as in Laxa group); *lacunae* present in the colorless parenchyma of the keel (absent in Laxa group); *metaxylem vessel*

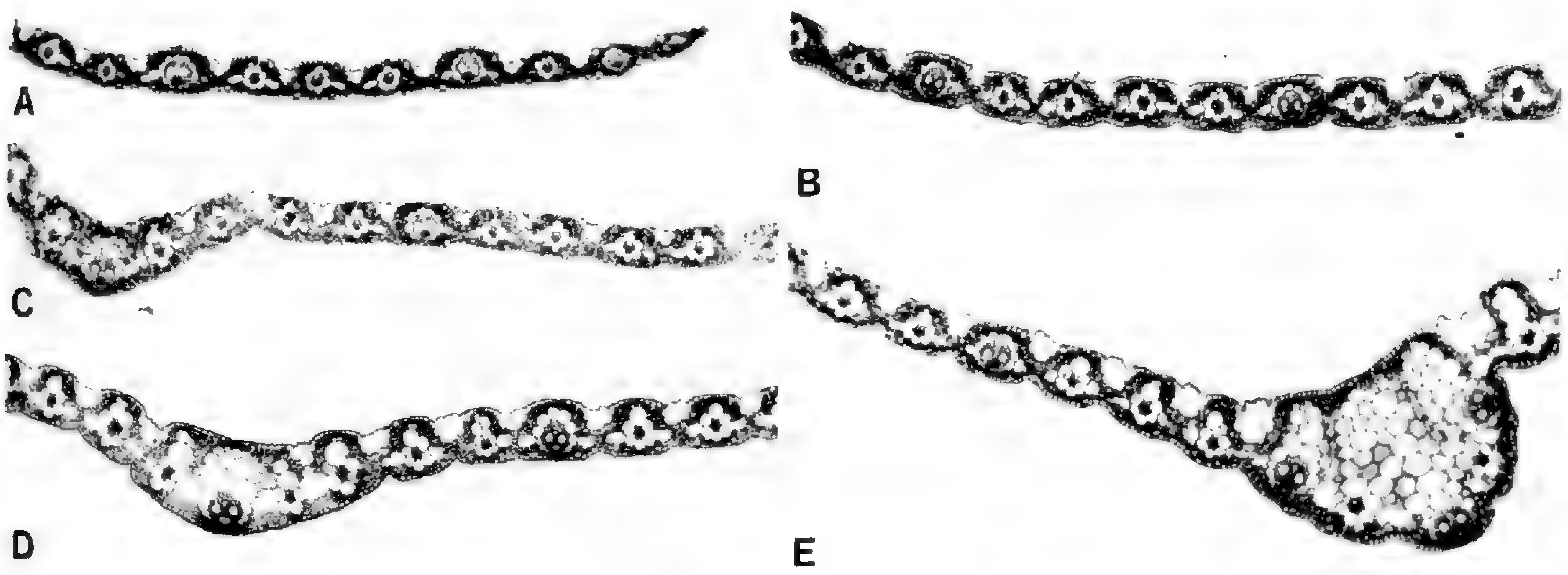

FIGURE 9. Transectional anatomy of the leaf blade outline of *Panicum laxum*.—A. Gently tapering margin with only the most laterally situated vascular bundles without associated fusoid cells.—B. Mid-lamina region showing four third-order vascular bundles located between successive first-order bundles; note fusoid cavities on either side of all bundles. C–E. Variation in the structure of the keel.—C. Insignificant keel incorporating only the median vascular bundle; this first-order bundle with small amount of adaxial colorless cell tissue.—D. Most common intermediate keel type incorporating 3 vascular bundles and adaxial colorless tissue.—E. Unusual elaborate V-shaped keel with 5 vascular bundles and extensive colorless parenchyma; note abrupt delimitation from lamina by bulliform cell groups (A, based on *Zuloaga 3290*; B, *Stevens 25354*; C, *Zuloaga 2337*; D, *Davidse 30703*; E, *Zuloaga et al. 4330*; A–E ×50).

diameters greater than in Laxa group (often wider than obs cells); *outer bundle sheath* with 8–10 cells around 3'vbs (5–6(–8) in Laxa group); 16–20 cells in obs of 1'vbs (8–11 in Laxa group); *bundle sheath extensions* always present (variable, from 1–4 cells deep); adaxial; uniseriate to biseriate; longest extensions closer to keel; *chlorenchyma cells* smaller and more compact, adaxial cells

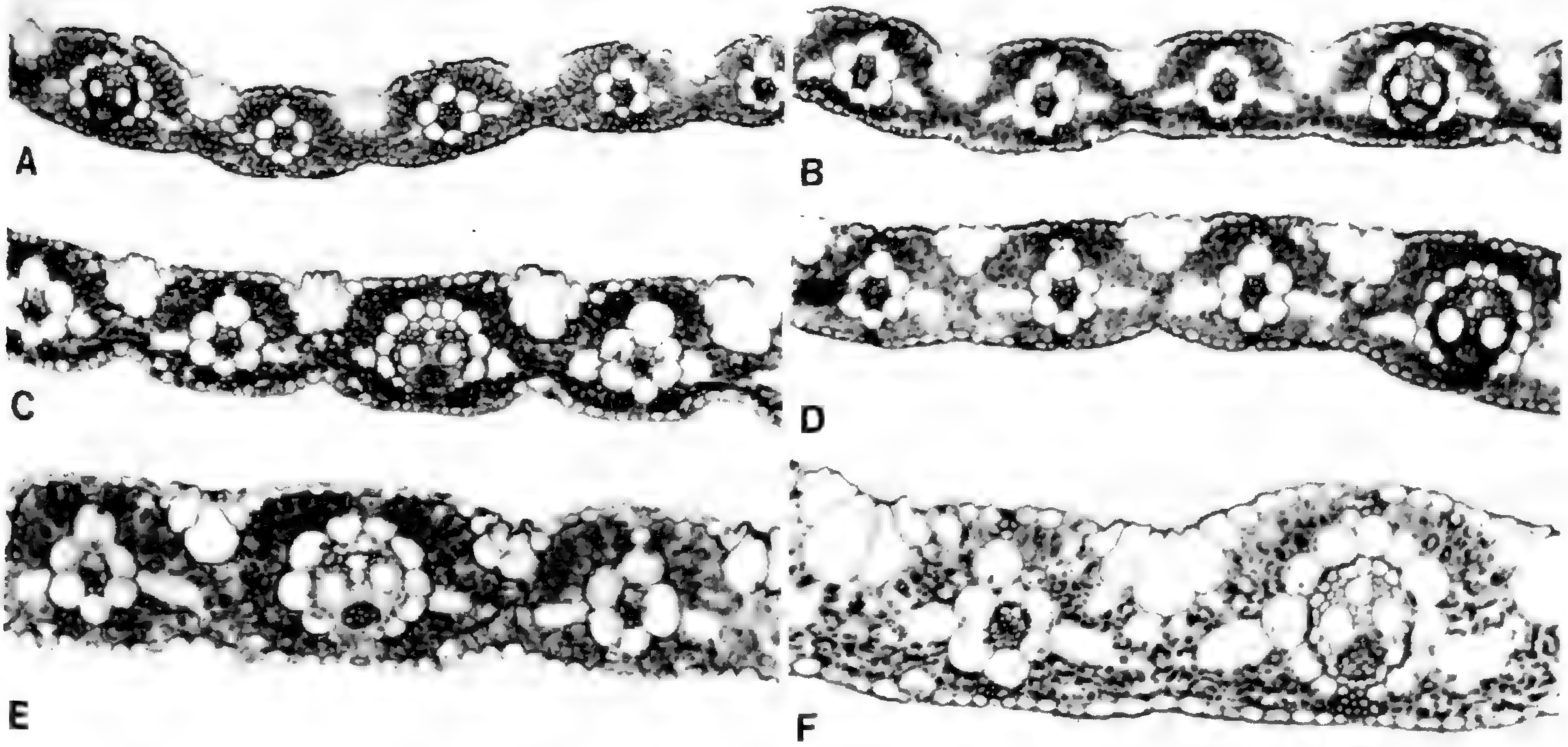

FIGURE 10. Detail of transectional leaf anatomy of *Panicum laxum*.—A. Thinner lateral part of lamina where fusoid cell occurrence is less regular; outer sheath cells without chloroplasts.—B. Specimen with typical anatomy of the Laxa group: regular fusoid cell presence and parenchyma sheath cells without chloroplasts.—C. Typical Laxa-type anatomy, but note well-developed adaxial ribs and furrows, very similar to those of *P. pilosum*.—D. Fusoid and bundle sheath cell structure.—E. Adaxial chlorenchyma tissue palisadelike, particularly above the fusoid cavities, whereas the abaxial chlorenchyma cells are equidimensional with discernible cell wall invaginations.—F. Specimen with anatomy tending to the intermediate C_3/C_4 type with a few, centripetally located chloroplasts, which differ structurally from those of the chlorenchyma; note the presence of fusoid cavities and that this leaf is thicker than other *P. laxum* specimens (A, based on *Stevens 25275*; B, *Zuloaga 3290*; C, *Zuloaga et al. 4330*; D, *Zuloaga et al. 4367*; E, *Zuloaga 2337*; F, *Brown 19*; A–D ×125; E, F ×200).

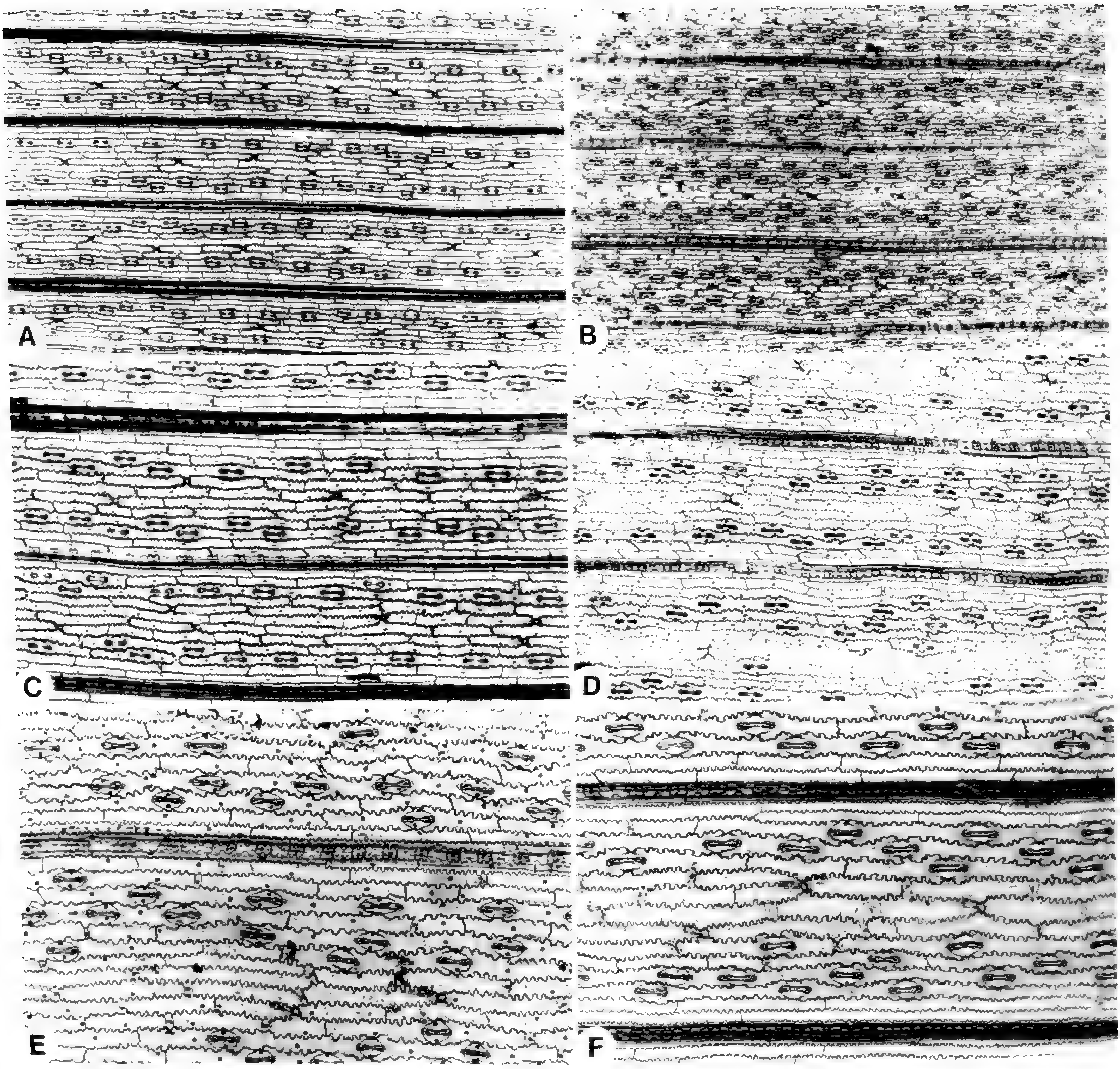

FIGURE 11. Consistent abaxial epidermis structure of *Panicum laxum*.—A. Epidermal zonation with narrow costal zones evenly spaced across lamina width.—B. Zonation with intercostal zones slightly wider than in A.—C. Narrow costal zones of 1 or 3 cell files and stomata in 1 or 2 files laterally situated in the intercostal zones.—D. Typical *P. laxum* epidermal structure.—E. Epidermal detail of dumbbell-shaped silica bodies, low dome or triangular nucleate subsidiary cells and microhairs in the center of the intercostal zones.—F. Dumbbell or nodular silica bodies, low triangular subsidiary cells and microhairs between long cells in center of intercostal zones (A, C, based on *Davidse 32998*; B, *Zuloaga 3290*; D, *Zuloaga s.n.*; E, *Zuloaga 2571*; F, *Davidse 30703*; A, B ×80; C, D ×125; E, F ×200).

without pallisade arrangement; *fusoid cells* irregular in occurrence, particularly laterally; may be virtually absent (*Zuloaga 3232*); fuse to form lacunae in keel; *intercostal long cells* short, generally less than 3× longer than wide; interstomatal cells often very short.

DISCUSSION

The possible affinities of section *Laxa* with other sections of *Panicum* and other genera of the Paniceae are summarized in Table 1.

Section *Laxa* conforms within *Panicum* to the anatomical and exomorphological diagnosis of subgenus *Phanopyrum*. Subgenus *Phanopyrum* is characterized anatomically by the presence of a double bundle sheath, the inner mestome sheath with thick-walled cells and the outer sheath parenchymatous, with slightly thickened walls, and completely devoid of, or with few, nonspecialized chloroplasts (Zuloaga, 1987). The number of mesophyll cells between the vascular bundles varies between 5 and 12, and the mesophyll tissue is irregularly arranged; this is typical of non-Kranz anatomy. All

TABLE 1. Comparison of section *Laxa* with other sections of *Panicum*, *P. grande*, and genera *Homolepis* and *Hymenachne*.

		Genus *Panicum*					
		Subg. *Steinchisma* sect. *Steinchisma*	Subg. *Phanopyrum* sect. *Laxa*		Subg. *Phanopyrum* *P. grande*	Subg. *Phanopyrum* sect. *Phanopyrum*	
	Genus *Homolepis*		Group Laxa	Group Grumosum			Genus *Hymenachne*
Photosynthetic type	C_3 (rarely C_3/C_4 intermediate)	C_3/C_4 intermediate	C_3 (rarely C_3/C_4 intermediate)	C_3	C_3	C_3	C_3
Fusoid cells present	+ (absent in *H. longispicula*)	–	+	+ (sometimes reduced)	–	–	–
Lacunae present	–	–	–	Present in keel only	Present in keel and mesophyll	Present in keel and mesophyll	Present in keel and mesophyll
Superposed bundles present	–	–	–	–	+	+	–
Upper anthecium consistency	Indurate	Indurate	Indurate to membranous	Membranous	Indurate	Indurate	Membranous
Palea covered at its apex by the lemma	+	+	+	+	+	+	–
Prickle hairs and papillae present	–	–	+	+	–	–	+
Inflorescence with unilateral branches	–	–	+	+	–	+	+
Lower palea expanded; compound papillae present	–	+	– (rarely present in *P. laxum*)	–	–	–	–

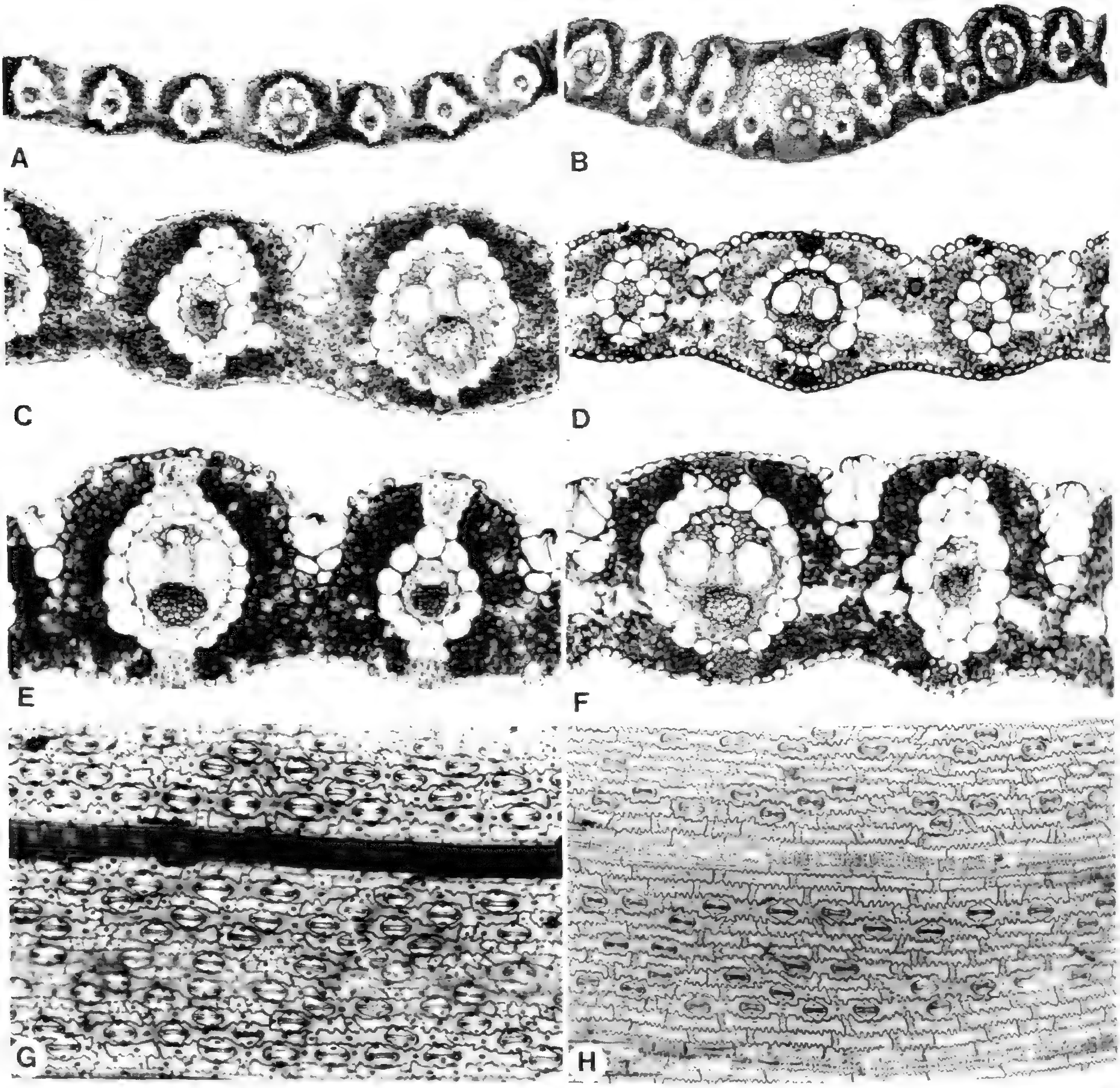

FIGURE 12. Leaf blade anatomy of *Panicum pernambucense*. A–F. Transectional anatomy.—A. Mid-lamina with first- and third-order bundles; note absence of fusoid cavities.—B. Keel with five bundles gradually intergrading with lamina; few lacunae present.—C. Anatomical detail showing virtual absence of fusoids and short adaxial bundle sheath extensions associated with the third-order bundles.—D. Specimen with irregular fusoid cell presence.—E. Detail of compact mesophyll without palisadelike tissue; no fusoid cells.—F. Irregular fusoid occurrence and compact mesophyll of arm cells. G, H. Abaxial epidermal structure.—G. Thickened long cell walls with stomata regularly distributed throughout intercostal zone; note nucleate nature of all intercostal cells.—H. All cells shorter than in Laxa type, particularly the intercostal long cells and the silica bodies (A, C, based on *Zuloaga et al. 3232*; B, E, G, *Zuloaga 2235*; D, *Zuloaga et al. 3323*; F, H, *Zuloaga 2494*; A, B ×50; G, H ×200; C–F ×125).

taxa in this subgenus possess the C_3 photosynthetic pathway. Plants of subgenus *Phanopyrum* are commonly found in humid and shady habitats and have membranous, small ligules; the inflorescences vary in this subgenus from spikelets disposed unilaterally in racemose branches (as in sections *Stolonifera*, *Phanopyrum*, and *Laxa*), to spikelets dispersed in lax or contracted panicles; spikelet nervation is constant, the lower glume 1–3-nerved and the upper glume and lower lemma 5-nerved, occasionally 7-nerved (Zuloaga, 1987). Zuloaga (1987) suggested two subgroups could be distinguished in subgenus *Phanopyrum*: one with a basic chromosome number of $x = 10$, spikelets disposed unilaterally on the branches, and upper anthecium smooth, without papillae and bicellular microhairs, which includes sections *Phanopyrum*, *Laxa*, and *Stolonifera*; the other one with $x = 9$, spikelets in open or contracted panicles, not unilaterally disposed, and upper anthecium papillate and with

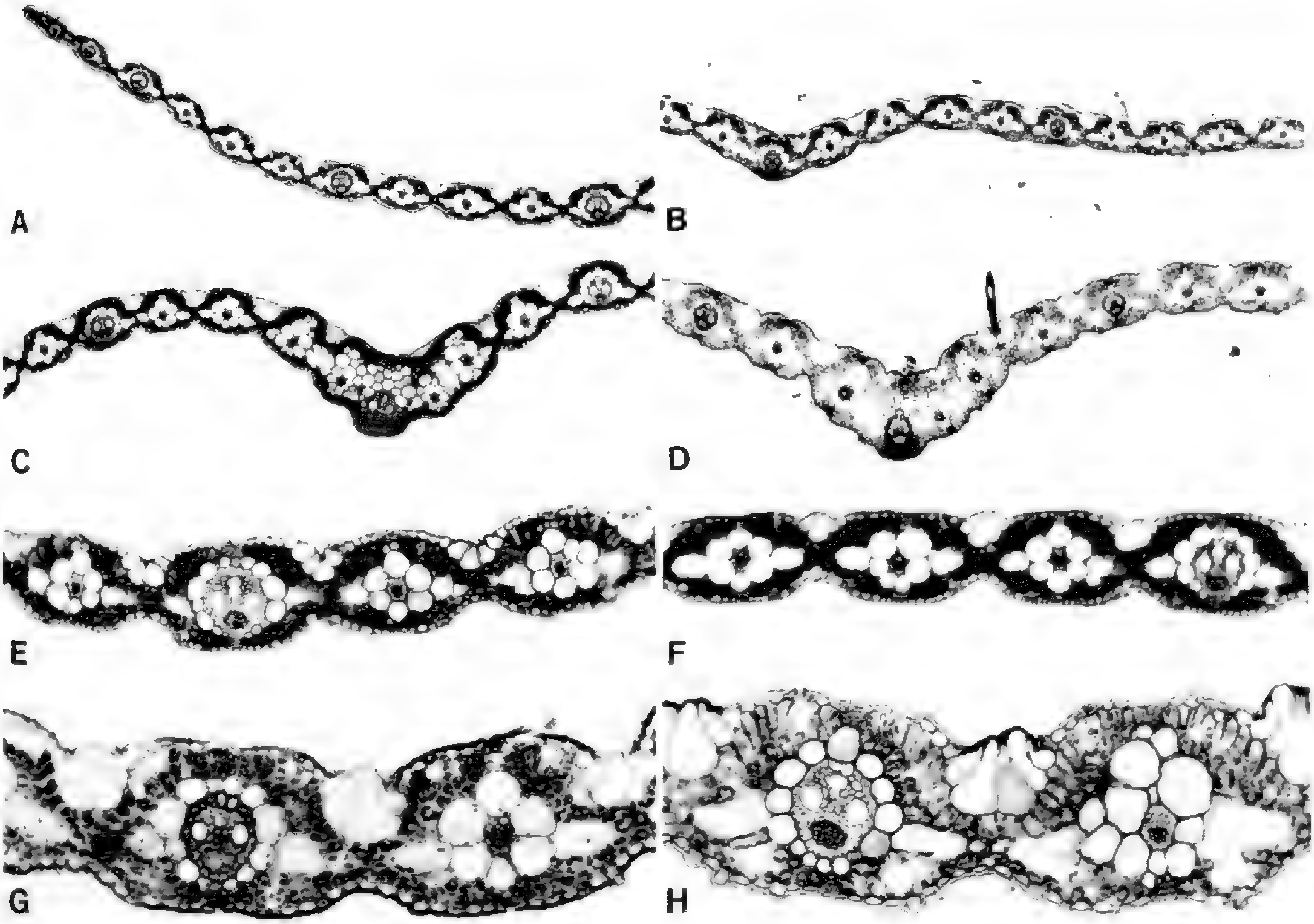

FIGURE 13. *Panicum pilosum* leaf blade in transverse section.—A. Margin showing fusoids associated with all vascular bundles except the most lateral ones. B–D. Structure of keel.—B. Median vascular bundle only, without associated colorless cell development.—C. Typical keel including three vascular bundles and with colorless parenchyma; median bundle with additional sclerenchyma girder development.—D. Typical keel but note lacunae in keel; unusual adaxial macrohair base evident.—E. Typical Laxa anatomy with palisadelike mesophyll, regular fusoid cell presence and parenchyma sheath cells without chloroplasts; presence of abaxial ribs and furrows characteristic.—F. Note that abaxial ribs and furrows larger than those of adaxial surface.—G. Few chloroplasts in outer sheath cells; note thick cuticle with evidence of abaxial epidermal hooks.—H. Typical palisade adaxial chlorenchyma; note breakdown of fusoid cavities to form lacunae (A, E, based on *Zuloaga 3289*; B, G, *Stevens 25219*; C, F, *Zuloaga 2303*; D, H, *Davidse 21866*; A–D ×50; E, F ×125; G, H ×200).

bicellular microhairs, with sections *Parviglumia*, *Parvifolia*, *Monticola*, and *Verrucosa* within this group. Section *Lorea*, originally placed by Zuloaga (1987) in this second group, is more closely related to the first one, with a similar upper anthecium ornamentation and a basic chromosome number of $x = 10$, although spikelets are scattered on the panicles.

Section *Laxa* is distinct from the other sections of *Phanopyrum* as well as from sections of *Dichanthelium*, the other C_3 subgenus, in that all representatives possess translucent fusoid cells in the mesophyll. The presence of these fusoidlike cells in section *Laxa* has been reported by Killeen & Clark (1986), who suggest that their presence lends support to Brown's (1977) revised evolutionary scheme for the Paniceae based on leaf anatomy and photosynthetic pathway. Fusoid cells in species of section *Laxa* are illustrated for *P. hylaeicum* (as *P. boliviense*) (Brown et al., 1985) and *P. pernambucense* (= *P. rivulare*) (Morgan & Brown, 1979; Wilson et al., 1983).

Fusoid cells are a distinguishing feature of the Bambusoideae and the peripheral bambusoid groups (Ellis, 1987) but have also been recorded in *Homolepis* (Watson et al., 1985) and *Streptostachys* (Clayton & Renvoize, 1986), in addition to section *Laxa* (Killeen & Clark, 1986). In all these non-bambusoid, panicoid taxa, the fusoid cavities are seen to be cellular in paradermal section, the cells being inflated and not constricted and girderlike as in most of the Bambusoideae. These structures therefore conform to the definition of fusoid cells and are not to be confused with lacunae, which are noncellular cavities in the mesophyll and which also occur in the Grumosum group of section *Laxa*.

Fusoid cells are, therefore, diagnostic for section *Laxa* within *Panicum* but are not restricted to

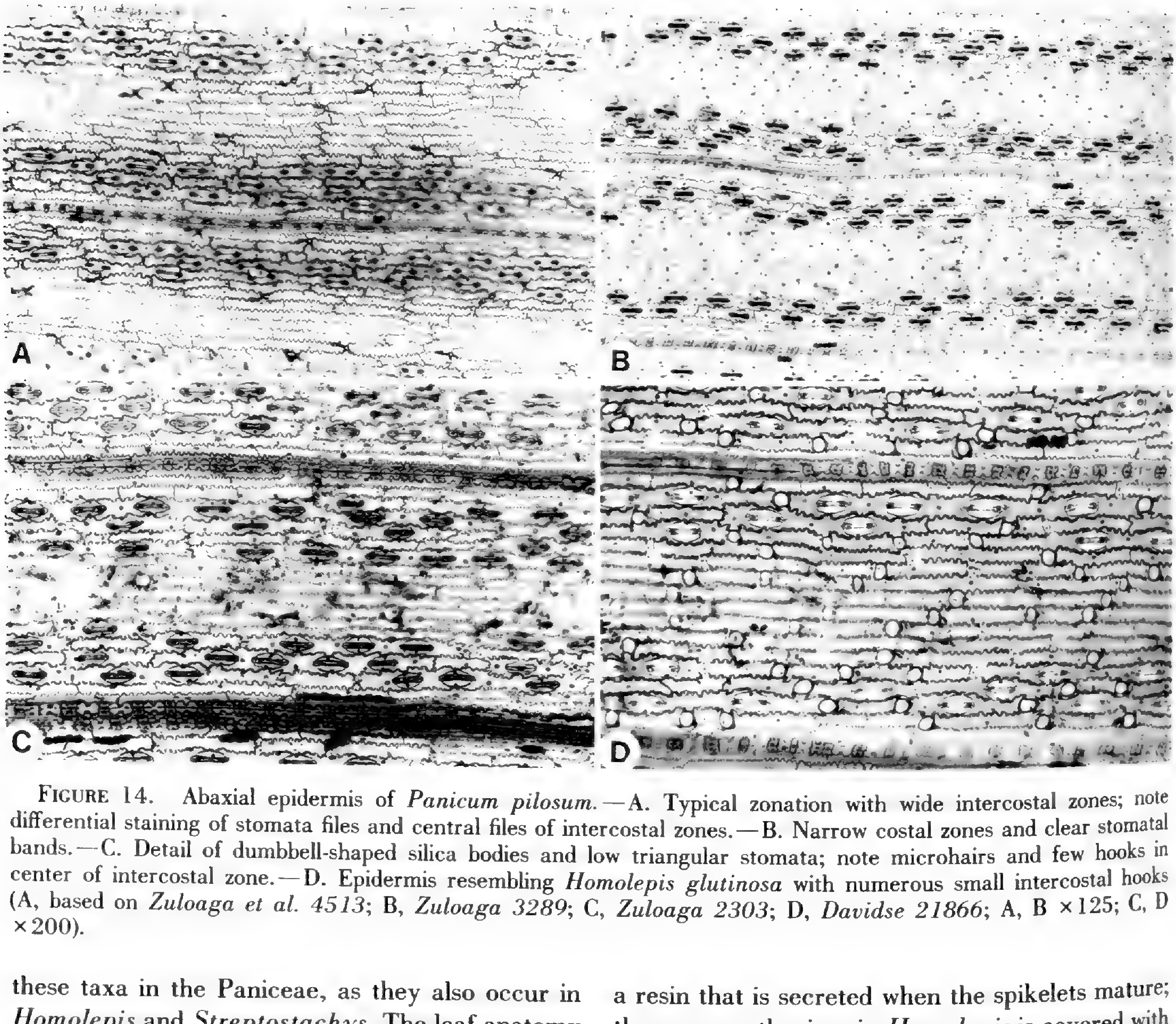

FIGURE 14. Abaxial epidermis of *Panicum pilosum*.—A. Typical zonation with wide intercostal zones; note differential staining of stomata files and central files of intercostal zones.—B. Narrow costal zones and clear stomatal bands.—C. Detail of dumbbell-shaped silica bodies and low triangular stomata; note microhairs and few hooks in center of intercostal zone.—D. Epidermis resembling *Homolepis glutinosa* with numerous small intercostal hooks (A, based on *Zuloaga et al. 4513*; B, *Zuloaga 3289*; C, *Zuloaga 2303*; D, *Davidse 21866*; A, B ×125; C, D ×200).

these taxa in the Paniceae, as they also occur in *Homolepis* and *Streptostachys*. The leaf anatomy of *Homolepis aturensis* (Kunth) Chase, *H. glutinosa* (Sw.) Zuloaga & Soderstrom, *H. isocalycia* (Meyer) Chase, and *H. villaricensis* (Mez) Zuloaga & Soderstrom, but not *H. longispicula* (Doell) Chase, closely resembles that of the Laxa group of section *Laxa* in most other respects as well. The only discernible anatomical difference between the Laxa group and *Homolepis* is that *Homolepis glutinosa*, in particular, often has numerous intercostal hooks, and macrohairs are sometimes present. These features, although rare, are not unknown in section *Laxa* and were observed on a specimen of *Panicum pilosum* (*Davidse 21866*), which is indistinguishable from most specimens of *H. glutinosa* on the basis of leaf anatomy.

Although the anatomy of section *Laxa* and *Homolepis* is similar, the exomorphological evidence does not suggest close affinities between these two taxa. In *Homolepis* spikelets are arranged in open, lax panicles; the lower glume reaches the same length and has the same nervation as the upper glume; the lower lemma has conspicuous bi- or tricellular secretory microhairs, which contain a resin that is secreted when the spikelets mature; the upper anthecium in *Homolepis* is covered with dumbbell-shaped silica bodies, bicellular microhairs toward the apex, and it lacks simple, evenly distributed papillae; and the hilum is linear, reaching one half to the entire length of the caryopsis.

Fusoid cells are also present in the leaf blades of the Grumosum group of section *Laxa*, although in these species they may be absent, particularly near the margin. In some specimens this reduction is extensive, with most vascular bundles without associated fusoid cells (Fig. 12A, C, E). Specimens of *P. pernambucense* in which the fusoid cells are rare or absent closely resemble those of *P. rude* Nees, of section *Stolonifera*, and *P. mertensii* Roth, of section *Megista*, in transectional leaf anatomy. The epidermal structure is also similar, and this may indicate affinity. *Panicum rude* has a similar mesophyll to species of the Laxa group, the adaxial cells tending to a pallisade-type of arrangement, with 6–8 cells in 3′vbs; metaxylem vessels are narrower than the obs cells as seen in cross section. *Panicum mertensii* has a similar mesophyll to that of *P. rude* and 6(–8) cells in 3′vbs. The keel is similar to that of *P. grumosum*. *Panicum rude*,

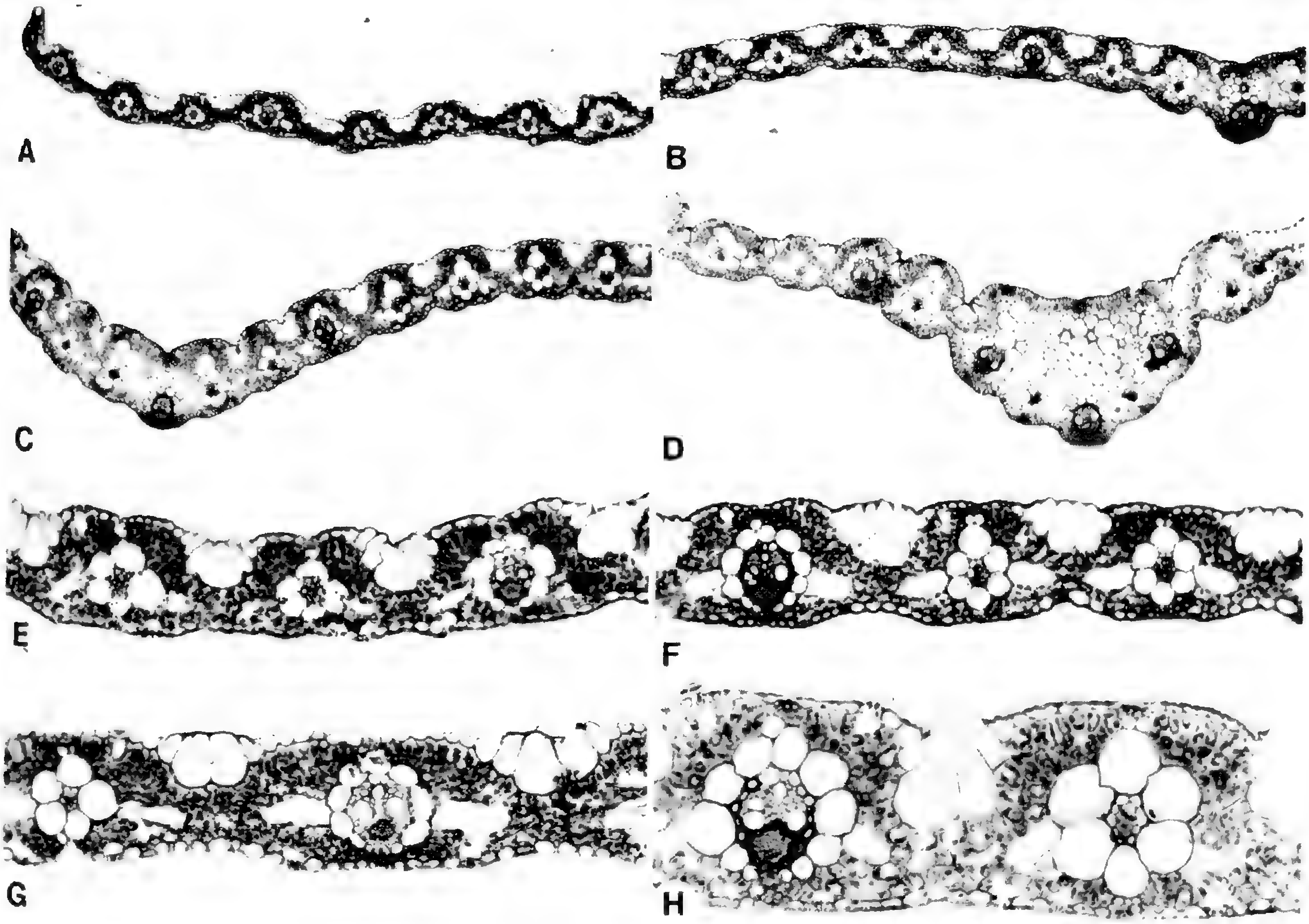

FIGURE 15. Transectional leaf anatomy of *Panicum polygonatum.*—A. Tapering leaf margin. B–D. Variation in structure of keel.—B. Keel with three vascular bundles; note that third-order bundles on either side of median bundle have additional colorless parenchyma cells associated with the outer bundle sheath.—C. Typical Laxa-type keel incorporating three vascular bundles.—D. Large keel of 3 first-order and 2 third-order vascular bundles and colorless parenchyma tissue.—E. Detail of parenchyma sheath cells with few, very small chloroplasts.—F. Conspicuous fusoid cavities present on either side of all vascular bundles.—G. Typical Laxa-type anatomy.—H. Detail of palisadelike adaxial chlorenchyma, fusoid cavities and parenchyma sheath cells devoid of chloroplasts (A, E, based on *Zuloaga 3913*; B, F, *Davidse 30413*; C, *Davidse 26917*; D, *Zuloaga & Londoño 4238*; G, *Stevens 25879*; H, *Davidse 21844*; A–D ×50; E–G ×125; H ×200).

together with other species of section *Stolonifera,* shares with section *Laxa* a similar inflorescence type and basic chromosome number. Section *Stolonifera* is differentiated by its stipitate, smooth, and glabrous upper anthecium and lower lemma with or without crateriform glands on the middle portion (Zuloaga & Sendulsky, 1988). Section *Megista* differs from section *Laxa* by the inflorescence type and spikelet outline and nervation, with branches of the inflorescence whorled and spikelets obovate, globose, with the upper glume and lower lemma 7–9-nerved (Zuloaga, 1987). Species of sections *Laxa, Stolonifera,* and *Megista* share a similar humid habitat, which may explain this superficial similarity in leaf anatomy.

Lacunae occur in the Grumosum group of section *Laxa* in the same location as fusoid cells in the mesophyll between the vascular bundles (Figs. 7D, 12D, F). Lacunae consist of a single lysigenous cavity between successive vascular bundles as seen in transection (and not two inflated cells as in fusoids) and are not cellular. In *P. grumosum* and *P. pernambucense* these lacunae are often only associated with the keel and intergrade into normal fusoid cavities in the mid-lamina.

The Grumosum group resembles *Hymenachne* rather closely on the basis of the lacunae, as well as leaf anatomy in general, a trend that is not shared by the Laxa group of species. This relationship between *Hymenachne* and species of section *Laxa* was emphasized by Zuloaga & Soderstrom (1985), who suggested that species of *Laxa* could be congeneric with *Hymenachne.* These authors pointed out that *Hymenachne* differs from *Panicum* by having the upper palea free at its apex. Pohl & Lersten (1975) considered that the presence of aerenchyma is a good character to separate *Hymenachne* from related genera, such as *Sacciolepis* and *Panicum.* Species of *Laxa,* including the Grumosum group, have the upper

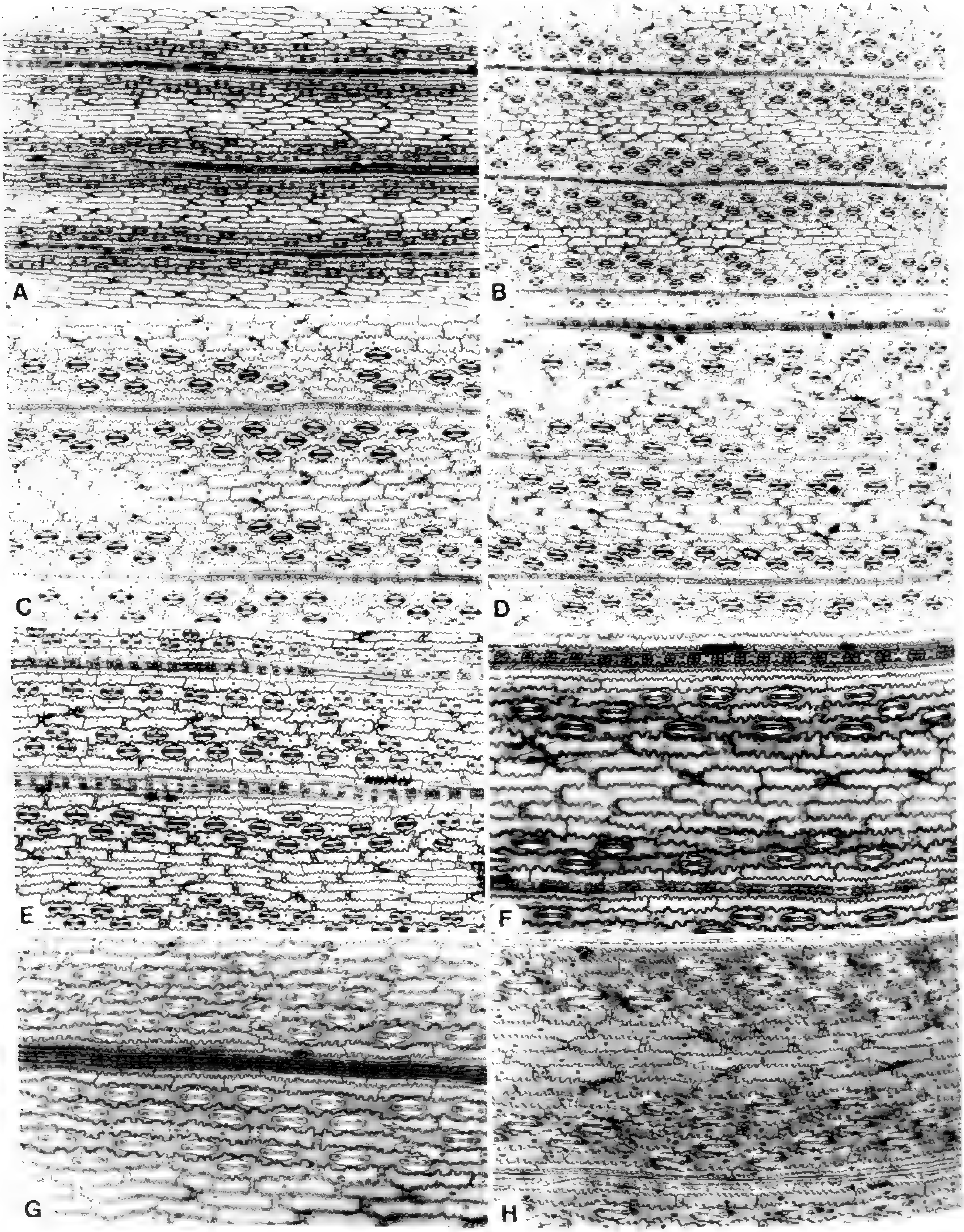

FIGURE 16. Typical Laxa-type abaxial epidermal structure of *Panicum polygonatum*.—A. Epidermal zonation with regularly spaced, narrow costal zones; note absence of stomata in center of intercostal zones.—B. Abaxial cellular pattern.—C. Costal zones 3 cell files wide, sinuous intercostal long cells and stomatal bands adjacent to the costal zones.—D. Typical Laxa-type abaxial epidermal structure.—E. Short dumbbell- to cross-shaped silica bodies alternating with darkly staining but similar shaped cork cells; stomata low dome-shaped; note that most epidermal cells have persistent nuclei.—F. Detail of dumbbell and nodular silica bodies and evaginations of subsidiary cells; note microhairs in center of intercostal zone.—G. Typical Laxa epidermal cellular structure and pattern; note differential staining of center of intercostal zone (without stomata) as compared to the stomatal files.—H. Interference contrast illumination showing nuclei in all long cells, short cells, and subsidiary cells; microhairs visible in center of intercostal zone (A, F, based on *Davidse 30113*; B, C, *Zuloaga 4087*; D, *Zuloaga 3913*; E, *Stevens 25879*; F, *Davidse 21844*; G, *Davidse 26917*; A, B ×80; C–E ×125; F–H ×200).

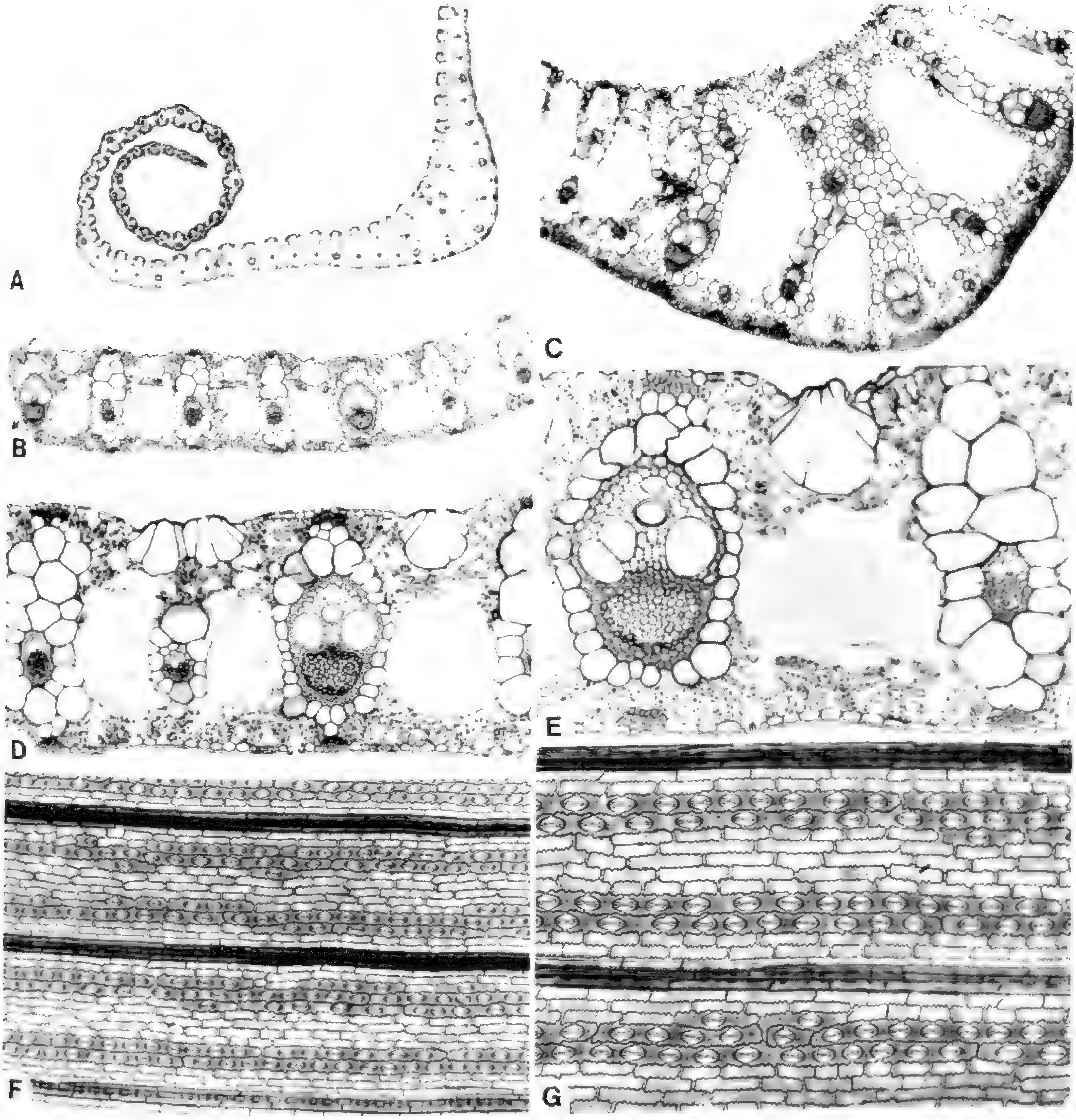

FIGURE 17. Atypical leaf blade anatomy of *Panicum grande*. A–E. Leaf anatomy as seen in transverse section. A. Outline of blade as seen in cross section showing continuously decreasing thickness from median vascular bundle to margin.—B. Mid-lamina, showing arrangement of vascular bundles (3 third-order bundles between successive first-order bundles) and the presence of a single lacunal cavity in the mesophyll between all bundles.—C. Keel structure showing gradual integration into lamina, definite lacunae and the superposed vascular bundles located away from the abaxial surface.—D. Outer bundle sheath cells without chloroplasts and wide adaxial extensions present, particularly on the sheaths of smaller bundles.—E. Detail of bundles, sheaths, and mesophyll; note that the lacunae are not bounded by cell walls but are just cavities in the chlorenchyma. F, G. Abaxial epidermis.—F. Epidermal zonation with stomata clearly grouped into 2–3 files of cells on either side of 4–5 files of long cells located in the center of the intercostal zones.—G. Detail of relatively short long cells, particularly the interstomatals; all intercostal cells nucleate, although these rather indistinct (A–G, based on *Davidse 21867*; A ×125; B, C ×50; F ×80; D, G ×125; E ×200).

palea covered at the apex by the lemma and lack stellate aerenchyma in culms, sheaths, and blades; they can also be separated by the presence of fusoid cells, although this can be controversial if reduction, or their replacement by lacunae has occurred. However, it could be argued that there has been a correlation with the presence of fusoid cells, upper anthecia consistency, and habitat in these taxa. Species of drier habitats, usually found on edges of woods, have indurate upper anthecia with fewer silica bodies and papillae, are less robust, have conspicuous fusoid cells, and lack lacunae in transverse section of the blade. By contrast, species such as *P. grumosum* and *P. pernambucense*, as well as those of *Hymenachne*, which inhabit streambanks, have membranous upper anthecia and leaves with lacunae and less conspicuous fusoid cells. There are, however, intermediate species between groups Grumosum and Laxa of section *Laxa*, such as *P. bresolinii*, *P. stagnatile*, and *P. leptachne*, which have membranous upper anthecia, conspicuous fusoid cells and lack lacunae in the leaves. There appears to be a developmental sequence from fusoid cavities through lacunae to aerenchyma: these structures may be ontogenetically homologous or merely correlated with shady, wet tropical habitats (Killeen & Clark, 1986).

Lacunae also occur in the keel and lamina of *P. gymnocarpon* Elliott, section *Phanopyrum*, a species that resembles the section *Laxa* in some respects of leaf anatomy. However, the keel differs from the one present in species of section *Laxa* by its superposed bundles and conspicuous lysigenous cavities. The midnerve has conspicuous pith aerenchyma, as is common in *Hymenachne amplexicaulis*. Taking into consideration the superposed bundles, pith aerenchyma, and conspicuous lacunae, this species seems to be more closely related to *P. grande* and *Hymenachne*. Alternatively, the presence of lacunae in these taxa may represent a convergence or similar adaptation to an aquatic habitat.

Subgenus *Steinchisma* is characterized by possessing an intermediate C_3–C_4 photosynthetic pathway in which the anatomy is Kranz but with fewer centripetal chloroplasts in the outer bundle sheath cells than is usual. The vascular bundles are also farther apart than in normal Kranz sections, with 5 to 7 chlorenchyma cells between bundles (Zuloaga, 1987). Fusoid cells are absent in all species of this subgenus. Physiologically these species are intermediate between C_3 and typical C_4 plants (Brown & Brown, 1975; Morgan & Brown, 1979; Brown et al., 1985) but all have carbon isotope ratios in the C_3 range. Exomorphologically, species of *Steinchisma* can be distinguished by open panicles, with spikelets not unilaterally disposed, lower palea expanded at maturity, and upper anthecium covered by verrucose papillae.

Section *Laxa* generally has typical C_3 leaf anatomy with very few or no chloroplasts in the outer bundle sheath cells. However, in a few specimens of *P. laxum* specialized chloroplasts are present in these cells, and the anatomy tends toward the C_3/C_4 intermediate type. Examples are *Stevens 25354*, *Zuloaga et al. 4330* and, in particular, *Brown 19* (Fig. 10F), which closely resembles *P. decipiens* Nees ex Trin. and *P. spathellosum* Doell, of subgenus *Steinchisma*, in the structure of the bundle sheath chloroplasts. A comparison of Figure 8 (Ellis, 1988) with Figure 10 clearly illustrates this similarity. Illustrations of *P. laxum* in Wilson et al. (1983) and *P. spathellosum* (Brown et al., 1985) support this observation. We have examined specimens of *P. laxum* with characters intermediate in relation to the ones present in species of subgenus *Steinchisma*, such as palea more or less expanded and upper anthecium with verrucose papillae. All these data confirm the relation between *Steinchisma* and section *Laxa*, supporting the decision of Zuloaga (1987) to retain *Steinchisma* in *Panicum*.

In all the physiological and hybridization work on *P. laxum* that has included leaf anatomy (Morgan & Brown, 1979; Wilson et al., 1983), it is significant that no illustrations of this species show fusoid cells. This is in marked contrast to the findings of the present study where all 14 accessions of *P. laxum* had conspicuous fusoid cavities present on both sides of virtually all vascular bundles. The specimens illustrated by Morgan & Brown (1979) and Wilson et al. (1983) also have C_3/C_4-type chloroplasts, and it is possible that their results were based on incorrect identifications or at least are not applicable to most populations of *P. laxum*. However, *P. laxum* leaf blade material received from R. H. Brown did have fusoid as well as C_3/C_4-type anatomy (Fig. 10F), which appears to confirm their determination.

The decision to recognize two informal anatomical species groups in section *Laxa* for the purpose of the anatomical description appears to be supported by this discussion of character distributions and possible affinities. Thus, the Laxa group shows links to *Homolepis* on the basis of fusoid cells and such characters as keel structure, but not morphological characters, and even to *Steinchisma*, on the basis of the photosynthetic anatomy and the keel structure. Similarly, the Grumosum group tends toward *Hymenachne* and other taxa in subgenus *Phanopyrum* because of similar reduction of fusoid cells and presence of lacunae, C_3 anatomy, and the possession of wide keels with lacunae.

Taxonomic Treatment

Panicum section **Laxa** (A. Hitchc. & Chase) Pilger. Notizbl. Bot. Gart. Berlin-Dahlem 104(11): 243. 1931. *Panicum* Group *Laxa* A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 110. 1910 (invalid name); A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 17(6): 201. 1915. TYPE SPECIES: *Panicum laxum* Sw.

Inflorescences with lax to contracted panicles, with spikelets ± crowded and unilaterally disposed on the branches or in short branchlets. *Spikelets* pilose or glabrous, elliptic to lanceolate. *Lower glume* ⅓ to ¾ the length of the spikelet, 1–3-nerved. *Upper glume and lower lemma* subequal or the upper glume shorter and not covering the upper anthecium. *Lower palea* conspicuous, with the same length of the lower lemma, to small or absent; lower flower present and male, occasionally bisexual, or absent. *Upper anthecium* membranous to indurate, papillose, with simple papillae all over its surface or toward the apex and with prickle hairs at the apex of lemma and palea; silica bodies present in the membranous anthecia, palea covered by the lemma at its apex; upper flower bisexual, lodicules 2, conduplicate; stamens 3, styles 2, stigma plumose. *Blades* lanceolate to ovate-lanceolate. *Ligules* membranous, with or without short hairs at the distal portion.

Plants perennial, usually growing in wet places at edges of woods or margins of ponds, streams or rivers.

Non-Kranz anatomy, basic chromosome number $x = 10$.

Section with 12 American species, growing from Mexico to Argentina, and with one Asiatic species.

KEY TO SPECIES OF SECTION *LAXA*

- 1a. Spikelets on first-order branches, second-order branchlets absent, occasionally present toward the base of the inflorescence; main axis and branches usually long-pilose to scabrous.
  - 2a. Spikelets 1.9–3.2 mm long; ligules present.
    - 3a. Blades narrowed at base; Mexico .... 8. *P. longum*
    - 3b. Blades cordate at base; Brazil.
      - 4a. Branches of inflorescences glabrous; panicles 13–24 cm long; spikelets 1.9–2.4 mm long .... 3. *P. condensatum*
      - 4b. Branches of inflorescences papillose-pilose; panicles 25–40 cm long; spikelets 2.1–3.2 mm long .... 7. *P. leptachne*
  - 2b. Spikelets 1.3–1.5 mm long; ligules usually absent, occasionally present .... 10. *P. pilosum*
- 1b. Spikelets mainly on short second-order branchlets; main axis and branches scabrous to short-pilose, occasionally long-pilose.
  - 5a. Blades amplexicaulous, cordate.
    - 6a. Spikelets 1.4–1.7 mm long, lower palea present, the culms rigid; Mexico to Argentina .... 5. *P. hylaeicum*
    - 6b. Spikelets 2.1–2.3 mm long, lower palea absent, the culms herbaceous; Santa Catarina, Brazil .... 2. *P. bresolinii*
  - 5b. Blades not amplexicaulous, rounded to subcordate, occasionally cordate in specimens of *P. stagnatile*, *P. stevensianum*, and *P. polygonatum*.
    - 7a. Spikelets pointed at apex, without lower flower; lower palea absent to reduced.
      - 8a. Plants 0.15–0.50(–1) m tall; blades 4–17 cm long; panicles 8–20 cm long; spikelets 1.3–1.6 mm long .... 11. *P. polygonatum*
      - 8b. Plants 1–3 m tall; blades 17–60 cm long; panicles 20–40 cm long; spikelets 1.6–2.2(–3) mm long.
        - 9a. Spikelets (2.2–)2.5–3 mm long. Asia .... 1. *P. auritum*
        - 9b. Spikelets 1.6–2.2(–2.5) mm long; America.
          - 10a. Panicles slender, with spikelets not crowded on second-order branches; Mexico to Panama .... 12. *P. stagnatile*
          - 10b. Panicles congested, with spikelets crowded on second-order branches; northeastern Brazil to Paraguay, Uruguay, and Argentina .... 9. *P. pernambucense*
    - 7b. Spikelets not pointed at apex, with a male lower flower, bisexual in specimens of *P. stevensianum*, occasionally absent; lower palea present.
      - 11a. Upper flower with two stamens, occasionally three; spikelets 1–1.7 mm long .... 6. *P. laxum*
      - 11b. Upper flower with three stamens; spikelets 1.9–3 mm long.
        - 12a. Culms spreading, decumbent at the base, 0.20–1 m tall; spikelets 1.9–2.6 mm long; lower flower bisexual, occasionally male or absent; West Indies and northern South America .... 13. *P. stevensianum*
        - 12b. Culms erect, 1.30–2 m tall; spikelets 2.3–3 mm long; lower flower male; eastern Brazil to Argentina .... 4. *P. grumosum*

1. **Panicum auritum** J. S. Presl ex Nees, Agrost. Bras.: 176. 1829. *Hymenachne aurita* (J. S. Presl ex Nees) Bal., Cat. Indo-China Française, Journ. de Bot. 4: 30. 1890. *Sacciolepis aurita* (J. S. Presl) A. Camus, in Lecomte, Fl. Gen. Indo-Chine 7: 459. 1922. TYPE: Philippines. "in Luzon insula" (holotype, PR? not seen; isotype, W).

Perennials, with erect *culms* 1.1–1.3 m tall, simple; internodes 5–17 cm long, terete, hollow, glabrous; nodes brownish, glabrous. *Sheaths* 4–10 cm long, shorter than the internodes, striate, glabrous, the margins membranous, ciliate or not at the upper portion. *Ligules* membranous, 0.4–1 mm long, laciniate or not, brownish. *Blades* lanceolate, 17–30 cm long, 0.8–1.6 cm wide, flat, cordate to subcordate at base, attenuate at the apex, short pilose on both surfaces to glabrous, the margins scabrous, the lower ones ciliate or not. *Inflorescence* exserted, peduncle 8–20 cm long, glabrous, smooth; panicles lax, 16–45 cm long, 3–15 cm wide; *main axis* wavy, scaberulous, pulvini pilose, with whitish hairs, to glabrous, first-order branches alternate, divergent, axis of the branches triquetrous, scabrous, spikelets short-pedicelled, appressed and paired on short second-order branchlets, pedicels triquetrous, scabrous. *Spikelets* narrowly ovate, (2.2–)2.5–3 mm long, 0.8–0.9 mm wide, glabrous, greenish and tinged with purple, upper glume and lower lemma subequal, acute, 5-nerved. *Lower glume* ovate, acute, 0.9–1.2 mm long, less than ⅓ the length of the spikelet, 3-nerved, midnerve scaberulous toward the apex. *Lower palea* elliptic, small, 1–1.4 mm long, 0.3 mm wide, hyaline, glabrous, the borders ciliolate or not; lower flower absent. *Upper anthecium* narrowly elliptic, 1.9–2.6 mm long, 0.6–0.8 mm wide, acuminate, membranous at maturity, brownish, glabrous, with simple papillae and prickles toward the apex. *Caryopsis* ovate, 1–1.3 mm long, 0.5–0.8 mm wide, brownish; hilum oblong, embryo less than ½ the length of the caryopsis.

Distribution and ecology. Found at edge of forest in humid places or in open, wet sites, from sea level to 1,200 m, in Southeast Asia, India, Sri Lanka, and southern China, in tropical Asia. It is a weed in plantations of rubber, tea, teak, and *Cinchona* (Lazarides, 1980).

Additional specimens examined. BORNEO. Sandakan and vicinity, *Ramos 1597* (P). MALAYSIA. Singapur, Park of the broadcasting Station Jureng, *Sinclair 9828* (M). PHILIPPINES. LUZON: Manila, *Merrill 101* (M, P, SI*), *238* (W); Prov. of Sorgoson, Irosin, *Elmer 14344* (P), *16398* (P, W); Prov. of Rizal, Morong, *Ramos s.n.* (W); San Francisco del Monte, *Loher 1719* (M); Luzón central, *Loher 1718* (P*). MINDANAO: Zamboanga district, Malangao, *Ramos & Edaño s.n.* (P). CEYLON [SRI LANKA]. Ratmapoora, *Thwaites 3242* (P, W). THAILAND. Khow-Yau National Park, *Larsen et al. 68* (W); Bangkok, *Kerr 7044* (P); Bangkok, Wat Lum, *Kerr 6952* (P). VIETNAM. Van-Yeu, *Balansa 4914* (P, W); Hue, Annam, *Hitchcock 19378* (P); Annam, Tourane, *Clemens 4045* (P); Tu-Phep, *Balansa 1630* (P).

Panicum auritum, the only non-American species of the section, was included in *Laxa* by Pilger (1940). It is related to *P. laxum*, differing by having spikelets pointed, with the lower palea reduced and lower flower absent.

2. P. bresolinii L. B. Smith & Wasshausen, Bradea 2(35): 245, fig. 2, A–D, 1978. TYPE: Brazil. Santa Catarina: Florianópolis, Morro Costa da Lagoa, 200 m, 19 Apr. 1967, *Klein & Bresolin 7360* (holotype, US 2536896). Figures 2, 18.

Plants of indefinite duration, probably perennials, the *culms* decumbent, rooting and branching at the lower nodes, then becoming erect, ca. 90 cm tall, internodes compressed, hollow, glabrous, nodes dark, densely pilose with whitish hairs. Leaves with *sheaths* usually shorter than the internodes, short-hirsute with stiff papillose-pilose hairs, one margin membranous, the other short-ciliate. *Ligules* small, 0.5 mm long, membranous with a short fringe of hairs at the apex. *Blades* lanceolate, 15–26 cm long, 2.2–3 cm wide, flat, shortly pseudopetiolate, pseudopetiole brownish, ca. 0.2 cm long, pilose, blades cordate at the base, amplexicaulous, acuminate, short-pilose and with long hairs toward the base on the adaxial surface, the abaxial surface glabrous with anastomosed nerves. *Inflorescence* a lax panicle 26 cm long, 10–13 cm wide; main axis wavy, scabrous, spikelets unilaterally disposed on short secondary branchlets, paired or solitary, axis of the branches, branchlets and pedicels triquetrous, scabrous, axils of the branches pilose. *Spikelets* narrowly elliptic, 2.1–2.3 mm long, 0.5–0.6 mm wide, acute, glabrous, upper glume and lower lemma subequal. *Lower glume* ovate, 1.1–1.4 mm long, ½ or more the length of the spikelet, 3-nerved, the nerves anastomosed toward the apex, the keel scabrous. *Upper glume* acute, 5-nerved, the nerves anastomosed, the keel scabrous. *Lower lemma* acute, 3-nerved, the keel scabrous. *Lower palea* absent; lower flower absent. *Upper anthecium* lanceolate, 1.7–2 mm long, 0.5 mm wide, membranous at maturity, whitish, smooth, with simple papillae and conspicuous, retrorse prickle hairs at the apex of lemma and palea, rachilla prolonged beyond the upper anthecium as a short mucro. *Caryopsis* not seen.

Distribution and ecology. Known from Santa Catarina, Brazil, where it grows in swamp forest. In flower from March to April.

Additional specimens examined. BRAZIL. SANTA CATARINA: 5 km NE of Papanduva along highway BR-116 to Curitiba, 780 m, *Davidse et al. 11056* (MO, SI*, SP).

Related to *P. hylaeicum* Mez, it differs by the spikelet size, 1.4–1.7 mm long in *P. hylaeicum*,

FIGURE 18. *Panicum bresolinii* (based on *Davidse et al. 11056*).—a. Habit, with panicle included.—b. Detail of ligule and lower portion of the blade.—c. Racemose branch.—d. Spikelet, lower glume view.—e. Spikelet, upper glume view.—f. Spikelet, lateral view.—g. Upper anthecium, lemma view.—h. Upper anthecium, palea view.—i. Upper portion of the upper lemma showing prickle hairs.

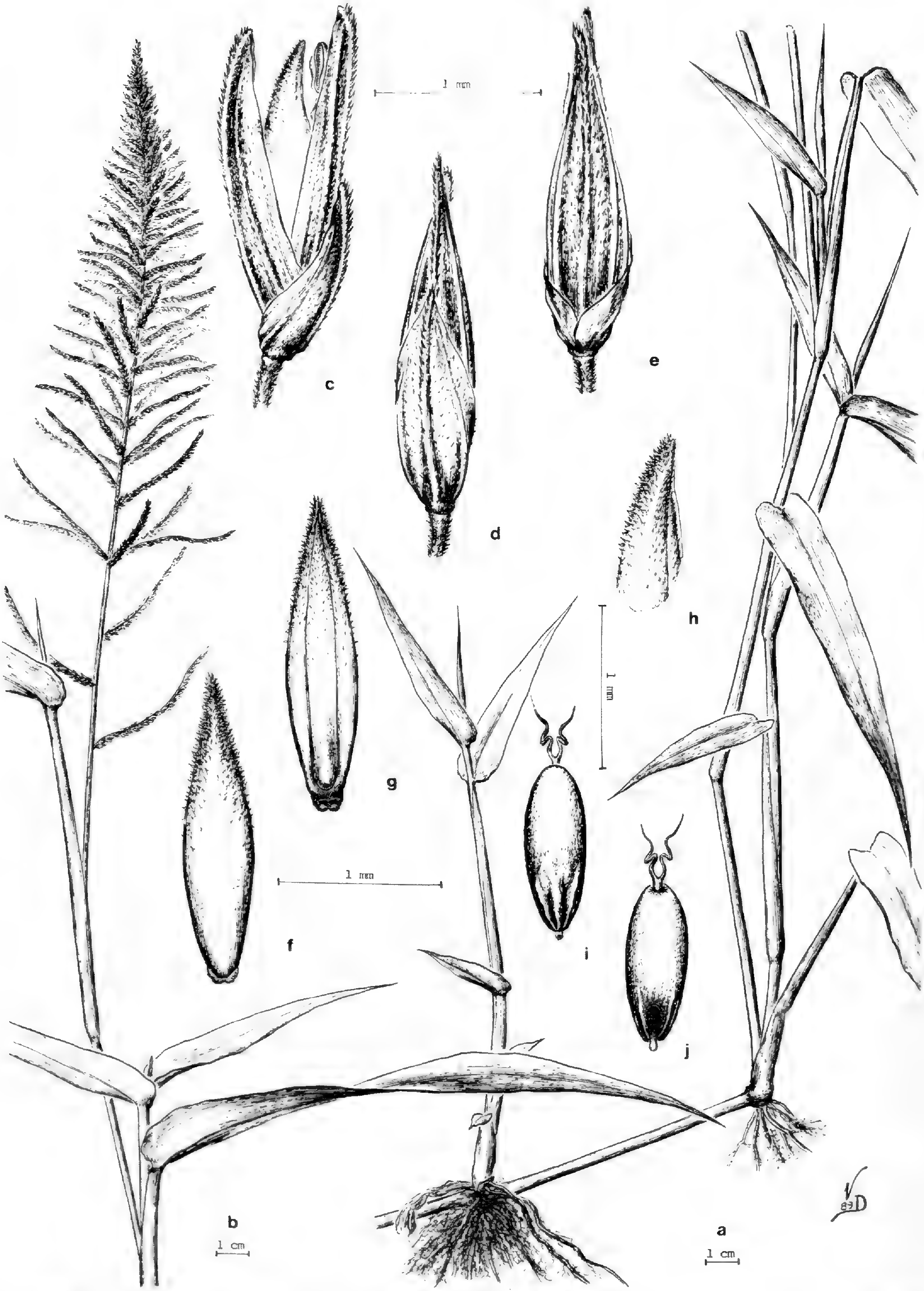

FIGURE 19. *Panicum condensatum* (a, based on *Chase 8101*; b–h, *Chase 12127*; i–j, *Davidse 11494*).—a. Habit. —b. Upper portion of a culm with panicle.—c. Spikelet, lateral view.—d. Spikelet, lower glume view.—e. Spikelet, upper glume view.—f. Upper anthecium, lemma view.—g. Upper anthecium, palea view.—h. Upper portion of the upper lemma showing prickle hairs.—i. Caryopsis, embryo view.—j. Caryopsis, hilum view.

and by the consistency of the upper anthecium, indurate in the latter species and membranous in *P. bresolinii.*

3. **Panicum condensatum** Bertol., Opusc. Sci. 3: 408. 1819. *Hymenachne condensata* (Bertol.) Chase, J. Wash. Acad. Sci. 13: 177. 1923. TYPE: Brazil. Rio de Janeiro: without precise locality, *Raddi s.n.* (holotype, PI; isotype, K, fragment, US 80598). Figures 5, 6, 19.

Panicum auriculatum Willd. var. *fasciculosum* Doell, in C. Martius, Fl. Bras. 2(2): 238. 1877. *Panicum januarium* Mez, in Engler, Bot. Jahrb. Syst. 56, Beibl. 125: 4. 1921. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, *Gaudichaud 288* (isotypes, P, W, fragment US 80476).

Annuals or perennials?, the *culms* decumbent, rooting and branching at the lower nodes, then erect, up to 100 cm tall, branching at the middle and upper nodes, internodes compressed, hollow, glabrous, (5–)10–23 cm long, nodes compressed, dark, glabrous. Leaves with *sheaths* shorter than the internodes, 4–10 cm long, with tessellate nerves, glabrous, the margins membranous. *Ligules* membranous at the base and shortly ciliate at the apex, 0.9–1.3 mm long; collar brownish, glabrous to shortly ciliate. *Blades* lanceolate, 7–17 cm long, 1–2 cm wide, flat, acuminate, cordate at the base and amplexicaulous, shortly pseudopetiolate, pseudopetiole brownish, short-pilose and sparingly papillose-pilose, blades glabrous, the margins scabrous, ciliate at the lower margins. *Inflorescence* 13–24 cm long, 1.5–6 cm wide, with approximately 50 unilateral, racemose branches, the branches verticillate, subopposite to alternate; *main axis* wavy, scabrous, lower branches 3–4 cm long, branches and pedicels scabrous, the branches triquetrous, flattened on one side, axils of the branches long-pilose, branchlets absent, the spikelets secund and paired, one subsessile, the other short-pedicellate on the branches, alternating in 2 rows. *Spikelets* lanceolate, brownish, somewhat laterally compressed, 1.9–2.4 mm long, 0.4–0.5 mm wide, scaberulous, acuminate, upper glume and lower lemma subequal, exceeding in length the upper anthecium. *Lower glume* ½ to ¾ the length of the spikelet, 1–1.6 mm long, ovate, acuminate, 3(–5)-nerved, the keel scabrous. *Upper glume* 1.8–2.1 mm long, 5-nerved, the keel scabrous. *Lower lemma* 1.7–2.1 mm long, 5-nerved, keel scabrous. *Lower palea* absent; lower flower absent. *Upper anthecium* lanceolate, 1.5–1.8 mm long, 0.5 mm wide, membranous at maturity, whitish, scabrous at the apex of lemma and palea and with simple papillae all over its surface, the lemma 5-nerved. *Caryopsis* lanceolate, brownish, hilum elliptic, embryo ⅓ or less the length of the caryopsis.

Distribution and ecology. Brazil, from Bahia to Minas Gerais, Rio de Janeiro, São Paulo, and Santa Catarina, in wet places on margins of streams or in marshy areas, up to 500 m elevation. In flower from November to April.

Additional specimens examined. BRAZIL. BAHIA: Cachoeira, *Chase 8101* (US, W). MINAS GERAIS: ca. 1 km S of São Pedro do Suacui along highway MG-3, *Davidse et al. 11494* (MO, SI, US). RIO DE JANEIRO: Rio de Janeiro, Recreio dos Bandeirantes, *Casari 552* (MO); Furnas de Agassiz, *Chase 12127* (US*); Tijuca, *Schott 4845* (US, W); Jacarepagua, *Chase 8414, 8418* (US*); without locality, *Kuhlmann s.n.* (US). SANTA CATARINA: Pedra de Amolar, *Condim 1* (US); Florianópolis, *Klein & Bresolin 9966* (US). SAO PAULO: Pindorama, *Viegas s.n.* (US); without state and locality, *Riedel s.n.* (W).

Pohl & Lersten (1975) indicated that *Panicum condensatum* (as *Hymenachne condensata*) did not have aerenchyma in culms as is typical in other species of the genus *Hymenachne. Panicum condensatum* also has the apex of the palea covered by the lemma, and fusoid cells are present in transverse section of the blades. This species has spikelets disposed in first-order branches, as in *P. pilosum* and related species. Its habit is similar to that of *P. grumosum* and *P. pernambucense.*

4. **Panicum grumosum** Nees, Agrost. Bras.: 182. 1829. *Panicum rivulare* var. *grumosum* (Nees) Hackel, Repert Spec. Nov. Regni Veg. 6: 343. 1909. SYNTYPES: "Habitat in Monte Video et in confinibus Regni Paraguayani (*Sellow*)" (syntype of "Uruguay, Sellow," B; isosyntypes P, W, fragments BAA, US). Figures 3, 7.

Panicum pycnanthum Steudel, Syn. Pl. Glumac. 1: 70. 1853. TYPE: Uruguay. Montevideo: Montevideo, *Deloche s.n.* (holotype, P, fragments BAA, US 2903523).

Panicum pavonii Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 5. 1921. TYPE: Peru. Without locality, *Pavon s.n.* (holotype, B, fragments, BAA, US; isotype, G).

Panicum knuthii Herter, Revista Sudamer. Bot. 6: 137, fig. 6, 1940. TYPE: Uruguay. Minas: Corrales, Feb. 1924, *Schroeder s.n.* (herb. Osten 16731) (fragment of the type, BAA).

Panicum schroederi Herter, Revista Sudamer. Bot. 6: 137, 138, fig. 7. 1940. TYPE: Uruguay. Barra del Santa Lucía, Jan. 1920, *Schroeder s.n.* (herb. Osten 15402). (fragment of the type, US 2903525).

Strongly rhizomatous perennials, *culms* erect, 1.3–2 m tall, freely branching at the upper nodes, internodes cylindric, hollow, glabrous, 8–30 cm long, nodes glabrous, purplish. *Sheaths* glabrous, shorter than the internodes, 9–20 cm long, the margins membranous, collar glabrous, brownish. *Ligules* membranous, 1.2–2 mm long. *Blades* lanceolate, 14–44 cm long, 0.6–3 cm wide, subcordate, glabrous, the margins scaberulous, midnerve conspicuous. *Inflorescence* a terminal panicle, 15–45 cm long, 3.5–13 cm wide; *main axis* scabrous, branches ascending, alternate or opposite, axis of the branches and pedicels scabrous, spikelets paired and densely crowded on short secondary branchlets, pedicels short. *Spikelets* long-elliptic, 2.3–3 mm long, 0.5–1 mm wide, glabrous, greenish or tinged with purple. *Lower glume* 1–1.7 mm long, ½ to ¾ the length of the spikelet, 3-nerved, the nerves anastomosed toward the apex, the keel scabrous. *Upper glume* 1.8–2.5 mm long, slightly shorter than the lower lemma, 5-nerved, the keel finely scabrous toward the apex. *Lower lemma* 5-nerved, 2.2–2.7 mm long. *Lower palea* 2.2–2.6 mm long, 0.5–0.6 mm wide, membranous, ciliolate on the margins; lower flower male, anthers 3. *Upper anthecium* long-elliptic, 2–2.6 mm long, 0.5–0.7 mm wide, membranous, scabrous toward the apex and with silica bodies and simple papillae; lemma 5-nerved. *Caryopsis* obovate, brownish, 1.1–1.3 mm long, 0.5–0.6 mm wide, plano-convex; hilum oblong, embryo approximately ½ the length of the caryopsis.

Distribution and ecology. South America, from Brazil and Paraguay to Uruguay and Argentina. It is common at margins of rivers and streams, in inundated areas. In flower between October and January.

Selected specimens examined. ARGENTINA. BUENOS AIRES: Isla Santiago, *Cabrera 3422* (F, NY, SI, SP, US); Punta Lara, *Zuloaga 3357* (SI), *3073* (SI*). DISTRITO FEDERAL: Palermo, *Burkart 238* (BAA). CORRIENTES: Isla Apipé Grande, Puerto Mora, *Krapovickas et al. 24388* (CTES, SI). CHACO: Colonia Benítez, *Schulz 1796* (BAB). ENTRE RIOS: Salto Grande, Casa de Piedra, *Renvoize et al. 2975* (K, MO, NY, SI); Concepción del Uruguay, Arroyo La China, *Zuloaga et al. 3087* (MO, SI*). MISIONES: Posadas, *Ekman 622* (CORD, US). SANTA FE: Villa Guillermina, *Meyer 3322* (BAA). BRAZIL. MINAS GERAIS: Caldas, *Regnell III-1361* (P, US). PARANA: Rio Jordão, Aguas Sta. Clara, *Hatschbach 10549* (US). RIO GRANDE DO SUL: Pelotas, *Sacco 212* (NY, RB, US); 20 km from Porto Alegre, grown at Athens, Georgia, *Brown & Barreto 107* (P). SANTA CATARINA: Mun. Caçador, 52 km west of Caçador near the eastern edge of the campos of Palmas, 1,000–1,200 m, *Smith & Reitz 9132* (NY, US); Lages, wet ground, bank of stream and margin of banhado, Fachinal, *Swallen 8126* (US). PARAGUAY. AMAMBAY: Sierra de Amambay, *Hassler 10155* (G, K, LIL, NY, P, W). CAAZAPA: Tavaí, Castor-Cué, 26°10′S, 55°20′W, *Mereles 2188* (MO). CENTRAL: Capiatá, *Schinini 4960* (G, MO, SI). CORDILLERA: Cordillera de Altos, *Fiebrig 421* (F). GUAIRA: prope Villa Rica, in paludosis, *Hassler 8773a* (G). PARAGUARI: Parque Nacional Ybicu'í, gallery forest along Arroyo Minas, on trail to Salto Guaraní, 26°03′S, 56°50′W, *Zardini 7474* (MO). PRESIDENTE HAYES: S de Villa Hayes, *Rosengurtt 5627* (BAA, US); Estancia de la "Copacar," El Milagro, *Ramírez 223* (US). URUGUAY. CANELONES: Río Santa Lucía, Estancia Paso Cuello, *Gallinal et al. PE-5571* (MO, P, US). COLONIA: bank of Arroyo de San Juan, *Bartlett 21266* (NY). RIO NEGRO: San Javier, *Chebataroff s.n.* (LIL 57356). SAN JOSE: Río Santa Lucía, *Rosengurtt B-4956* (P, SI). TACUAREMBO: Arazatí, *Rosengurtt 1676* (US).

This species is related to *P. pernambucense*, from which it differs by being commonly smaller in overall size (2–3 m tall in *P. pernambucense*) and by having bigger spikelets (1.7–2.2(–2.5) mm long in *P. pernambucense*) with a conspicuous lower palea and lower flower. *Panicum grumosum* is common in Uruguay and northeastern Argentina, but becomes less common north of these areas. It ranges as far north as Minas Gerais, Brazil, but becomes quite rare. It is difficult to separate the two species in Paraguay.

There is a gradation in the pilosity of leaves and panicles. Some specimens have densely papillose-pilose sheaths covered with rigid, caducous hairs and inflorescences with papillose-pilose rachis and branches; others are glabrous.

Panicum pavonii was described by Mez on the basis of material presumably collected in Peru. We considered this to be an error on the label of the type specimen since the known geographical range of *P. grumosum* does not come close to Peru.

Three-flowered spikelets were found in *Quarín et al. 2745*, *Hunziker 4614* (also with geminate spikelets), and *Millán 568*.

5. **Panicum hylaeicum** Mez, Notizbl. Bot. Gart. Berlin-Dahlem 7: 75. 1917. *Panicum laxum* Sw. var. *pubescens* Doell, in C. Martius, Fl. Bras. 2(2): 213. 1877, pro parte. TYPE: Brazil. Pará: in vicinibus Santarem, Aug 1850, *Spruce 1061*^{2} (*Panicum 26*) (holotype, M, fragment, US; isotypes, K, P). Figures 3, 8, 20.

Panicum minutiflorum Doell, in C. Martius, Fl. Bras. 2(2): 253. 1877. Not *Panicum minutiflorum* Raspail, 1825. LECTOTYPE: Brazil. Pará: prope Santarem, *Spruce 720* (lectotype, here designated, P; isolectotype, K, fragment, US).

Panicum potamium Trin. var. *pubescens* Doell, in C. Martius, Fl. Bras 2(2): 214. 1877, pro parte. TYPE: Brazil. "Ad Tocantins fluvium inter Porto Imperial et Funil," *Burchell 8795* (holotype, K; isotype, W).

Panicum laxum Sw. var. *amplissimum* Hackel, Repert. Spec. Nov. Regni Veg. 6: 343. 1909. TYPE: Paraguay. "in reg. curs. inf. fl. Pilcomayo," *Rojas 276* (holotype, W; isotypes, G, K, P, US, W; fragment of the type, BAA, US).

Panicum schiedeanum Mez, Bot. Jahrb. Syst. 56, Beibl.

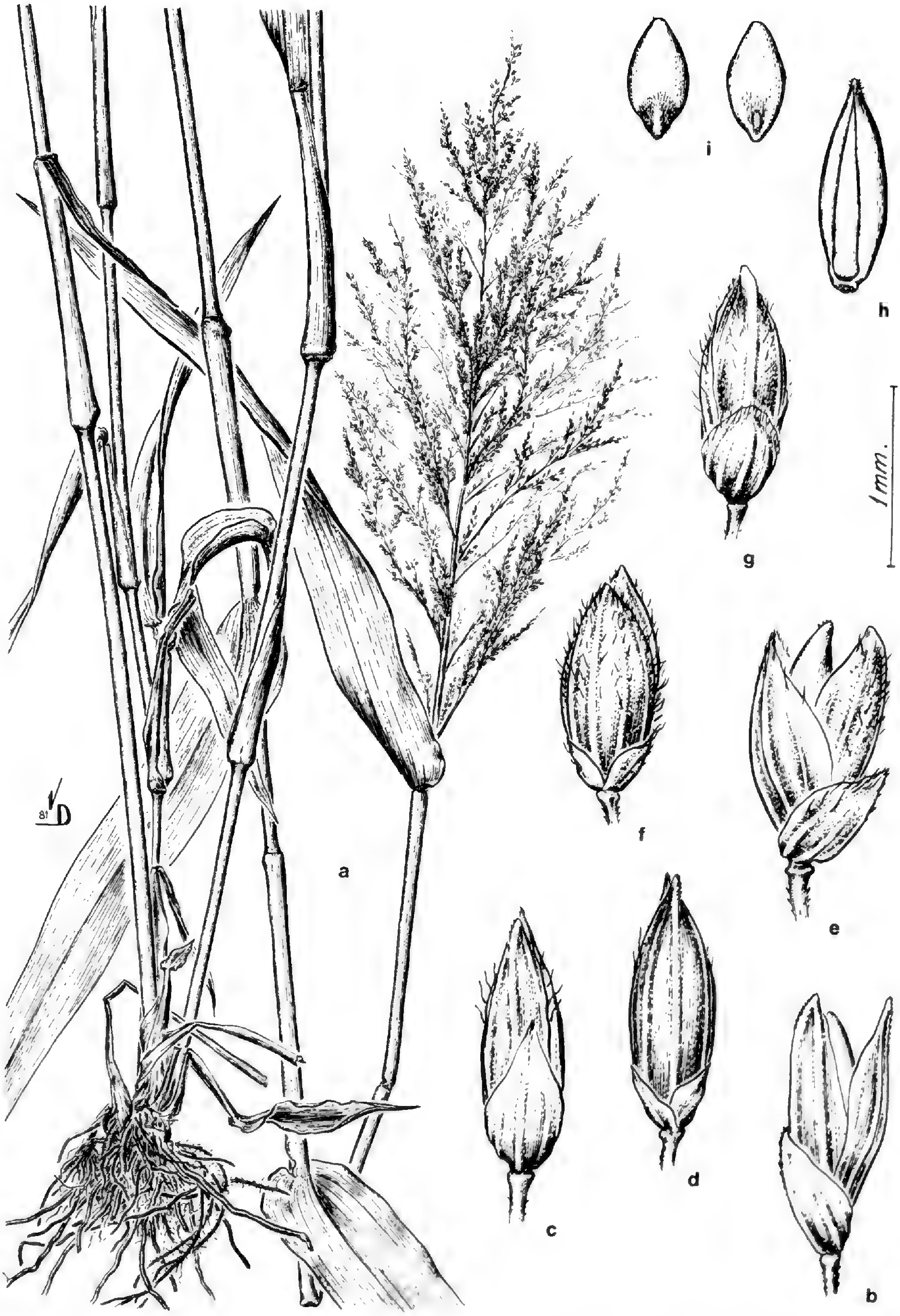

FIGURE 20. *Panicum hylaeicum* (a, based on *Guaglianone et al. 728*; e–g, *Spruce 26*).—a. Habit.—e. Hispid spikelet, lateral view.—f. Hispid spikelet, upper glume view.—g. Hispid spikelet, lower glume view.—*Panicum polygonatum* (based on *Buchtien 2501*).—b. Spikelet, lateral view.—c. Spikelet, lower glume view.—d. Spikelet, upper glume view.—h. Upper anthecium, palea view.—i. Caryopsis, hilum and embryo view.

125: 4. 1921. Not *Panicum schiedeanum* Trin. ex Beal, 1886. LECTOTYPE, here designated: Mexico. Without locality, *Schiede 29* (lectotype, B; isolectotype, P, fragment and photo, US 2830931).

Panicum schaffneri Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 4. 1921. Not *Panicum schaffneri* Kuntze, 1898. TYPE: Mexico. Without locality, *Schaffner 156* (holotype, B, fragment, US 2830930).

Panicum doellii Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 6. 1921. SYNTYPES: Brazil. Pará: Santarem, *Spruce 347* (*Panicum n. 18*). Paraguay. Central: Asunción, Apr. 1874, *Balansa 49*; in regione cursus inferiores fluminis Pilcomayo, *Fiebrig 4689*; without locality, *Rojas 276* (isosyntype of *Spruce 347* (*Panicum n. 18*), P, fragments, BAA, US; isosyntype of *Balansa 49*, G, K, P, US; isosyntype of *Rojas 276*, G, P, US, fragments, BAA, US; fragment of the syntype *Fiebrig 4689*, US).

Panicum guianense A. Hitchc., Contr. U.S. Natl. Herb. 22: 487, f. 83. 1922. TYPE: Guyana. Rockstone, 1 Jan. 1920, *Hitchcock 17313* (holotype, US 1038517; isotypes, BAA, F, G, K, NY, W).

Plants perennial, robust, 1–2(–3) m tall, *culms* cylindric, rooting and branching or not at the lower nodes, then erect, sprawling and clambering, many-noded, internodes 4–20 cm long, rigid, hollow, glabrous, tinged with purple, nodes glabrous, purplish. Leaves with *sheaths* equal to or shorter than the internodes, 3.5–10 cm long, stramineous to purplish, pilose to glabrescent, with papillose-pilose, caducous hairs on the upper margins, collar pilose, glabrous. *Ligules* membranous, laciniate to short pilose on the upper portion, 0.3–0.7 mm long. *Blades* ovate-lanceolate, flat, 7–26 cm long, 1–3 cm wide, cordate, clasping at base, shortly pseudopetiolate, attenuate at the apex, densely pilose to glabrescent on both surfaces, the lower margins long-ciliate, otherwise scabrous, the nerves tessellate. *Inflorescence* a terminal, diffuse to contracted panicle 10–32 cm long, 4.5–17.5 cm wide, included or not at the upper sheaths; *main axis* and branches and pedicels scabrous, pulvini short-pilose, first-order branches alternate to opposite, spreading, spikelets unilateral on short, second- or third-order appressed branches, paired on short pedicels 0.5–1.3 mm long. *Spikelets* narrowly elliptic, 1.4–1.7 mm long, 0.4–0.6 mm wide, greenish to purplish, hispid with caducous hairs, to glabrous. *Lower glume* 0.7–1 mm long, less than ½ the length of the spikelet, ovate, acute, amplexicaulous, 3-nerved, the keel scabrous on the upper portion. *Upper glume* 1–1.7 mm long, covering or not the upper anthecium, 5-nerved, blunt. *Lower lemma* 5-nerved, acute. *Lower palea* elliptic, 0.9–1.3 mm long, 0.3–0.5 mm wide, membranous, small in some specimens; lower flower male or absent. *Upper anthecium* elliptic, 1–1.4 mm long, 0.4–0.6 mm wide, scabrous at the apex, otherwise smooth, glabrous, indurate. *Caryopsis* elliptic, 0.9 mm long, 0.5 mm wide, hilum punctiform, embryo less than half the length of the caryopsis.

Distribution and ecology. Mexico, Mesoamerica, Cuba, Dominica, and South America, from Colombia to Argentina. It is common at margins of rivers and swamps or at edge of forest in humid soils, usually scandent over the vegetation, from sea level to 1,500 m.

Selected specimens examined. ARGENTINA. CHACO: Puerto Vilelas, *Schulz 3379* (BAA, CTES, SI). CORRIENTES: Ituzaingó, Puesto de Prefectura, 42 km al E de Ituzaingó, *Zuloaga et al. 624, 2293** (MO, SI). FORMOSA: Estancia Bouvier, *Guaglianone et al. 728* (SI). MISIONES: Santa Ana, camino al balneario Municipal, *Zuloaga et al. 2218* (MO, SI*). BELIZE. Temash River, *Schipp 1372* (G, US). BOLIVIA. BENI: Río Yata, 30 km W de Guayamerím, camino a Riberalta, *Krapovickas & Schinini 35086* (CTES, K). BRAZIL. ALAGOAS: without locality, *Gardner 1435* (K). AMAPA: Igarapé do Lago, *Black & Froes 51-12342* (IAN). AMAZONAS: Rio Solimoes, *Froes 20549* (IAN, US). BAHIA: Rio Itapicuru, *Pinto 687* (US). GOIAS: Santa Rita do Paranahyba, *Chase 11622* (US). MARANHAO: Caxias to Barra do Corda, *Swallen 3595* (IAN, US). MATO GROSSO: bank of Rio S. Lourenço, Barça S. Lourenço, *Chase 11966* (US). MATO GROSSO DO SUL: Porto Esperança, *Chase 11073, 11099* (US). MINAS GERAIS: Capinópolis, Cachoeira Dourada, *Macedo 4545* (US). PARA: Santarem, *Swallen 3311* (US), *Spruce 347* (P, US), *436* (US). PARANA: mouth of Rio Ivaí, *Lindeman & Haas 4322* (K, NY, US). RONDONIA: Forte da Principe da Beira, *Rodriguez 3490* (US). RORAIMA: Rio Mucajaí, Colonia Fernando Costa, *Black & Magalhaes 51-12877* (IAN, US). SAO PAULO: Porto Pulador on the Rio Moji-Guaçu, 8.9 km NNE of RR Station at Santa Eudóxia, *Eiten & Campos 3487* (MO, US). COLOMBIA. CASANARE: Río Casanare, barranco de Atahuarpa, *Cuatrecasas & García Barriga 4238* (COL), *4284* (COL, US). META: Río Meta, Orocué, *Cuatrecasas & García-Barriga 4432* (COL, US). COSTA RICA. ALAJUELA: Cariblanco, *Pohl & Davidse 11024* (US). CUBA. ORIENTE: Sierra de Nipe, Río Pilabo, *Ekman 15105* (G). PINAR DEL RIO: Baños de San Vicente, *Britton et al. 7452* (US). SANTA CLARA: banks of Banao River, *León 5460* (US). DOMINICAN REPUBLIC. Santo Domingo, Cuenca, *Ekman 13305* (G). FRENCH GUIANA. Haut Itany, *Hoock s.n.* (NY). GUATEMALA. ALTA VERAPAZ: Cobán, *von Tuerckheim 1254* (US). ESCUINTLA: South of Río Burrión, northeast of Escuintla, 700 m, *Standley 89612* (US). HUEHUETENANGO: entre Ixcán y Río Ixcán, Sierra de los Cuchumatanes, *Steyermark 49333* (F). IZABAL: Chickasaw Farm of the United Fruit Company, about 15 km north of Quirguá, *Standley 24623* (US). SANTA ROSA: plains north of Los Cerritos, on road between Chiquimulilla and El Ahumado, *Standley 79566* (US). SOLOLA: around lake at Finca Mocá, slopes of Volcán Atitlán, 1,000 m, *Steyermark 47887* (US). GUYANA. Crab Fall, Cuyuni River, *Tutin G-69* (K, US). HONDURAS. COMAYAGUA: below Barranco Trincheras, *Williams & Williams 18435* (US). COPAN: entre Acrópolis y Jaguarteple, *Molina 26236* (F, US). MEXICO. CHIAPAS: 13 km south of Ocozocoautla, *Breedlove & Davidse 54040* (US). SAN LUIS POTOSI: in a tropical forest along Mexico Highway

55 to Xilitla, *Sohns 1449* (US). VERACRUZ: Córdoba, *Hitchcock 6435* (BAA, LIL, P, US). PARAGUAY. AMAMBAY: Pedro Juan Caballero, *Fiebrig 4760* (M). CONCEPCION: zwischen Río Apa und Río Aquidabán, Villa Sana, *Fiebrig 4689* (G, K, US). NEEMBUCU: Alberdi, *Reales 231* (LIL). PRESIDENTE HAYES: Colonia Inglesa, frente a Trinidad, *Sparre & Vervoorst 898a* (LIL). PERU. LORETO: Río Mamón near Río Nanay, *Croat 19893* (MO). VENEZUELA. AMAZONAS: Dpto. Atures, terraplén y área de rebalse del Río Orinoco, en el muelle de Puerto Ayacucho, *Guánchez 2357* (MO, VEN). APURE: Hato San Juan del Río Claro, a orillas del Río Claro, al S de Cunaviche, 1 Feb. 1956, *Borsotti s.n.* (VEN). BARINAS: en cercanías de Ciudad Nutrias, *Zuloaga et al. 4315* (MO, SI*, VEN). GUARICO: at intersection of Río Orituco and road from Calabozo to Cazorla, along river bank, wet soil, semi-erect in shrubs, up to 2 m tall, *Davidse 3716* (K, MO, VEN). ZULIA: Distrito Perijá, 14 airline km NE of the intersection of the Río Aricuaisa and the Maracaibo–La Fría Hwy, 9°26′N, 72°29′W, *Davidse et al. 18411* (MO, NY, VEN).

Panicum hylaeicum is distinguished from *P. laxum* mainly by its cordate and amplexicaulous leaves, and the culms usually rigid. It differs from *P. polygonatum* also by its amplexicaulous leaves, and by having spikelets not pointed, with the lower palea well developed and a lower flower staminate.

Zuloaga (1981) considered this species to be a synonym of *P. boliviense* Hackel. A detailed study revealed that *P. boliviense* is a synonym of *P. polygonatum*, representing only a robust form of the latter species. There is in *P. hylaeicum* a gradation in the pilosity of the spikelet, from some specimens with spikelets densely pilose to others with spikelets completely glabrous.

6. **Panicum laxum** Sw., Prodr.: 23. 1788. TYPE: Jamaica. Without locality, *Swartz s.n.* (holotype, S, photo of the type, K; isotype, M). Figures 4, 9–11.

Panicum agrostidiforme Lam., Tabl. Encycl. 1: 172. 1791. TYPE: "Ex Amer. merid. Communic. A. D. Richard" (holotype, P, fragments, BAA, US 80537).

Panicum tenuiculmum G. Meyer, Prim. Fl. Esseq.: 58. 1818. TYPE: Guyana (holotype, LE, fragment, US).

Panicum leptomerum J. S. Presl, Reliq. Haenk. 1: 311. 1830. TYPE: Without locality, *Haenke s.n.* (holotype, PR, fragment, US 2903500).

Panicum diandrum Kunth, Revis. Gramin. 2: 393, pl. 110, 1831. TYPE: "Crescit in insula Guadelupae inque Brasilia" (type, B not seen, photo and fragment, US 80660).

Panicum ramuliflorum Hochst. ex Steudel, Syn. Pl. Glumac. 1: 65. 1853. TYPE: Surinam. Without locality, *Kappler 1523* (holotype, P, fragment of the type, US 2830942; isotypes, G, M, W).

Panicum psilanthum Steudel, Syn. Pl. Glumac. 1: 66. 1853. TYPE: Uruguay. Without locality, *Deloche s.n.* (not seen).

Panicum laxum Sw. var. *pubescens* Doell, in C. Martius, Fl. Bras. 2(2): 213. 1877, pro parte. SYNTYPES: Brazil. Goiás: Porto Real, *Burchell 8705*. Pernambuco: Without locality, *Gardner 1182*. Without state and locality, *Riedel 943*, *Burchell 3456* (syntype of *Burchell 8705*, W, fragment, US; of *Gardner 1182*, G, K, P, W; of *Riedel 943*, G, K, W; of *Burchell 3456*, W).

Panicum pilosum Sw. var. *epilosum* Fourn., Mexic. Pl. 2: 24. 1886.

Panicum luticola A. Hitchc., Contr. U.S. Natl. Herb. 22: 485, fig. 82, 1922. TYPE: Guyana. Mazaruni River, Penal Settlement, 5 Dec. 1920, *Hitchcock 17313* (holotype, US; isotypes, F, G, K, NY, P, US, W).

Panicum hondurensis Swallen, Contr. U.S. Natl. Herb. 29: 270. 1949. TYPE: Honduras. Valle: San Lorenzo, 10 Sep. 1945, *Rodríguez 3323* (holotype, US 1869140; isotypes, MO, US 1869141).

Panicum caroniense Luces, Bol. Soc. Venez. Ci. Nat. 15: 26, f. 12. 1953. TYPE: Venezuela. Bolívar: cercanías de Santa Elena, 28 Mar. 1946, *Tamayo 3209* (holotype, VEN; isotype, US 80558).

Panicum laxum Sw. var. *vestitum* L. B. Smith & Wasshausen, Bradea 2(35): 245. 1978. TYPE: Brazil. Santa Catarina: Joinville, Palacio Episcopal, 8 Nov. 1957, *Reitz & Klein 5665* (holotype, US 2240919).

Plants perennial, *culms* decumbent and rooting at the lower nodes to stoloniferous, then ascending to erect, 0.15–0.80 m tall, simple or branching at the upper nodes, internodes 2–15 cm long, glabrous, nodes dark, pilose to glabrous. Leaves with *sheaths* 2–11 cm long, pilose with papillose-pilose, caducous hairs to glabrous, the margins ciliate with tuberculate hairs, more so toward the distal portion, collar pilose to glabrous. *Ligules* membranous, shortly laciniate or ciliate at the distal portion, 0.4–0.8 mm long. *Blades* lanceolate, 4–30 cm long, 0.3–1.4 cm wide, flat, rounded to occasionally subcordate at base, sparingly pilose to glabrous, the margins scaberulous. *Inflorescence* terminal, lax to contracted, 6–29 cm long, 2–14 cm wide; *main axis*, branches and pedicels scabrous, axils of the branches short- to long-pilose, first-order branches alternate or occasionally opposite, ascending or spreading, spikelets crowded on short secondary branchlets, pedicels 0.5–1.4 mm long. *Spikelets* narrowly elliptic, 1–1.7 mm long, 0.4–0.6 mm wide, pilose, with caducous hairs, to glabrous, greenish or tinged with purple. *Lower glume* ovate, 0.6–1.1 mm long, ⅔ to ½ the length of the spikelet, 3-nerved, the keel scabrous on the upper portion. *Upper glume* 1–1.6 mm long, covering or not the upper anthecium, 5-nerved, the keel scabrous. *Lower lemma* 0.9–1.6 mm long, 5-nerved. *Lower palea* oblong, 1.1–1.5 mm long, 0.4–0.6 mm wide, membranous, shortly ciliate on the margins, occasionally expanded or not at maturity; lower flower staminate, stamens 3, or occasionally absent. *Upper anthecium* elliptic, 1–1.4 mm long, 0.4–0.5 mm wide, scabrous toward the apex, papillose, indurate, shining; anthers 2, occasionally 3, 0.3–0.7 mm long. *Caryopsis* elliptic, 0.8–0.9 mm long, 0.4–0.6 mm wide; hilum oblong, embryo ½ the length of the spikelet.

Distribution and ecology. Widely distributed in America, from Mexico to Argentina, and introduced in Africa. It is common in wet and open, disturbed places, in margins of roads, swamps, and rivers, between 0 and 1,500 m.

Selected specimens examined. ARGENTINA. BUENOS AIRES: Isla Martín García, *Parodi 4662b* (BAA). CHACO: Puerto Antequera, *Zuloaga et al. 3319* (SI*). CORRIENTES: 42 km E de Ituzaingó, puesto de Prefectura, *Zuloaga et al. 593, 2298* (SI). ENTRE RIOS: Concepción del Uruguay, borde del Río Uruguay, *Zuloaga et al. 2337* (MO, SI*). FORMOSA: Estancia Monteagudo, *Guaglianone et al. 326* (MO, SI). JUJUY: Calilegua, toma del Río Zora, *Cabrera et al. 30378* (SI). MISIONES: Santa Ana, camino al balneario municipal, *Zuloaga et al. 3170**, *3178* (SI). SALTA: de Río Pescado a Orán, *Cabrera et al. 26510* (SI). SANTA FE: Alto Verde, *Pensiero 116* (SI). TUCUMAN: Acheral, *Venturi 1635* (SI). ANTIGUA. Without locality, *Wullschaegel 623bis* (M). BELIZE. BELIZE: 41 mi. northwest of Belize along Northern Highway, *Croat 23967* (MO). CAYO: 4 km W of Hattieville along the Western Highway to Belmopan, *Davidse & Brant 32998* (MO*). TOLEDO: near border of Stann Creek along Southern Highway, *Croat 24185* (MO). BOLIVIA. BENI: Prov. Ballivián, Estancia El Porvenir, 50 km E of the Río Maniqui (San Borja) on the road to Trinidad, *Solomon 14775* (MO). COCHABAMBA: Campamento Izarzama, *Beck 1587* (LPB). LA PAZ: Zonga valley, below the dam at Lago Zongo, *Solomon 12901* (MO, SI). PANDO: Prov. Manuripi, along Río Madre de Dios, 80 km (by air) downstream from and NE of Chibe, *Nee 31529* (MO). SANTA CRUZ: Montero to Puerto Grether, *Renvoize & Cope 3953* (K, MO, SI). TARIJA: camino a Bermejo, Río Seco, *Coro-Rojas 1434* (LPB). BRAZIL. ACRE: NW of Cruzeiro do Sul, along road from Cruzeiro do Sul to Barao do Rio Branco, *Croat & Rosas 62653* (SI). AMAPA: Campo Experimental do Cerrado, km 45 da rodovia BR-156, *Valls 11644* (CEN). AMAZONAS: Fazenda Santa Terezinha, Costa da Terra Nova, Ilha do Careiro, *Prance & Ramos 23298* (US). BAHIA: by Rio Cumbuca, ca. 3 km S of Mucugé, *Harley et al. 15968* (CEPEC, K, MO). CEARA: Serra do Baturité, S. Inácio do Azevedo, *Eugenio 267* (RB). DISTRITO FEDERAL: Taguatinga Norte, *Silva 257* (IBGE, SP). ESPIRITO SANTO: Mirassol, *Mattos et al. 10849* (SP). GOIAS: ca. 20 km W of Veadeiros, 1,000 m, *Irwin et al. 12931* (MO, NY). MARANHAO: Barra do Corda to Grajaú, *Swallen 3625* (RB). MATO GROSSO: Poconé, Fazenda Ipiranga, *Allem & Vieira 1011* (CEN). MATO GROSSO DO SUL: Fazenda Bodoquena, *Allem et al. 2188* (CEN, MO). MINAS GERAIS: Serra do Espinhaço, 18 km W of Grão Mogol, *Irwin et al. 23558* (MO, P, UB, US). PARA: Santarém, *Spruce Panicum 5* (G, MO, P, M, W). PARANA: Parque Nacional de Sete Quedas, Ilhas dos Saltos, *Sendulsky 1824* (SI, SP). PERNAMBUCO: Beberibe, vicinity of Recife, *Chase 7760* (MO). PIAUI: between Floriano and Oeiras, *Swallen 4166* (US). RIO DE JANEIRO: Leblon, near Lagoa Rodrigo de Freitas, Rio de Janeiro, *Chase 8227* (MO). RIO GRANDE DO SUL: Tenente Portela, Reserva Florestal do Turvo, *Valls et al. 1791* (CEN). RONDONIA: vicinity of Santa Bárbara, 15 km east of km 117, *Prance & Ramos 7168* (MO). RORAIMA: vicinity of Caracaraí, along BR-174 road, between Caracaraí and Rio Branco, *Coradin & Cordeiro 1040* (CEN). SANTA CATARINA: 6 km N of Abelardo Luz, *Smith & Klein 15617* (SI). SAO PAULO: 1 km NE of Juquitiba along Highway 116 to Curitiba, *Davidse et al. 10914* (MO). COLOMBIA. AMAZONAS: Trapecio Amazónico, between Amazon and Putumayo water sheds, *Black & Schultes 46-396* (COL). ANTIOQUIA: Medellín, *Archer 351* (COL). ARAUCA: kilometro 13 al Sur de Arauca, Laguna El Venero, Hato de Tiberio Sosa, *Jorgenson 28* (COL). BOYACA: Villa de Leyva, *Zuloaga et al. 4181, 4183* (COL, MO, SI*). CALDAS: La Dorada, Hacienda "El Palmar," *Restrepo s.n.* (COL). CAQUETA: Florencia, Granja Macagual del I.C.A., *Echeverry 2477* (COL). CASANARE: Río Casanare, Hato "El Mochuelo," *Jaramillo 164* (COL). CAUCA: Guapi, Parque Nacional de Isla Gorgona, camino a Pablo Sexto, *Lozano & Rangel 5218* (COL). CHOCO: Hoya del Río San Juan, Andagoya, *Forero et al. 5120* (COL). GUAINIA: Río Inírida, Caranacoa, *Fernández et al. 7091* (COL); MAGDALENA: Santa Marta, *Smith 202* (COL, SI, W), *204* (COL, G, P). META: Puerto Gaitán, 4 km al W, borde de arroyo, *Zuloaga 3983* (COL, MO, SI*). NARINO: El Pedregal y Pilcuan, *Mora 2491* (COL). NORTE DE SANTANDER: Abrego, *García & Cabrales 6* (COL). SANTANDER: Barrancabermeja, carretera a El Llanito, *Schmidt-Mumm 450* (COL). TOLIMA: Ibagué, Planta Eléctrica de Mirolindo, 1,200 m, *Echeverry 1188* (COL). VALLE: Cartago, Santa Ana de los Caballeros, *Cuatrecasas 23036* (P). VAUPES: raudal de Yuruparí, *Schultes & Cabrera 19735* (US). VICHADA: 20 km NW of San José de Ocuné, *Hermann 10944* (COL). COSTA RICA. ALAJUELA: Carrillos de Poas, *Brenes 20172* (NY). GUANACASTE: Finca La Pacífica, 5 km NW of Cañas, *Pohl 12959* (MO). HEREDIA: roadside in pasture, 10 km SSE of Puerto Viejo, E side of Río Puerto Viejo, *Pohl 12819* (MO). LIMON: north shore or the mouth of the Río Colorado at Barra del Colorado, between the village and the Caribbean sea, *Davidse & Herrera 30979* (SI). PUNTARENAS: along west side of Río Grande de Tarcoles, ca. 0.5 km S of mouth of Río Turrubares, *Grayum et al. 5238* (MO). SAN JOSE: along Río Conejo in the valley of the Río Alumbre, *Pohl & Davidse 11059* (MO). CUBA. CAMAGUEY: vicinity of La Gloria, *Shafer 174* (US). ISLA DE LA JUVENTUD: San Pedro and vicinity, *Britton & Wilson 14803* (US). HABANA: Laguna de Ariguanabo, *Ekman 13092* (G). ORIENTE: Bayate, *Ekman 6065* (G). PINAR DEL RIO: Sierra de los Organos, Grupo del Rosario, *Ekman 12957* (US). SANTA CLARA: Minas de Motembo, *León et al. 8613* (US). DOMINICAN REPUBLIC. LA VEGA: vicinity of Jarabacoa, 500–1,200 m, *Allard 14513* (US). PACIFICADOR: Pimentel, near sea level, *Abbott 687* (US). ECUADOR. GUAYAS: Milagro, *Asplund 5761* (P). IMBABURA: Lita, *Acosta Solís 12150* (F). LOS RIOS: 14 km SE of Quevedo, *MacBryde 1119* (MO). NAPO: Carretera Hollín–Loreto, km 40–50, *Hurtado 688* (MO). PASTAZA: Mera, *Asplund 18340* (P). PICHINCHA: Puente Gloria de María, *Asplund 7271* (G). EL SALVADOR. AHUACHAPAN: vicinity of Ahuachapán, *Standley 19824* (US). LIBERTAD: Hwy. 2, ca. 20 km E of La Libertad, crossing of Río Tihuapa, *Pohl 11856* (MO). FRENCH GUIANA. Passoura, *Black & Klein 54-17230* (IAN, NY). GRENADA. Without locality, *Broadway 1870* (M). GUADELOUPE. Montebello, *Questel 503* (P, US). GUATEMALA. ALTA VERAPAZ: Panzos, along road to Hidrochulac and Cahabon from Tactic–El Estor road, *Stevens et al. 25354* (MO*). IZABAL: between El Estor and plant of abandoned nickel mine, *Stevens & Martínez*

25275 (MO*). PETEN: Sabanas y bosque secundario de Santa Rita, 20 kms al sur de Santa Elena, *Molina 15523* (MO). GUYANA. Rupununi, *Chan Choong 25* (US). HAITI. Massif de la Hotte, western group, Dame-Marie, Etang-Dérémond, *Ekman 10473* (US). HONDURAS. ATLANTIDA: Orillas del Río Piedras Gordas, Tela, *Ordonez 6* (MO). CHOLUTECA: Marcovia, 20 km NE de Choluteca, *Argenal 33* (MO). COMAYAGUA: Vado Alto, orilla del Río Sulaco, *Nelson et al. 7671* (MO). COPAN: Ocoteseco, 20 km NE de Santa Rosa de Copán, 1,300 m, *Portillo 47* (MO). EL PARAISO: near Piedra Herrada, drainage of the Río Yeguare, *Williams 15982* (MO). GRACIAS A DIOS: Alrededores del Río Platano, *Clewell & Cruz 4167* (MO). FRANCISCO MORAZAN: Alrededor de Nueva Tatumbla, 20 km al SE de Tegucigalpa, *Maradiaga 68* (MO). OLANCHO: Montaña de Chifiringo, 20 km del campamento, *Izaguirre 36* (MO). SANTA BARBARA: Trinidad, Finca Las Colmenas, *Salguero 15* (MO). VALLE: 3 km E of San Lorenzo along the road to the new sea harbor, *Davidse & Pilz 31687* (MO*). YORO: Victoria, orilla del Río Sulaco, *Nelson et al. 7055* (MO). JAMAICA. Hope Grounds, *Harris 11800* (P). MARTINIQUE. St. Pierre, *Hahn 757, 1536* (G). MEXICO. CAMPECHE: about 9 miles W of Escarcega in calcareous soil, *Reeder & Reeder 6101* (MO). QUINTANA ROO: 15 km SSW of Puerto Morelos on Hwy. 307 to Felipe Carrillo Puerto, *Davidse et al. 20645* (MO). TABASCO: km 10.2 de Huimanguillo hacia Malpaso en carretera Huimanguillo–Malpaso, *Cowan et al. 2574* (MO). TAMAULIPAS: Hacienda Santa En Gracia, *V. Chase 7592* (MO). VERACRUZ: about 2 miles W of Minatitlán in area of tropical vegetation, *Reeder & Reeder 6027* (MO). NICARAGUA. CHINANDEGA: Los Balcones, a 9 km de Somotillo, carretera a Cinco Pinos, *Moreno 11511* (MO). CHONTALES: Hacienda Veracruz, including Cerro La Batea and Cerro Los Charcos, *Stevens 22372* (MO). ESTELI: 1.5 km al N del valle San José de la Laguna, camino a San Nicolás, *Moreno 11361* (MO). JINOTEGA: along road from Hwy. 3 through La Fundadora, between Las Camelias and La Salvadora, *Stevens & Grijalva 15305* (MO). MATAGALPA: Ranchería, 11 km al NE de Muy muy, *Moreno 24430* (MO). RIO SAN JUAN: meadow along Río San Juan, *Seymour 5295* (MO). ZELAYA: Puerto Cabezas, ca. 14°01′N, 83°23′W, *Stevens 17805* (MO). PANAMA. BOCAS DEL TORO: Alrededores de Quebrada Chica, *Correa et al. 3830* (MO). CANAL ZONE: Cerro Gordo, near Culebra, *Standley 25995* (MO). COLON: vicinity of San Miguel de La Borda, *Croat 9878* (MO). DARIEN: vicinity of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al. 834* (MO). LOS SANTOS: one mile south of Pedasi, *Correa 70* (F). PANAMA: between Pacora and Chepo, *Woodson et al. 1632* (MO). VERAGUAS: roadside savanna 2–4 miles E of Santiago, *Duke 12346* (MO). PARAGUAY. ALTO PARANA: Puerto Bertoni, *Bertoni 4951, 3673, 3602, 5831, 5846* (W). AMAMBAY: Pedro Juan Caballero, *Fiebrig 4776* (G, W). CAAGUAZU: Caaguazú, *Balansa 56a* (P). CAAZAPA: Tavaí, *Mereles 2297* (MO). CENTRAL: Asunción, *Balansa 57, 58* (G, P). CONCEPCION: Río Apa, *Hassler 8189* (P). CORDILLERA: Cordillera de Altos, Cerro Tobatí, *Schinini 24029* (G, MO). GUAIRA: Azucarera de Tebicuary, Río Tebicuary, *Schinini 5907* (G, SI). MISIONES: Santiago, Estancia La Soledad, *Pedersen 3260* (SI). PARAGUARI: Paraguarí, *Balansa 57c* (G, P). PRESIDENTE HAYES: Pilcomayo River, *Morong 977* (G, MO). PERU. AMAZONAS: ridge above Cikan Ece Creek, *Berlin 1643* (MO). CUZCO: entre Otalaya y Salvación, *Vargas 16277* (US). HUANUCO: Tingo María, *Asplund 13003* (P). JUNIN: Prov. Satipo, km 41 on road to Satipo, 1,000 m, *Smith et al. 1438* (MO). LORETO: Prov. Alto Amazonas, Capahuari Sur (Campamento Petrolero), *Vásquez et al. 3023* (MO). MADRE DE DIOS: Prov. Manú, Parque Nacional del Manú, Cocha Cashu Station, *Foster 9864* (MO). PASCO: Oxapampa, Río Iscozacín, tributary of Río Palcazu, *Knapp et al. 7830* (MO). SAN MARTIN: Quebrada de Canuto, *Schunke Vigo 10661* (K, SI). PUERTO RICO. 8 km SW of Vega Baja, *Mac Kee 10605* (P). SURINAME. Near Kayser Airstrip, *Irwin et al. 57554* (MO, NY, P, US). TRINIDAD & TOBAGO. Piarco Savanna, south of Arouca, *Hitchcock 10343* (US). URUGUAY. San José, Río Santa Lucía, Colonia Etchejare, *Rosengurtt B-4957* (P). VENEZUELA. AMAZONAS: Depto. Atabapo, Salto Yureba, Cerro Yureba, *Liesner 18764* (MO). ANZOATEGUI: Morichal El Pinal, 3 km norte de San Diego de Cabrotica, *Montes 1756* (MO). APURE: N de casa principal de UNELLEZ, en médano grande, *Zuloaga et al. 4330* (MO, SI*, VEN). BARINAS: cercanías de Ciudad Nutrias, 8°5′N, 69°19′W, *Zuloaga et al. 4313* (MO, SI, VEN). BOLIVAR: entre Piedra de la Virgen y la parte alta de la Escalera, carretera a la Gran Sabana, *Zuloaga et al. 4401* (MO, SI, VEN). COJEDES: San Carlos, *Burkart 16161* (SI). FALCON: Carretera Coro–Mirimire, cerca del Río Hueque, *Wingfield 6227* (MO). GUARICO: 21 km SSE of Calabozo along road to Cazorla, 95 m, *Davidse 3752* (MO, PORT). LARA: en potreros irrigados de Sicarigua, *Burkart 16657* (SI). MIRANDA: Cerros del Bachiller, near east end, between Quebradas Corozal and Santa Cruz, south of Santa Cruz, *Steyermark & Davidse 116468* (MO). MONAGAS: Alrededores de Laguna Grande, a unos 15 km, *Aristeguieta 3909* (MO). PORTUGUESA: a 4 km al Oeste de Guanare hacia Ciudad Barinas, *Zuloaga et al. 4302* (MO, SI, VEN). SUCRE: 8 km al N de Santa Fé, entre Barcelona y Cumaná, *Zuloaga et al. 4367* (MO, SI*, VEN). TACHIRA: alluvial flats, at El Vado, along Río Lobatera, in Parcelamiento Guarumito, 5.5 km west of La Fría (by air), *Steyermark et al. 120340* (MO). YARACUY: San Felipe, orilla del Río Yaracuy, *Burkart & Tamayo 16430* (SI). ZULIA: Distrito Perijá, between the Ríos Yasa and Tucuco along the Machiques and Los Angeles de Tucuco road, *Davidse et al. 18393* (MO).

This species has a wide distribution and a great amount of variability. There are small to medium specimens, some with contracted panicles, described as *P. luticola* and *P. caroniense*; others have open panicles, spikelets pilose or glabrous, and flowers with two (unusual in *Panicum*) or three anthers.

Specimens previously included in *Panicum hondurensis*, a species considered here as a synonym of *P. laxum*, are characterized by having the upper anthecium covered by verrucose papillae regularly distributed. This character links the species to subgenus *Steinchisma*. Also, there are other specimens of *P. laxum*, such as *Smith 202, Schunke Vigo 10661, 10802, Duke 11684 (2), Lewis & Pire 808*, and *Arbo et al. 1348*, that have the upper anthecium with verrucose papillae all over its surface; these specimens are intermediate in this character with species of subgenus *Steinchisma*.

FIGURE 21. *Panicum leptachne* (based on *Chase 8803*).—a. Habit.—b. Detail of ligule, sheath and blade.—c. Racemose unilateral branch.—d. Axis of a branch with hairs and pedicels.—e. Detail of paired, short pedicels on a branch.—f. Spikelet, lateral view.—g. Spikelet, lower glume view.—h. Spikelet, upper glume view.—i. Lower palea with lodicules and filaments of stamens.—j. Upper anthecium, lemma view with prickle hairs at the upper portion.—k. Upper anthecium, palea view.

7. **Panicum leptachne** Doell in C. Martius, Fl. Bras. 2(2): 195. 1877. TYPE: Brazil. Without locality, *Widgren 1157* (holotype, S, fragment US 80737). Figures 4, 21.

Panicum pilosum Sw. var. *polychaetum* Hackel, Ergeb. Bot. Exped. Akad. Wiss. Sudbras.: 9. 1906. TYPE: Brazil. São Paulo: prope Rio Grande inter Santos et Urbem São Paulo, 750–800 m, 1902, *Wacket s.n.* (holotype, W, fragment, US 2907505).

Plants of indefinite duration, probably perennial, the *culms* erect, ca. 100 cm tall, simple, internodes compressed, hollow, glabrous, nodes compressed, dark, densely pilose with appressed, whitish hairs to glabrous. *Sheaths* 11–14 cm long, longer than the internodes, with tessellate nerves, covered by short, appressed papillose-pilose hairs to glabrous, the margins short-ciliate with papillose-pilose hairs. *Ligule* membranous, 0.8–1 mm long, laciniate at apex. *Blades* lanceolate, 13–22 cm long, 1.8–2.5 cm wide, shortly pseudopetiolate, pseudopetiole sparingly pilose, brownish, blades flat, cordate, acuminate, glabrous. Peduncle ca. 10 cm long, glabrous. *Inflorescence* a terminal, ovate panicle 25–40 cm long; *main axis* wavy, scaberulous and sparingly pilose near the axils of branches, first-order branches ascending, numerous, axis triquetrous, with one side flattened, scabrous and covered with conspicuous, long papillose-pilose hairs; second-order branches absent; spikelets paired and secund on short, scabrous pedicels. *Spikelets* narrowly elliptic, 2.1–3.2 mm long, 0.5–0.8 mm wide, greenish or tinged with purple, scabrous on glumes and lower lemma. *Lower glume* 1–2 mm long, ⅖ to ½ or more the length of the spikelet, 3(–5)-nerved, the keel scabrous above, acute. *Upper glume* 5(–7)-nerved, not covering the apex of the upper anthecium, cucculate. *Lower lemma* 3(–5)-nerved, the keel scabrous above. *Lower palea* lanceolate, brownish, 1.7 mm long, 0.4 mm wide, hyaline, glabrous, to absent; lower flower present, with 2 lodicules and 3 anthers, or absent. *Upper anthecium* narrowly elliptic, 1.8–2.5 mm long, 0.6–0.7 mm wide, brownish, membranous, scabrous at the apex of lemma and palea; lemma 5-nerved. *Caryopsis* obovate, 1.2 mm long, 0.6 mm wide, plano-convex, brownish; hilum oblong, embryo ⅓ the length of the caryopsis.

Distribution and ecology. This species grows in Brazil in the states of Minas Gerais, Rio de Janeiro, Paraná, and São Paulo, in wet places up to 650 m elevation.

Additional specimens examined. BRAZIL. MINAS GERAIS: Juiz de Forá, Faz. da Cachoeira, *Roth 1323* (RB, US); Lavras, *Chase 8771* (F, MO, RB, W), *8803* (US*); Viçosa, *Bailey 1177* (US), *Chase 9432* (F, MO, US), *Kuhlmann 1936* (RB), *s.n.* (RB 110562, SI, US); Belo Horizonte, Ressaca, *Mello Barreto 3019* (R, US). PARANA: Serra do Mar, Ypiranga, *Dusén 3664* (R, SI, US, W); Gral. Carneiro, Rio Lajeadao, *Hatschbach 13727* (K). RIO DE JANEIRO: Petrópolis, Caetitú, *Goes & Dionisio 762* (RB). SANTA CATARINA: Canoinhas, campo, 17 km W of Canoinhas on the road to Pôrto Uniao, *Smith et al. 10701* (NY, US). SAO PAULO: Horto Botanico, *Edwall 3859* (SP, US*); Pirajussura, *Gehrt s.n.* (SP 30558); São Paulo, Mogí das Cruzes, *Pickel 5222* (US); without locality, *St. Hilaire 623* (P), *Burchell 4495-2* (K, W), *4355* (K).

Related to *P. pilosum*, *P. leptachne* has bigger spikelets, 2.1–3.2 mm long, and a membranous upper anthecium.

Renvoize (1988) regarded *P. leptachne* as similar to *Hymenachne donacifolia*, differing by having the upper palea enclosed by the lemma at the apex.

8. **Panicum longum** A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 111, fig. 106. 1910. *Panicum pilosum* Sw. var. *macranthum* Scribner, U.S.D.A. Div. Agrost. Circ. 19: 1. 1900. Not *P. macranthum* Trin. 1826. TYPE: Mexico. Veracruz: swamps near Jalapa, *Pringle 8195* (holotype, US* 354552; isotypes, M, NY, P, W). Figure 2.

Plants perennial, ascending or spreading from a ± geniculate base; *culms* 1 to 2 m long, many-noded, simple or sparingly branching from the lower nodes, internodes glabrous, compressed, hollow, nodes dark, compressed, glabrous. *Sheaths* shorter or longer than the internodes, papillose-pilose with long caducous hairs, the margins ciliate. *Ligule* 0.6 mm long, a membrane with a fringe of hairs at the upper portion. *Blades* lanceolate, 10–25 cm long, 0.6–1.2 cm wide, shortly pseudopetiolate, pseudopetiole dark, blades flat, narrowed at base, acuminate, sparsely papillose-pilose on the adaxial surface, glabrous beneath, margins scabrous, the midnerve manifest. *Inflorescence* a terminal panicle 18–25 cm long, 2–5 cm wide, short-exserted or included at base; *main axis* wavy, with long, stiff hairs toward the distal portion, first-order branches ascending, the lower alternate, middle and upper opposite or whorled, axis of the branches triquetrous, flattened on one side, densely papillose-pilose with hairs exceeding the length of the spikelets, second-order branches absent; spikelets secund and paired or occasionally singly on short, scabrous pedicels. *Spikelets* narrowly elliptic, 2.3–2.5 mm long, 0.6–0.7 mm wide, acuminate, scabrous, especially over the nerves of glumes and lower lemma. *Lower glume* 1.3–1.5 mm long, ½ or more the length of the spikelet, acuminate, 3-nerved, nerves anastomosed toward the apex.

Upper glume shorter than the lower lemma, 5-nerved. *Lower lemma* exceeding the upper anthecium in length, 3(–5)-nerved. *Lower palea* absent; lower flower absent. *Upper anthecium* narrowly elliptic, 2–2.2 mm long, 0.6–0.7 mm wide, membranous, scabrous toward the apex and covered with silica bodies. *Caryopsis* unknown.

Distribution and ecology. Mexico, known only from the type collection, growing in swamps.

This species is related to *P. leptachne,* from which it differs slightly by having leaves narrow at their bases and spikelets usually smaller; the two species may be conspecific. However, due to the geographic distribution of *P. longum* and *P. leptachne,* both are maintained as separate species in the present treatment.

9. **Panicum pernambucense** (Sprengel) Mez ex Pilger in Engler, Nat. Pflanzenfam. (ed. 2) 14e: 15. 1940. *Agrostis pernambucensis* Sprengel, Syst. Veg. 1: 258. 1825. TYPE: Brazil. Pernambuco: Without locality and collector. Figures 5, 12, 22.

Panicum rivulare Trin., Gram. Panic.: 213. 1826. TYPE: Brazil. Rio de Janeiro: Serra dos Orgaos, *Langsdorff s.n.* (holotype, LE, fragments, BAA, US 974638, photo of type, K).

Panicum excelsum Nees, Agrost. Bras.: 180. 1829. TYPE: Brazil. "Habitat in Brasilia meridionale (*Sellow*)" (holotype, B; isotypes, K, US 1061585, fragments, BAA, NY, US 974640, 1061585, 2907336).

Panicum urticans L. B. Smith & Wasshausen, Bradea 2(35): 246, fig. 2 E–G, 1978. TYPE: Brazil. Paraná: Porto Vitoria, barranco do Rio Jangada, 7 Dec. 1971, *Smith & Klein 15715* (holotype, US 2849460).

Robust rhizomatous perennial, 2–3 m tall, *culms* erect, branching at the middle and upper nodes; internodes 8–22 cm long, 0.8–1 cm diam., stramineous, hollow, hirsute to glabrous; nodes pilose to glabrous, dark. *Sheaths* 8.7–18 cm long, glabrous or densely papillose-pilose with caducous hairs. *Ligules* 0.5–1.3(1.8) mm long, membranous; collar brownish. *Blades* lanceolate, 17–60 cm long, 0.8–2 cm wide, subcordate, attenuate at the apex, the margins scaberulous, sparsely pilose to glabrescent, the midnerve conspicuous. *Inflorescence* a terminal, lax panicle 27–40 cm long, 8–12 cm wide; *main axis* scabrous, with or without short hairs, axils of the branches short-pilose, spikelets short-pedicelled, crowded on short, second-order branches, first-order branches ascending to spreading, distant, alternate to opposite, occasionally whorled, appressed, the branchlets short, appressed; pedicels scabrous, short, 0.4–2 mm long. *Spikelets* narrowly elliptic, 1.7–2.2(–2.5) mm long, 0.4–0.8 mm wide, glabrous. *Lower glume* ovate, 0.8–1.2 mm long, ½ the length of the spikelet, 3-nerved, the keel scabrous toward the apex. *Upper glume* 1.4–2.1 mm long, shorter than the lower lemma, 3–5-nerved, the keel scaberulous. *Lower lemma* oblong, 1.7–2.2 mm long, 3–5-nerved, the keel scabrous. *Lower palea* usually absent, when present elliptic, hyaline; lower flower absent. *Upper anthecium* narrowly elliptic, 1.7–2.2 mm long, 0.4–0.8 mm wide, membranous, stramineous, scabrous at the apex of lemma and palea, the rest of its surface with simple papillae and silica bodies. *Caryopsis* elliptic, 0.9–1 mm long, 0.5–0.6 mm wide.

Distribution and ecology. South America, from northeastern Brazil, in the state of Paraiba, to Paraguay and Argentina. It is found at margins of streams and rivers, where it forms huge colonies. In flower between October and February.

Selected specimens examined. ARGENTINA. BUENOS AIRES: San Pedro, Isla del Recreo, *Nicora 3610* (SI). CHACO: Puerto Antequera, *Zuloaga et al. 3323* (SI*). CORRIENTES: ruta nacional 12, 5 km antes del Arroyo Itaembé, *Zuloaga et al. 3232* (SI*). ENTRE RIOS: San Carlos, *Meyer 10811* (LIL); ruta entre Concepción del Uruguay y Gualeguaychú, *Zuloaga & Deginani 2494* (SI*). FORMOSA: Formosa, *Jorgensen 2418* (SI, US). MISIONES: de Apóstoles a Concepción de la Sierra, Arroyo Las Tunas, 2 km de Concepción de la Sierra, *Zuloaga et al. 3251* (SI*); Santa Ana, camino al balneario municipal, *Zuloaga et al. 2235* (MO, SI*). SANTA FE: Reconquista, Isla Mascota, *Job 956* (LP, NY). BRAZIL. BAHIA: Serra do Sincorá, on road to Cascavel, 3 km S of Mucugé, *Harley et al. 15961* (CEPEC, K, MO, NY, P, US). ESPIRITO SANTO: Rodovia BR-101, Rio Santa Maria, *Hatschbach 48776* (K). MATO GROSSO: Porto Frangeli, *Hatschbach 40611* (MO, NY). MATO GROSSO DO SUL: vicinity of Dourados, *Chase 10957* (MO, RB, US). MINAS GERAIS: 9 km NE of Camundacaia, *Davidse & D'Arcy 10563* (K, MO, SP). PARAIBA: Soledade, *Glaziou 16632* (F, P, US, W). PARANA: Pitanga, Borboleta, *Hatschbach 46007* (K, NY, US). PERNAMBUCO: near Santa Esmeralda, *Pires Furtado 119* (RB). RIO DE JANEIRO: Monte Serrat, below Serra de Itatiaia, near Campo Bello, *Chase 8365* (MO, NY, RB, US). RIO GRANDE DO SUL: Vacaria, Vale do Rio Ibitiriá, *Valls et al. 1897* (CTES, US). SAO PAULO: city of São Paulo, 6–7 km SW of center of city, along the Rio Pinheiros, *Skvortzov 90* (K, UB, US). PARAGUAY. ALTO PARANA: Puerto Bertoni, *Bertoni 3889, 4177, 5134* (W). CAAGUAZU: Tacurú, *Sparre & Vervoorst 2229* (LIL). CENTRAL: in regione lacus Ypacaraí, *Hassler 11468* (G, NY, US). CORDILLERA: Cordillera de Altos, Cerro Tobatí, *Schinini 23974* (G, SI). GUAIRA: Itapé, *Joergensen 4089* (F, MO, NY, SI, US). PARAGUARI: prope Sapucay, *Hassler 12904* (G, US). SAN PEDRO: Puerto Antequera, *Rojas 2326* (SI).

There is variation in the pilosity of culms and sheaths of this species. In *P. pernambucense* there are specimens with culms and sheaths with abun-

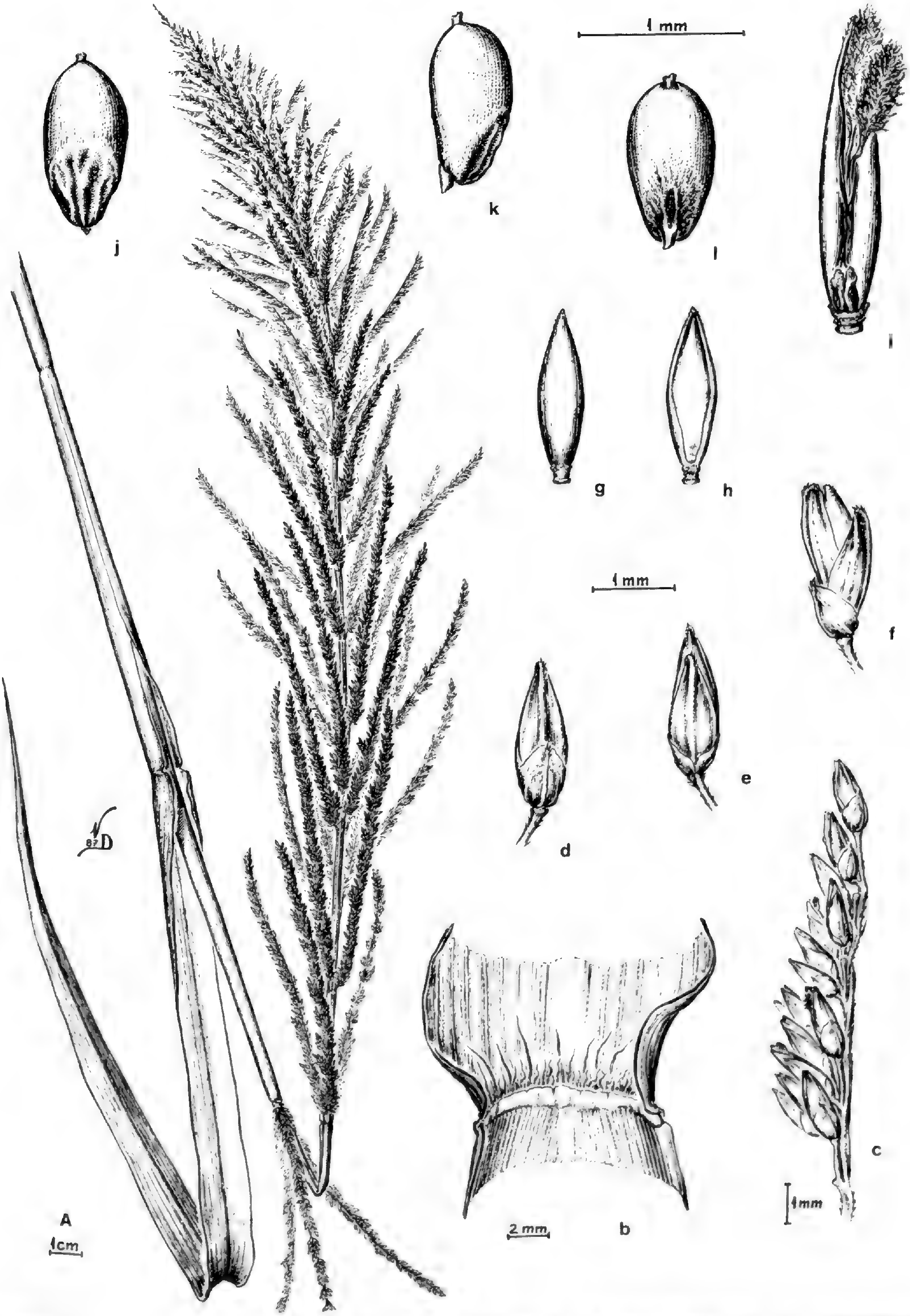

FIGURE 22. *Panicum pernambucense* (based on *Joergensen 2418*).—a. Upper portion of a culm with blade and terminal panicle.—b. Detail of membranous ligule and hairs at the lower portion of the blade.—c. Racemose unilateral branch with paired spikelets.—d. Spikelet, lower glume view.—e. Spikelet, upper glume view.—f. Spikelet, lateral view.—g. Upper anthecium, lemma view.—h. Upper anthecium, palea view.—i. Upper palea with lodicules and stigmas.—j. Caryopsis, embryo view.—k. Caryopsis, lateral view.—l. Caryopsis, hilum view.

dant rigid and caducous papillose-pilose hairs, while others are almost glabrous; the presence or absence of hairs is not correlated with any other character. For this reason, *P. urticans*, which is similar in other respects to *P. pernambucense*, has been included in synonymy.

Panicum pernambucense is similar to *P. grumosum*, and in some cases specimens are difficult to assign to one or the other species, as in several collections from Paraguay (e.g., *Hassler 11468*, *Schinini & Bordas 25190*). However, *P. pernambucense* can be distinguished by its usually smaller spikelets, lower palea absent or less commonly present, lower flower absent, and a wider range of distribution.

10. Panicum pilosum Sw., Prodr.: 22. 1788. *Setaria pilosa* (Sw.) Kunth, Revis. Gramin. 1: 47. 1829. *Panicum distichum* Lam. var. *pilosum* (Sw.) Griseb., Fl. Brit. W. Ind.: 548. 1864. TYPE: Jamaica. Without locality, *Swartz s.n.* (holotype, S; isotype, M, fragment, US 80916). Figures 2, 13, 14.

Panicum distichum Lam., Encycl. 4: 731. 1798. *Setaria disticha* (Lam.) HBK, Nov. Gen. & Sp. 1: 112. 1816. TYPE: "Cette plante croit a la Jamaique" (holotype, P, fragment, US 80650).

Panicum pilisparsum G. Meyer, Prim. Fl. Esseq.: 57. 1818. *Setaria meyeri* Kunth, Revis. Gramin. 1: 47. 1829. TYPE: Guyana. Essequibo: "in graminosis humidis plantitionis Hamburg" (holotype, GOET not seen, fragment, US 2907509).

Panicum pennisetum Roth, Nov. Pl. Sp.: 55. 1821. TYPE: Guyana. Essequibo: *Mertens s.n.* (holotype, B not seen, photo of type, K).

Panicum trichophorum Schrad. ex Schultes, Mantissa 2: 247. 1824. *Setaria schraderi* (Schrad. ex Schultes) Kunth, Revis. Gramin. 1: 47. 1829. TYPE: Brazil: "In Brasilia, Princeps Sereniss. Maximil. Neowidens" (type not seen).

Panicum densiflorum Willd. ex Sprengel, Syst. Veg. 1: 320. 1825. TYPE: "*P. densiflorum* Willdenow. America merid. *Humboldt*" (holotype, B not seen, fragment, US 2903513, photo of type, SI).

Panicum distichum Lam. var. *luxurians* G. Meyer, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 768. 1825.

Panicum distichum Lam. β *lancifolium* Griseb., Fl. Brit. W. I.: 548. 1864. *P. distichum* Lam. var. *lancifolium* (Griseb.) A. Hitchc., Man. Grasses W. Ind.: 267. 1936. *Panicum distichum* Lam. γ *lancifolium* Griseb., Fl. Brit. W. I.: 548. 1864. *Panicum pilosum* Sw. var. *lancifolium* (Griseb. ex A. Hitchc.) Pohl, Fieldiana, Bot. 4: 381. 1980. TYPE: Trinidad. Without locality, *Crueger 84* (fragment and photo of the type, US 80649).

Panicum coenosum Doell, in C. Martius, Fl. Bras. 2(2): 191. 1877. TYPE: Brazil. Amazonas: Manaus, *Spruce 1235* (*Panicum 38*) (isotypes, G, K, M, NY, P, US 1445789, W, fragment, US).

Panicum pilosum Sw. var. *latifolium* Doell, in C. Martius, Fl. Bras. 2(2): 212. 1877. SYNTYPES: Brazil. Rio de Janeiro: Tijuca, 27 Feb. 1870, *Glaziou 4300*, *Raben 169* (isosyntype of *Glaziou 4300*, P, fragment of *Raben 169*, US 80918).

Panicum milleflorum A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 17: 494. 1915. TYPE: Panama. Canal Zone: Frijoles, *Hitchcock 8387* (holotype, US 693327; isotypes, G, K, NY, P, US, W).

Plants of indefinite duration, probably perennial, stoloniferous, *culms* decumbent, rooting and branching at the lower nodes, then erect, 10–70 cm tall, internodes 1.5–13 cm long, compressed, glabrous, nodes brownish to purplish, glabrous to densely pilose with long, whitish hairs. *Sheaths* usually shorter than the internodes, 3–9 cm long, densely papillose-pilose to glabrous, the margins pilose, more so toward the distal portion, collar brownish, pilose to glabrous. *Ligules* small, membranous, to commonly absent. *Blades* lanceolate, 6–28 cm long, 0.5–2 cm wide, shortly pseudopetiolate, subcordate and asymmetric at the base, glabrous to sparsely covered with papillose-pilose hairs on both surfaces, the margins scabrous. *Inflorescence* lax, 9–20 cm long, 2–8 cm wide; *main axis* and branches scabrous and with long hairs, axils of the branches pilose, spikelets crowded and paired, unilaterally disposed on first-order branches, second-order branches absent to occasionally present at the base of the inflorescence, the branches divergent to ascending, pedicels scaberulous, short, 0.4–1 mm long. *Spikelets* narrowly elliptic, 1.2–1.5 mm long, 0.5–0.6 mm wide, biconvex, glabrous to sparsely pilose. *Lower glume* 0.7–1 mm long, 3-nerved, the keel scabrous toward the apex. *Upper glume* 1.3–1.5 mm long, 5-nerved, the keel scabrous. *Lower lemma* 1.2–1.4 mm long, 3-nerved. *Lower palea* 0.4–1.1 mm long, 0.2–0.5 mm wide, equaling in length the lower lemma to small, membranous. *Upper anthecium* narrowly elliptic, 1.2–1.4 mm long, 0.4–0.6 mm wide, glabrous, smooth, finely scabrous at the apex and with simple papillae over the lemma and palea. *Caryopsis* broadly elliptic, brownish, 0.8 mm long, 0.5 mm wide; hilum punctiform, embryo ½ the length of the caryopsis.

Distribution and ecology. Widely distributed from Mexico and the West Indies to South America, from Colombia to Argentina. It is usually found at margins of woods or in disturbed places.

Selected specimens examined. ARGENTINA. CORRIENTES: Puesto de Prefectura, 42 km E de Ituzaingó, *Zuloaga et al. 623, 2303* (SI*). MISIONES: San Ignacio, Peñón del Teyucuaré, *Zuloaga et al. 3194* (SI*). BELIZE. CAYO: Cave Branch Section, Humming Bird Highway, *Gentle 8868, 8869* (F). TOLEDO: upper reach, Golden Stream, *Gentle 4582* (MO). STANN CREEK: along road and stream at Dry Creek, *Croat 24516* (MO, SI). BOLIVIA. BENI: Guayamerín, *Krapovickas & Schinini 35017* (SI). COCHABAMBA: San Rafael, *Steinbach 482* (GH, NY). LA PAZ: Mapiri, *Buchtien 78* (BAF, SI, SP). SANTA CRUZ: Ichilo, de Montero a Puerto Grether, *Renvoize & Cope 3956* (K, LPB). BRAZIL. ACRE: Rio Branco, *Calderón & Soderstrom 2308* (US). ALAGOAS: Porto Calvo, Fazenda Macaitá, *Campelo 2181* (CEN). AMAPA: Estrada de Fazendinha, Macapá, *Rabelo et al. 3319* (MO). AMAZONAS: km 65, on road from Manaus to Bôa Vista, *Lasseign P21166* (US). BAHIA: Itacararé, near the mouth of the Rio de Contas, *Harley et al. 17567* (CEPEC, MO). CEARA: Guaramiranga, Serra do Baturité, *Fernández & Matos 9649* (IBGE). DISTRITO FEDERAL: 10 km S of Brasilia, Fazenda Vargem Bonita, *Irwin et al. 12285* (F, NY, US). GOIAS: Serra do Morcego, ca. 35 km NE of Formosa, *Irwin et al. 15255* (MO, SP, US). MARANHAO: Caxias to Barra do Corda, *Swallen 3532* (SP), *3603*, *3589* (US). MATO GROSSO: Poconé, Porto Cercado, *Allem & Viera 1608* (CEN, MO). MINAS GERAIS: ca. 15 km N of São João da Chapada, *Irwin et al. 28155*, *28158* (MO). PARA: Conceição do Araguaia, range of low hills ca. 20 km West of Redenção, *Plowman et al. 8595* (MO). PARAIBA: Areia, Escola de Agronomia do Nordeste, *Coelho de Moraes 750* (P). PARANA: Porto de Cima, *Dusén 14334* (MO, SI). PERNAMBUCO: vicinity of Recife, *Chase 7668* (MO). PIAUI: Serra de Araripe, *Luetzelburg 26304* (M). RIO DE JANEIRO: Parque Nacional Itatiaia, Picada Macieiras, *Zuloaga et al. 2355* (MO, RB, SI, US). RIO GRANDE DO SUL: São Leopoldo, *Rambo 41663* (LIL). RONDONIA: Forte Príncipe da Beira do Igarapé da Viúva, *Rodríguez & Wilson 4224* (NY). RORAIMA: along Boa Vista-BV 8 road (BR-174), km 197, *Coradin & Cordeiro 895* (CEN, IAN). SANTA CATARINA: Azambuja, *Smith & Reitz 6005* (SI). SAO PAULO: São Paulo, grounds of the Instituto Botânico, 860 m, *Davidse 10440* (MO). COLOMBIA. AMAZONAS: Río Igará–Paraná, Puerto Buenaventura, *Sastre 2423* (COL). ANTIOQUIA: road to Nechi, ca. 14 km from Caucasia–Planeta Rica road, Hacienda Candelaria, *Brant & Escobar 1253* (MO). BOLIVAR: ca. 16 km NW of San Jacinto, Cerro Maco, ca. 200 m SE of radar installation, *Zarucchi & Cuadros 4029* (MO). CALDAS: Santa Cecilia, *von Sneidern 5064* (F, LIL). CAQUETA: 23 km N of Florencia along main road to Garzón, E slope of Eastern Cordillera, 560 m, *Davidse et al. 5760* (COL, MO). CASANARE: Tauramena, *Uribe 4054* (COL). CAUCA: Guapi, Parque Nacional Isla de Gorgona, camino a Playa Blanca, *Lozano & Rangel 5616* (COL). CHOCO: Bahía de Solano, *Gentry & Forero 7177* (COL, MO). GUAINIA: Raudal Pilón, en el Río Guainía, *Pabon et al. 308* (COL). MAGDALENA: Santa Marta, *Smith 203* (COL, G, MO, W). META: de Cumaral a San Nicolás, 10 km del desvío a San Nicolás, 480 m, *Zuloaga 3868*, *3882* (COL, MO, SI). NARINO: Mocoa, *Bristol 235* (GH). PUTUMAYO: selva higrófila del Río San Miguel en la quebrada del Sipenae, *Cuatrecasas 10986* (COL). VALLE: Buenaventura, Vereda Puerto Patiño, *Muñoz 14-48* (COL). VAUPES: Alto Vaupés, alrededores de Miraflores, *Gutiérrez & Schultes 725* (COL). VICHADA: 27 km NE de San José de Ocuné, *Hermann 11013* (COL). COSTA RICA. ALAJUELA: 6 km W of Venicia, 450 m, *Pohl & Davidse 11254* (US). GUANACASTE: road to Upala, ca. 24 km NNE of CIA, *Pohl 12635* (MO). HEREDIA: La Selva, 3 km SE de Puerto Viejo, *Opler 551A* (MO, SI). LIMON: hills 2 airline km SSE of Islas Buena Vista in the Río Colorado, *Davidse & Herrera 31121* (MO, SI). PUNTARENAS: Osa Península, Rincón, *Pohl & Davidse 10744* (US). SAN JOSE: Basin of El General, *Skutch & Barrantes 5111* (MO, US). CUBA. HABANA: Herradura, *van Hermann 763* (W). ISLA DE LA JUVENTUD: Sierra Las Casas, *Killip 44160* (US). ORIENTE: Sierra de Nipe, in pinares, *Alain et al. 8797* (US). PINAR DEL RIO: vicinity of Sumidero, limestone hills, *Shafer 13505* (P). SANTA CLARA: banks of Guayabo River, Banao hills, *León 3982* (US). DOMINICA. South Chiltern Estate between Pointe Michel and Soufrière Bay, *Ernst 1318* (US). DOMINICAN REPUBLIC. LA VEGA: vicinity of Piedra Blanca, *Allard 13145* (US). SEIBO: along road between Miches and El Seibo at crest of Cordillera Oriental, 30 km from El Seibo, 600 m, *Gastony et al. 710* (US). ECUADOR. CARCHI: trail from Pailón to Gualpi Chico area of Awa Reservation, 1.5 km past Río Blanco, *Hoover et al. 2388* (MO). ESMERALDAS: Parroquia de Concepción; Playa Rica, *Mexía 8482* (MO). NAPO: Reserva Biológica Jatún Sacha, Río Napo, 8 km al E de Misahuallí, *Ceron 1038* (MO). PASTAZA: Curaray, *Neill & Palacios 6569* (MO, SI). PICHINCHA: Carretera Quito–Puerto Quito, km 113, 10 km al norte de la carretera principal, *Balslev & Balseca 4703* (MO). FRENCH GUIANA. Haut Marony, *Sastre & Moretti 3847* (MO, P). GRENADA. St. Georges, *Broadway s.n.* (US). GUATEMALA. ALTA VERAPAZ: Panzós, along road to Hidrochulac and Cahabón from Tactic–El Estor road, *Stevens et al. 25341* (MO*). IZABAL: slopes WNW (above) El Estor, along margin of open pit nickel mine, *Stevens & Martínez 25219* (MO*). SUCHITEPEQUEZ: near Patulul, *Standley 62150* (US). GUYANA. Wismar, *Hitchcock 17447* (F, IAN, NY, P, US). HONDURAS. ATLANTIDA: vicinity of La Ceiba, *Yuncker et al. 8203* (MO). COLON: Trujillo, Río Negro, SE del cerro Copiro, *Clotter 12* (MO). COMAYAGUA: Centro Acuícola El Carao, *Casco 48* (MO). COPAN: San Francisco mountain, between San Isidro and San Cristóbal, about 10 miles south of Copán Ruinas, *Molina 30696* (MO). CORTES: just S of Puerto Cortés, *Pohl & Davidse 12054* (MO). GRACIAS A DIOS: Alrededores de Puerto Lempira, *Gorgun 19* (MO). OLANCHO: montaña Chifiringo, 20 km de Campamento, *Izaguirre 113* (MO, SI). SANTA BARBARA: above El Mochito, *Pohl & Davidse 12094* (MO). YORO: Cerro between Río Guan Guan and Río Texiguat, E of Cerro Guan Guan, *MacDougal et al. 3258* (MO). JAMAICA. Near Claverty Cottage, Portland, *Harris 11524* (P). MARTINIQUE. Près St. Pierie, *Hahn 787* (G, P). MEXICO. GUERRERO: 8 km al NE de Paraíso, carretera a Puerto del Gallo, *Tenorio et al. 1401* (MO). NAYARIT: steep hillsides 2 miles west of Mazatán, *McVaugh 19104* (US). OAXACA: 8 km del Río Lana rumbo a Palomares, *Beetle M-5063* (MO). QUINTANA ROO: a 25 km al Sur de F. Carrillo Puerto, *Tellez 3025* (MO). SAN LUIS POTOSI: 2 miles east of Tamzunchale, on north side of river, *Hitchcock & Stanford 7304* (US). TABASCO: near the 21 km post W of Huimanguillo on the Huimanguillo–Francisco Rueda road, *G. & J. Davidse 9383* (MO). VERACRUZ: El Mirador, *Beetle M-2254* (MO). NICARAGUA. MATAGALPA: carretera al Tuma, approx. 28 km NE de la ciudad de Matagalpa, finca El Diamante, en los márgenes del Río Yasica, *Guzmán et al. 914* (MO). RIO SAN JUAN: Quebrada Santa Crucita, *Moreno 23441* (MO). ZELAYA: Corn Island, N and W shore, Sand Fly Point to Southwest Bay, *Stevens 19943* (MO). PANAMA. BOCAS DEL TORO: Al NW del campamento Changuinola 1 de Corriente Grande, Cerro Bracha, *Correa et al. 3157A* (MO). CANAL ZONE: between Mindi and Colón, *Hitchcock 7942* (US). COCLE: along road to Coclesito near Saw Mill, *Hammel 4062* (SI). COLON: 5 miles northeast of Sabanita towards Portobello, *Wilbur & Luteyn 11629* (MO). DARIEN: vicinity of Paya, Río Paya, *Stern et al. 380* (MO). HERRERA: disturbed area surrounding Chepo de las Minas, *Folsom et al. 7026* (MO). PANAMA: Cerro Ancón, *González 12* (MO). SAN BLAS: mainland opposite Playón Chico, 0–3 miles from Caribbean, *Gentry 6357* (MO). VERAGUAS: roadside adventives, road at base of Cerro Tuti, Santa Fé, *Folsom 3002* (MO). PARAGUAY. ALTO PARANA: in regione fluminis Alto Paraná, *Fiebrig 6008* (G, K, LIL, SI). AMAMBAY: in altiplanitie Sierra de Amambay, *Hassler 11993* (G). CAAGUAZU: Coronel Oviedo, *Rojas 14402* (BAF). CANINDEYU: ruta 10, 80 km W de Guairá, cruce Ybyrobara, *Carnevali 3763* (SI). CANTERA: Cantera, *Montes 7222* (SI). GUAIRA: Azucarera de Tebicuary, Arroyo Yhacá, *Schinini 5842* (G, SI). PARAGUARI: Mbocaiatí, près de Paraguarí, *Balansa 2944* (BAF, G, K, P). PERU. HUANUCO: Tingo María, *Vera 4080* (LIL). LORETO: Dtto. Iquitos, Río Nanay, de Pampachica al caserío de Santa Rita, *Rimachi 8014* (MO). MADRE DE DIOS: Rio La Torre, Explorer's Inn, near confluence of Río Tambopata & Río La Torre, 39 km SW of Puerto Maldonado, *Smith 359* (NY). SAN MARTIN: Tingo María, 625–1,100 m, *Allard 20431* (US). SURINAME. Lucie Rivier, 2 km below affluence of Oost Rivier, *Irwin et al. 55199* (MO, NY, US). ST. LUCIA. Savanne Edmund district, southeast of Piton Troumassée, *Proctor 17958* (US). ST. VINCENT. Along Chateubelair River, *Morton 5216* (US). TRINIDAD-TOBAGO. Castara, *Broadway 4063* (G, P). VENEZUELA. AMAZONAS: tall rainforest ESE of Puerto Ayacucho, 10–30 km on road to Gavilán, *Steyermark et al. 113908* (MO). APURE: Dtto. Paéz. Selva de Cutufí, between Cutufí on the Río Cutufí and the Río Sanare, *Davidse & González 21866* (MO*). ARAGUA: Parque Nacional Henry Pittier, Estación Rancho Grande, camino a La Toma, *Zuloaga & Ortíz 4513* (MO, SI*, VEN). BARINAS: Boca de Uribante, 19 km más allá del Caño Anaru, *Trujillo et al. 14951* (F). BOLIVAR: 35 km SW of Caicara del Orinoco, *Steyermark et al. 131246* (SI). DELTA AMACURO: without locality, *Tamayo 3635* (SI). LARA: 30 km SW of Barquisimeto, near road to Cerrata, *Meijer et al. 51* (LIL). FALCON: F6, entre Sanare y el Río Tocuyo, *Wingfield 6855* (MO). GUARICO: Dtto. Infante, Parque Nacional Aguaro-Guariquito, Caño Carnestolendo, *Delascio et al. 11482* (MO). MIRANDA: Guatopo, selvas pluviales, *Bernardi s.n.* (NY). PORTUGUESA: Camino hacia "La Estación," Municipio de Ospino, 1,200 m, *Stergios et al. 4616* (MO, PORT). SUCRE: entre Barcelona y Cumaná, carretera secundaria a 8 km al sur de Santa Fé, 300 m, *Zuloaga et al. 4366* (MO, SI, VEN). TACHIRA: Dtto. Córdoba, Cerro La Camiri, just south of the town of Río Negro, *Davidse & González 21545* (MO). ZULIA: Dtto. Colón, forested slopes at the settlement of Río de Oro along the Río de Oro, *Davidse et al. 18667* (MO).

Panicum pilosum is a very variable species, ranging from small specimens with a reduced panicle to others nearly 1 m tall with large inflorescences. For this reason, *P. coenosum* and *P. milleflorum* are synonymized, the first representing the smaller plants and the latter the larger ones.

In *P. pilosum* the spikelets are paired on secondary branches, as is the case in *P. leptachne* and *P. longum*. Occasionally, small branchlets may be present toward the base of the inflorescence on large specimens. Another peculiar feature of *P. pilosum* is the absence of ligules in most specimens.

11. Panicum polygonatum Schrader in Schultes, Mantissa 2: 256. 1824. *Setaria polygonata* (Schrader) Kunth, Rev. Gram. 1: 47. 1829. *Panicum pilosum* Sw. var. *polygonatum* (Schrader) Doell, in C. Martius, Fl. Bras. 2(2): 211. 1877. TYPE: Brazil. Bahia: Ilheus, 1816, *Prince Maximilian s.n.* (holotype, LE, fragment, US 80925). Figures 3, 15, 23.

Panicum potamium Trin., Gram. Panic.: 239. 1826. TYPE: Brazil. Without locality, *Langsdorff s.n.* (holotype, LE, fragment, US 81301).

Panicum bourgaei Fourn., Mexic. Pl. 2: 25. 1886. TYPE: Mexico. Veracruz: "In valle Cordovense, Januario," *Bourgeau 1662*, pro parte (isotype, P).

Panicum boliviense Hackel, Repert Spec. Nov. Regni Veg. 11: 19. 1912. TYPE: Bolivia. La Paz: Antahuacana, Espírito Santo, 1909, *Buchtien 2501* (holotype, W, fragment, US 80488; isotype, US*, photo of type, K).

Panicum ecuadorense Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 3. 1921. TYPE: Ecuador. Without locality, *Eggers 15064* (holotype, B, fragment, US 80635).

Plants perennial, shortly rhizomatous, with *culms* decumbent, rooting and branching at the lower nodes, then becoming erect, 0.15–0.50(–1) m tall, upper nodes branching or not, internodes cylindric, glabrous to sparsely papillose-pilose, 5–12 cm long, nodes dark, compressed, densely pilose with appressed, retrorse hairs, occasionally glabrous. *Sheaths* shorter than the internodes, 2.7–3.5 cm long, glabrous or rarely papillose-pilose toward the distal portion, the margins membranous, with one margin long-ciliate with papillose-pilose hairs toward the distal portion, collar pilose. *Ligules* membranous, laciniate, 0.3–0.5 mm long. *Blades* lanceolate, 4–15(–20) cm long, 0.6–1.5(–2.5) cm wide, shortly pseudopetiolate, pseudopetiole pilose or glabrous, cordate to subcordate, sparsely pilose with appressed hairs on both surfaces or glabrous, the margins scaberulous, the lower ones ciliate with caducous hairs. *Inflorescence* a lax, pyramidal panicle 8–20(–25) cm long, 3–15 cm wide; *main axis* sparingly hirsute to scabrous, first-order branches alternate, ascending, triquetrous and with or without long hairs, with one side flattened, the spikelets paired on short pedicels on short second-order branches. *Spikelets* narrowly elliptic, 1.3–1.6 mm long, 0.5–0.6 mm wide, pointed at the apex, greenish, pubescent or more commonly glabrous. *Lower glume* ovate, 0.7–0.9 mm long, ½ the length of the spikelet, 1–3-nerved, the keel scaberulous toward the apex. *Upper glume* 1.2–1.4 mm long, glabrous, 5-nerved, acute. *Lower lemma* 1.2–1.4 mm long, 3–5-nerved, acute. *Lower palea* 1.1–1.3 mm long, 0.2–0.4 mm wide, hyaline, glabrous to more commonly absent; lower flower absent, occasionally present with 3 stamens. *Upper an-*

FIGURE 23. *Panicum polygonatum* (a, based on *Chase 8555*; b–h, on type specimen).—a. Habit.—b. Ligule and base of blade.—c. Branch of a panicle with spikelet.—d. Spikelet, lateral view.—e. Upper anthecium, lemma view.—f. Upper anthecium, palea view.—g. Caryopsis, embryo view.—h. Caryopsis, hilum view.

thecium elliptic, 1.1–1.3 mm long, 0.5 mm wide, stramineous, smooth, indurate, scabrous at the apex; anthers 3, 0.3–0.5 mm long. *Caryopsis* elliptic, brownish, 0.8 mm long, 0.5 mm wide; hilum oblong, embryo ⅓ the length of the caryopsis.

Distribution and ecology. Widely distributed from Mexico to Paraguay, Bolivia and Brazil, occasionally present in Northwestern Argentina. It is found at borders of woods, swamps or in wet places, to 1,600 m elevation.

Selected specimens examined. ARGENTINA. MISIONES: Acaragua, *Bertoni 2822* (LIL, MO, US). BELIZE. STANN CREEK: along road and stream at Dry Creek, near District of Cayo border, *Croat 24517* (MO). TOLEDO: in high ridge, at base of hill near Manga Camp, Edwards Road beyond Columbia, *Gentle 6537* (MO, US). BOLIVIA. COCHABAMBA: San Rafael, *R. Steinbach 484* (MO, NY). LA PAZ: along road between Unduavi and Caranavi, 83.5 km beyond Unduavi, *Croat 51586* (MO*); Tipuani, Hacienda Simaco, *Buchtien 5334* (MO, NY, US*). SANTA CRUZ: Río Surutu, bañados, *Steinbach 6840* (G, K, LIL, MO, NY, US). BRAZIL. ACRE: trail to Rio Iaco from 7 km of road Sena Madureira to Rio Branco, *Prance et al. 7703* (M, MO, P). AMAZONAS: Solimoes, Copatana, beira do Rio Jutahy, *Froes 20594* (IAN, US). BAHIA: Ilheus, area do CEPEC, *dos Santos 3397* (CEPEC, RB), *3789* (CEPEC, K, RB). ESPIRITO SANTO: Santa Barbara do Caparaó, *Chase 10073* (US). GOIAS: Santa Rita do Paranahyba, *Chase 11630* (US). MINAS GERAIS: Juiz de Forá, *Chase 8555* (F, NY, US). PARANA: 9 km E of Guaraniau along highway BR-277 to Curitiba, *Davidse et al. 11283* (MO, UB). RIO GRANDE DO SUL: São Leopoldo, Quinta São Manuel, *Dutra 601* (R). RIO DE JANEIRO: Jardim Botânico, caminho dos Macacos, *Chase 8434* (F, MO, RB, US). RONDONIA: Island in Rio Madeira at mouth of Rio Jaciparana, *Prance et al. 5343* (MO). SANTA CATARINA: Florianópolis, *Zuloaga & Deginani 1878* (SI, US). SAO PAULO: Morro das Pedras, *Brade 7815* (R, SP), *9162* (IAN, R). COLOMBIA. AMAZONAS: Río Loretoyacu, *Black & Schultes 46-122* (US). ANTIOQUIA: carretera al mar en los alrededores del Río Ampurrumiado, *Gutiérrez & Barkley 17C172* (LIL, SI, US). CALDAS: Chinchina, *Cuatrecasas 23387* (US). CAQUETA: Miramar, Río Caquetá, *Soderstrom 1401* (K, MO). CASANARE: Tauranema, *Uribe 4268* (COL, NY). CAUCA: entre El Estrecho y Balboa, *Zuloaga & Londoño 4238* (COL, MO, SI*). CHOCO: Río Atrato, bocas del Río Tanando, *Idrobo & Cuatrecasas 2665* (US). CORDOBA: 3 km SW of Popales, Planta Providencia, *Alverson et al. 196* (MO, NY). CUNDINAMARCA: San Francisco-Alto Guarama, *Wood 3642* (COL). HUILA: La Plata, Hacienda La Limona, *Lozano et al. 4826* (COL). MAGDALENA: Santa Marta, *Smith 206* (COL, G, K, MO, P). META: entre Villavicencio y Restrepo, 6 km de Restrepo, *Zuloaga 4087* (COL, MO, SI*); Restrepo, Salinas, subida al cerro, *Zuloaga 3913* (COL, MO, SI*). NARIÑO: Trayecto San Isidro–La Planada, 1,500–1,800 m, *Olga de Benavides 9214* (MO). RISARALDA: Santa Cecilia, *von Sneidern 5192* (F, US). SANTANDER: vicinity of Barrancabermejo, Magdalena valley, *Haught 1923* (COL, NY, US). VALLE DEL CAUCA: Alto del Dinde, entre Cartago y Alcala, *Cuatrecasas 22941* (US). VICHADA: Caño Urimica, *Cabrera 2276* (COL). COSTA RICA. ALAJUELA: edge of cleared fields and wooded area bordering steep slopes above the Río Aguas Zarcas, south of Aguas Zarcas, *Burger & Stolze 5136* (MO). CARTAGO: Turrialba, *Pittier & Tonduz 4092* (M). HEREDIA: roadside in pasture, 10 km SSE of Puerto Viejo, E side of Río Puerto Viejo, *Pohl 12818* (MO). LIMON: 6 km W of Guapiles, *Pohl & Calderón 10017* (MO). PUNTARENAS: forest along trail between Las Alturas and Lotonsito, *Davidse 24387* (MO, SI). SAN JOSE: 10 km by road SW of Santiago de Puriscal, *Pohl & Pinette 13287* (MO). ECUADOR. CHIMBORAZO: entre Bucay y Heda, Rosa Mercedes, *Acosta Solís 5254a* (F). COTOPAXI: Tenefuerte, Río Pilato, *Dodson & Gentry 12248* (MO). EL ORO: Porto Velho, *Hitchcock 21256* (US). ESMERALDAS: Parroquia de Concepción, Playa Rica, *Mexía 8417* (MO, US). GUAYAS: Teresita, 3 km west of Bucay, *Hitchcock 20433* (US). IMBABURA: Lita, 500 m, *Acosta Solís 12239* (US). LOS RIOS: Río Palenque Field Station halfway between Santo Domingo de los Colorados and Quevedo, *Gentry 10191* (MO). MORONA-SANTIAGO: near Mendez, *Camp 865* (NY, US). NAPO: Baeza–Tena rd., 46 km S of Baeza, *Luteyn & Boom 8360* (MO, NY). PASTAZA: Hacienda San Antonio de Baron von Humboldt, 2 km al NE de Mera, *Palacios et al. 137* (MO). PICHINCHA: Nanegalito, al NW de Tandapaya, *Acosta Solís 17166* (US). TUNGURAHUA: valley of Río Pastaza, Machai, *Asplund 8527* (G, LIL, NY, P). EL SALVADOR. Ateos, in swamp, *Calderón 1880* (US). FRENCH GUIANA. Crique la Boue de l'Approuague, *Oldeman B-2225* (MO). GUADALOUPE. Without locality, *Bertero s.n.* (G). GUATEMALA. ALTA VERAPAZ: Finca Mercedes, Teleman, Panzos, faldas de la Sierra de las Minas, *Martínez et al. 22729* (MO). IZABAL: Quebradas, *Pittier 8564* (US). GUYANA: Issorora, Aruka River, *Hitchcock 17589* (K, MO, NY, P, US, W). HONDURAS. ATLANTIDA: Lancetilla Valley, near Tela, *Standley 53181, 53529* (US). CORTES: alrededores del centro ceremonial de Pulapanza, *Torres Flores 176* (SI). SANTA BARBARA: San Pedro Sula, 350 m, *Thieme 5578* (US). FRANCISCO MORAZAN: Montaña La Tigra, 30 km NE de Tegucigalpa, *Soihet 200* (MO, SI). OLANCHO: Orillas del Riachuelo Aguaquire, 30 km NE de Culmi, 700 m, *Nelson & Vargas 2660* (MO). YORO: 17–19 km SE of Río Viejo, on road to Olanchito, *Pohl & Davidse 12089* (MO). MARTINIQUE. Without locality, *Sieber 121* (W). MEXICO. CHIAPAS: Finca Mexiquito, *Purpus 7408* (US). VERACRUZ: Jesús Carranza, 1.5 km N del Poblado 2, *Zambrano 1165* (MO). NICARAGUA. BOACO: Cerro Mombachito, al SE de la ciudad de Boaco, *Moreno 248* (MO). CHONTALES: vicinity of La Libertad, *Standley 8848* (F). JINOTEGA: El Cedro, 19 km al N del Cuá, *Moreno 849* (MO). MATAGALPA: falda NW del Cerro Musún, trocha de Palan, *Araquistain & Moreno 2438* (MO). RIO SAN JUAN: El Castillo, 0–100 m, *Nelson 5190* (MO). RIVAS: Ladera N del volcán Concepción, Isla de Ometepe, *Martínez Salas et al. 1493* (MO). ZELAYA: El Salto, along Río Pis Pis and surrounding hills, *Pipoly 3578* (MO). PANAMA. BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel 1121* (MO). CANAL ZONE: Barro Colorado Island, at end of Fuertes Cove, *Croat 5255* (MO). CHIRIQUI: Burica Peninsula, Quebrada Mellize, 6 mi south of Puerto Armuelles, *Liesner 450* (MO). COCLE: El Valle de Antón and vicinity, *Seibert 485* (MO). COLON: trail from head waters of Río Boqueron back to fork with Río Escandaloso, *Hammel 3973* (MO). DARIEN: vicinity of Boca Quebrada Venado, Río Tuqueza, *Bristan 1101* (MO). PANAMA: Tocumen International Airport, *Dwyer 1864* (MO). VERAGUAS: Río Primero Braso, 2.5 km beyond Agriculture School Alto Piedra near Santa Fé, *Croat 25464* (MO). PARAGUAY. ALTO PARANA: Puerto Bertoni, *Bertoni 5356* (US). CAAGUAZU: Caaguazú, *Balansa 55* (BAF, G, P, US). CENTRAL: Asunción, *Jiménez 11190* (SI). CORDILLERA: Valenzuela, *Schwarz 11078* (LIL). GUAIRA: Santa Bárbara, près de Villa Rica, *Balansa 54a* (G, P). PERU. AMAZONAS: La Poza, Río Santiago, strip between Calle Piura and the Río Santiago, *Berlin 3678* (MO). HUANUCO: Prov. Pachitea, Comunidad Nativa Santa Marta, on bank of Sungaruyacu, *Smith 1251* (MO, NY). JUNIN: Colonia Perené, *Hitchcock 22059* (US), *22124* (US). LORETO: lower Río Huallaga, *Williams 4469* (US). MADRE DE DIOS: Tambopata Nature Reserve, *Barbour 5245* (MO, NY). PASCO: Oxapampa, Río Iscozacín, tributary of Río Palcazu, *Knapp et al. 7821* (MO). SAN MARTIN: on trail from Lamas to San Antonio east of Río Chupiseña, *Belshaw 3497* (MO, SI, US). TRINIDAD-TOBAGO. Mason Hall, *Broadway 4476* (G, P). VENEZUELA. AMAZONAS: Neblina base camp, on the Río Mawarinuma, *Davidse & Miller 26917* (MO*, NY, SI); along Río Mawarinuma, 1 to 3 km west of Cerro de La Neblina Base Camp, *Liesner 15696* (MO). APURE: selva de Cutufí between Cutufí on the Río Cutufí and the Río Sanare, *Davidse & González 21844* (MO*, PORT, SI). ARAGUA: Parque Nacional Henry Pittier, Estación Rancho Grande, camino a La Toma, *Zuloaga & Ortíz 4515* (MO, SI, VEN). BOLIVAR: El Dorado, *Couret 258* (US). DISTRITO FEDERAL: alrededores de la Planta Eléctrica de Mamo, *Pittier 11082* (VEN). FALCON: Cerro Socopo, east side above Socopito, 10°30′N, 70°45′W, riverside in shade, *Liesner et al. 8278* (MO, VEN). LARA: Dtto. Iribarren, Laguna Los Papelones, en la selva nublada en la Fila de las Goteras, *Steyermark et al. 103711* (VEN). MERIDA: La Llorona, on road to Amparo, *van der Werff & Ortíz 5754* (MO, NY, PORT, SI). MIRANDA: Dtto. Páez, Quebrada Chaguaramas, *González & Davidse 946* (MO, NY, PORT, VEN). MONAGAS: 10 km WSW of Jusepín, *Pursell 9094* (US, VEN). PORTUGUESA: 5 km NW de la Concepción, *van der Werff et al. 7521* (MO, PORT, SI). TACHIRA: Dtto. Uribante, Empresa Las Cuevas near La Fundación, 71°47′W, 8°50′N, *van der Werff 4900* (MO, VEN). ZULIA: along Río Cachiri, just north of hacienda Salamanca, *Steyermark et al. 123448* (MO, NY, VEN).

Panicum polygonatum is related to *P. laxum*, from which it differs in having narrow, elliptic spikelets, pointed at the apex, the lower palea commonly absent (or when present usually without a lower flower), and cordate to subcordate blades.

Panicum polygonatum differs from *P. pilosum* by having spikelets on short second-order branches, lower palea usually absent and ligule membranous, always present.

The pilosity of the plants varies, with sheaths and blades usually glabrous and nodes densely pilose; branches of the inflorescences vary also from hirsute, similar to *P. pilosum*, to scabrous and without long hairs.

Panicum boliviense Hackel was considered by Hitchcock & Chase (1910), and Zuloaga (1981) to be the species here considered *P. hylaeicum*, which has cordate and amplexicaulous leaves and rigid culms. *Panicum boliviense* actually represents a robust form of *P. polygonatum* that is approximately 1 m tall with cordate leaves and large panicles; specimens of this latter form range from Central America to Ecuador, Peru, and Bolivia.

The specimen *Idrobo & Cuatrecasas 2665* has the lower lemma indurate, similar to the one on the upper anthecium.

12. **Panicum stagnatile** A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 17: 528, fig. 141. 1915. TYPE: Panama. Canal Zone: Frijoles, 12 Oct. 1911, *Hitchcock 8388* (holotype, US* 693328; isotypes, F, G, K, MO, NY, P, US, W, fragment of type, BAA). Figure 5.

Panicum bernoullianum Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 3. 1921. TYPE: Guatemala. Mazatenango: *Bernouille 543* (holotype, B; isotypes, G, K, NY, fragment of type, US 80485).

Plants perennial, the *culms* prostrate, decumbent and rooting at the lower nodes, then ascending, 1 to 2 m tall, simple or occasionally with sterile branches, internodes 12–20 cm long, cylindric, hollow, glabrous, compressed, brownish, puberulent; nodes compressed, glabrous. *Sheaths* striate, glabrous, the margins ciliate. *Ligules* membranous, short-ciliate at apex, ca. 0.8 mm long. *Blades* lanceolate, 22–35 cm long, 1.5–3 cm wide, flat, with long hairs at the base of the adaxial surface behind the ligule, short-pilose on the adaxial surface and glabrous on the abaxial surface, subcordate to cordate, acuminate at the apex. *Inflorescence* a terminal, pyramidal panicle, 20–40 cm long; *main axis* wavy, scabrous, pulvini pilose, numerous slender first-order branches ascending or spreading, spikelets unilateral on slender second-order branches, axis of the branches and pedicels triquetrous, scabrous. *Spikelets* loosely clustered, lanceolate, 1.6–1.8 mm long, 0.4–0.5 mm wide, pointed, brownish to purplish, scabrous, especially on the keels of glumes and lower lemma. *Lower glume* 0.6–0.9 mm long, ⅓ to ½ as long as the spikelet, 1–3-nerved, acute. *Upper glume* 3(–5)-nerved, not covering the apex of the upper anthecium, obtuse to acute. *Lower lemma* 3-nerved, acute. *Lower palea* absent; lower flower absent. *Upper anthecium* lanceolate, 1.5 mm long, 0.4 mm wide, membranous, scabrous at the apex, whitish, the margins of the lemma inrolled only at the base; anthers 0.4–0.8 mm long. *Caryopsis* unknown.

Distribution and ecology. Southern Mexico to Panama, growing commonly in swamps or margins of rivers or ponds, from sea level to 100 m.

Additional specimens examined. BELIZE. CAYO: Humming Bird Highway, Pry Creek, *Gentle 8909* (G). STANN CREEK: Humming Bird Highway, *Gentle 8408* (US*); Middlesex, *Gentle 3029* (NY). EL SALVADOR. LA LIBERTAD: Near Ateos, 31 km W of San Salvador, *Fassett 28272* (US). GUATEMALA. IZABAL: Puerto Barrios, *Hitchcock 9153* (US). RETALHULEU: Río Coyote, along road 4 km W of Retalhuleu, 300 m, *Standley 87507* (US). HONDURAS. ATLANTIDA: vicinity of Tela, *Standley 54473* (US). MEXICO. CHIAPAS: Escuintla, *Matuda 1861* (GH, US); Acacoyagua, *Matuda 18416* (US). TABASCO: between San Juan Bautista and San Sebastián, *Rovirosa 625* (K, US). VERACRUZ: Campo Experimental de Hule, El Palmar, Zongolica, *Vera Santos 2655* (US). PANAMA. Without locality, *Hayes 214* (K).

Panicum stagnatile is related to *P. pernambucense*; it differs by its lax panicles, with the spikelets more diffuse on the branchlets, plants smaller with culms decumbent, rooting or not at the lower nodes. Spikelets are similar to those of *P. polygonatum*.

13. Panicum stevensianum A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 17: 498, fig. 77. 1915. TYPE: Puerto Rico. Campo Alegre, near Laguna del Tortuguero, 25 Nov. 1913, *Chase 6616* (holotype, US* 693323; isotypes, NY, US). Figure 5.

Plants of indefinite duration, probably perennials, *culms* prostrate, spreading, decumbent and rooting at the lower nodes, then becoming erect, 20–100 cm tall, internodes glabrous, nodes brownish, glabrous. *Sheaths* striate, glabrous or sparsely papillose-pilose with caducous hairs, one margin ciliate toward the apex, collar brownish, glabrous. *Ligules* membranous, shortly ciliate at the apex, 0.4–1 mm long. *Blades* lanceolate, 10–25 cm long, 0.5–1.7 cm wide, flat, subcordate to cordate at the base, the lower margins ciliate to sparsely pilose on the adaxial surface or completely glabrous. *Inflorescence* a terminal, lax to contracted panicle, 8–28 cm long, 1–6 cm wide; *main axis* wavy, scabrous, first-order branches alternate, axis of the branches and pedicels scabrous, spikelets secund or in short second-order branchlets, paired on short pedicels. *Spikelets* narrowly elliptic, 1.9–2.6 mm long, 0.6–0.7 mm wide, greenish or tinged with purple, glabrous, biconvex, upper glume and lower lemma subequal or the upper glume slightly shorter, pointed. *Lower glume* 0.8–1.1 mm long, nearly ½ the length of the spikelet, acuminate, 3-nerved, the keel scabrous. *Upper glume* 5-nerved, the keel scaberulous. *Lower lemma* 5-nerved. *Lower palea* lanceolate, 2 mm long, 0.6 mm wide, hyaline, the margins scaberulous; lower flower bisexual to male or occasionally absent, lodicules 2, truncate, anthers 3, 1.2 mm long, stigma purple, plumose. *Upper anthecium* narrowly ovate, 1.7–1.9 mm long, 0.5 mm wide, whitish, firmly membranous, scabrous at the apex, the rest of its surface papillose and with silica bodies. *Caryopsis* unknown.

Distribution and ecology. West Indies, in Cuba, Puerto Rico, and Guadaloupe, and South America, collected in Colombia, Venezuela, and occasionally in northeastern Brazil.

Additional specimens examined. BRAZIL. PERNAMBUCO: Dois Irmaos, vicinity of Recife, *Chase 7717* (US*). COLOMBIA. CASANARE: cerca del Hato Gandul, al sur del Río Pauto, *Blydenstein s.n.* (SI, US). CUBA. HABANA: Laguna de Ariguanabo, *Ekman 11516, 13093* (both G, NY, P, R, UB, US*), *16929* (US), *León 9030* (NY, US); Laguna de Castellano, *Ekman 16796* (NY, P, R, UB, US*), *Wilson 9558* (NY, US); Batabanó, *Ekman 12630* (US*); clearing in a swampy wood, W of Batabanó, *León 14200* (US). GUADALOUPE. Without locality, *L'Herminier s.n.* (G, P, US). VENEZUELA. GUARICO: Hato Flores Moradas, carretera Calabozo–Camaguán, *Ramia 1213, 1288* (both VEN).

EXCLUDED SPECIES

Panicum scabridum Doell in Martius, Fl. Bras. 2(2): 201. 1877. TYPE: Brazil. Amazonas: Manaus, Campo de Jauari, *Spruce 1281-3* (holotype, K, fragment, US; isotype, P).

Panicum prieurii Mez, Bot. Jahrb. Syst. 125: 3. 1921. TYPE: French Guiana. Without locality, *Leprieur s.n.* (holotype, B? not seen, fragment, US 2830932).

Panicum manacalensis Swallen, Phytologia 14: 77. 1966. TYPE: Venezuela. Amazonas: Río Atabapo, *Wurdack & Adderley 42986* (holotype US; isotypes, F, GH, K, MO, NY, VEN).

This species was included by Zuloaga (1987) in section *Laxa*. *Panicum scabridum* resembles *P. laxum* in that it has a similar habit, ligule, inflorescence and spikelet type, with the lower glume 3-nerved, ½ the length of the spikelet, and the upper glume and lower lemma subequal, 5-nerved. It differs by having an indurate and smooth upper anthecium, with scattered simple papillae toward the apex, but without prickle hairs or silica bodies; also, the caryopsis is completely black in *P. scabridum*.

The leaf anatomy of *P. scabridum* has shown major differences in relation to species of section *Laxa*. In this species there are no fusoid cells, and there are usually two to four cells between contiguous vascular bundles. Aerenchyma is associated with the keel, and the inner mestome sheath has abundant starch grains.

Vouchers for anatomical study: *Eiten & Eiten 10293, Leprieur 14, 452, Davidse 5444, 14617, Wurdack & Adderley 42986, Zuloaga 3984.*

Panicum grande A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 17: 529, fig. 143. 1915. TYPE: Panama. Gatun Lake, *Hitchcock 9178* (holotype, US 693329; isotypes, G, K, NY, P, US, W).

Panicum myrianthum Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 3. 1921. Not *P. miryanthum* Buse, in Miquel, 1854. SYNTYPES: Suriname. Without locality, *Hostmann 434* (syntypes, K, US 974637), *Hostmann et Kappler 253* (syntype, G).

This species differs from the others placed in section *Laxa* by having the upper anthecium indurate with bicellular microhairs toward the apex, a character not present in the species of this section as here defined. Also, the spikelets are not disposed in unilateral branches as is characteristic of species in *Laxa*. In addition, *P. grande* lacks fusoid cells and has conspicuous lacunae in the mesophyll and superposed bundles.

Vouchers for anatomical study: *Black 15352, Pires & Silva 4855, Gentry et al. 51575.*

Panicum aristellum Doell, in C. Martius, Fl. Bras. 2(2): 22. 1877. TYPE: Brazil. Minas Gerais: without locality, *Widgren s.n.* (holotype, S not seen; isotype, US, fragment, US).

Related to section *Laxa* by its spikelet and upper anthecium type, it differs mainly by having aristate glumes and by lacking fusoid cells in the leaves.

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Valls 1037 (4); 1038 (4); 1791 (6); 1806 (10); 1897

(9); 2067 (10); 2077 (11); 2586 (10); 3077 (4); 4657 (4); 11644 (6). van der Werff 4900 (11); 5754 (11); 7521 (11). van Donseelar 2576 (6). van Hermann 763 (10). Vanni 69 (5); 72 (5); 378 (5). Vargas 16277 (6). Vásquez 788 (11); 3023 (6). Vautier 352 (10); 354 (10). Vázquez 1419 (6); 3023 (6). Vázquez Avila 323 (11); 436 (10). Velez 2716 (10). Venturi 1635 (6); 8127 (6). Vera 4080 (10). Vera Santos 2227 (10); 2655 (12). Vidal 952 (10). Viegas 5459 (10); s.n. (3). Villamil 4 (6). Vincelli 976 (6). von Sneidern 1022 (11); 4969 (11); 5064 (10); 5192 (11); A.1174 (10). von Tuerckheim 1254 (5); 1451 (10). von Wedel 1121 (11).

Wachencheim 235 (10). Warming s.n. (11). Wawra 234 (10); 285 (5). Weatherwax 1643 (11). Weddell 149 (5); 3142 (10). Whitefoord 87 (11); 411 (11); 1507 (10); 2753 (6). Widgren 904 (9). Wilbur 11629 (10). Williams 240 (11); 2575 (10); 4469 (11); 6740 (11); 7034 (11); 7404 (11); 7516 (11); 15982 (6); 18345 (11). Wilson 9444 (10); 9558 (13). Wingfield 5380 (11); 6227 (6); 6370 (11); 6855 (10). Wood 3642 (11). Woodson 1632 (6). Woolston G-48 (11); G-95 (11). Woronow 4453 (11). Wright 759 (6). Wullschaegel 623bis (6).

Young 284 (11). Yuncker 8203 (10).

Zambrano 1165 (11). Zardini 4263 (9); 7474 (4); 8187 (9). Zarucchi 4029 (10); 5586 (11). Zuloaga 73 (4); 438 (6); 593 (6); 623 (10); 624 (5); 657 (10); 744 (10); 808 (6); 864 (9); 1469 (6); 1878 (11); 1973 (10); 1994* (10); 2218* (5); 2235* (9); 2293 (5); 2298 (6); 2303 (10); 2337 (6); 2355 (10); 2371 (10); 2494* (9); 2571* (6); 3073* (4); 3087* (4); 3090 (6); 3170* (6); 3178 (6); 3177 (10); 3194* (10); 3197* (5); 3232* (9); 3251* (9); 3289* (10); 3290* (6); 3319* (6); 3323* (9); 3357 (4); 3868 (10); 3882 (10); 3913* (11); 3956 (11); 3983* (6); 4087* (11); 4181* (6); 4183* (6); 4238* (11); 4302 (6); 4313 (6); 4315* (5); 4330* (6); 4366 (10); 4367* (6); 4401 (6); 4513* (10); 4515 (11); s.n.* (9); s.n. (4).

A TREATMENT OF AMERICAN XYRIDACEAE EXCLUSIVE OF *XYRIS*[1]

Robert Kral[2]

ABSTRACT

This work is the first part of a treatment of New World Xyridaceae, exclusive of *Xyris*, and is focused on the other four genera that make up this family, namely *Abolboda* (21 species), *Achlyphila* (one species), *Aratitiyopea* (one species), and *Orectanthe* (two species). The treatment is conventional, providing (1) a general description, (2) a key to the genera, (3) detailed descriptions of each of the four genera and keys to their species where needed, and (4) illustrations of species and varieties together with synonymy and geographic distribution. Some realignment of taxa is presented. Two new species, *Abolboda dunstervillei* and *A. scabrida*, and one new variety, *Abolboda acaulis* var. *scaposa*, are proposed.

This treatment is directed toward a final reckoning of Xyridaceae for the New World and is based on studies commencing in the late 1950s, when my own interest in the family was confined to those of the southeastern United States, where *Xyris* is the only genus. At that time taxonomists considered the family to have two genera, *Abolboda* and *Xyris*, or followed the lead of Nakai (1943), who considered these to be monotypic in two families, Abolbodaceae and Xyridaceae, respectively. However, during that period and forward, extensive field exploration within the Neotropics resulted in discovery and description of many morphologies that escaped these traditional generic concepts. *Orectanthe* was described by Maguire (1958) as distinct from *Abolboda*, and shortly thereafter the monotypic *Achlyphila* Maguire & Wurdack was described (1960), the latter representing such morphological intermediacy between Abolbodaceae and Xyridaceae (Carlquist, 1960) as to convince most workers that the two families are indeed one. Finally, after this manuscript was being formed, Steyermark & Berry (1984) published yet a fifth genus, *Aratitiyopea*, based upon material previously described as a part of the bromeliaceous genus *Navia*. Thus, as this much revised manuscript is being done for what amounts probably to my last attempt, the Xyridaceae are thought by most to be comprised of five genera.

My objective is two-fold, first to present a synopsis of the four smaller taxa and second to present a synopsis of the much larger genus *Xyris*, in order ultimately to have something for all known New World species of Xyridaceae that would be similar to what was done for *Carex* in North America by K. K. Mackenzie (1931 et seq.). This first objective, a treatment of *Abolboda* (21 species), *Achlyphila* (one species), *Aratitiyopea* (one species), and *Orectanthe* (two species), will be a tight presentation. An all-inclusive description of the family will be followed by a key to all genera now known. Next, the treatment for each genus is presented, including (1) a full description of the genus, (2) a key to the species and varieties, (3) a full description of species and varieties, and (4) accompanying illustrations of all species and most varieties. Some discussion of the morphology peculiar to each of the four genera will be included under these genera, but this will be (and should be in such a synopsis) brief.

Lectotype designations are given here uniformly

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[1] Many hundreds of specimens have been examined in the preparation of the work, and I acknowledge the assistance of curators and staffs of F, GH, K, L, MO, NY, P, U, and US who kindly made loans and facilities available. Particular thanks are due Otto Huber, ecologist and authority on tropical American savanna, and the late Julian A. Steyermark, outstanding authority on the Venezuelan flora, who provided both specimens and encouragement and without whom this work would have been impossible. Fieldwork in the Guayana Highlands was accomplished in part with the assistance of National Geographic and National Science Foundation funding: fieldwork in Brazil during 1988 was made possible through a travel grant from the National Geographic Society (National Geographic Society Travel and Research Grant #3471-86). Thanks are gratefully given to the editors of the *Annals of the Missouri Botanical Garden* for patience in seeing the editorial process through with equanimity. Likewise, I am very grateful to Grace Monty, technical secretary, Department of Biology, Vanderbilt University, for invaluable assistance in rendering script to the word processor.

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to represent work of all authors who, post-1935, applied instead the term "type" to such material. Therefore, none of these lectotype designations are mine; authors such as B. Maguire, Lyman B. Smith, etc., are the ones whose choice of material and places of deposit is followed, their intent being plain even if they did not use the term "lectotype."

Throughout the descriptions the terms coarse and fine, when referring to the plant as a whole, describe the plant's general aspect. Thus, coarse implies large and robust, while fine implies small and delicate.

I should stress here that I judge my efforts to be preliminary, even though they are based on field and herbarium work over more than 30 years. Real credit should go to the pioneers in neotropical botany whose extensive field and laboratory work have provided a proper basis for such a study as this. I refer particularly to Malme, L. B. Smith, Steyermark, Maguire, Wurdack, and Otto Huber, whose contributions have more than facilitated my own.

Xyridaceae Agardh, Aphor. Bot. 158. 1823. "Xyrideae," nom. cons.

Rosulate or caulescent, fine or coarse monocotyledonous, terrestrial (rarely aquatic) herbs, mostly of high-hydroperiod acidic soils. Roots mostly slender, diffuse-fibrous, with root hairs. Axis sympodial or monopodial. Leaves alternate, distichous or spiral, ligulate or eligulate, the bases broad, open-sheathing, frequently equitant and keeled, the blades laterally to dorsiventrally compressed, less often terete, angulate or variously channeled. Inflorescence lateral or terminal, scapose (rarely subsessile), the scapes of 1 to few from axils of scape sheaths or inner leaves, naked or with distant to approximate pairs of bracteal leaves, each scape bearing apically 1 or more imbricate-bracted spikes or heads or panicles of spikes. Flowers perfect, 1 to many, solitary and subsessile to pedicellate in axils of chaffy, leathery, or scarious bracts. Perianth in 2 differentiated whorls. Sepals (2–)3, the anterior (inner) one a reduced scale, or subequal to the others, or (*Xyris*) membranous and wrapped around the corolla, abscissing as the flower opens, the other 2 subopposite, connivent to basally connate, chaffy, mostly navicular, often keeled, persisting around the ripe capsule. Petals 3, equal or subequal, distinct to united and salverform or bilabiate, yellow to white, blue, lavender, or purple, mostly narrowed to connivent claws or to a narrow tube. Stamens 3, epipetalous; anthers tetrasporangiate, usually bilocular at anthesis, introrsely or laterally dehiscent, dehiscing longitudinally; pollen monosulcate or inaperturate. Staminodia (1–)3, scalelike, filamentous or bibrachiate and plumose, or lacking. Gynoecium 3-carpellate, the ovary 1-locular to completely or incompletely 3-locular, the placentation marginal, parietal, basal, free-central or axile (all conditions found in *Xyris*, in all other genera strictly axile); style terminal, distally tubular, slender, appendaged or exappendiculate, apically 3-branched or variously laminar, papillate, or fimbriate; stigmas 3. Fruit capsular, mostly loculicidal. Seeds usually numerous (rarely 1), mostly with strong longitudinal ridges and finer cross-lines, translucent or farinose-opaque, the embryo small, situated at base of an abundant mealy endosperm.

KEY TO THE GENERA OF AMERICAN XYRIDACEAE

1a. Petals gamopetalous; leaves polystichous; styles with appendages or ovary summit appendaged; pollen with spines or papillate; corolla regular or irregular; sepals 2–3.
  2a. Stylar appendages mostly well above style base on style; capsule apex thickened; flowers 1–several, the inflorescences sessile or on variously elongated, opposite-bracted scapes; sepals 2(–3) .... *Abolboda*
  2b. Stylar appendages at or around style base; capsule apex not appreciably thickened; flowers many in dense globose or hemispheric large heads; sepals 3.
    3a. Corollas arching-spreading, irregular, yellow (rarely red-purple); stigma capitate, lateral-terminal, papillate; seeds winged, irregular .... *Orectanthe*
    3b. Corollas erect, regular, salverform, purple; stigma terminal and trilobed, the lobes pilose; seeds wingless, ridged-and-pitted, symmetric .... *Aratitiyopea*
1b. Petals usually distinct; leaves distichous, mostly equitant; styles unappendaged; pollen lacking spines or other protuberances; corolla regular; sepals 3.
  4a. Flowers distinctly pedicelled; sepals alike; staminodia lacking; style unbranched, the stigma capitate, trilobed .... *Achlyphila*
  4b. Flowers subsessile; sepals not alike, the lateral ones chaffy and keeled, the inner one membranaceous and infolding the corolla bud; staminodia usually present, bibrachiate; style 3-branched, the stigmas "U"-shaped or annulate .... *Xyris*

1. **Abolboda** Kunth in Humb. & Bonpl., Pl. Aequinoct. 2: 25, pl. 114. 1809.

Chloerum Willd. ex Link in Sprengel, Jahrb. 3, pt. 1: 74. 1833.

Poarchon C. Martius ex Seub. in C. Martius, Fl. Bras. 3, pt. 1: 223. 1855.

Coarse to low and mosslike (annual–)perennial, caulescent to essentially acaulescent, rosulate herbs with rarely fine, commonly thickened fibrous roots, perennating by axillary lateral buds. Foliage externally smooth to variously papillose or tuberculate, rarely scabro-ciliate or ciliate, the leaves frequently dimorphic, those of rhizome or early rosettes either scalelike or subulate, the principal ones polystichously arranged, with bases typically open-sheathed, the sheaths broadly clasping, the blades variously linear-triangular or linear, flat, angled or lingulate, usually narrowly acute, at apex frequently and eccentrically or symmetrically aristate or conic-subulate. Inflorescence a single sessile flower or 2 or more flowers in spikes and sessile or (commonly) the flowers in spikes raised and terminal on scapes, the spikes either single and terminal *or* clustered and terminal *or* (rarely) terminal on branches of a branched inflorescence, the scape itself either naked or usually with 1 or more pairs of subopposite, sessile, erect, leafy but mostly short, bracts. Spike bracts paired at spike base, spirally arranged upward, or all spike bracts spirally set, all fertile or the lowermost 1(–2) sterile, mostly glumaceous, usually rigid and lanciform-navicular with thickened dorsal areas and broad, mostly entire, scarious borders, apically frequently produced into stiff mucros, cusps, or subulation. Sepals 2–3, often similar to fertile bracts, rarely 3 and subequal, more often with 2 (the laterals) thinner with narrower, thickened curvate-keeled backs and subopposite, the third (inner) sepal reduced, usually of different design and still thinner, or entirely lacking. Petals 3, equal, the corolla salverform, the tube variously elongate, the 3 lobes broad, blue, lavender, or white, ephemeral. Stamens 3, the short filaments adnate near base of petal blades and opposite them, shorter or longer than anthers, flat or terete, the anthers mostly narrow, tetrasporangiate and bilocular, the locules with bases variously divergent on a broadened, flattened connective. Staminodia 1–3, variously reduced, or lacking (the common condition). Ovary trilocular, the placentation axile, the ovules usually numerous, the style typically elongate, wing-angled at or toward the base and (except in complex including species 8 and 9) bearing 2–3, usually pendent, less often erect, claviform appendages, at apex with 3, usually distally dilated and flattened, stigma branches, these variously divided and fimbriate. Capsules loculicidal, the 3 valves firm, mostly much thickened at the crested, lobed or toothed apex. Seeds usually tumid and irregularly obovoid, mostly 0.5–1 mm long, short-apiculate or umbilicate, the broad body dark, spirally longitudinally coarsely ribbed, frequently with strong irregular cross-ridges.

Distribution. Neotropical plants of boggy warm or cool habitats, centering in the savannas of northern South America but with two taxa extending south to the southern Brazilian planalto, one into Paraguay.

KEY TO SPECIES OF *ABOLBODA*

In this key priority is given to vegetative characters (rosette leaves, rootstocks, scapes, and bracts) and easily observed externals of spikes (sterile and fertile bracts, sepals). The key applies only to normal, healthy growth in flowering or fruiting condition. Features involving more dissection (floral parts from the corolla inward, fruit, seed) perhaps deserve more emphasis than they get here, but the average *Abolboda* specimen often is quite limited in some or all of these structures. A suggestion to collectors is that they make more effort to gather extra spikes, thereby increasing the value of the collection exponentially. The best characters are yet to be explored sufficiently and thus are used here with some reservation. It is recommended to check these features against the species treatments and their accompanying figures.

1a. The plants e-scapose, the spikes sessile with basal bracts forming part of the involucre; leaves usually less than 4 cm long.
  2a. Rosette leaves mostly uniform, smooth, gradate only in size, with bases tightly imbricate in high spirals on elongate stems, the longest ones toward and at shoot tip, narrowly linear-triangular, stiff, tapering gradually, with an arista at apex at least 1 mm long; flowers mostly 2–4 per spike, the corolla pale blue; stylar appendages short-stalked, often erect, broadly clavate-spathulate; sepal keels smooth .... 1a. *A. acaulis* var. *acaulis*
  2b. Rosettes often dimorphic or of 2 sorts of leaves, one type with stubby fleshy angulate, blunt and often papillose linear blades (mostly less than 1 cm long), the others longer, broader-based (with narrower, more tapering blades), sometimes aristulate or aristate; flowers 1–2 per spike, the corolla pale blue or white; stylar appendages longer-stalked, mostly reflexed, narrowly claviform; lateral sepals often with papillose keels .... 2. *A. killipii*
1b. The plants scapose, the scapes sometimes shorter than the principal leaves but mostly projecting the spikes beyond them; leaves various in shape and size.
  3a. Scapes ebracteate (exclusive of those at very base of scape) or if bracteate, the bracts a single pair (rarely 2 pair) at or near the scape summit.
    4a. Plants with comparatively coarse foliage, the principal leaves over 15 cm long, their blades 3–5 mm wide; spikes (excluding involucres) 1.5–2.5 cm long; perennials with stout, short rhizomes.

5a. Inflorescence overtopped by longer leaves, these with strongly thickened, pale, cartilaginous margins; spike bracts and sepals strongly excurved; scape bracts mostly ca. 2 cm long, inserted 5–20 mm below spike base; stylar appendages with basal auricles .... 3. *A. bella*

5b. Inflorescence overtopping longer leaves, the leaf blades lacking strongly thickened, pale cartilaginous margin; spike bracts and sepals not excurved; scape bracts 3–7 cm long, inserted 0–40 mm below spike, in either case making a leafy involucre; stylar appendages lacking auricles .... 4. *A. sprucei*

4b. Plants with comparatively fine or short leaves, these rarely over 11 cm long, their blades less than 3 mm thick or wide; spikes 0.5–1.5 cm long; perennials or short-lived perennials or annuals.

6a. Perennials with firm leaves and linear scapes.

7a. Scapes 2 or more times longer than principal leaves; tips of capsule valves bifid-toothed; stylar appendages pendulous.

8a. Lower spike bracts exceeding, rarely equaling, the rest of the spike; longer leaves over ½ as long as scape; lateral sepals narrowly acute, mostly overtopped by tips of subtending bract; stylar appendages exauriculate .... 5a. *A. ebracteata* var. *ebracteata*

8b. Lower spike bracts shorter than the rest of the spike; longer leaves up to ½ as long as the scape; lateral sepals broadly and bluntly acute, their tips equaling or surpassing tips of subtending bract; stylar appendages auricled .... 5b. *A. ebracteata* var. *brevifolia*

7b. Scapes barely if at all overtopping principal leaves; tips of capsule valves shallowly bilobed, not toothed; stylar appendages erect or ascending, not pendulous .... 1b. *A. acaulis* var. *scaposa*

6b. Annual or short-lived perennial, with soft, filiform, flat leaf blades and filiform scapes; sepals oblong or obovate, obtuse, often retuse and mucronate .... 6. *A. americana*

3b. Scapes with 1 or more pairs of scape bracts, at least one of these pairs at or toward middle of scape.

9a. Spikes solitary and terminal at scape tips or at tips of scape branches.

10a. Fertile flowers 4 or fewer per spike (reduced, probably sterile florets may be produced internal to the fertile ones); spikes to 1.5 cm long.

11a. Scape bracts in 4 or more pairs; bract tips remaining erect, thus fruiting inflorescence narrowly ellipsoid; sepals always 3, lacking evident keel, subequal in length but the inner one strongly stipitate.

12a. Inflorescence much branched, the spikes terminal on the elongate branches; style base appendaged .... 7. *A. paniculata*

12b. Inflorescence not branched or with one short branch from the penultimate node or the second spike sessile there; style base in *A. uniflora* not observed (but condition assumed to be the same).

13a. Leaves tapering gradually from base to tip, thus linear-triangular, the blades flattened and with conic-subulate, even aristate, tips .... 8. *A. neblinae*

13b. Leaves narrowed above clasping base, not tapering-bladed, the blades narrowly linear, thickened, their tips with an eccentric apiculus .... 9. *A. uniflora*

11b. Scape bracts nearly always in 3 or fewer, usually 1, rarely 2–3, pairs; bract tips ascending or spreading, the spikes typically broadly ellipsoid or ovoid to turbinate or hemispheric; sepals mostly 2, lateral and strongly keeled, the inner sepal if present much shorter and thinner.

14a. Spike bracts prevalently ovate, abruptly blunt-mucronate; tips of lateral sepals conspicuously projected beyond tips of subtending bracts.

15a. Spikes broadly turbinate, the sepals strongly bowed outward beyond the bract tips; leaf blades strongly flattened, mostly (1.5–)2 mm or wider, uniformly nerved abaxially; scapes barely overtopping longer leaves .... 10. *A. abbreviata*

15b. Spikes narrower, mostly ovoid to ellipsoid, the sepals more erect in orientation; leaf blades with midnerve strongest abaxially; scapes usually at least twice as long as longer leaves.

16a. Rhizome usually producing a stubble of short-stubby-leaved rosettes, and longer-leaved floriferous rosettes; longer leaves with costa strongly raised abaxially, the blades silvery green; stylar appendages narrowly claviform, exauriculate .... 11. *A. egleri*

16b. Rhizome with or without dimorphic-leaved rosettes; longer leaves with costa level or slightly raised abaxially, the blades not silvery green; stylar appendages broadly clavate, mostly auriculate .... 12. *A. pulchella*

14b. Spike bracts prevalently lanciform, more taper-tipped, mucronate or cuspidate; tips of lateral sepals mostly not projecting beyond tips of subtending bracts, at most equaling them.

17a. Leaves and/or scapes liberally frosted with prominent tubercles, thus tuberculate-scabrid and also often rugose; leaves essentially monomorphic, these and bracts with blunt, callused tip bearing a small eccentric mucro.

18a. Leaves and scapes tuberculate-rugose; keel of both bract and sepals scabridulous from middle to tip; bifurcate staminodia present ..... 13. *A. scabrida*

18b. Only scapes tuberculate-rugose; keel of bract and sepals smooth or nearly so; staminodia not evident ..... 14. *A. dunstervillei*

17b. Leaves and/or scapes smooth or no more than papillate-granular; leaves of a tuft mostly dimorphic, these and bract apices more tapering, often spinulose-tipped.

19a. Leaf blades smooth, most of the principal ones subulate-setose-tipped; spike bracts > 1 cm long, spinulose at tip; stylar appendages raised well above the ovary apex ..... 15a. *A. acicularis* var. *acicularis*

19b. Leaf blades or most of them granular-papillose, also often rugulose, averaging wider, with blunter tips, these apiculate or aristulate; spike bracts no longer than 1 cm, aristulate or apiculate; stylar appendages basal and erect ..... 15b. *A. acicularis* var. *granularis*

10b. Fertile flowers 5 or more, usually many, per spike; spikes at least 1.5 cm long.

20a. Spikes broadly ellipsoid to ovoid or globose to hemispheric, the sepals (except in no. 16) strongly exserted and attenuate to sharply acute or with keel excurrent as cusp or arista.

21a. Scape bracts 1 pair; leaf blades <5 mm wide.

22a. Leaf sheaths long-ciliate; leaf blades scabro-ciliate; sepals about as long as subtending bracts or shorter; staminodia present; stylar appendages without basal auricle ..... 16. *A. ciliata*

22b. Leaf sheaths and blades entire; sepals much longer than subtending bracts; staminodia lacking; stylar appendages with basal auricles.

23a. Flowering in morning; larger leaves 3–10 cm long ..... 17a. *A. poarchon* var. *poarchon*

23b. Flowering in afternoon; larger leaves prevalently >10 cm long ..... 17b. *A. poarchon* var. *intermedia*

21b. Scape bracts 2 or 3 pairs (rarely 4); leaf blades mostly <5 mm wide; sepal tips much exserted.

24a. Lowest (largest) pair of scape bracts mostly 2–3(–3.5) cm long; spikes broadly ovoid to hemispheric or subglobose, rarely >2 cm long ..... 18a. *A. grandis* var. *grandis*

24b. Lowest (largest) pair of scape bracts (3–)3.5–6 cm long; spikes broadly ovoid to ellipsoid or narrowly ovoid, mostly at least 2.5 cm long ..... 18b. *A. grandis* var. *rigida*

20b. Spikes narrowly ellipsoid, narrowly lanceoloid or cylindric, the sepals blunt-tipped and slightly projecting beyond the erect, strongly imbricate subtending bracts.

25a. Leaves mostly linear-triangular to gladiate or linear-lorate, the blades tapering evenly to acute tips, thin-edged and plane, finely multinerved and comparatively smooth on both surfaces.

26a. Scapes with mostly 2(–3) pairs of bracts, these 1.5–3 cm long; plants mostly not >6 dm high ..... 19a. *A. macrostachya* var. *macrostachya*

26b. Scapes mostly with 1(–2) pairs of bracts, these mostly 4–6 cm long; plants mostly 6–10 dm high ..... 19b. *A. macrostachya* var. *robustior*

25b. Leaves narrowly linear, the tips blunt, the edges thick, the surfaces with few, coarse and raised nerves ..... 20. *A. linearifolia*

9b. Spikes numerous, subsessile in glomerules at scape tip; fertile flowers not produced ..... 21. *A.* ×*glomerata*.

1. **Abolboda acaulis** Maguire, Bull. Torrey Bot. Club 75: 1. 1948. TYPE: Guyana. In white sand from conglomerate and sandstone, Kaieteur Plateau, British Guiana, 30 Apr. 1944, *Maguire & Fanshawe 23096* (holotype, NY; isotypes, F, GH, K, US).

1a. **Abolboda acaulis** var. **acaulis**. Figure 1.

Densely caespitose, smooth perennial, forming tight, dome-shaped cushions 4–5 cm high, these a compaction of ascending stems densely cloaked by tightly spirally imbricate chaffy old leaves, the roots

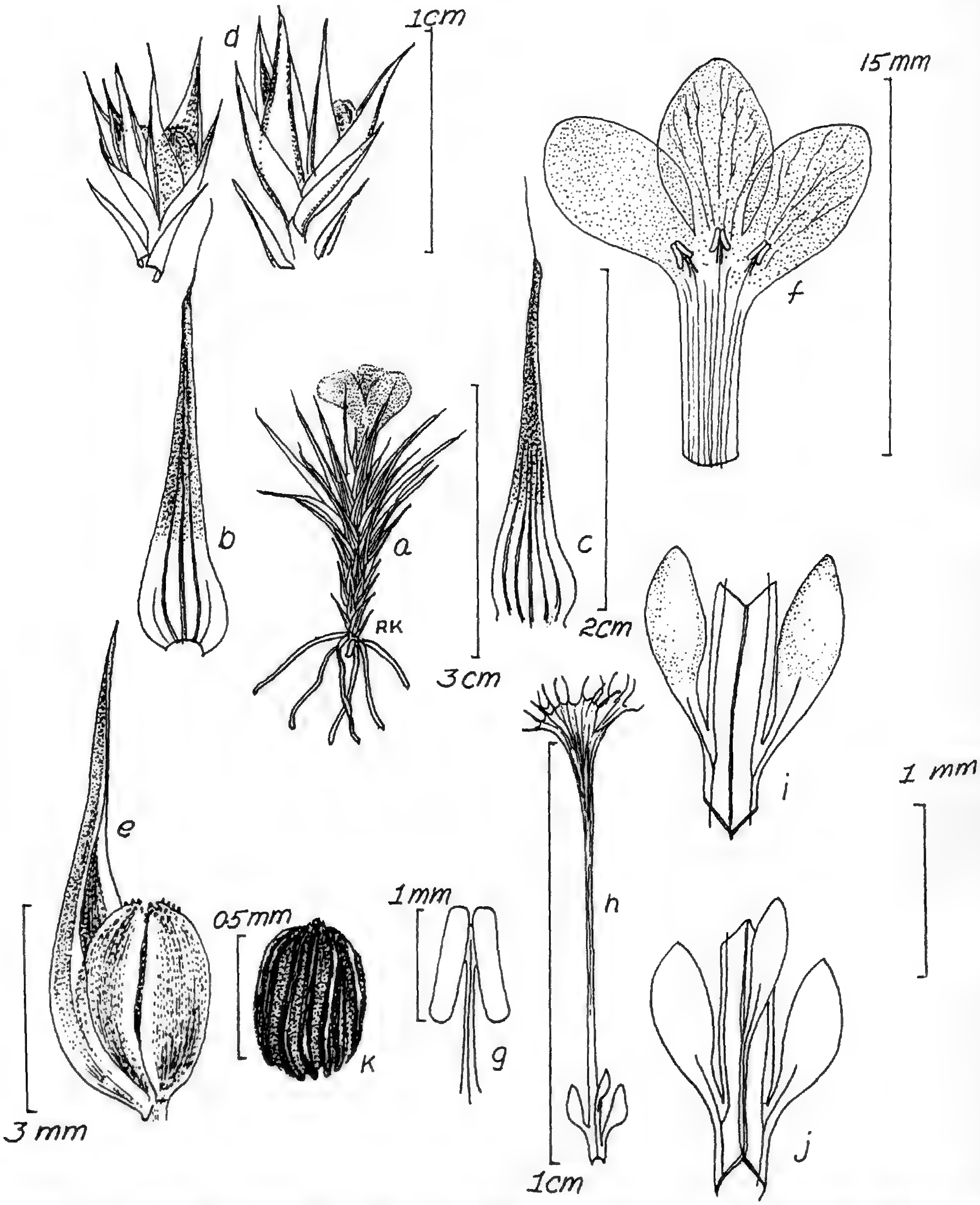

FIGURE 1. *Abolboda acaulis* var. *acaulis* (*Steyermark et al. 12863*).—a. Habit.—b. Leaf, adaxial side.—c. Leaf, abaxial side.—d. Two spikes.—e. Lateral sepal and capsule.—f. Corolla and stamens.—g. Stamen.—h. Stylar apparatus.—i. Style base showing lateral appendages.—j. Style base showing lateral appendages and adaxial appendage.—k. Seed.

spongy-thickened. Lower stem leaves shortest, narrowly triangular with setaceous tips, erect or ascending, 5–15 mm long, the upper gradually more spreading, broadly to narrowly triangular-linear, to 20(–30) mm long, the clasping base thin, pale, dilated, 2–3 mm wide, 3–11-nerved, narrowing gradually or abruptly to a thicker, narrowly linear-subulate blade, this for most of its length flat or lingulate adaxially, convex and with 1–3 raised nerves abaxially, the tip usually narrow but blunt, obliquely spinulose-trichomiferous, the "spine" 1.5–3 mm long; inner leaves of rosette usually spreading or ascending, bent outward, those at base of spikelet buds abruptly shorter, thinner, and passing into floral bracts, some also subtending initials for new rosettes. Spikes sessile or subsessile, (1–)2(–4)-flowered, the bracts and sepals stramineous, keeled; sterile bracts 1–3, broadly lanceolate or oblong-lanceolate, 5–6 mm long, acuminate, the lowest one shortest; fertile bracts mostly 2–3(–4), alternate-spiral, ca. 6 mm long with the innermost one often shorter and presumably subtending an aborted floret; sepals 2, rarely 3, the inner mostly aborted, the laterals slightly unequal, lanceolate, strongly keeled, 6–7 mm long, subequilateral, the bases broadly scarious-bordered, the blade narrowing and conduplicate toward apex; corollas salverform, pale blue, ca. 15 mm long, the tube ca. 6–7 mm long, the spreading lobes broadly ovate, 8–9 mm long, entire; stamens with anthers near-white, ca. 1 mm long, the two cylindric locules joined by connective above middle, their bases divergent, on slender filaments ca. 1.5 mm long; stylar apparatus fully 1 cm long, slender, triquetrous at base with 3 ascending, claviform-spathulate appendages to 1 mm long, these distally thickened, the laterals slightly larger and set slightly below the anterior appendage, the style above becoming narrowly tubular, 3-lobed at the stigma, the broad, fimbriate-lacerate lobes forming a short funnel. Capsules oblong-obovoid, 2.5–3 mm long, the 3 valves thickened at the incurved-acute, sometimes slightly emarginate and always papillose-tuberculate tips. Seeds nearly round, 0.6–0.7 mm long, dark red-brown to nearly black, strongly and somewhat spirally 11–12-ribbed.

Distribution. Common in acidic, moist, rocky soil, medium to high elevations (200–2,400 m), usually savanna, from western Guyana west into Territorio Federal Amazonas in Venezuela.

Additional specimens examined. GUAYANA. Kaieteur Plateau, *Cowan & Soderstrom 1814* (US); Soeschifhe, *Cooper 292* (U); Imbaimadal, *Maguire & Fanshawe 32167* (NY); Pakaraima Mts., *Maguire & Fanshawe 32516* (F, NY); Upper Mazaruni River, *Maguire & Fanshawe 32609* (K, NY, US); Mt. Ayanganna, *Maguire & Fanshawe 40618* (GH, NY), *40669* (K, NY), *Maguire & Fanshawe 40700* (GH, K, NY, US), *40701* (K, NY); Pakaraima Mts., *Maguire 45917* (K, NY), *Maguire et al. 46121* (NY, US), *Maguire et al. 46916* (F, GH, NY); Kaieteur Falls, *Prance 16558* (NY); Upper Mazaruni River, *Tillett & Boyan 45227* (NY). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Río Coro-Coro, *Holst & Liesner 3349* (MO, VDB); Cerro Sipapo, *Maguire & Politi 27659* (NY, US), *27700* (F, K, NY), *27923* (NY, US), *28691* (NY); Cerro Huachamacari, *Maguire et al. 30154* (NY); Río Manapiare, *Maguire et al. 31703* (NY), *31773-A* (NY); Serranía Yutajé, *Maguire 35214* (NY), *35249* (NY); Cerro Huachamacari, *Steyermark & Manara 2192*. BOLIVAR: Kama-meru, *Holst et al. 2192* (MO, VDB); Río Apongao, *Huber & Alarcon 7443* (MYF, VDB); Kavanayen, *Huber & Alarcon 7718* (MYF, VDB); Chimantá Massif, *Huber et al. 8853* (NY, VDB, VEN); Kavanayen, *Huber & Alarcon 10578* (MYF, VDB); Salto Angel, *Huber 11238* (MYF, VDB); Río Soruape, *Huber 11837* (MYF, VDB); Meseta Guaiquinima, *Huber & Rull 12256* (MYF, VDB); Kavanayen, *Kral & Gonzalez 70414* (MO, NY, VEN, VDB), *70538* (MO, NY, US, VDB, VEN); Cerro Guaiquinima, *Maguire et al. 32820* (F, NY, US); Ilu-tepui, *Maguire 33179* (F, NY, US), *33730* (GH, NY); Chimantá Massif, *Steyermark & Wurdack 457* (F, K, NY); Luepa, *Steyermark & Nilsson 607* (NY); Apacara-tepui, *Steyermark 75784* (F, MO, NY, WIS); Auyan-tepui, *Steyermark 93509* (F, K, NY, US, VDB), *116059a* (F, MO); Guaiquinima, *Steyermark et al. 117481* (MO), *117501* (MO); Cerro Marutani, *Steyermark et al. 123872* (MO); Chimantá, *Steyermark et al. 128089, 128683* (MO, VDB, VEN); Amuri-tepui, *Steyermark et al. 123797*; Acopan-tepui, *Steyermark et al. 129926, 129977* (MYF, VDB, VEN).

This is one of the prettiest and most distinctive abolbodas of the Gran Sabana of Bolívar, Venezuela, and it is particularly abundant in and around rocky, wet, rapateaceous bogs, where it produces pale blue flowers year-round. Its commonest xyridaceous associates are *Orectanthe sceptrum*, *Xyris bicephala*, and *X. setigera*. Some of the larger clones are of considerable age, and the growth of these makes interesting study. Young plants may have a simple, single rosette with the leaves all spreading. As the plant grows older and into the first flowering season, buds form around spikes at rosette center and will be the shoots for the next flush of growth, then elongate to produce spirals of imbricate, short-triangular scale leaves that progressively elongate upstem to form successive flowering rosettes, and so on. The end result is a dome-shaped cushion of rosettes at tips of sometimes quite elongate, chaffy-cloaked stems. Other e-scapose abolbodas (*A. killipii*, extremes of *A. americana*), while often forming tight clusters of rosettes, appear not to have as much stem.

1b. Abolboda acaulis var. **scaposa** Kral, var. nov. TYPE: Venezuela. Bolívar: sandy seeps around rocks at edge of rapateaceous savanna by road, ca. 1.5 km E of Kavanayen, ca. 1,200 m, 27 July 1983, *R. Kral with A. C. Gonzalez 70537* (holotype, VEN; isotypes, F, GH, K, MO, NY). Figure 2.

Ab *A. acaulis* var. *acaulis* foliis aliquantum longioribus (vulgo 3–5 cm longis), habitu breviscaposa differt.

Similar in habit to *A. acaulis* var. *acaulis* but coarser, stems typically shorter, though cloaked with short, triangular old leaves and their bases, or very short with all leaves in low, flat spirals, the short outer ones grading more abruptly into spreading rosette leaves; principal leaves rigid, spreading

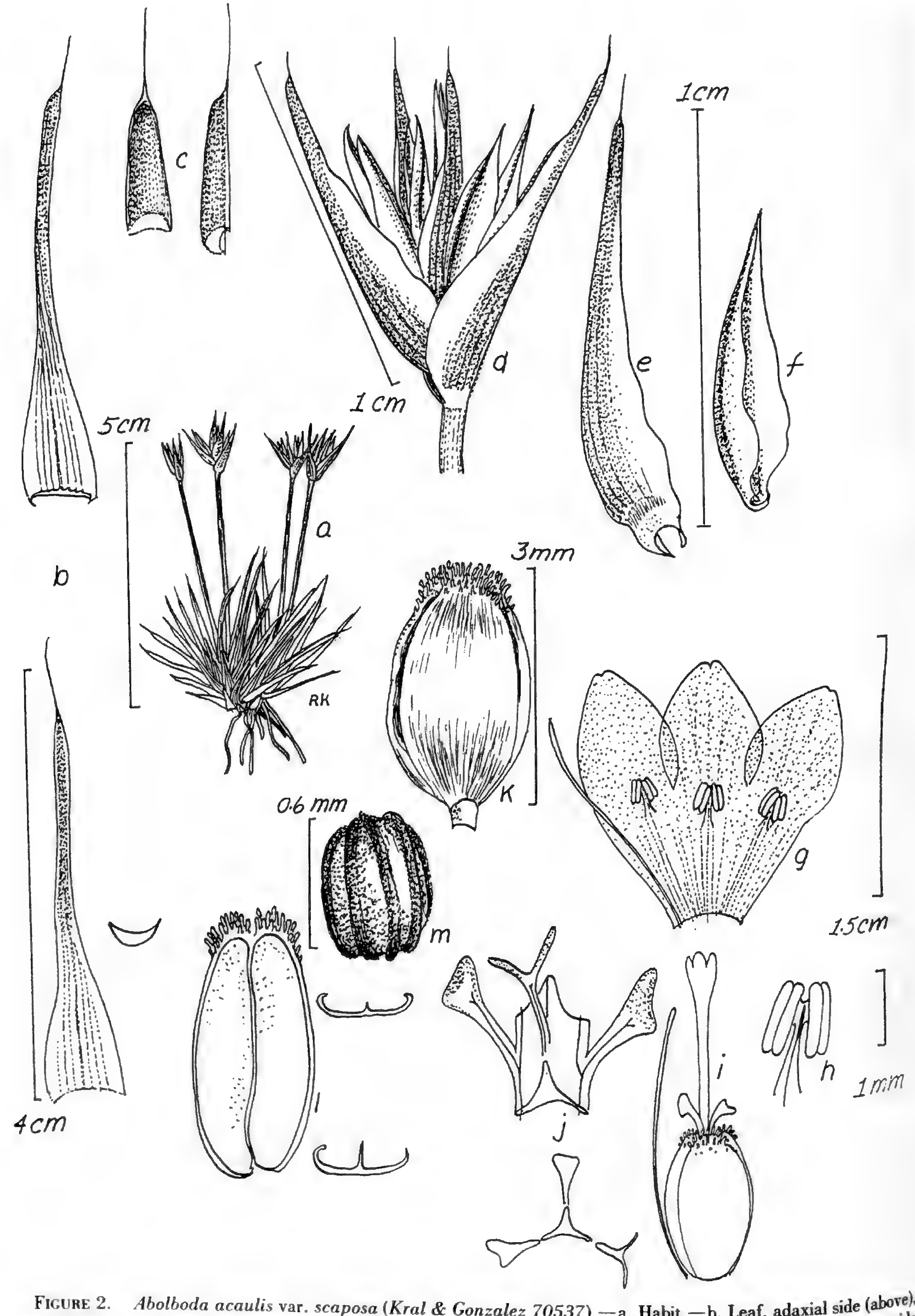

FIGURE 2. *Abolboda acaulis* var. *scaposa* (*Kral & Gonzalez 70537*).—a. Habit.—b. Leaf, adaxial side (above), abaxial side (below).—c. Leaf blade tip, adaxial side (left), side view (right).—d. Spike.—e. Lowest spike bract, side view.—f. Lateral sepal, side view.—g. Spread corolla showing stamens and a staminode.—h. Stamen.—i. Portion of excised gynoecium plus detached staminode.—j. Side view (above) and cross-sectional view (below) of stylar base showing appendages.—k. Capsule.—l. Capsule valve showing median septum.—m. Seed.

or spreading-ascending, mostly 3–5 cm long, subulate-aristate-tipped as in the type variety. Scapes evident, erect or ascending, few to several per rosette, 0.5–4 cm long, shorter than leaves to slightly longer, stiff, 0.5–1 mm thick, oval or terete in cross section, ecostate, subtended by 2–3 keeled, lance-linear, subulate-tipped, broadly scarious-bordered bracts, the lowest shortest, the innermost 9–10 mm long; spikes turbinate, ca. 1 cm long, (2–)3(–4)-flowered, each flower subtended by a bract; bracts lanciform, 8–10 mm long, the lowermost longest, all with clasping bases, thickened, medially, 7-nerved, with strongly convex dorsal areas, broad, pale, scarious borders, and tapering to thickened, cusplike tips, these setose at tip; sepals 2, obliquely lateral, subequal, subequilateral, lanciform-navicular, 6–7 mm long, narrowly acute, the broad borders pale-scarious, the thickened carina curved, entire; corolla salverform, ca. 15 mm long, pale blue as in variety *acaulis* but sometimes with filiform-clavate staminodia attached low in the tube; anthers, gynoecium, and fruit essentially as in the type variety.

Distribution. Less common than the type variety, sometimes occurring with it in acidic, sandy, rocky soils, medium-to-high-elevation savanna (200–2,400 m), from Guyana west into Territorio Federal Amazonas, Venezuela.

Additional specimens examined. GUYANA. Pakaraima Mts., 15 Oct. 1981, *Maas et al. 5697* (K, NY). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Yapacana, 3 Jan. 1951, *Maguire et al. 30720* (NY). BOLIVAR: Piar, Chimantá Massif, 26–29 Jan. 1983, *Huber & Steyermark 6912* (MYF, VDB, VEN); 20 km E Canaima, 31 Aug. 1983, *Huber et al. 8219* (MYF, NY, VDB); Apacará-tepui, 6–9 Feb. 1984, *Huber et al. 8879*; Guaiquinima Massif, 2 abr. 1984, *Huber 9363* (MYF, NY, VDB); Sifontes, Río Soruape, 9 Sep. 1986, *Huber 11837* (MYF, VDB); Ilu-tepui, 4 Apr. 1952, *Maguire 33749* (NY); El Jardín, 22 June 1983, *N. Ramirez 834* (PORT, UCV, VDB); campamento 150, km 150, NE Luepa, 24–25 abr. 1960, *Steyermark & Nilsson 608* (NY).

This variety has much to distinguish it from the type, its tufts being shorter-stemmed and longer-leaved, its spikes larger and with (usually) more flowers and longer bracts with sepals proportionately shorter. Of particular interest but requiring larger samples for a more detailed study, are the staminodia, which may or may not be evident (and if present then unequal in length and position on the corolla), and the stylar appendages, which likewise vary considerably in shape and length as well as in number. It is probably best to treat this as a variety, at least until the characters of staminodia and stylar appendages are evaluated properly. It now seems that in *Abolboda* these floral features are in transition.

2. **Abolboda killipii** Lasser, Bol. Soc. Venez. Ci. Nat. 9: 179. 1944. TYPE: Venezuela. Bolívar: muddy sabana, Río Torono, Alto Río Paragua, 20 ago. 1943, *F. Cardona 832* (holotype, VEN; isotypes, F, NY, US). Figure 3.

A. psammophila Maguire, Bull. Torrey Bot. Club 75: 193. 1948. TYPE: Surinam. Grass savanna, Sanderij II, 3 June 1944, *Maguire & Stahel 23667* (holotype, NY; isotypes, GH, U).

A. minima Maguire, Mem. New York Bot. Gard. 10: 7. 1963. TYPE: Venezuela. Territorio Federal Amazonas: Sabana Manacal, 15 km above Guarinumo, Río Atabapo, 125–140 m, 12 June 1959, *J. J. Wurdack & L. S. Adderley 42977* (holotype, NY; isotypes, GH, NY, US).

Diminutive, rosulate annual or short-lived perennial, the foliage uniform or of one of two sorts, usually the early leaves stubby, 3–5 mm long, their bases clasping but constricted below the blade, this fleshy, either narrowly triangular with flat upper surfaces or slightly lingulate, or in cross section triquetrous to terete, the tips blunt to acute, mucronulate or subulate; longer leaves usually appearing later and just below flower, 3(–4) cm long, the bases thin, broadly clasping, to 3 mm wide, variously tapering to narrowly triangular or filiform-linear blades, these somewhat compressed and abaxially triple-ribbed or triquetrous, the midrib prominent, or triangular to terete, toward apex terete, the tips blunt, short-conic, subulate or subulate-aristate; leaf surfaces from smooth to quite granular-papillose or even scabridulous, occasionally rugulose-tuberculate, bright green, the papillosity best developed on the shorter leaves. Flowers 1–2 per inflorescence, the spikes usually with at least the base hidden by surrounding rosette leaves and only the spread corolla evident and exsert, the bracteal leaves transitional to rosette leaves, spirally disposed around the spike base, lance-subulate, 5–9 mm long, the medial areas narrow, green, smooth or papillate, excurrent as outcurved, green, subulate, often aristate cusps, the border broad, pale, scarious; sepals 2, eccentrically lateral to ovary, lanciform, 4.5–8 mm long, somewhat inequilateral, navicular, firm, variously papillate, the apex variously subulate; corolla 10–13 mm long, pale blue or white, the lobes ca. as long as the narrowly campanulate tube; staminodia not evident; anthers bilocular, the ellipsoid thecae oblique (Fig. 3), ca. 1 mm long, pale, the slender filaments ca. 1.5 mm long; style open toward base, trique-

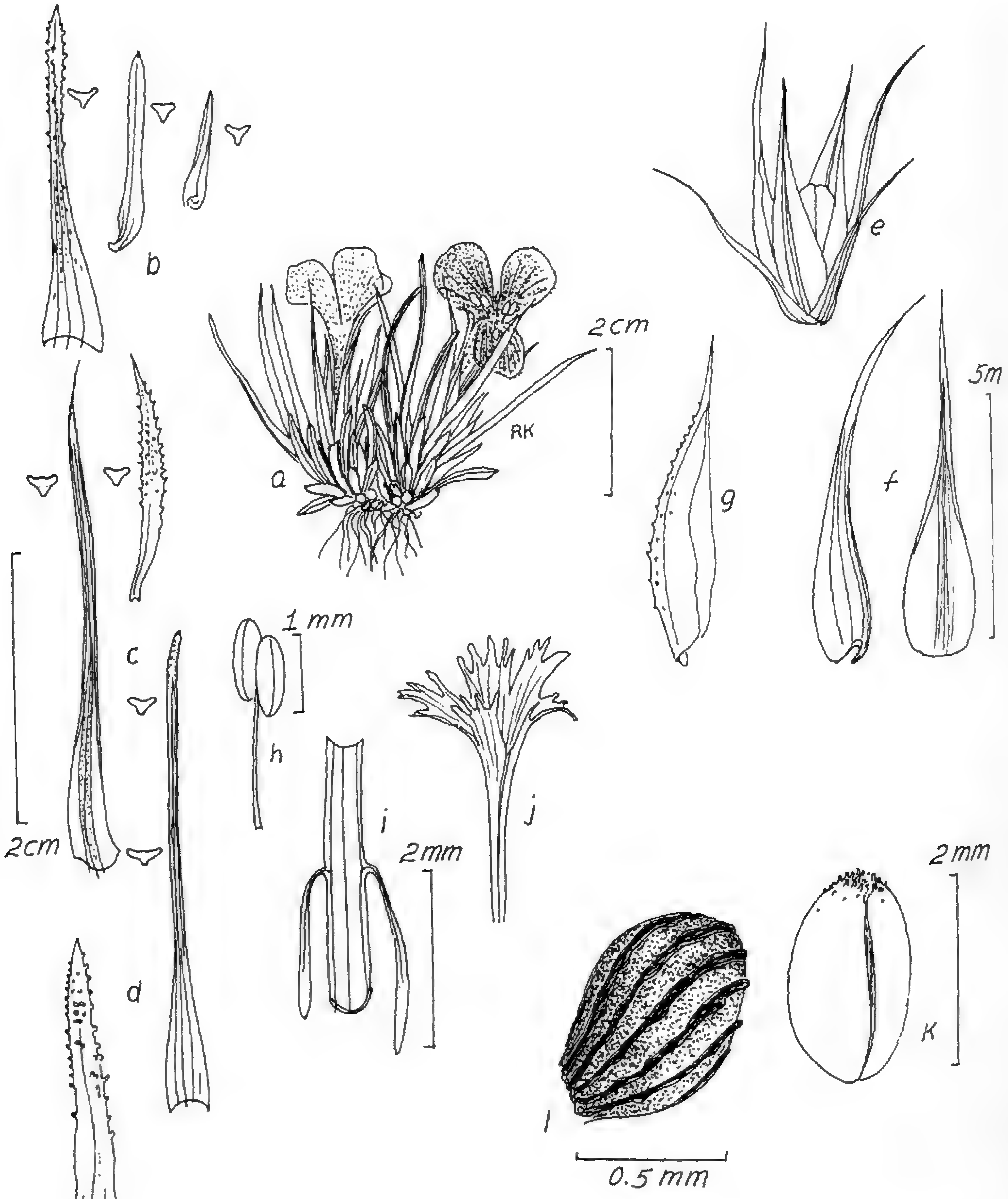

FIGURE 3. *Abolboda killipii* (*Cardona 832*).—a. Habit.—b.–d. A spread of "short" and "long" leaves, with accompanying cross sections, to show range.—e. Spike.—f. Fertile bract, side view (left), adaxial view (right).—g. Lateral sepal.—h. Stamen.—i. Stylar base.—j. Stylar apex.—k. Capsule.—l. Seed.

trous-alate, the appendages narrowly claviform, reflexed, ca. 1 mm long, only 2 evident (the laterals); style apex flaring to a funnelform, fibriate-bordered, 3-lobed tip. Capsule ellipsoid, ca. 2 mm long, the valves papillate at thickened, narrowly rounded tips. Seeds obovoid, ca. 0.7 mm long, deep red-brown or near black, with 5–6 strong, longitudinally spiral ribs per side.

Distribution. Infrequent in low-elevation sandy savanna (mostly under 500 m), Surinam west through Bolívar and Territorio Federal Amazonas in Venezuela and south in Amazonian Brazil.

Additional material examined. BRAZIL. AMAZONAS: Manaus-Caracaraí Hwy., 17 Feb. 1974, *W. C. Steward et al. P20345* (INPA, NY, U); Itapiranga, Rio Uatumã, 19 Aug. 1979, *C. A. Cid et al. 526* (INPA, NY, VDB).

GUYANA. ATKINSON: St. Cuthbert's Trail, 26 Feb. 1969, *U. G. Bio. 106* (BRG, K, NY); Demarara: Kara Savanna, 21 Feb. 1910, *C. W. Anderson 510* (K, NY), *569* (K); Soesdijke, Sep. 1973, *A. Cooper 291* (U); trail to St. Cuthbert's, 8 June 1976, *Grewal & Persaud 201* (U). SURINAM. Gros-savanna (prope km 103), 8 Apr. 1959, *J. van Donselaar 730* (U); Zanderij I, 8 May 1959, *van Donselaar & T. B. Huinink D-C 12* (U); RR near km 62, 20 Apr. 1949, *Lanjouw & Lindeman 3009* (U); Zanderij savanna, 19 Sep. 1976, *Mori et al. 8339* (NY; note that this has scapes); Zanderij II, 6 Feb. 1942, *Stahel s.n.* (NY), 3 June 1944, *Maguire & Stahel 23667* (GH, NY, U; type of *A. psammophila* Maguire), 1 Mar. 1944, *Stahel s.n.* (K, U). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: San Carlos, 30 Mar. 1978, *H. Clark 6574* (NY; some of this has scapes); Sabana Cucurital, 29 abr.-04 Mayo 1979, *Huber et al. 3674* (NY); E del cerro Yapacana, 28 June 1979, *Huber 3895* (NY); 4 km W Serranía Cuao, 14 July 1980, *Huber & Tillett 5300* (VEN, US); 2 km W San Antonio del Orinoco, 20 July 1980, *Huber & Tillett 5424* (US, VEN); San Carlos-Solano, 16 Sep. 1980, *Huber et al. 5679* (VEN); Serranía Vinilla, 13 June 1981, *Huber 6263* (NY); above Pimichin, 2 July 1959, *Wurdack & Adderley 43296* (NY). BOLIVAR: Trianna Savanna, Cerro Pitón, 4 Sep. 1962, *Maguire et al. 53593* (NY); 50 km SE El Dorado, 1 Sep. 1961, *Steyermark 89682* (NY, US); Sabana de Cusimi, Río Cusimi, 7 Mar. 1964, *Steyermark 93174* (NY).

This is indeed a "belly plant," and the great extremes of leaf length, flatness, and indumentum are, at least regarding the first two characters, perhaps a seasonal expression. Particularly conspicuous on most specimens are the rosettes exclusively of little, stubby leaves, these often developed severally on older stem bases and in strong contrast to the longer principal leaves in the same or different rosettes. While few collections are as yet available of this species, they grade in regard to nearly all features that are supposed to distinguish *Abolboda killipii* from *A. minima* Maguire. Two specimens (*S. Mori et al. 8339*, NY, and *Clark 6574*, NY) are of particular interest in that they have flowers ranging from sessile to produced on scapes 1.5–5 cm long. These specimens have the dimorphic leaves as in *A. killipii*, and the bract and sepal characters agree; some have granular foliage. These could show intergradation with *A. americana*.

3. **Abolboda bella** Maguire, Mem. New York Bot. Gard. 10: 15. 1958. TYPE: Venezuela. Territorio Federal Amazonas: Alto Río Orinoco, marshy areas, Yapacana Savanna III at 125 m, 17 Mar. 1953, *Maguire & Wurdack 34514* (holotype, NY; isotype, US). Figure 4.

Perennial, smooth herb from a horizontal stiff rhizome, the roots coarse, the leaves with bases imbricate and secund along the rhizome, leaving a scaly residue of old sheaths, the principal leaves ascending to erect, firm, 9–17 cm long, the longer ones much overtopping scapes, with sheath ca. 10 mm across the clasping base, here stramineous to pale purple or brown, strongly multicostate and ecarinate, gradually narrowing into blade, the blades much longer than the sheaths, elongate-linear, compressed but firm, narrowing slightly above the middle then abruptly to a conic or subulate-spinose tip, the margins entire, forming a thickened, pale, cartilaginous border on the abaxial side, the surface pale to dark green, sometimes violet-tinted toward base, abaxially evidently ribbed, finely striate adaxially. Scapes erect and central, solitary, 5–10 cm long, terete, 1–1.2 mm thick, pale green, enfolded at base by short, erect, sheathing bracts 1–2 cm long and toward apex bearing a single pair of erect, unequal, lance-linear, involute scape bracts 3–20 mm below spike base, the outer one 1.3–1.5(–2) cm long, the inner one 2–2.5 cm long, these convex, green with pale scarious borders and subulate tips; spikes broadly, deliquescently turbinate or more narrowly turbinate (depending on stage), ca. 2 cm high from base to spreading sepal tips, the bracts much shorter than the sepals, the lowermost lance-ovate, ca. 13–14 mm long, cuspidate-subulate, the convex back green except for the pale costa and narrow, scarious, pale borders, the second bract ca. 12–13 mm long and similar but subtending the lowest floret, the third and fourth bracts slightly smaller still but similar in design and also subtending florets, the spike apex with 2–3 green, much smaller and narrower, sterile lanciform bracts; sepals 2 per floret, eccentrically lateral, lanciform-falciform, ca. 15 mm long, bent outward with broad, thin but firm, entire keels, narrowly acute, thick except for the thin margins; corolla salverform, the tube ca. 2 cm long, narrowly funnelform apically, the spreading lobes broadly elliptic, dark blue, ca. 12–15 mm long; filaments flattened, ca. 3 mm long, departing above median petal trace below the level of the corolla lobes; anthers lanciform-sagittate, ca. 3 mm long, dehiscence lateral-introrse; staminodes present as 3 filaments alternating with filament bases and set ca. 2–3 mm below them; style 23–24 mm long, the basal portion winged-triquetrous, each wing with a vein, this base geniculate ca. 5 mm above, here with traces departing into appendages, each appendage with a calloused "hook" or auricle distally and a downward-projecting spur ca. 2 mm long, the 3rd trace less distinct, into the 3rd wing and supplying a reduced narrower median appendage, this with a somewhat narrower "hook" and a filamentous spur much

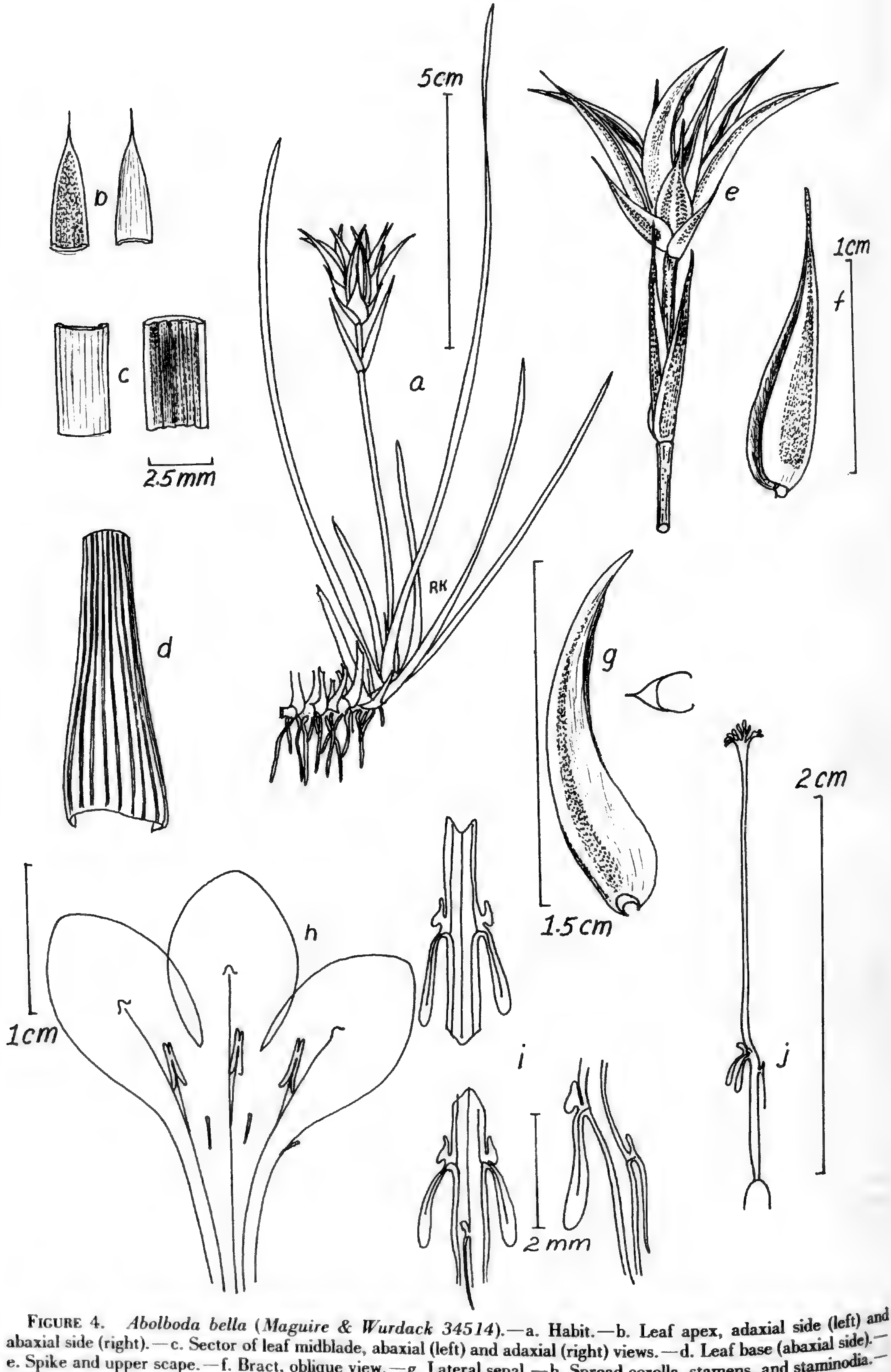

FIGURE 4. *Abolboda bella* (*Maguire & Wurdack 34514*).—a. Habit.—b. Leaf apex, adaxial side (left) and abaxial side (right).—c. Sector of leaf midblade, abaxial (left) and adaxial (right) views.—d. Leaf base (abaxial side).—e. Spike and upper scape.—f. Bract, oblique view.—g. Lateral sepal.—h. Spread corolla, stamens, and staminodia.—i. Three views of stylar base.—j. Style and stigma.

longer than the others (Fig. 4); style thence erect above the geniculation, becoming strongly involute and tubular just below the fimbriate-funnelform stigma apparatus. Capsule and seed not seen.

Distribution. Known only from the type, from the Yapacana savannas, at low elevations.

The rarity of this well-marked species is evidenced by the fact that, despite the frequency of visits by skilled field botanists, no further examples of the plant have been found since Maguire and Wurdack found it in 1953. In regard to its general habit, its almost distichously arranged leaves, and its floral features, this species shares many features with *Abolboda sprucei*, another rarity of the Orinoco savannas, and with *A. abbreviata*, still another rare one from Brazilian Amazonia.

4. **Abolboda sprucei** Malme, Ark. Bot. 25A(12): 17. 1933. TYPE: Venezuela. Territorio Federal Amazonas: Río Guainia, near mouth of Río Casiquiare, *R. Spruce 3456* (lectotype, K; isolectotypes, P, S; phototype at NY). Figure 5.

A. schultesii Idrobo & Lyman B. Smith, Caldasia 6(29): 246, fig. 31. 1954. TYPE: Colombia. Vaupés: Río Guainia, Puerto Colombia (opposite Venezuelan town of Maroa) and vic., ca. 800–850 ft., 31 Oct.–2 Nov. 1952, *R. E. Schultes, R. E. D. Baker & I. Cabrera 18177* (holotype, COL; isotypes, GH, US).

Solitary or caespitose, smooth, pale green perennial, the rosettes from a short, thick caudex, the roots coarse. Leaves elongate-linear to linear-lorate, 10–25 cm long, mostly erect to spreading-outcurved, the sheaths pale or distally purple, broadly clasping and convex at base, thence contracted and lingulate, gradually broadened to the elongate, compressed, flattened or conduplicately folded blades, these 4–10 mm wide with acute to acuminate, somewhat thickened tips, the margins thin and entire, the adaxial surface finely indented-nerved, the abaxial surface strongly raised-nerved, the median nerve forming a strong and elevated costa. Scapes 1–several per rosette, erect or outcurved, 15–30 cm long, strongly unisulcate, thus in cross section forming a "U" or "V," 2–3 mm thick, the bracts confined to the distal part, leafy, lance-linear, 4–7 cm long, subequal, 1–2 or more pairs, the lowest pair sometimes as much as 3 cm below the spike or spikes; inflorescence a single spike or a cluster of a few spikes, the spikes ca. 2 cm long; all spike bracts subtending flower, 9–12 mm long, shorter than the sepals subtended, ovate, acuminate to strongly cuspidate, very firm, the backs frequently carinate toward apex; sepals 2, lanciform, 12–13 mm long, rigid and strongly curved, acute, the margins chartaceous, the dorsal area thickened, with a broad, chartaceous, alate keel; corolla from base to petal tip 22–24 mm long, pale blue, the broadly ovate lobes ca. 12 mm long; stamens with anthers oblong-linear, deeply emarginate and sagittate, ca. 2 mm long on filaments ca. 1.5 mm long; staminodia when present linear, peglike; ovary ca. 3 mm long, ellipsoid, 1 carpel bilobed at apex, this confluent with the style base, the other carpel tips rounded; style including stigma 6 mm long, the appendages midway up, 3, the laterals compressed-clavate, ca. 1.5 mm long, the median one reduced to a filament; stigma funnelform, of 3 connivent but excurved fimbriate lobes. Capsule oblong-cylindric, very thickened, 5 mm long. Seed nearly round to obovoid-prismatic, dull brown, the outer coat finely and irregularly ribbed longitudinally, the ribs anastomosing to produce an irregularly and narrowly alveolate pattern, the body 1–1.2 mm long.

Distribution. Frequent in low-to-medium-elevation sandy savanna, southwestern Venezuela (Territorio Federal Amazonas), and contiguous southeastern Colombia (Vaupés).

Additional material examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: 1 km E of Maroa, 16 Apr. 1953, *Maguire & Wurdack 35688* (GH, NY, US), *Maguire et al. 36419* (F, K, NY, U); 0.5 km E of Maroa, 6 Oct. 1957, *Maguire et al. 41721* (K, NY, US); 1 km W La Cieba, 4 Oct. 1957, *Maguire et al. 41919* (NY, US).

The most unusual feature of this species is the size and disposition of the scape bract pairs, which form what appears to be a leafy involucre, this sometimes with the 1(–2) spikes sessile above it or removed by a short but distinctive internode.

5. **Abolboda ebracteata** Maguire & Wurdack, Mem. New York Bot. Gard. 10: 17–18. 1958. TYPE: Venezuela. Territorio Federal Amazonas: Yapacana Savanna III at 125 m, 31 Dec. 1950, *Maguire, Cowan & Wurdack 30469* (holotype, NY; isotype, US).

5a. **Abolboda ebracteata** var. **ebracteata**. Figure 6.

Caespitose, stiff, smooth perennial, the stems short, cloaked in chaffy old leaf bases, the roots coarsely fibrous. Leaves usually of two sorts, those of new shoots short-linear, rarely longer than 2 cm, grading into main rosette leaves, these ascending to spreading, mostly outcurved, 5–12(–15) cm long, the thin bases broadly dilated, multinerved, pale, to 5 mm broad, with scarious entire borders, narrowing rather abruptly to elongate-linear, green blades, tapering gradually from ca. 1.5 mm broad to 0.5–0.7 mm broad, at apex blunt,

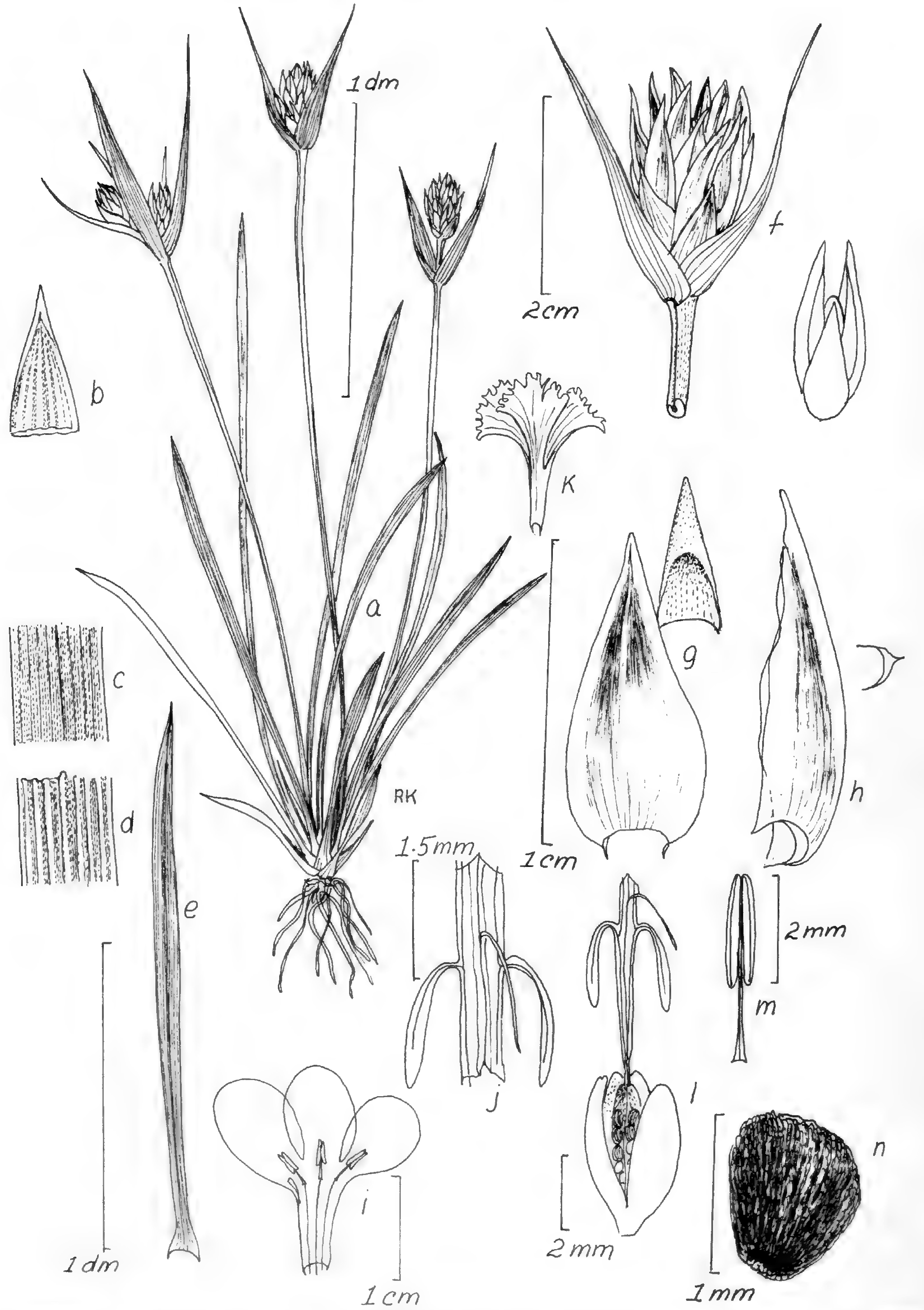

FIGURE 5. *Abolboda sprucei* (composite of collections from vic. Maroa, Territorio Federal Amazonas, Venezuela).—a. Habit.—b. Leaf tip.—c. A section from midblade, adaxial surface.—d. A section from midblade, abaxial surface.—e. Entire leaf.—f. Spike (left); sepal pair subtended by fertile bract (right).—g. Fertile bract and (slightly above, right) inside view of its tip.—h. Lateral sepal.—i. Spread corolla, outline, with stamens and a staminodium to scale.—j. Stylar base.—k. Stylar apex.—l. Ovary and style base.—m. Stamen.—n. Seed.

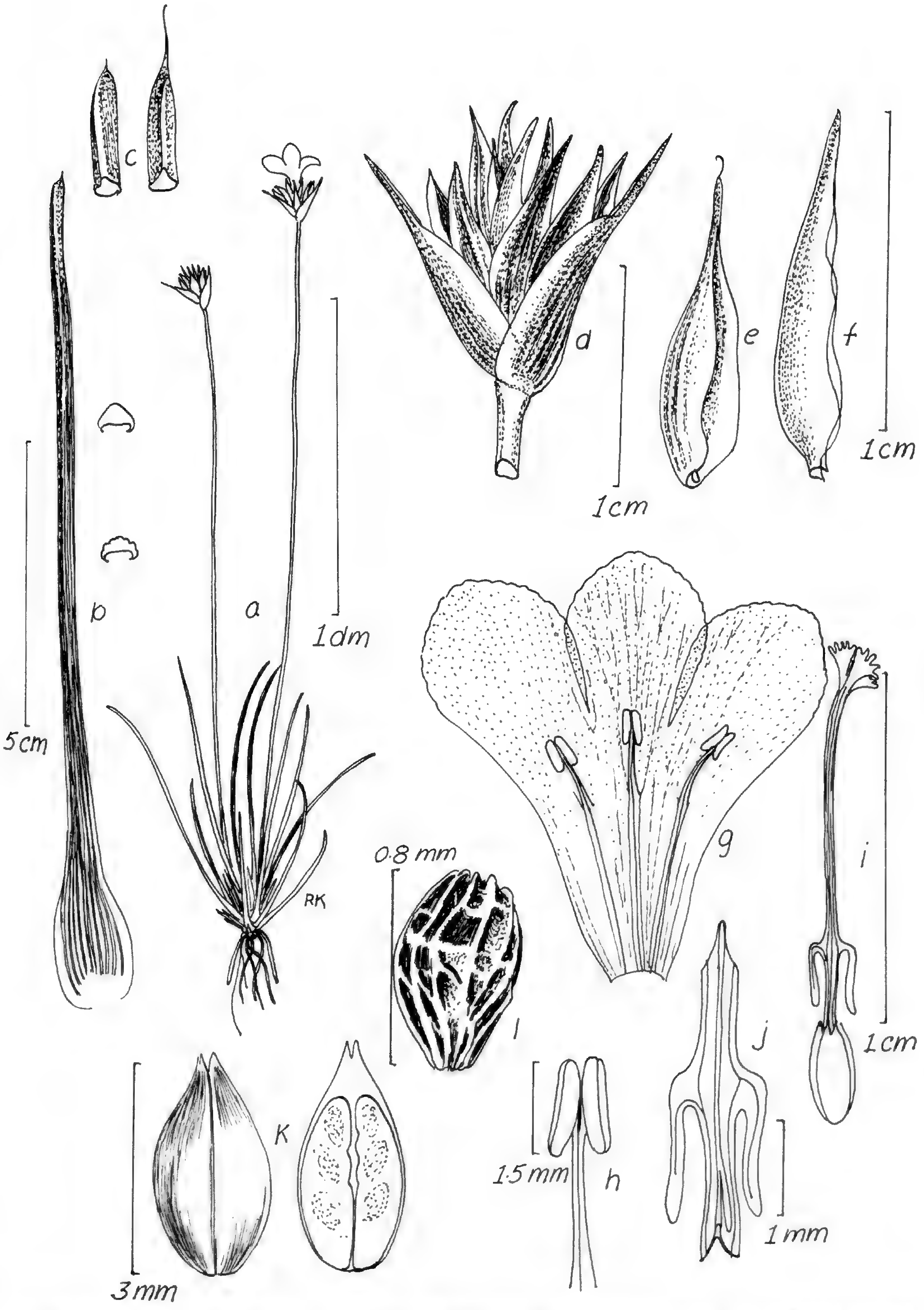

FIGURE 6. *Abolboda ebracteata* var. *ebracteata* (*Maguire, Cowan & Wurdack 30469, Steyermark & Bunting 103242*).—a. Habit.—b. Leaf, adaxial view, with appropriate cross sections.—c. Two common sorts of leaf tip (idealized).—d. Spike.—e. Inner fertile bract.—f. Associated lateral sepal.—g. Spread corolla, stamens.—h. Stamen.—i. Gynoecium.—j. Style base showing appendages.—k. Capsule, external view (left); valve, inner view (right).—l. Seed.

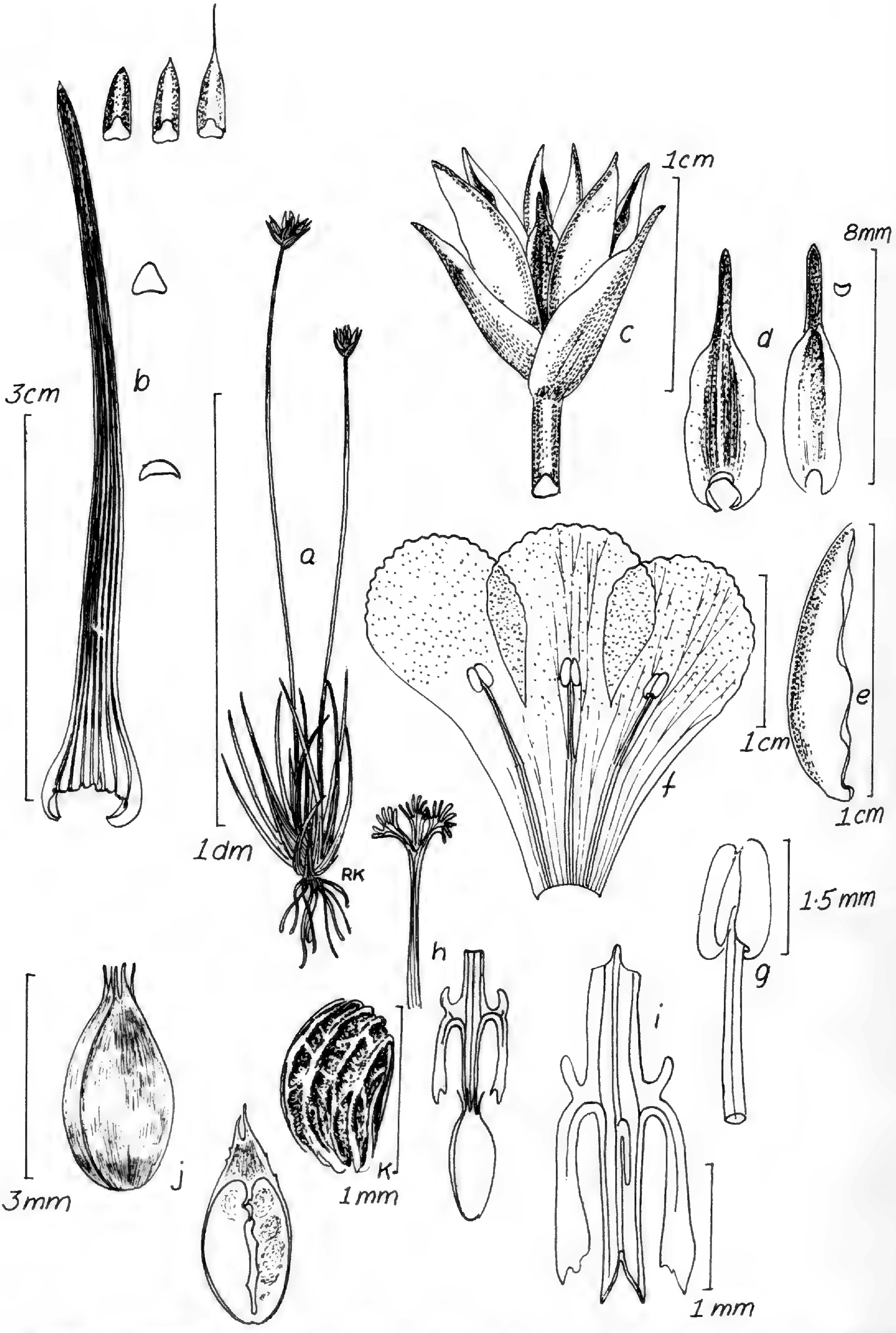

FIGURE 7. *Abolboda ebracteata* var. *brevifolia* (*Wurdack & Adderley 43689; Huber & Tillett 2813*).—a. Habit.—b. Principal leaf (left); 3 common types of tip (above).—c. Spike.—d. Inner fertile bract, abaxial view (left);

narrowly rounded or conic-subulate, either with or without a mucro or (occasionally) a terminal bristle 1–3 mm long, at midblade usually semiterete or plano-convex, abaxially coarsely multicostate and convex, adaxially level or somewhat concave, upblade toward tip becoming subtriangular or triquetrous, abaxially with a strong costa. Scapes stiffly ascending or erect, 1–2 per rosette, 1–2 dm long, at some or all levels subterete to obtusely triangular, ca. 1–1.2 mm thick, bractless except for 2–3 conduplicate, scarious, subulate-setaceous-tipped basal bracts to 2 cm long; spikes post-anthesis broadly turbinate, ca. 1.5 cm long, mostly 4-flowered (sometimes with an additional pair of reduced florets), the bracts all fertile, the 2 outermost ones to 15 mm long, lanciform, with broad, scarious, pale borders and thickened, convex, green or purple-tinged, low-costate dorsal areas, these narrowed and excurrent as a prominent, blunt to aristate-tipped cusp; inner fertile bracts slightly shorter (10–11 mm long), broader in outline; sepals 2, navicular, curved-lanciform, ca. 1 cm long, acute, the keels narrow, entire, and firm, bordered by a green or purple-tinted zone, the outer border broad, pale, scarious; corolla 12–13 mm long, bright dark blue, the lobes broadly obovate, crenulate, shorter than the tube; staminodia lacking; anthers broadly oblong, bilocular, the locules slightly divergent proximally, 1.5 mm long, on filaments ca. 2 mm long, these attached below the corolla sinus level; gynoecium with stylar apparatus proximally alate-triquetrous, appendaged ca. ¼ way up from the ovary, the lateral appendages claviform, recurved, ca. 1.5 mm long, the medial appendage set slightly lower, reflexed, filamentous, ca. 1 mm long; stigmatic part with 3 spathulately dilated lobes, distally fimbriate. Capsule ovoid-ellipsoid, 3–3.5 mm long, the valves distally much thickened, acuminate, at apex sharply bifid. Seeds few, asymmetrically obovoid or wedge-shaped, 0.7–0.8 mm long, dark red-brown, coarsely and sharply ribbed longitudinally, with somewhat lower and irregular crossribs.

Distribution. Locally abundant in moist to wet white sand savanna around the base of Cerro Yapacana, on the upper Orinoco in Territorio Federal Amazonas, Venezuela, at 100–125 m, one locality 30 km above confluence of Orinoco–Ventuari.

Additional material examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: W base of Cerro Yapacana, Savanna III, 6 May 1979, *Davidse et al. 17246* (MO, VDB), *Huber 1626* (US), *Huber 2037* (K, MYF, NY, VDB); 30 km SE of confluence Orinoco–Ventuari, 30 nov.–1 dic. 1978, *Huber 2183* (MYF, VDB); Yapacana Savanna 3, 17 Mar. 1953, *Maguire & Wurdack 34516* (paratype, NY); Cerro Yapacana, savanna, 7 mayo 1970, *Steyermark & Bunting 103242* (NY, VEN).

5b. Abolboda ebracteata var. **brevifolia** Maguire, Mem. New York Bot. Gard. 10: 8. 1963. TYPE: Venezuela. Territorio Federal Amazonas: righthand bank of Río Orinoco, 10 km above mouth of Río Ventuari, 125 m, 21 July 1959, *Wurdack & Adderley 43689* (holotype, NY; isotypes, GH, NY, US, VDB). Figure 7.

Similar to the type but leaves ranging shorter and tending to be more dimorphic, the innovations with several series of short, stubby-bladed, sharply triquetrous and curved, linear-subulate leaves, later grading to more elongate ones, these (2–)3–10 cm long, strongly curved, with character much as in the type variety but with blade tips more often spinulose. Spikes ranging shorter, mostly not over 1 cm long, the bracts thus shorter, with shorter cusps; lateral sepals 9–10 mm long; corolla and stamens as in the type variety; gynoecium with somewhat more elaborate stylar appendages, recurved as in the species but each producing a narrow, erect but curved auricle at base (on the upside of appendage). Capsule likewise ovoid, ca. 3 mm long, the valves similarly bifid, the teeth narrower, sharper. Seeds as in the species but slightly longer (to 1 mm).

Distribution. Moist to wet savanna, at 100–150 m, along the Orinoco and near confluence of major streams with it, Territorio Federal Amazonas, Venezuela, and in Amazonas, Colombia.

Additional material examined. COLOMBIA. AMAZONAS: Alto Río Orinoco, Cacagual Savanna, 13 Sep. 1957, *Maguire et al. 41439* (NY). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: vic. Canaripó, Río Ventuari, 29 May 1978, *Huber 1875* (US); 30 km SE confluence of Orinoco–Ventuari, 30 nov.–1 dic. 1978, *Huber & Tillett 2781* (NY, US), *2813* (K, NY); 30 km W Serranía El Tigre, 29 Feb. 1980, *Huber 4848* (NY); 30 km N Puerto Ayacucho, 19 May 1980, *Huber 5216* (NY—a mix with *A. pulchella*).

This variety is a little weak. The character stressed by Maguire, namely, that the cephalar bracts (outer ones) are shorter than the inner,

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adaxial view (right).—e. Lateral sepal.—f. Spread corolla, stamens.—g. Stamen.—h. Stylar apparatus.—i. Enlarged view of style base showing appendages.—j. Capsule, outer view (left); valve of capsule, inner view (right).—k. Seed.

appears to vary more widely, as do leaf lengths, and this variation does not appear to be as little as was first observed.

6. **Abolboda americana** (Aublet) Lanjouw, Recueil Trav. Bot. Neerl. 34: 492. 1937. *Xyris americana* Aublet, Hist. Pl. Guiane 1: 140, 3: pl. 14. 1775. TYPE: French Guiana, *Aublet s.n.* (lectotype, P; isolectotype, BM; phototype, NY). Figure 8.

Xyris caerulea Lam., Tabl. Encycl. 1: 136, t. 36, fig. 2, as "*X. bleue.*" 1791.

Abolboda imberbis Kunth in HBK, Nov. Gen. Sp. 1: 256. 1816. *A. americana* Aublet var. *imberbis* (Kunth in HBK) Maguire, Bull. Torrey Bot. Club 75: 193. 1948. TYPE: "crescit in arenosis guayanae ad flumen Atabapo" (international boundary between Colombia and Venezuela). Ostensibly collected by Humboldt.

A. poeppigii Kunth, Enum. Pl. 4: 27. 1843. TYPE: Campina Grande de Colares (Pará), June 1832, *Poeppig 2993* (holotype not formally designated, specimens at B, F, M, P; phototype, NY).

Soft, glabrous, solitary or caespitose annual or short-lived perennial, the stems leaf-cloaked, mostly short, rarely to 2.5 cm long, the roots spongy-thickened. Leaves typically of 2 lengths, those of secondary rosettes (which arise on buds around scapes on primary rosettes) stubby, short-linear, 3–10 mm long, abruptly narrowed from clasping thin bases, fleshy-linear, acute, mostly trigonous or triquetrous, upstem later in season grading longer, distinctly narrower, mostly spreading, or ascending with incurved tips, 15–120 mm long, narrowing from (mostly) triplinerved soft pale bases to elongate-linear, flattened blades, these for most of their length 0.3–0.7 mm wide, dorsiventrally compressed, triplinerved, the adaxial face usually plane, the abaxial face showing thickened margins and a distinct costa, pale to deep green, or tinged with maroon or red, toward apex variously thickened, blunt and with an eccentric short mucro at tip. Scapes rarely shorter than leaves, usually equal to them or much longer, usually wrapped at base in 2–3 scarious, ovate-lanciform, mucronate or cuspidate basal bracts, otherwise bractless, 2.5–15 cm long, terete, sometimes low-fluted or striate; spikes by seeding time broadly turbinate to hemispheric, 5–6(–7) mm high, 2–3(–4)-flowered, typically with 2 lance-ovate, cuspidate or mucronate, keeled sterile bracts 2.7–6 mm long at base, the lowest one usually 1–2 mm shorter than the other or all bracts fertile, 5–6 mm long, ovate-lanceolate, strongly keeled, broadly scarious-bordered, the median area thickened and with a strong green to maroon costa, this mostly much excurrent as an outcurved cusp; sepals 2 or sometimes accompanied by a reduced inner one, this mostly oblanceolate, ca. 3 mm long, scarious, broadly acute to rounded at apex, the 2 lateral sepals navicular-conduplicate, oblong-obovate, 5–5.5 mm long, shallowly emarginate, pale-scarious except for the strong, short-excurrent, entire keel; corolla mostly 13–15 mm long, the lobes oblong-ovate, narrowly rounded at tip, light blue; staminodia not evident; anthers bilocular, pale, the thecae divergent at base, the flattened filaments 1.2–1.3 mm long; style ca. 10 mm long, triquetrous at base and with 2 recurved-clavate, lateral appendages 1–1.5 mm long, and a reduced, short-filamentous adaxial one. Capsule broadly ovoid, 2.5–3.5 mm long, smooth, the valves thickened, especially distally at the incurved, entire, smooth, acute tips. Seeds broadly obovoid to inequilaterally subglobose, ca. 0.5 mm long, coarsely 9–11-ribbed, the broad ribs bedecked with deep red-brown papillae and often somewhat rugulose, the intervals paler and irregularly transversely rugulose.

Distribution. Frequent, mostly in low-elevation, wet, sandy substrates of savanna, caatinga, restinga, and broad, wet, open grass-sedge campo, often in recently disturbed, wet, burned areas, South America from French Guiana west to southeastern Colombia, south into Amazonian and northeast-coastal Brazil (Amapá, Amazonas, Bahia, Paraiba, Pará).

Additional representatives examined. Because of large amount of material seen, only selected specimens are cited here to demonstrate geographical and morphological range): BRAZIL. ACRE: Cruzeiro do Sul, Ponto 10, 10 Feb. 1976, *Rosa 696* (US, VDB). AMAPA: Campo de Aviacas, 25 Apr. 1960, *Egler 1417* (US); between Rios Cujubim and Flechal, 8 Aug. 1962, *Pires & Cavalcante 52000* (U). AMAZONAS: Bella Vista, 15–18 Mar. 1944, *Baldwin 3558* (F, K, US). BAHIA: 5 km SE Marau, 2 Feb. 1977, *Harley 18462* (K, NY, VDB), *18463* (NY, VDB); Alcobaça, *Mori et al. 10614* (K, NY). PARA: Maracana, 6 Dec. 1978, *Bastos et al. 106* (F, NY); Vigia, 24 Jan. 1950, *Black, herb. no. 50.8817* (US); 36 km SE Vigia, 29 Mar. 1980, *Davidse et al. 17539* (F, GH, US, VDB); Marudá, 3–4 Apr. 1980, *Davidse et al. 17856* (F, MO, NY, VDB); Collares, 16 Aug. 1913, *Ducke 12576* (U, US). PARAIBA: Paraíba, *Moraes 2A38* (NY, US). RORAIMA: Carecarai, 7 Feb. 1974, *Pires & Leite 14855-14861* (US). COLOMBIA. GUAINIA: Puerto Inirida, 14 ago. 1975, *Garcia-Barriga 20.823* (US), *20.824* (F); San Filipe, 6 Apr. 1984, *Gentry & Stein 46389* (MO, VDB). VAUPES: Araracuara, 5 Sep. 1959, *Maguire & Fernandez 44125* (NY). GUYANA. Wanama River, 10–23 May 1923, *J. S. de la Cruz 4378* (NY); Kaieteur Plateau, 30 Apr. 1944, *Maguire & Fanshawe 23116* (GH, NY, U, US), 3 May 1944, *Maguire & Fanshawe 23178* (F, GH, K, MO, U, US), *23188* (F, GH, K, MO, NY, U, US); Partang Savanna, 13 June 1960, *Maguire & Tillett 43815* (K, NY, U). SURINAM.

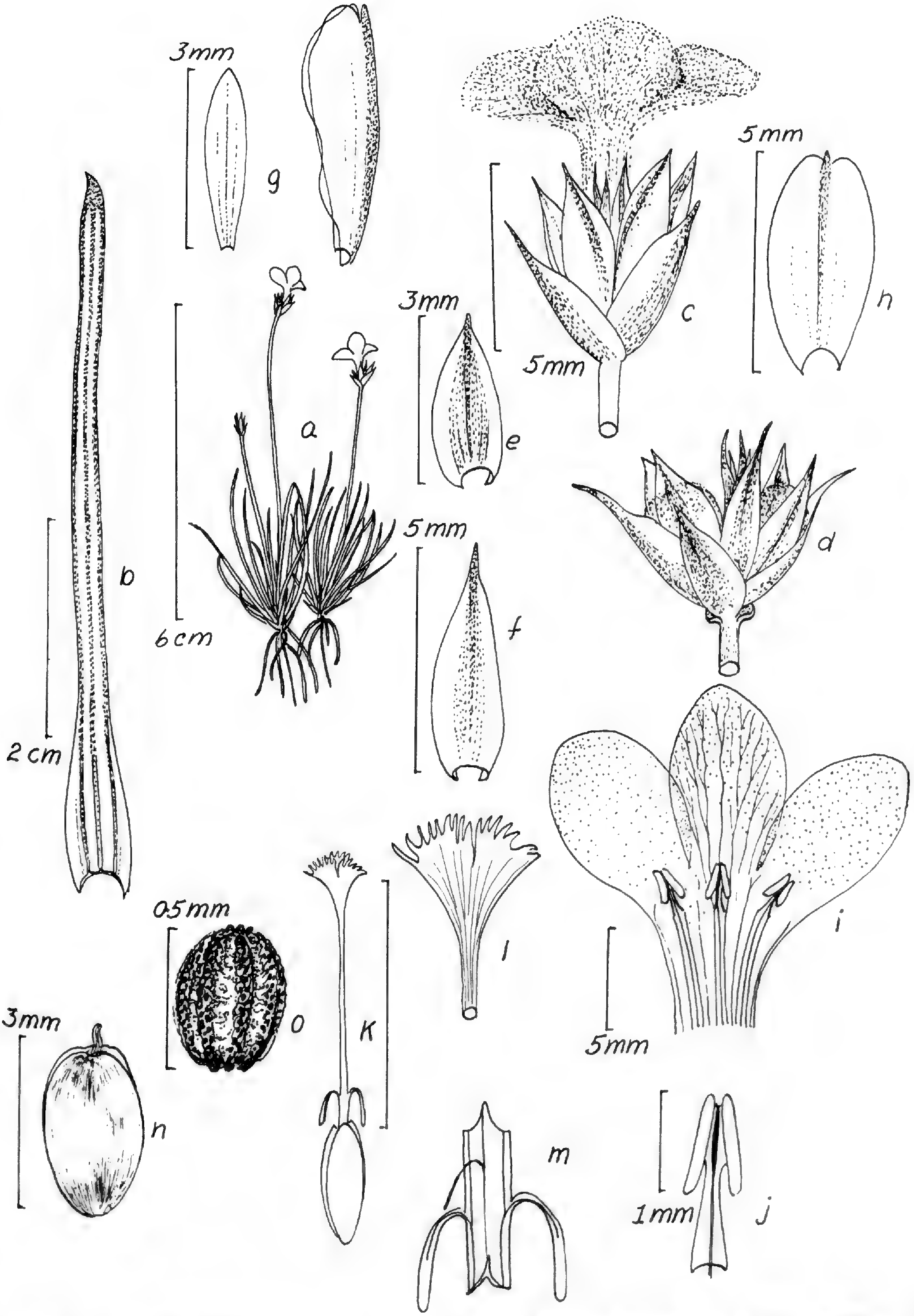

FIGURE 8. *Abolboda americana* (*Huber & Alarcon 8002*; *Wurdack & Adderley 43757*).—a. Habit.—b. Principal leaf.—c. Flowering spike.—d. Fruiting spike.—e. Lower sterile bract.—f. Fertile bract.—g. Inner sepal (at left), side view of lateral sepal (at right).—h. Spread lateral sepal, outer side.—i. Spread corolla and stamens.—j. Stamen.—k. Gynoecium.—l. Stigmatic apparatus.—m. Stylar base with appendages.—n. Capsule.—o. Seed.

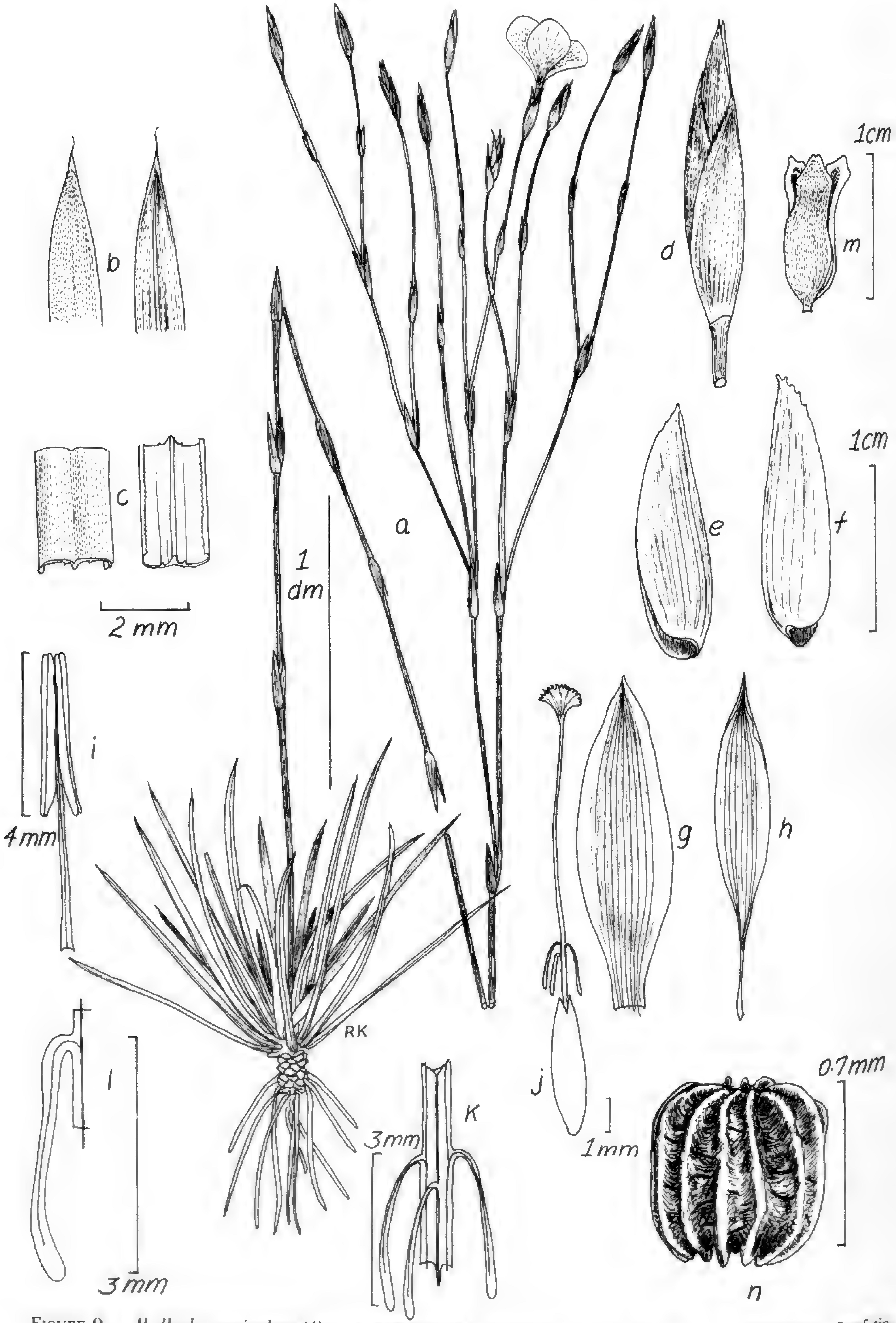

FIGURE 9. *Abolboda paniculata* (*Cowan & Wurdack 31387*; *Tavares & Silva 31*).—a. Habit.—b. Leaf tip, upper surface (left), lower surface (right).—c. Sector of leaf midblade, adaxial side (left) and abaxial side (right).—

Zanderij, 22 Mar. 1976, *Jansma LBB 15685* (U), *3284* (U); Zanderij I, 29 July 1933, *Lanjouw 294* (K, U); *Lanjouw & Lindeman 108* (NY, US); Morengo tapoe to grote Zwiebelzwamp, 22 Oct. 1948, *Lanjouw & Lindeman 1007* (U); E of Kopie Penninica, 16 July 1953, *Lindeman 4378* (F); Zanderij II, 3 June 1944, *Maguire & Stahel 23666* (GH, NY, U, US); Natioureservaat Brinkheuvel, 20 Oct. 1967, *Teunissen & Wildschut 11870* (U—a little plant, long spike bracts and short scapes). TRINIDAD. Aripo Savanna, 9–23 Feb. 1950, *Howard 10515* (GH); Long Stretch Savanna, 2 Apr. 1953, *Baker & Simmonds 14931*, 26 Aug. 1977, *Philcox & Maas 8228* (K), 13 July 1976, *Adams & Kalloo 14013* (K). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: San Carlos, 3 June 1979, *Clark 7188* (MO, NY); Cerro Yapacana, 3 June 1978, *Huber 2018* (NY); Caño Caname, Cucurital, 29 Apr.–5 May 1979, *Huber et al. 3694* (MYF, NY, VDB); 15 km SSW Cerro Autana, 26 June 1979, *Huber 3821* (NY); Yapacana Savanna III, 10 Aug. 1983, *Kral & Huber 70712* (F, GH, MO, NY, U, US, VEN, VDB); San Carlos, 26 Nov. 1977, *Liesner 3910* (MO, NY); Maroa, 16 Sep. 1957, *Maguire et al. 42503* (NY, U, US); base of Cerro Duida, 22 Aug. 1944; *Steyermark 57831* (F, NY, US), *57847* (F, GH, NY, US); Esmeralda, 1 Nov. 1928, *Tate 299* (NY); above Pimichin, 2 July 1959, *Wurdack & Adderley 43297* (GH, NY, U); Caño Cumaré, 5 Aug. 1959, *Wurdack & Adderley 43757* (NY, US), *43767* (NY, US). BOLIVAR: Salto Aicha, 27–28 Nov. 1982, *Davidse & Huber 22898* (MO, VDB); W of Canaima, 25 ago. 1983, *Huber & Alarcon 8002* (MYF, NY, VDB); Guaiquinima, Salto Carapo, *Huber 12426* (MYF, VDB); Cerro Pitón, 4 Sep. 1962, *Maguire & Steyermark 53594* (NY); Sabana de Triana, SE de El Dorado, 1 Sep. 1961, *Steyermark 89681* (NY, US); Icabaru, 18 dic. 1978, *Steyermark et al. 117802* (NY); Cerro Guaiquinima, 20–25 enero 1977, *Steyermark & Dunsterville 113137* (K, NY—a very small plant with short scapes).

This is the commonest and most widespread *Abolboda* in low-elevation sites (much less common in elevations over 1,000 m). It is probably the nearest thing to a weed in the genus and is also the most variable in leaf, scape length, length and character of spike bracts, and number of flowers. It is most often confused with *Abolboda killipii*, which usually has nearly sessile spikes with fewer flowers and thicker, usually shorter, scabridulous foliage, or with *A. acaulis*, which has larger, sessile or stouter-scaped spikes and more rigid and linear-triangular, mostly setaceous-tipped leaves. Both of these latter species have a very different seed sculpture (see figures). While I have no trouble interpreting the Aublet material as type for the species (identification of the two elements on the type sheet is possible from the phototype), there is some problem with the synonymy, as I have seen only paratype material of the Poeppig collections ("Para, *Poeppig s.n.*, L"). However, the phototype of *Poeppig D. 2993* taken at Geneva is still legible enough to make an identification. Essentially this material represents a lower, shorter leaved-and-scaped extreme that grades through other transitional specimens to taller forms and does not appear to me to be varietally distinct.

7. **Abolboda paniculata** Maguire, Mem. New York Bot. Gard. 10: 10, fig. 2a–g. 1958. TYPE: Venezuela. Territorio Federal Amazonas: cumbre at 2,000 m, Cerro Parú, 10 Feb. 1951, *R. Cowan & J. Wurdack 31387* (holotype, NY; isotypes, US, VEN). Figure 9.

Smooth, rosulate, perennial herb, the stem short, stout (to 1 cm thick), caudiciform or attached to a stouter horizontal or ascending, knobby rhizome. Leaves of rosette monomorphic, spreading or ascending, usually outcurved, 5–15(–17) cm long, the bases thin, scarious, pale, convex and strongly costate, constricted to a narrow "U"-shaped attachment with blade and dilating just above the blade, this linear-triangular, rigid, stiff and thin but not fleshy, tapering to a narrowly acute, acuminate, or subulate tip, sometimes prolonged variably to an arista, the margins thin, pale, narrowly revolute, frequently papillate, the adaxial surface dark green, lustrous, the midnerve depressed, the abaxial surface with a strong, elevated median costa and often 2–4 strong laterals convergent apically to a single costa. Scape solitary, 5–12 dm high (including inflorescence), terete and multistriate, usually purple-brown, to 5 mm thick at base, tapering gradually into a (usually) "V"-shaped, dichotomously branched panicle, the scape bract pairs numerous, lance-oblong or lance-triangular, likewise purple-brown, subequal, the proximal pairs longest, to 2 cm long, gradually reduced upward, the upper ones ca. 1 cm long, with a pair at each inflorescence fork and a pair usually median on the ultimate flowering branches; spikes colored as in bracts, terminal on branches, fusiform, ca. 2.5 cm long, terete; fertile bracts 2, ovate-lanciform, involute and with rounded backs as in scape bracts, the lower one ca. 1.5 cm long, the inner one slightly longer, ca. 1.7 cm, both with narrow scarious borders, and erose or lacerate, narrowly acute or acuminate tips; sepals 3, 2–2.2 cm long, the lateral

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d. Spike.—e. Sterile spike bract.—f. Fertile bract.—g. Lateral sepal.—h. Inner sepal.—i. Stamen.—j. Gynoecium.—k. Stylar base and appendages.—l. Lateral stylar appendage, enlarged.—m. Open capsule.—n. Seed.

ones lanciform, clasping at a narrow base, the inner sepal strongly clawed, the blade elliptic, thinner than in the lateral ones, the margins somewhat involute distally, the apex acuminate; corolla bright lavender-blue or blue-violet, ca. 4 cm long, the spreading lobes broadly ovate, ca. 2 cm long; anthers linear, 4 mm long, deeply sagittate, emarginate, on narrow, flattened filaments to 3 mm long; ovary ellipsoid, ca. 5 mm long, its tip tridentate, the style ca. 2 cm long, with 3 recurved, subequal, narrowly clavate, terete appendages to 3 mm long toward its base; stigma broadly funnelform, the receptive border glandular-erose. Capsule oblong-ellipsoid, ca. 1 cm long, the 3 valves woody, particularly thickened distally. Seeds broadly obovoid to subglobose, ca. 0.7 mm long, a glistening dark brown or nearly black, with ca. 6 spiral ribs per side, these strongly and irregularly raised, sometimes forming narrow wings and interconnected by narrow, less-raised irregular cross-lines.

Distribution. Frequent but local in acidic, sandy-peaty, open or shrubby bog savanna, tepui summits and surrounding plateaus, at 1,150–2,100 m, from southern Bolívar and Territorio Federal Amazonas, Venezuela, southward just inside the border of contiguous Amazonas, Brazil.

Additional material examined. BRAZIL. AMAZONAS: arredores de serra Aracá, 29 Jan. 1978, *Rosa & Lira 2297* (F, NY); SE parte de Serra Norte, plato da Serra Aracá, 14 Feb. 1984, *Tavares & Silva 31* (INPA, NY, VDB); plateau savanna, N massif of Serra Aracá, 11 Feb. 1984, *Prance et al. 28987* (NY, VDB). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Serranía Parú, 2,000 m, cumbre along W rim, 1 Feb. 1951, *Cowan & Wurdack 31300* (paratype, NY). BOLIVAR: Meseta de Jaua, Cerro Jaua, cumbre, 1,922–2,100 m, 22–27 Mar. 1967, *Steyermark et al. 109328* (F, K, NY).

On the basis of most characters, particularly the number and arrangement of spike bracts and sepals, the highly anthocyanic pigmentation, and its general large size and color of corolla, this species is closely allied to *Abolboda uniflora* and *A. neblinae*. However, it is a much more coarse species, unique in its much-branched inflorescence. Unlike *A. neblinae* (presumably also *A. uniflora*), this species has well-developed stylar appendages.

8. **Abolboda neblinae** Maguire, Mem. New York Bot. Gard. 17: 80. 1967. TYPE: Venezuela. Territorio Federal Amazonas: common in boggy area in open places, *Bonnetia* woodland, at 2,400 m, Venezuelan side of Brazilian Divide, 2 km E Boundary Marker no. 4, Cerro de la Neblina, 1 Nov. 1965, *B. Maguire, J. M. Pires & N. T. Silva 60523* (holotype, NY; isotypes, NY, UB, US). Figure 10.

Glabrous rosulate perennial, the rosettes in dense domelike mats, the roots coarse, the stems short. Leaves mostly curved, spreading to spreading-out-curved, linear-triangular, stiff, 3–7 cm long, narrowing from thin, strongly costate, convex pale bases into flattened, linear blades, these thickening toward apex and at tip narrowly acute and usually prominently spinulose, the margins very thin, the upper surface proximally with a shallow median groove, otherwise nearly smooth, the abaxial surface more prominently ribbed, the median nerve a strong costa. Scapes 1 per rosette, 20–40 cm long, distally 1.5–2 mm thick, terete, striate longitudinally, these and the bracts maroon or purple-brown; scape bracts appressed, in 2–3 well-spaced pairs, members of a pair subequal, lance-oblong or oblong-elliptic, 1.5–2 cm long, apically acute to acuminate-subulate with narrow, pale scarious borders; spikes 1(–2, sometimes an additional spike from next bract axil down), terminal, fusiform or lanciform, 15–18 mm long; sterile bracts 2, ca. 16–18 mm long, the laterals elliptic, obtuse, except for the thin, pale base purple-brown as in bracts, finely nerved, the inner sepal thinner, strongly stipitate, the blade narrowly elliptic with a broad, pale scarious border; corolla bright blue-violet, from base to lobe tips 30–33 mm long, the lobes spreading, ovate with fine dark nerves; stamens with anthers linear, pale, ca. 3 mm long, nearly basifixed, shallowly sagittate, on filaments ca. 1.5 mm long; ovary ellipsoid, ca. 5 mm long, tridentate at apex; style and stigma ca. 2 cm long, the slender style base exappendiculate, then dilating to a narrowly funnelform apex, the stigma funnelform with 3 ascending-triangular, papillate-edged lobes; capsule lanceoloid, 1.3–1.4 cm long, thickened throughout, valve tips narrowed acuminately to a blunt tip. Seeds broadly obovoid, ca. 1 mm long, light red-brown, longitudinally with 5–6 dark ribs per side, these connected by slightly finer cross-ribs to form a reticulum.

Distribution. Frequent in wet, boggy, rocky cold meadows and in *Bonnettia* woodland at and toward summit elevations, 1,900–2,300 m, Cerro Neblina along the Brazil–Venezuela border.

Additional material examined. BRAZIL. AMAZONAS: ridgeline, Venezuela–Brazil border, Cerro Neblina, Sep. 1985, *Gentry & Stein 46712* (MO, VDB). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Neblina, Camp II, 2.5–3.5 km NE Pico Phelps, 17–22 Feb. 1984, *V. A. Funk 6262* (US, VDB); Amazonas–Brazil frontier, summit Serra Neblina, 3 Dec. 1965, *Maguire & Pires 60539* (paratype, F, NY); Valle de Titirico N of Pico Phelps, Cerro Neblina, 1 Dec. 1984, *Kral with Brewer-Carias 71922* (NY, VDB, VEN); Brazil frontier, Planicie de Zuloaga, Río Titírico, 10–15 Oct. 1970, *Steyermark*

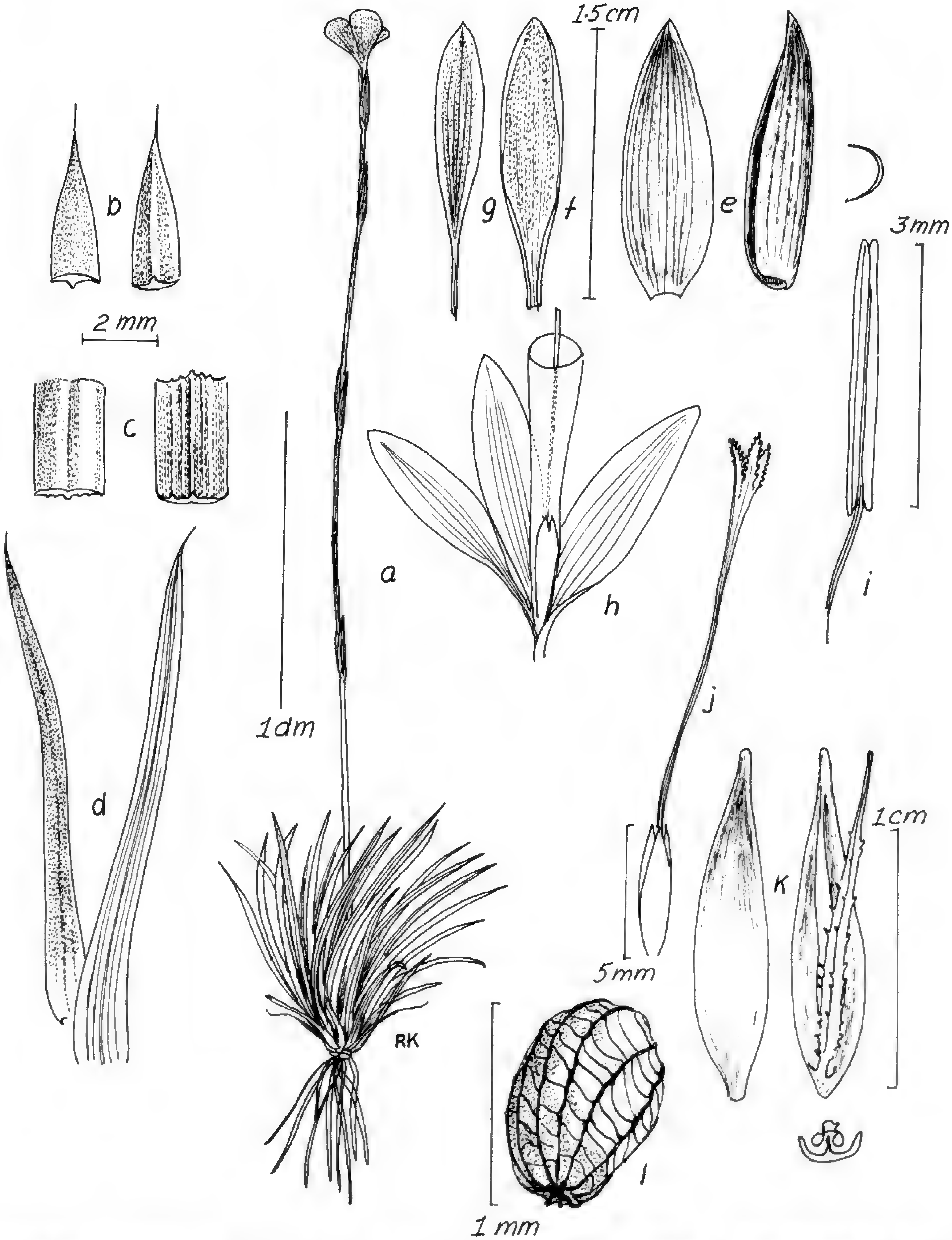

FIGURE 10. *Abolboda neblinae* (*Kral with Brewer-Carias 71922*).—a. Habit.—b. Leaf tip, adaxial side (left) and abaxial side (right).—c. Sector of leaf midblade, adaxial side (left) and abaxial side (right).—d. Two leaves.—e. Bract, spread, outer side (left), side view (right).—f. Lateral sepal.—g. Inner sepal.—h. Sepals spread so as to show corolla base, gynoecial base.—i. Stamen.—j. Gynoecium.—k. Views of capsule valve and placentation.—l. Seed.

103754 (NY, US), 17 Apr. 1984, *Gentry & Stein 46712* (MO, VDB).

This species is locally abundant atop Cerro Neblina and is, on a basis of foliar features, subequal and ecarinate sepals, corollas, stamens, fruit, and seeds, a part of a sharply distinguishable complex, which it forms with *Abolboda paniculata* and *A. uniflora*.

9. Abolboda uniflora Maguire, Mem. New York Bot. Gard. 10: 12. 1958. TYPE: Venezuela. Territorio Federal Amazonas: summit of Cerro Duida, Brocchinia Hills, 1,700–1,980 m, 1 Sep. 1944, *J. A. Steyermark 58169* (holotype, F). Figure 11.

Glabrous, rosulate perennial, the stems short, stout, the rosettes in dense clumps, the roots spongy-thickened. Principal leaves erect to spreading-recurved, grass-green, mostly 2–2.5 cm long, stiff, the pale, clasping bases mostly triplinerved, otherwise thin, tapering into and shorter than the narrowly linear blades, these in cross section mostly thick, 3–4-angled, blunt with an excurved, short, mucro-prickle, the upper side 3-ribbed toward the blade base with the central rib strongest, toward the apex unicostate, the abaxial side with a strong median costa from base to near apex. Scapes 1 per rosette, erect, purple-brown, to 48 cm long, terete and striate-costulate toward apex, there ca. 1.5 mm thick; scape bracts 7 pairs, these ca. equidistant along the scape, appressed, the bracts of a pair subequal, lance-oblong, 1.5–1.8 cm long, convex, subulate-acuminate with narrow, pale scarious borders and purple-brown backs, the uppermost pair slightly shorter and directly below the terminal spike, the penultimate pair bearing a second, nearly sessile, spike; spikes fusiform, ca. 1.5 cm long, colored as in the scape bracts, the 2 bracts ca. 1 cm long, lance-oblong, acute or acuminate, subtending a single flower; flowers in number and dimensions of parts presumably as in *Abolboda neblinae*, the closest relative.

Distribution. Known only from the type collection, not collected since.

The limited material available, consisting of three specimens (of which I have seen only the holotype), is distinguishable from *Abolboda neblinae* on the basis of its shorter, less-tapering, blunter-tipped, thicker, and strongly 3–4-angled leaf blades. When (if) further material with mature fruit and flowers becomes available, a decision can be made as to the precise relationship of *A. uniflora* to *A. neblinae*. On the basis of existing evidence, the relationship is very close and perhaps varietal.

10. Abolboda abbreviata Malme, Ark. Bot. 19(13): 5. 1925. TYPE: Brazil. Pará: Campos do Ariramba, 7 May 1912, *A. Ducke, Herb. Amaz. Mus. Para 11895* (lectotype, S; isolectotypes, K, MG, NY, RB, U, US). Figure 12.

Smooth, rosulate, annual or short-lived perennial, the stems short in tufted rosettes, the roots slender, fibrous. Earliest rosette leaves several, triangular, scalelike, ca. 1 cm long, the later and principal ones spreading to ascending, linear, 3–7.5(–9) cm long, the sheaths soft, thin and multicostate, convex-backed, the base clasping, narrowing to elongate-linear, stiff, flat, pale green blades, these abruptly acute, eccentrically short-subulate or apiculate, the margins a narrow incrassate-cartilaginous band, the abaxial surface with several fine, slightly raised nerves, the adaxial surface with fine indented nerves. Scapes overtopping leaves, 8–19 cm long, terete, their bases enfolded by short bracteal leaves, and with 1 pair of bracts at midscape or upward, sometimes to near 1 cm below spike, and there ca. 1 mm thick; scape bracts erect, lance-linear, 1–1.5 cm long, convex-backed, green with pale scarious borders and acute, apiculate tips; spikes narrowly to broadly turbinate, 1–1.5 cm high and 4–5-flowered; all bracts fertile, the lowest one ca. 5–7 mm long, lance-ovate, the median zone broad, green, the costa excurrent as a blunt cusp, the inner bracts similar, progressively slightly shorter; sepals 2, lance-elliptic, ca. 10 mm long, acute, sharply keeled with narrow green bands flanking keel and thin, entire, scarious borders; corolla blue-violet, 1.7–2 cm long, the lobes ca. 7–9 mm long; stamens with anthers ca. 2 mm long, deeply sagittate and emarginate, on filaments 1.5 mm long; staminodia not evident; lateral stylar appendages ca. 1 mm long, reflexed, stipitate-clavate, the median one reduced to a nub. Capsule obovoid to broadly ellipsoid, ca. 5 mm long. Seeds angulate-obovoid, 0.5–0.7 mm long, strongly but narrowly few-ribbed, red-brown with fine cross-etching.

Distribution. Rare in low-elevation riverine campos, thus far known only from two localities in Amazonian Brazil (Pará).

Additional material examined. Other than the type there seem to be only three specimens to cite, but these have amplified several details in the original description. They are BRAZIL. PARA: Campo do Jaramacarú, perto do Barracão, região do Ariramba, 26 May 1957, *G. A. Black, W. Egler, P. Cavalcante & Antonio Silva 57-19603* (NY); Obidos, Jaramacarú River, overflowed and sandy field, 27 May 1957, *W. A. Egler 271* (US), 2 June 1957, *P. Cavalcante 173* (US).

On the basis of most characters, this rare species appears to be part of a complex including *Abolboda bella* and *A. sprucei*. From comments on some labels it would seem that the plant is very localized but quite abundant within a small geographic area.

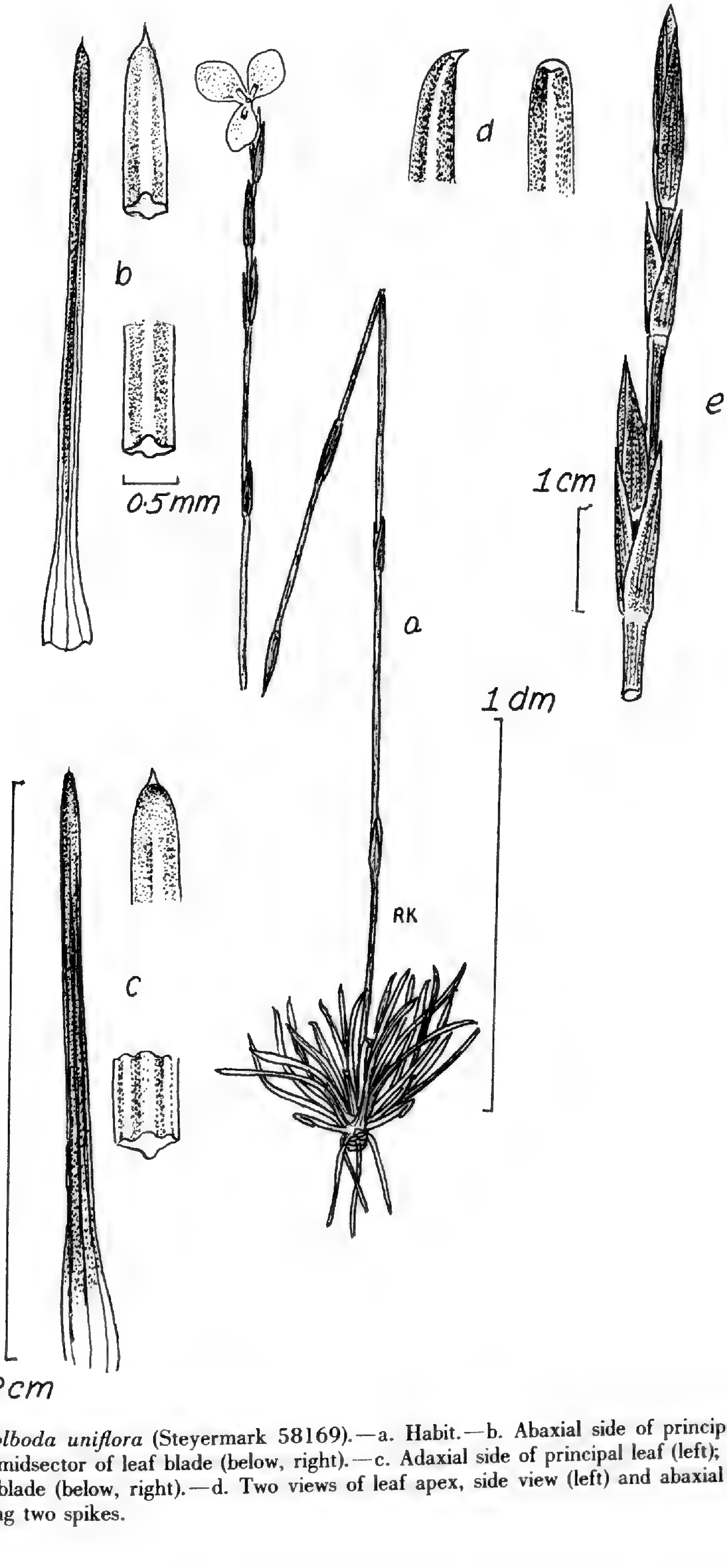

FIGURE 11. *Abolboda uniflora* (Steyermark 58169).—a. Habit.—b. Abaxial side of principal leaf (left); leaf apex (above, right); midsector of leaf blade (below, right).—c. Adaxial side of principal leaf (left); leaf apex (above, right); sector of midblade (below, right).—d. Two views of leaf apex, side view (left) and abaxial view (right).—e. Inflorescence, showing two spikes.

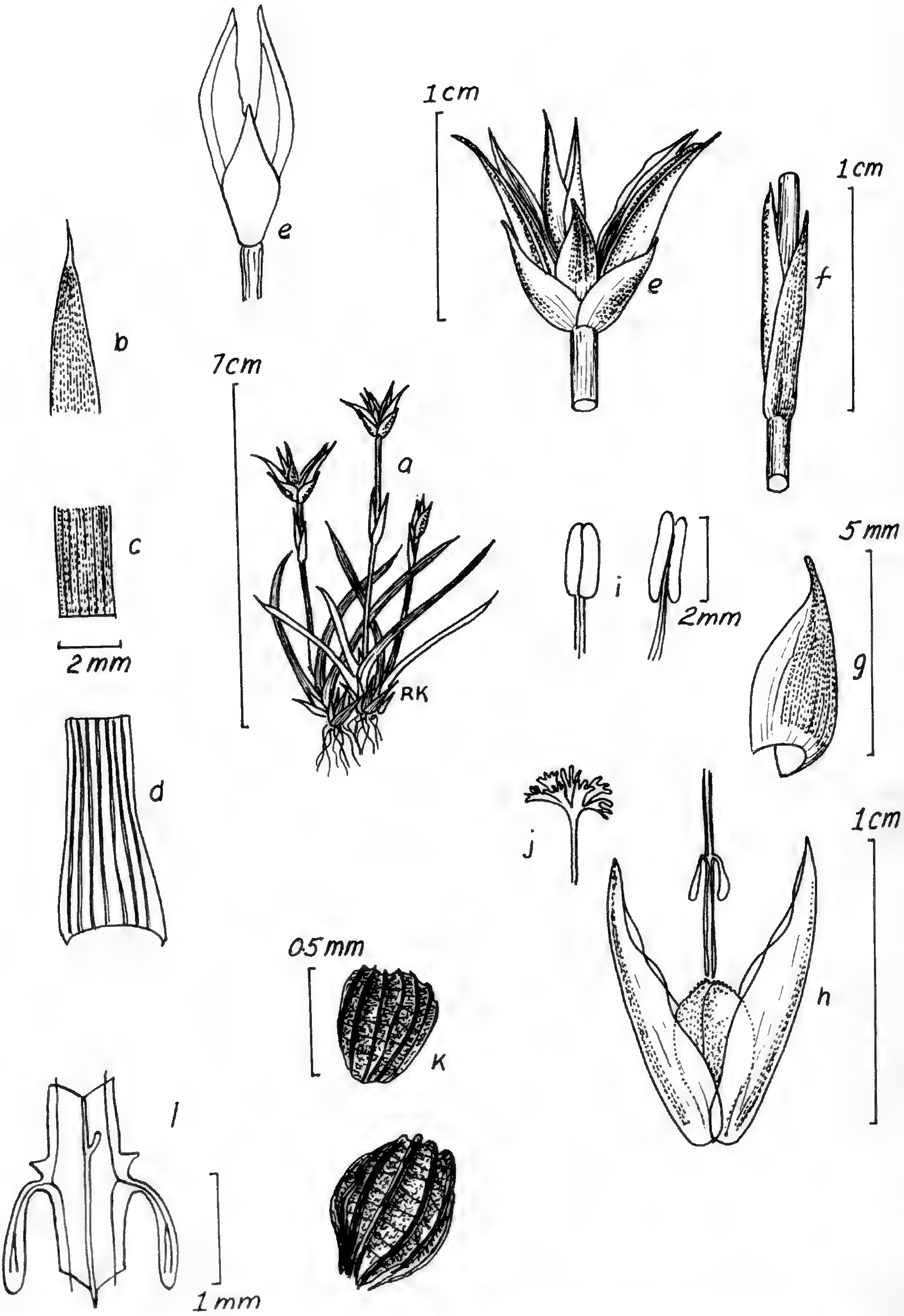

FIGURE 12. *Abolboda abbreviata* (*A. Ducke, Herb. Amaz. Mus. Para 11895*; *Cavalcante 173*; *Egler 271*).—a. Habit.—b. Leaf apex.—c. Sector of midblade, adaxial view.—d. Leaf base, abaxial side.—e. Spike (right); idealized view of spike base showing basal bract and its lateral sepals (left).—f. Scape bracts.—g. Inner spike bract.—h. Lateral sepals with enclosed ovary and style base.—i. Anthers.—j. Stigma.—k. Seeds, showing size range.—l. Style base with appendages.

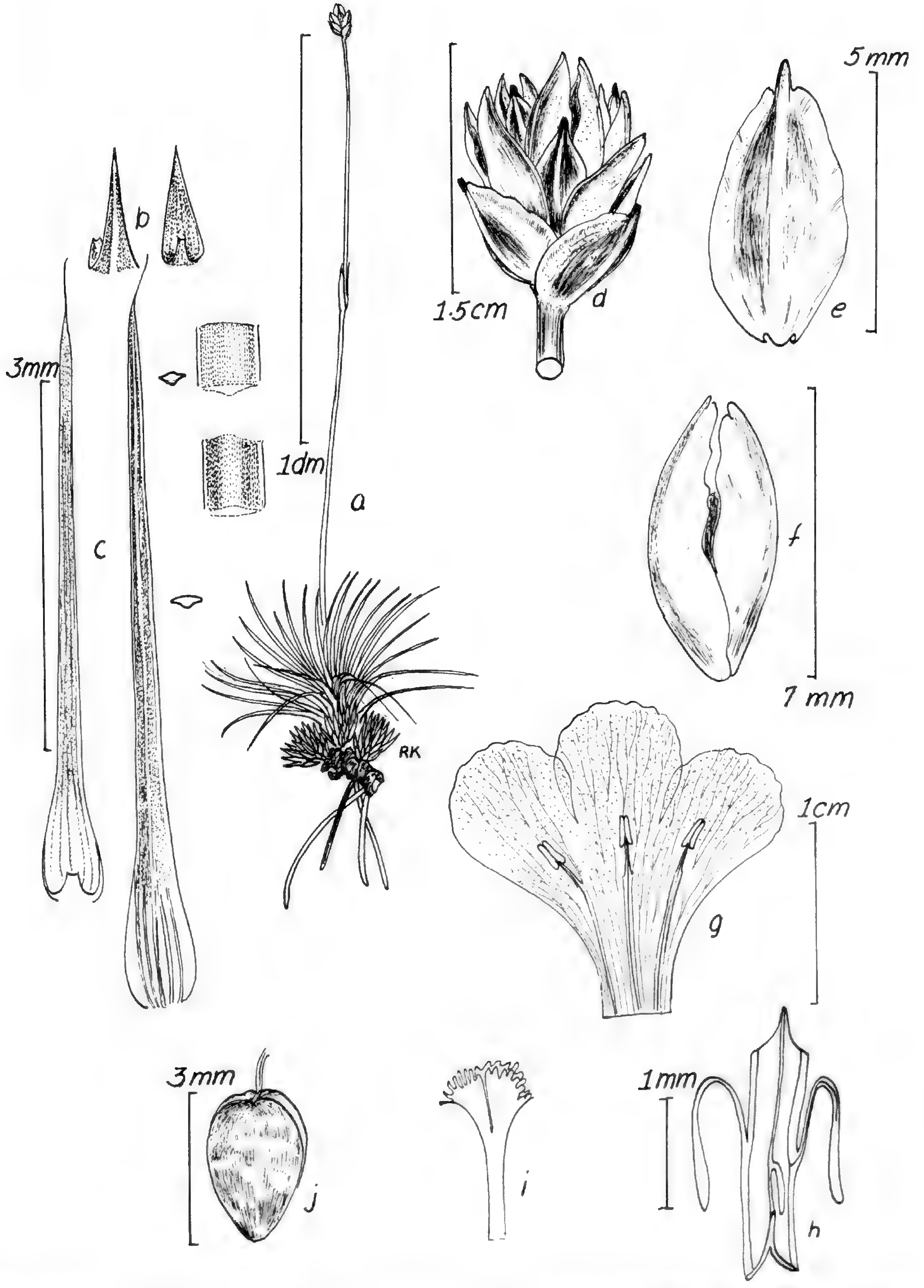

FIGURE 13. *Abolboda egleri* (*W. A. Egler & Raimundo 1271*; *Plowman, Rosa & Rosario 9714*).—a. Habit.—b. Early rosette leaves, adaxial side (left), abaxial side (right).—c. Two secondary rosette leaves, adaxial side (left), abaxial side (right), at far right two short sectors of blade.—d. Spike.—e. Lowest bract.—f. Corresponding sepal pair.—g. Corolla and stamens.—h. Style base and appendages.—i. Stigmatic apex.—j. Capsule.

11. Abolboda egleri Lyman B. Smith & Downs, Proc. Bol. Soc. Washington 73: 258, fig. 10a–b. 1960. TYPE: Brazil. Pará: Alto Tapajos, Rio Cururú, Rio Ereri, on wet sandy places, 8 Jan. 1960, *W. A. Egler & Raimundo 1271* (holotype, US; isotypes, MG, NY). Figure 13.

Caespitose, smooth perennial, the rosettes tufted on stubby branches from a thick, knotty, much-branched rhizome, the roots thickened-spongy. Leaves dimorphic, the initial rosette buds forming closely imbricate, ascending or spreading, narrowly triangular, rigid leaves up to 1.5 cm long, these with subulate, spinulose tips, the abaxial surface with a strong, raised midrib, the adaxial surface flat or slightly convex, faintly few-nerved; later leaves of a rosette abruptly much longer, relatively narrower, (2–)3–5 cm long, the thin base broadly dilated above its narrower clasping attachment, pale, 5-nerved, thence narrowing abruptly to a narrowly linear, gradually tapering, subulate-tipped, silvery-green blade, this apically long-spinulose, the adaxial surface at midblade slightly convex or level and finely few-nerved, the abaxial face strongly and broadly costate medially, the blade toward tip subquadrate or trigonous. Scapes mostly 1 per rosette, terete, gray-green, (7–)10–20(–40) cm long, sheathed at base by 2–3 scarious, setaceous-tipped basal bracts 1–2 cm long, the scape bracts 1 pair, mostly at ca. midscape, erect, subequal, lance-oblong, 8–15 mm long, conduplicate, the convex backs pale green with tints of purple, low-ribbed, with strong, broad, scarious pale borders narrowing to blunt mucros, these sometimes tipped with a short, slender hair; spikes at maturity ellipsoid to narrowly ovoid (or by seeding time obovoid), 1–1.5 cm long, pale, mostly 4-flowered or with an additional pair of undeveloped flowers, all bracts fertile, the lowest pair slightly larger and firmer than the inner ones, broadly ovate, 5–6 mm long, with thickened, convex, green or purple-tinged medial areas bisected by a pale, raised costa, this excurrent as a short, stubby blunt mucro, the border scarious, pale or submarginally with a lilac band, the apex emarginate; sepals 2 per flower, ovate, strongly conduplicate, curvate-lanceolate when viewed from the side, 7–8 mm long, broadly acute or blunt at tip, sometimes mucronulate, the wide keel entire, chartaceous; corolla ca. 12–13 mm long, the obovate lobes shorter than the tube; staminodia not evident; stamens with anthers ca. 1.5–2 mm long, oblong, the thecae slightly divergent below, on filaments ca. 2 mm long; style base strongly alate-triquetrous, the appendages produced ca. 3 mm above the ovary and with the lateral ones filiform-clavate, reflexed, 2 mm long, the central appendage set slightly lower, filamentous, shorter. Unripe fruit obovoid, ca. 3 mm long, the valves strongly bilobed apically, the lobes broadly rounded and thickened. Ripe seed not seen.

Distribution. Wet sandy campos and savanna at 100–450 m, Pará and adjacent Mato Grosso, Brazil.

Additional material examined. BRAZIL. MATO GROSSO: 38 km SE of Pontes and Lacerda, 30 Oct. 1985, *W. Thomas et al. 4683* (INPA, MG, NY, VDB); Serra do Roncador NNE Xavantina, 7 Dec. 1969, *G. & L. Eiten 9800* (NY). PARA: Serro do Cachimbo Corrego São Bento, 21 Feb. 1977, *Kirkbride & Lleras 2973* (NY, US, VDB); 16 km E of Represa Tucri, 18 Mar. 1980, *Plowman et al. 9714* (GH, NY, VDB).

The relationships of this rare species are definitely with *Abolboda pulchella,* which occurs, apparently more frequently, throughout the Amazon Basin and northern planalto of Brazil. *A. egleri* may be distinguished quickly from it mostly by its denser rosette of more strongly tapered, firm, more costate leaves, which have a definite silvery sheen. While no ripe capsules have been found so far, those available show a broader outline and a more umbilicate summit. The stylar appendages are longer and more slender.

12. Abolboda pulchella Humb. & Bonpl., Pl. Aequinoct. 2: 1109, pl. 114. 1813. TYPE: Venezuela. Territorio Federal Amazonas: vicinity "mission de Maypures" by the Río Orinoco, *Alexander von Humboldt* [I have not seen the type, this presumably at P. The excellent figures of habit, leaf, bracts, and flowers, plus the quite detailed description, allow me to suggest these to serve as lectotype. Maguire has annotated a Richard Spruce collection "prope Maypures, ad flumen Orinoco, Junio 1864, *R. Spruce 3651*" as a probable topotype (K, NY). This material agrees satisfactorily with the plate and protologue]. Figure 14.

A. brasiliensis Kunth, Enum. Pl. 4: 26. 1843. TYPE: "Brasilia, *Sellow legit*" (lectotype, BR; isolectotypes, K, L, S).

A. vaginata (Sprengel) Nilsson, K. Sv. Vet.-Akad. Handl. 24(14): 63. 1892. TYPE: Brazil. Goiás: "marsh Lima de Natividade, July 1840," *Gardner 4024* (lectotype, here designated, K; isolectotype, NY).

A. longifolia Malme, Bih. Sv. Vet.-Akad. Handl. 22: (Afd. III, No. 2): 20. pl. 2. 1897. TYPE: Brazil. Mato Grosso: "lugar arenoso-umido, Arica, entre São Jeronimo e Cuiabá, 17 Feb. 1894," *Malme 1402* (lectotype, S; isolectotype, S).

A. gracilis Huber, Bol. Mus. Goeldi Paraense Hist. Nat. Ethnogr. 5: 323. 1909. TYPE: Brazil. Pará: "campos de Ariramba, Rio Trombetas, 22 Dec. 1906," *A. Ducke Hb. no. 8074* (lectotype, MG).

A. pulchella var. *longifolia* (Malme) Lyman B. Smith & Downs, Arq. Bot. Estado São Paulo, nov. ser. 4, fasc. 2: 26. 1966.

Glabrous, solitary or caespitose, slender perennial, perennating by slender rhizomes or by lateral buds from ascending or erect caudices, the roots spongy-thickened. Leaves often dimorphic with "juvenile" rosettes of stubby, triangular-linear, strongly tapering blades, the smallest leaves often scalelike, the largest to 2 cm long, with broad, clasping, scarious-bordered bases, tapering upward to subulate, triquetrous, mostly spinulose-tipped blades; principal (larger) leaves mostly developing later on shoot, highly variable in outline and length, 2–15 cm long, those of the short range mostly recurved and linear-triangular, strongly tapering from broad (to 4 mm wide) clasping bases into stiff, compressed by lingulate blades, these thus strongly convex-backed, the adaxial face smooth or scarcely raised-nerved, the lower (abaxial) side more strongly nerved, the costa raised; in the longer leaf length range, the clasping base narrower, thinner, gradually or abruptly narrowing to narrowly linear, less folded, more often flat blades, both sorts of leaf usually with thin, entire, pale contrasting borders, both with variously thickened, attenuated, usually triquetrous tips, these either subulate or short-conic, sometimes spinulose or with a short, eccentric prickle. Scapes 1–several per rosette, mostly stiffly erect, distally 0.8–1.5 mm thick, terete, less often slightly angled or sulcate, sheathed at base by 2–3 lance-oblong, imbricate, scarious-bordered basal bracts with narrow, strongly nerved, greenish or maroon median areas, the midrib strongest and often long-excurrent or spinulose; scape bracts usually 1 pair, slightly to very unequal, narrowly lance-oblong, 1.5–3 cm long, conduplicate, the convex backs raised-nerved, the costa forming a blunt or subulate, spinulose or eccentrically spinose mucro or cusp; spikes mostly ellipsoid to narrowly obovoid (turbinate), 8–15 mm long, highly variable in pigmentation, from pale yellow-green to deep red-purple or brown-purple, the bracts (2–)4(–6), the lowest usually broader and slightly longer than the inner, all navicular, broadly ovate, 6–11 mm long, with broad, scarious borders and broadly ovate, thickened medial areas, these few-ribbed, the midrib (costa) mostly excurrent as a short, thick cusp, this sometimes with a short eccentric prickle; sepals 2, lateral, lanciform, ca. as long as the subtending bract but slightly elevated above its base, therefore with tips frequently exsert, the sides scarious, the keel firm, curved, entire, excurrent or not as the acute apex; corolla 14–15 mm long, the lobes broadly obovate to ovate, ca. as long as the tube, light blue-violet; staminodia not evident; anthers deeply emarginate and sagittate, oblong, 2–2.5 mm long on flattened filaments 2–3 mm long; style base narrow, sharply triquetrous, with 2 reflexed, broadly short-clavate lateral appendages and a low, auriclelike median appendage, all ca. 2–3 mm above ovary tip, the laterals each with an upswept short-oblong auricle at its base; style apex 3-branched, each branch apically broadly dilated and fimbriate-papillate. Capsule broadly ellipsoid or short-cylindric, ca. 4 mm long, rather uniformly firm-valved, apically umbilicate, each valve with 2 low lobes. Seeds nearly black, variously angled, mostly broadly obovoid, 0.5–0.6 mm long, coarsely irregularly thick-ribbed longitudinally, the intervals paler, broad, nearly smooth.

Distribution. Moist to wet sandy peats, clays or silts, mostly fine-textured substrate, in grass-sedge campos, 25–1,600 m, from French Guiana west to the low savannas of southeastern Colombia, southward through Amazonian Brazil to Minas Gerais and São Paulo.

Additional material examined (a selection to represent geographical and morphological range). BRAZIL. AMAZONAS: Transamazonica, Pedra Caida, 13 Apr. 1983, *N. A. Rosa et al. 1062* (MG, NY, VDB); Rio Branco, 1909, *Ule 7762* (K). BAHIA: Serra do Rio Contas, 21 Mar. 1977, *Harley 19785* (NY, US). DISTRITO FEDERAL: Brasilia, dez. 1961, *Cobra & Belem 106-61* (NY, UB). GOIAS: 16–17 km N Alto Paraiso, 8 Mar. 1973, *W. R. Anderson 6637* (F, K, MO, NY, U, US); Morro do Redondo, 7 Aug. 1895, *Glaziou 22284* (K, US); 7 km W of Veadeiros, 15 Feb. 1966, *Irwin et al. 12907* (F, GH, MO, US, VDB); Alto do Paraiso, 21 Mar. 1971, *Irwin et al. 32870* (F, K, NY, US, VDB); Jataí to Goiania, 1 Oct. 1963, *Maguire et al. 57001* (F, US). MATO GROSSO: Salgareira Bridge, Cuiabá, *Antonia & Assumcao 1456* (NY, this the "brasiliensis" morph); Serra do Roncador, NNE Xavantina, 6 Oct. 1968, *G. & L. Eiten 9140* (NY, UB); Santa Fe, Sidrolandia, 23 Jan. 1970, *Hatschbach 26047* (US); Rio Langrador, *Lindman A. 2421* (MO); Xavantina–Cachímbo Rd., *D. Philcox et al. 3432* (K). MINAS GERAIS: 35 km SW Gouveia, *Anderson et al. 35089* (MO, US); Carandai-Brejão, *Duarte 682* (US); Bom Successo, *M. Barreto 9659* (F); 5 km de Itacambira, *Kawasaki et al. 6608* (K). PARA: Alto Tapajos, Rio Cururu, Anderson 10963 (F, MO, NY, US); campos do Ariramba, *Ducke, Herb. no. 11454* (US); Ilha do Marajo, *R. Lima 42* (US). RORAIMA: Rio Branco, *Maguire 40118* (K). GUYANA. St. Ignatius, *R. Goodland 335* (NY); Ite Swamp, *Goodland 884* (NY); Nuinatta, Rupununi River, *Jenman 5720* (K); Palaime Savanna, *J. G. Wessels Boer 801* (NY, U). SURINAM. Gros-savanna (prope km 103, *J. van Donselaar 722* (U); Sipaliwini Savanna, *Oldenburger et al. 959* (U). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Río Orinoco 2 km rio arriba de Macuruco, *Berry 792* (MO); Puerto Ayacucho to El Burro, *Davidse & Huber 14520* (MO, US); sabanas de Santa Barbara, *Huber &*

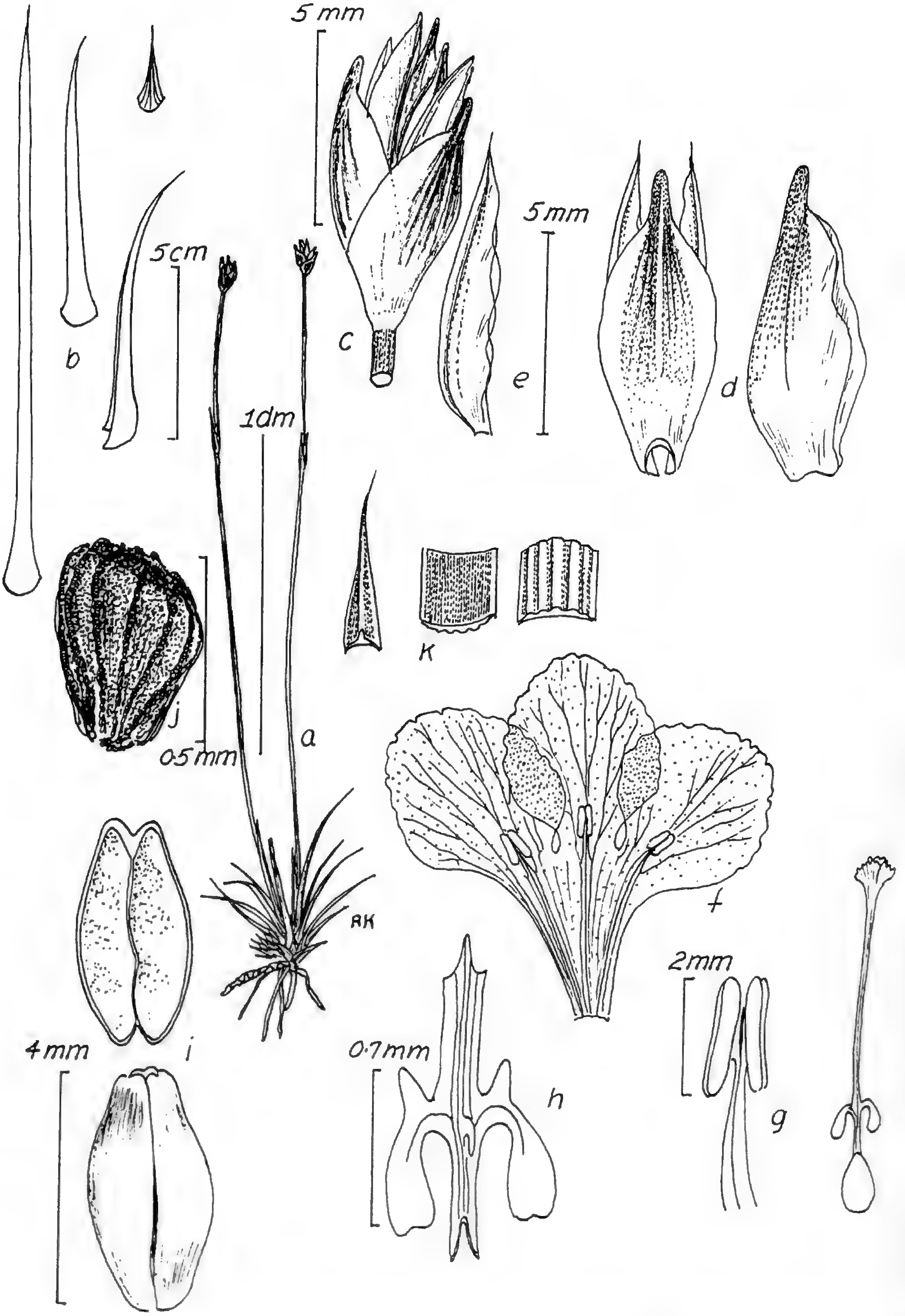

FIGURE 14. *Abolboda pulchella* (*Irwin, Harley & Smith 32870; Kral & Huber 70731*).—a. Habit.—b. Various leaf outlines.—c. Spike.—d. Fertile bract, external view (left), side view (right).—e. Lateral sepal.—f. Spread corolla, stamens.—g. Stamen (left); gynoecium (right).—h. Stylar base with appendages.—i. Capsule (below), inner view of valve (above).—j. Seed.—k. One type of leaf apex, abaxial side (left); two midblade sectors, adaxial side (center), abaxial side (right).

Tillett 5390 (US, VEN); bajo Río Ventuari, *Huber 1958* (MO, NY, U, US); 30 km N Puerto Ayacucho, *Huber 3806* (K, MYF, NY, VDB); 5 km NE Galipero, *Kral & Huber 70731* (MO, VEN, VDB); Orinoco 10 km above mouth of Río Ventuari, *Wurdack & Adderley 43688* (GH, US). ANZOATEGUI: Cienaga del morichal del Tigrito, *Pittier 15080* (US). BOLIVAR: 8–10 km SSE Yuruani, *Huber & Febres 9181* (MYF, VDB); 3 km SW Peraytepui, *Huber & Alarcon 9689* (MYF, NY, VDB, VEN); Salto Aponguao, *Kral & Gonzalez 7041* (GH, MO, NY, US, VDB, VEN); Ruemeru, S of Mt. Roraima, *Steyermark 59178* (F, K, NY, US); Urimán, *Steyermark 75244* (NY); Agua Amena, *Steyermark et al. 131437* (MO, VDB, VEN); between Ciudad Piar and S base of Cerro Bolívar, *Wurdack 35751* (NY).

This is, along with *Abolboda americana*, the widest-ranging and most morphologically variable of the abolbodas; thus it is not suprising that the synonymy is so elaborate. In the Brazilian planalto *A. pulchella* is a common associate of *A. poarchon*, though where the two share the same wet campo *A. pulchella* tends to be lower, usually more slender, with narrower, thinner, more tapering leaves, narrower scapes, smaller and fewer-flowered spikes, and more slender rhizomes. Typically, the flowers of *A. pulchella*, while of about the same size and color, are open sooner in the day. Some recently described variations, such as the variety *longifolia* (Malme) Lyman B. Smith & Downs, have leaves and scapes in the long range of the above description, but with bracts similar to those in the type variety. However, such elongate-leaved extremes might be seasonal and moisture expressions, in that the same variation can be found to the north of the described Brazilian range (Pará, Mato Grosso). The variety of *intermedia* Lyman B. Smith & Downs, understood by them to be a variant with a larger number of flowers per spike and with spike bracts bristle-tipped, appears to me to be a part of *A. poarchon*.

13. **Abolboda scabrida** Kral, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Río Negro, Cerro Aracamuni, summit, Proa Camp, medium height, semi-open forest, 28 Oct. 1987, *R. Liesner & G. Carnevali 22598* (holotype, VEN; isotypes, MO, VDB). Figure 15.

Herba perennis densicaespitosa, praeter inflorescentiam et bases scabrida et scabrido-rugosa. Radices spongiosae. Caules breves, ascendentes, usque ad 2–3 cm longi, per bases persistentes veternas foliorum obtecti. Folia extima rosularum pro parte maxima vaginalia, anguste triangulata; folia principalia erecta vel expansa, leviter excurvata, 3–6 cm longa, ad basim dilatata, ca. 5-costata, sursum abrupte contracta, 2–3-costata; laminae 0.5–1 mm latae, pallide virides, leviter compressae, transversim irregulariter rugosae et tuberculatae; apices gradatim vel abrupte contracti, incrassati, ad apicem obtusati vel excurvato-mucronati; margo leviter vel valde incrassata, scabra; paginae superiores planae aut leviter convexae, inferiores concavae vel planae aut prominente 2–3-costatae. Scapi solitarii, scabrosi, 6–10 cm alti, 0.5–0.7 mm lati, ad basim leviter compressi vel tricostati et sulcati, ad apicem teretes. Vaginae scaporum erectae, linearo-lanceolatae, subulatae, convexae, leviter striatae, inaequales, 2-jugatae, pari infimo basali, pari supero ca. ⅔ distanti a basi scaporum, vaginis exteriores 1–1.5 cm longis, longitudine ¾–⅘ interiores aequantibus. Spica anguste turbinata, 1.1–1.4 cm longa, pauciflora (flores praeter 4); bracteae 2-jugatae, subdecussatae, lanceolatae, incrassato-subulatae, 1–1.4 cm longae, convexae, a medio ad apicem carinatae, scabridulae, ad apicem obtusae, mediane virides, late scariomarginatae. Sepala 2, lateralia, subopposita, lanceolata, inequilateralia, ca. 1 cm longa, curvata, anguste acuta, a medio ad apicem acute carinata scabridula. Corolla azurea, ca. 1 cm longa. Staminodia bibrachiata, brachiis planis, anguste oblongis, ca. 1 mm longis. Antherae oblongae, ca. 1 mm longae; filamenta ca. 1.5 mm longa. Appendices stylorum 3, recurvatae, clavatae, 1-redactae. Capsula obovoidea, ca. 2.5 mm longa, obscure trilobata, valvis ad apicem inflexis et erosis. Semina late asymmetrice obovoidea, ca. 0.5 mm longa, longitudine valde 12–14-costata, anthracina.

Perennial, densely caespitose herbs, all but the bases and inflorescence scabrid and scabrid-rugose. Roots spongy. Stems short, ascending up to 2–3 cm long, the bases covered by old leaves. Outer leaves of a rosette for the most part sheath, narrowly triangular; principal foliage leaves erect to spreading, slightly recurved, 3–6 cm long, dilated at base, ca. 5-costate, then above abruptly contracted, 2–3-costate; blades 0.5–1 mm wide, pale green, somewhat compressed, transversely irregularly rugose and tuberculate; apices gradually to abruptly narrowed, thickened, at tip obtuse or excurved-mucronate; margin slightly to very thickened, scabrid; upper surface flat to somewhat convex, the lower surface concave to flat or prominently 2–3-costate. Scape solitary, scabrous, 6–10 cm high, 0.5–0.7 mm wide, at base somewhat compressed to tricostate and sulcate, toward apex terete. Scape bracts erect, linear-lanceolate, subulate, convex, slightly striate, unequal, in 2 pairs, the lower pair basal, the upper pair ca. ⅔ way up from scape base, the lower ones 1–1.5 cm long, ¾–⅘ as long as the upper. Spike narrowly turbinate, 1.1–1.4 cm long, few-flowered (flowers usually 4); bracts 2 pairs, subdecussate, lanceolate, thickened-subulate, 1–1.4 cm long, convex, from middle to tip carinate, scabridulous, at tip obtuse, medially green with margins broadly scarious-bordered. Sepals 2, lateral, subopposite, lanceolate, inequilateral, ca. 1 cm long, curvate, narrowly acute, from middle to tip sharply and scabridulously carinate. Corolla blue, ca. 1 cm long. Staminodia bibrachiate, the branches flat, narrowly oblong, ca. 1 mm long.

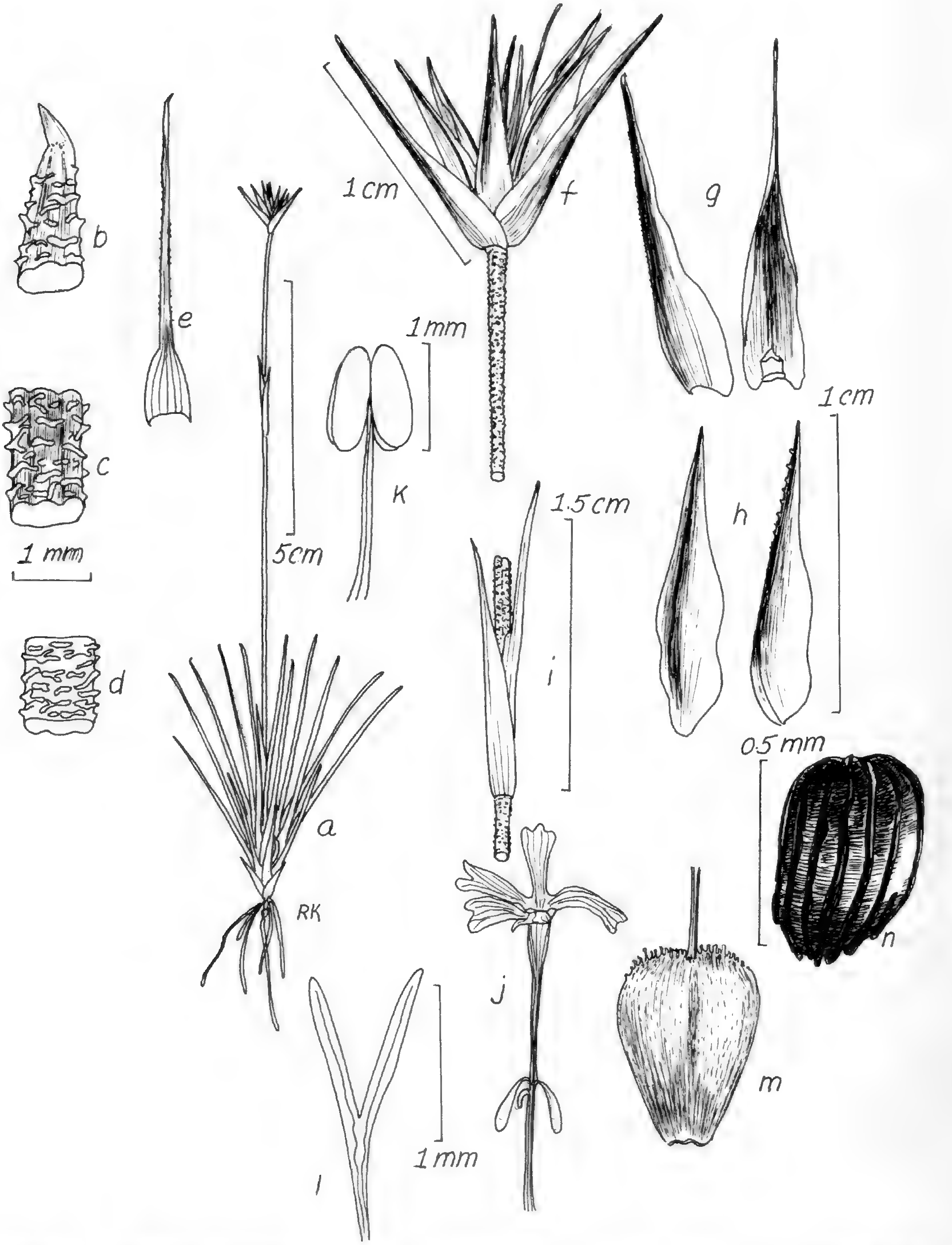

FIGURE 15. *Abolboda scabrida* (*Liesner & Carnevali 22598*).—a. Habit.—b. Leaf tip.—c. Sector of leaf blade, abaxial side.—d. Sector of leaf blade, adaxial side.—e. Leaf.—f. Spike and upper scape.—g. Outer spike bract, side view (left), adaxial view (right).—h. Lateral sepal, abaxial side (left), side view (right).—i. Scape bract pair, side view.—j. Style, showing appendages and stigma.—k. Stamen.—l. Staminode.—m. Capsule and style base.—n. Seed.

Anthers oblong, ca. 1 mm long; filaments ca. 1.5 mm long. Stylar appendages 3, reflexed, claviform, 1 appendage reduced. Capsule obovoid, ca. 2.5 mm long, obscurely trilobed, the valves at apex inflexed and erose. Seeds broadly asymmetrically obovoid, ca. 0.5 mm long, longitudinally strongly 12–14-ribbed, coal black.

Distribution. Known only from the type.

Abolboda scabrida is closely related to *A. acic-*

ularis Idrobo & Lyman B. Smith, particularly to the variety *granularis* Maguire, but foliage and scapes are rugose and scabrid (rather than smooth or granular), petals are blue (rather than white), the staminodial character is unique, and the seeds are smaller.

14. Abolboda dunstervillei Maguire ex Kral, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: summit of Cerro Avispa, Río Siapa, 1°30′N, 65°51′W, 1,510 m, 5 Dec. 1972, *G.C.K. & E. Dunsterville s.n.* (holotype, NY). Figure 16.

Planta perennis, dense rosulata, densicaespitosa; radices graciles; caules breves. Folia principalia erecta vel leviter expansa, rigida, 2–4 cm longa, pallide viridia, glabra, aut ad basim et apicem versus leviter papilloso-rugulosa; vaginae scariosae, ad basim 2.5–3.5 mm latae, 5-costatae, sursum gradatim contractae; laminae vaginis 2–3-plo longiores, anguste lineares, 9–10 cm altae, rectae, teretes, 0.7–0.8 mm crassae, ecostatae, transversim tuberculato-rugosae; bractae scaporum 1-jugae, ad circum medium scaporum involutae, oblongo-lanceolatae, leviter impares, bracteis extimis valde convexis, viridibus, margine late scariosis, acutis, mucronatis, leviter imparibus, bractea extima 9–10 mm longa, bractea intima 12–14 mm longa. Spicae turbinatae, circa 1 cm longae, 4–5-florae, si 5-florae hoc detactae; bracteae 4–5, lanceolatae, convexae, virides, margine late scariosae, a medio ad apicem carinatae, subulatae, ad apicem excentrice mucronatae, usae, duabas extimis 9–10 mm longis, ceteris aequantibus vel parum longioribus. Sepala 2, leviter inequilateralia, navicularia, 6.5–8 mm longa, acuta, valde unicostata, costis breviter excurrentibus. Corolla, stamina et apex stylorum non visa. Appendices stylorum 2, clavatae, pendulae, ca. 1 mm longae. Capsula obovoidea 2.3 mm longa, valvis ad apicem incrassatis, obtusis vel leviter emarginatis, tuberculato-papillosis. Semina late obovata, ca. 0.5 mm crassa, atroferruginea, longitudine spiraliter 12–14-costata.

Plants perennial, densely rosulate, densely caespitose; roots slender; stems short. Principal leaves erect to slightly spreading, rigid, 2–4 cm long, pale green, smooth or slightly papillose-rugulose at base and toward apex; sheaths scarious, at base 2.5–3.5 mm wide, 5-costate, gradually narrowing upward; blades 2–3 times longer than the sheaths, narrowly linear, 0.4–0.7 mm wide, for the most part straight, compressed, triplinerved, toward the tip thickened, at tip obtuse, eccentrically mucronate. Scapes linear, 9–10 cm high, straight, terete, 0.7–0.8 mm thick, ecostate, transversely tubercular-rugose; scape bracts 1 pair, toward midscape involute, lance-oblong, slightly unequal, the outer one 9–10 mm long, the inner 12–14 mm long. Spikes turbinate, ca. 1 cm long, 4–5-flowered, fifth flower, if present, reduced; bracts 4–5, lanceolate, convex, green with broad scarious margins, carinate from middle to tip, subulate, at tip eccentrically mucronate, blunt, the outer two 9–10 mm long, equaling the rest or a little longer. Sepals 2, slightly inequilateral, navicular, oblong-elliptic, 6.5–8 mm long, acute, strongly but narrowly unicostate, the sides thin, the costa entire, short-excurrent. Corolla, stamens, and apex of style not seen. Stylar appendages 2, clavate, reflexed, ca. 1 mm long. Capsule obovoid, 2.3 mm long, the valves apically thickened, obtuse or slightly emarginate, tuberculate-papillate. Seeds broadly obovoid, ca. 0.5 mm thick, dark red-brown, longitudinally spirally 12–14-costate.

This plant, thus far known only from the type, is closest taxonomically to the varieties of *Abolboda acicularis* and to *A. scabrida* Kral. From the former it is distinguished by its uniform leaves, which are flatter and have blunter, uniformly eccentrically mucronate tips, and by the coarser indument of scape. From the latter it is distinguished by its smoother, flatter leaf blades and by its smooth, rather than granular-papillate, bract costas and sepal keels.

15. Abolboda acicularis Idrobo & Lyman B. Smith, Caldasia 6: 250. 1954. TYPE: Colombia. Vaupés: terrestrial herb, savanna de Yapoboda, Alto Río Cuduyari, 10 Dec. 1943, *P. H. Allen 3150* (holotype, COL; isotypes, NY, US).

15a. Abolboda acicularis var. **acicularis**. Figure 17.

Tufted glabrous perennial, or rosettes solitary, the stems short or slightly elongate, in either case invested by chaffy remnants of old rosette leaves, the roots spongy-thickened. Initial rosette leaves (including those of new shoots) short, linear-subulate, mostly 1 cm long or less, straight or curved outward, stiff, bases broad, pale, thin, clasping, triplinerved, broadly scarious-margined, abruptly narrowed to linear-triangular, thickened blades, these subulate-tipped or with short prickles, pale to deep green, the adaxial face plane or lingulate with pale hyaline, narrow border, the abaxial side convex, usually strongly pale-costate medially, these initial leaves sometimes passing directly to basal scape bracts but more often abruptly changing to spirals of longer rosette leaves, these 1.5–3(–5) cm long, with narrower, shorter bases in relation to the longer, more evenly linear, mostly recurved blades 0.3–0.5 mm broad, these eccentrically mucronate, mucronulate or short-setaceous-subulate, thickened, mostly plane or lingulate adaxially, convex and commonly costate medially, in cross section triangular. Scapes 1–few per rosette, erect or

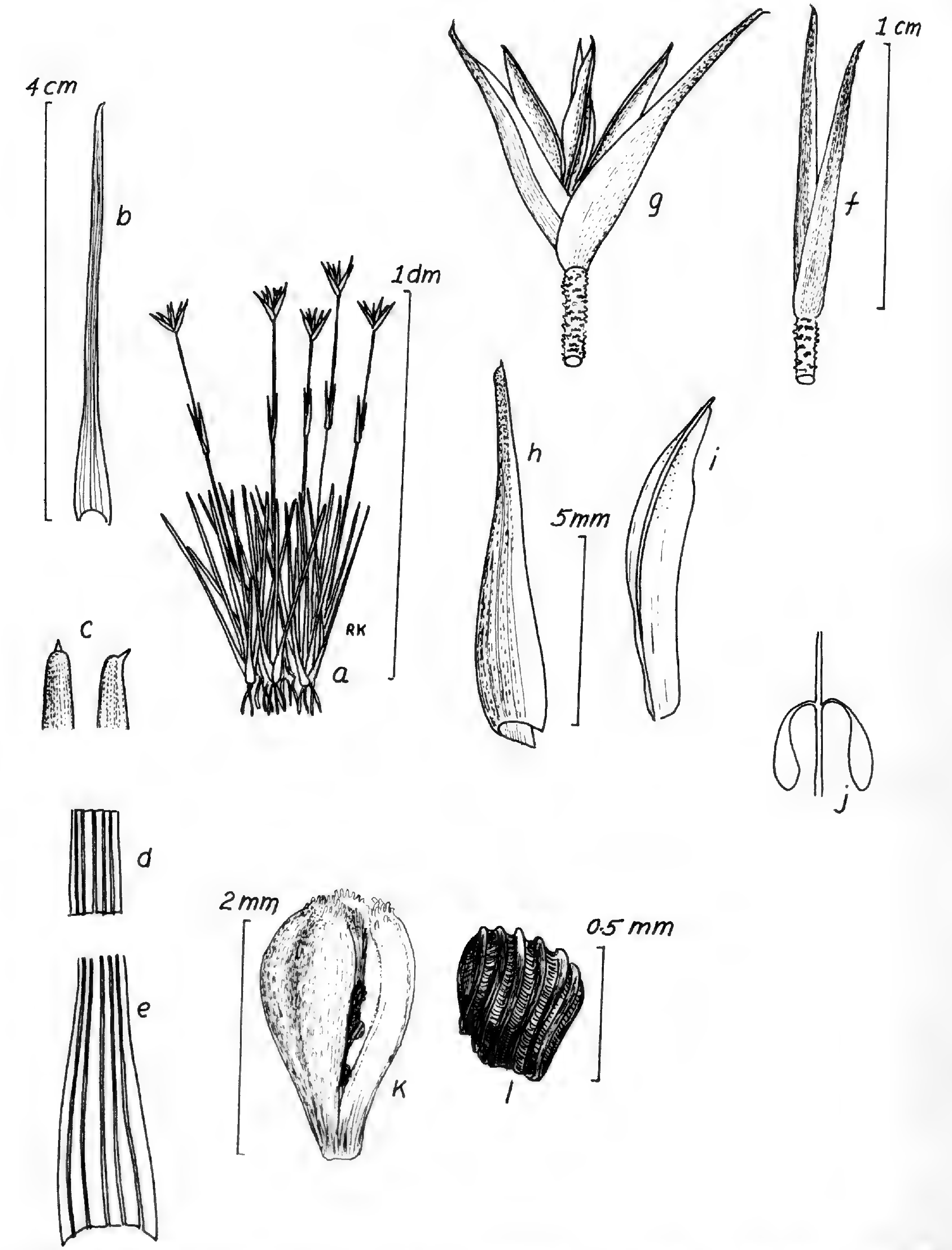

FIGURE 16. *Abolboda dunstervillei* (*C. C. K. & E. Dunsterville s.n.*).—a. Habit.—b. Leaf.—c. Adaxial (left) and side (right) views of leaf tip.—d. Sector of midblade, abaxial side.—e. Leaf base, abaxial side.—f. Scape bracts.—g. Spike.—h. Side view of basal bract of spike.—i. Lateral sepal.—j. Stylar appendages.—k. Capsule.—l. Seed.

ascending, terete, (7–)10–30 cm long, pale green, smooth or papillose, sometimes longitudinally striate, the bracts unequal, those at scape base usually 3–4, conduplicate-clasping, imbricate-spiral, linear, unequal, the innermost longest, 2–3 cm long, stramineous, with broad scarious borders and narrow firm costae, these tapering to subulate-setaceous tips; scape bracts rarely lacking, mostly 1

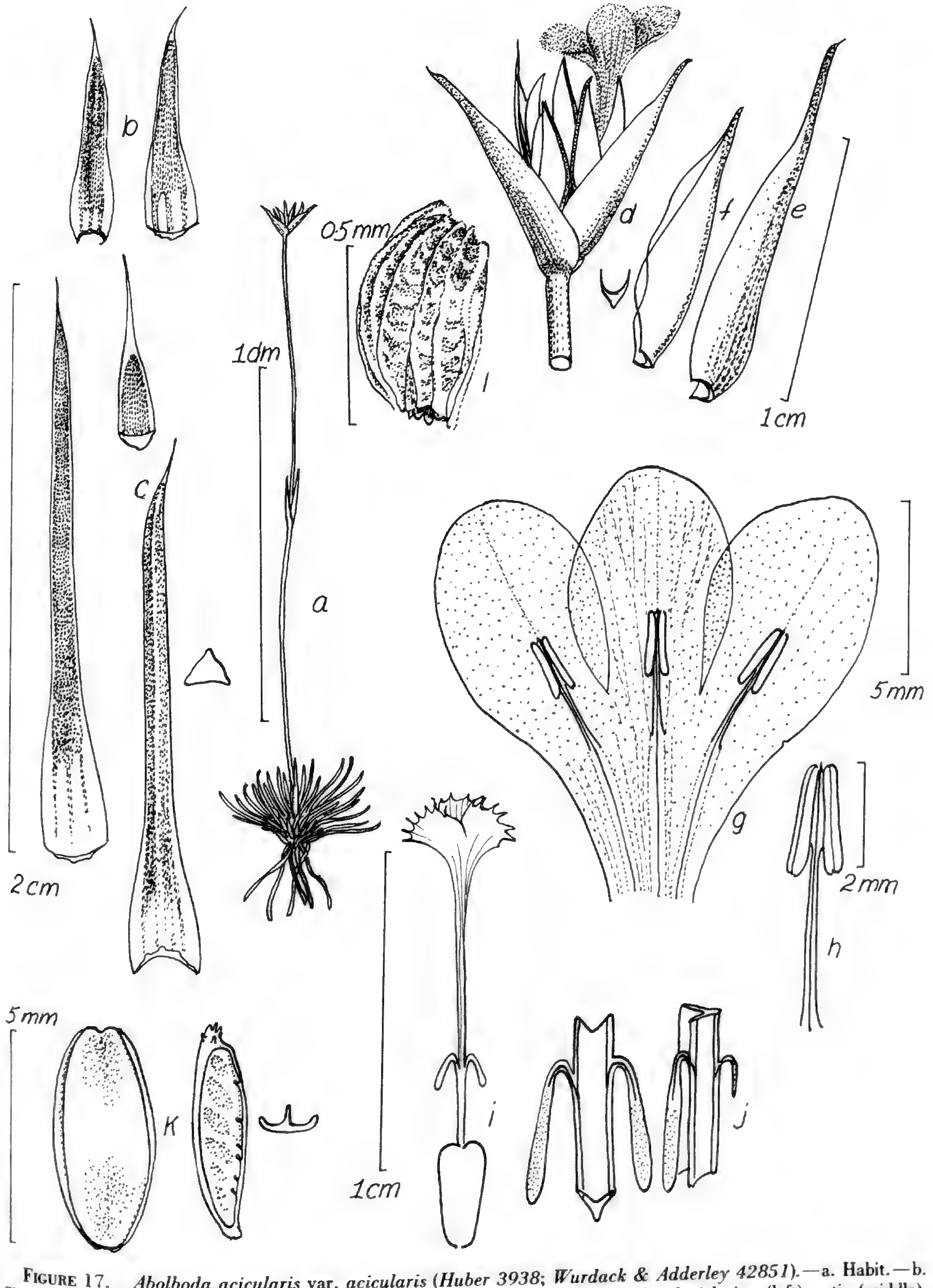

FIGURE 17. *Abolboda acicularis* var. *acicularis* (*Huber 3938*; *Wurdack & Adderley 42851*).—a. Habit.—b. Short rosette leaf, abaxial view (left), adaxial view (right).—c. Long rosette leaf, adaxial view (left), a tip (middle), abaxial view (right).—d. Spike.—e. Lowest spike bract.—f. Lateral sepal.—g. Spread corolla with stamens.—h. Stamen.—i. Gynoecium.—j. Enlarged style base showing lateral appendages (left), a side view showing reduced appendage (right).—k. Capsule (left), a side view of a valve (right).—l. Seed.

pair, subequal, subopposite, lance-linear, 1.5–2 cm long, conduplicate, erect, the bases with broad, pale, scarious borders, the medial zone thick, convex, mostly 3-ribbed, the costae convergent above to a prominent, cusplike, thickened, linear, often triangular apex, this ending in an eccentric-subulate-spinulose tip or a bristle-mucro; spikes pale green, broadly turbinate, 1–1.5 cm long, 1(–3)-flowered; spike bracts all fertile, longer than the sepals, loosely spirally set, the lowest slightly longer, 9–14 mm long, oblong-lanciform, all navicular, with thickened, convex, pale green, low-nerved medial areas and at base broadly pale-scarious-bordered, toward apex convergent to a thickened-linear, trigonous, apiculate to short-spinulose tip; inner sepal usually lacking, if present oblanceolate, ecarinate, apically narrowly rounded and scarious, shorter than the laterals; lateral sepals subequal, lanciform and navicular, 7–9 mm long, curvate-keeled, scarious and pale except along the thickened, entire keel; corolla 15–17 mm long, near white (cream), the spreading lobes broadly ovate, apically rounded, entire; staminodia apparently lacking; anthers lance-oblong, ca. 2 mm long, shorter than the filaments, the connective widest at base, apiculate at apex; style 8–10 mm long, the base triquetrous, producing 3 reflexed appendages at ca. 3 mm above base, the laterals narrowly claviform, the median one filamentous or very narrowly clavate. Capsule ellipsoid-cylindric, ca. 5 mm long, the valves thickened, particularly at apex, there slightly emarginate, sparsely tuberculate-papillose. Seeds wedge-shaped or eccentrically oblong, 6–9 mm long, longitudinally irregularly-and-sinuously-ribbed, some ribs narrowly hyaline-alate, the ribs connected transversely by many low, indistinct, rounded ridges.

Distribution. Infrequent at low elevations (100–150 m), white sand savanna, Territorio Federal Amazonas, Venezuela, west to southeastern Colombia (Amazonas, Vaupés).

Additional specimens examined. COLOMBIA. VAUPÉS: 1 km W Cacagual, *Maguire et al. 36288* (NY, US); Cacagual Savanna, Río Atabapo, *Maguire et al. 42435* (GH, K, US); Río Paraná-Píchuna, *Schultes & Cabrera 19966* (GH, US); Mitu, *Zarucchi 1354* (GH, US). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: cerro Yapacana–caño Yagua, *Huber 2518* (NY); sabanas de Curital, *Huber et al. 3677* (NY); Río Guayapo, *Huber 3838* (MYF, NY, VDB); sabana NE Caño Canamé, *Huber 4050* (NY); SE Cerro Cucurito, *Huber 6236* (MYF, NY, VDB); Cacagual savanna, Río Atabapo, *Maguire et al. 42435* (F, NY); Sabana Canamé, Caño Canamé, *Wurdack & Adderley 42851* (GH, NY). BOLIVAR: 3 km SW Peraytepui, *Huber & Alarcon 9689* (NY).

15b. Abolboda acicularis var. **granularis** Maguire, Mem. New York Bot. Gard. 10: 18. TYPE: Venezuela. Territorio Federal Amazonas: Sabana Venado, left banks Caño Pimichín above Puerto Pimichín, Río Guainia, above Puerto Pimichín, 140 m, 23 Nov. 1953, *Maguire, Wurdack & Bunting 36341* (holotype, NY; isotype, US). Figure 18.

Low, stiff, rosulate, short-lived perennial, the stems short, tufted, the roots spongy-thickened. Leaves fairly uniform, erect to ascending or (commonly) spreading-recurved, the principal ones (excluding juvenile or new shoots) 1–3(–5) cm long, tapering from broadened, spongy-dilated, 5-nerved clasping bases, gradually to fairly abruptly tapering into linear, thickened blades, these pale green or olivaceous, variously papillate or low-tuberculate, their tips eccentrically acute-mucronate or mucronulate, the adaxial side lingulate to level or slightly convex, thickened toward margin, the abaxial side with a strongly raised median costa and thickened borders, in cross section subtriquetrous, the angles rounded. Scapes stiff, terete, low-fluted, papillate to nearly smooth, 3–12 cm high, sheathed at base by 2–3, lance-linear, scarious-bordered, strongly carinate-costate basal bracts to 1 cm long, their tips subulate; scape bracts 1 pair (rarely lacking), subequal, lance-linear, 5–13 mm long, erect, costate and tipped as in basal bracts, located ⅓–⅔ the scape length from the base; spikes solitary or 2, the lower one on a narrowly ascending branch 1.5–3 cm long from the axil of a scape bract, all spikes turbinate, to 1 cm long, 2–4-flowered, the uppermost flower usually reduced; bracts lanceolate, the lowest slightly longer, ca. 1 cm long, all conduplicate, clasping-based, scarious-bordered, with thickened, pale green, convex, indistinctly 5-nerved dorsal areas, and narrowed above to a thickened, subtriquetrous, cuspidate tip as in leaves; sepals 2, rarely 3, the inner (if present) shortest, oblanceolate, ecarinate, to 5 mm long, distally scarious, rounded, the laterals unequal, 6–7 mm long, lanceolate, navicular, sharply acute, scarious except for the thickened, strong, pale green, smooth, keeled midzone; corolla white or near white, ca. 15 mm long, the spreading lobes broadly ovate, rounded, staminodia none or 1, arising low in the corolla tube, narrowly filiform with a clavate, incurved apex; anthers ca. 1 mm long, the oblong thecae divaricate at base by dilated connective, the filaments ca. 1 mm long; style base triquetrous-alate, the appendages arising at its base, erect, clavate, ca. 1 mm long, the lateral one reduced, short-linear, the stylar apex infundibular and la-

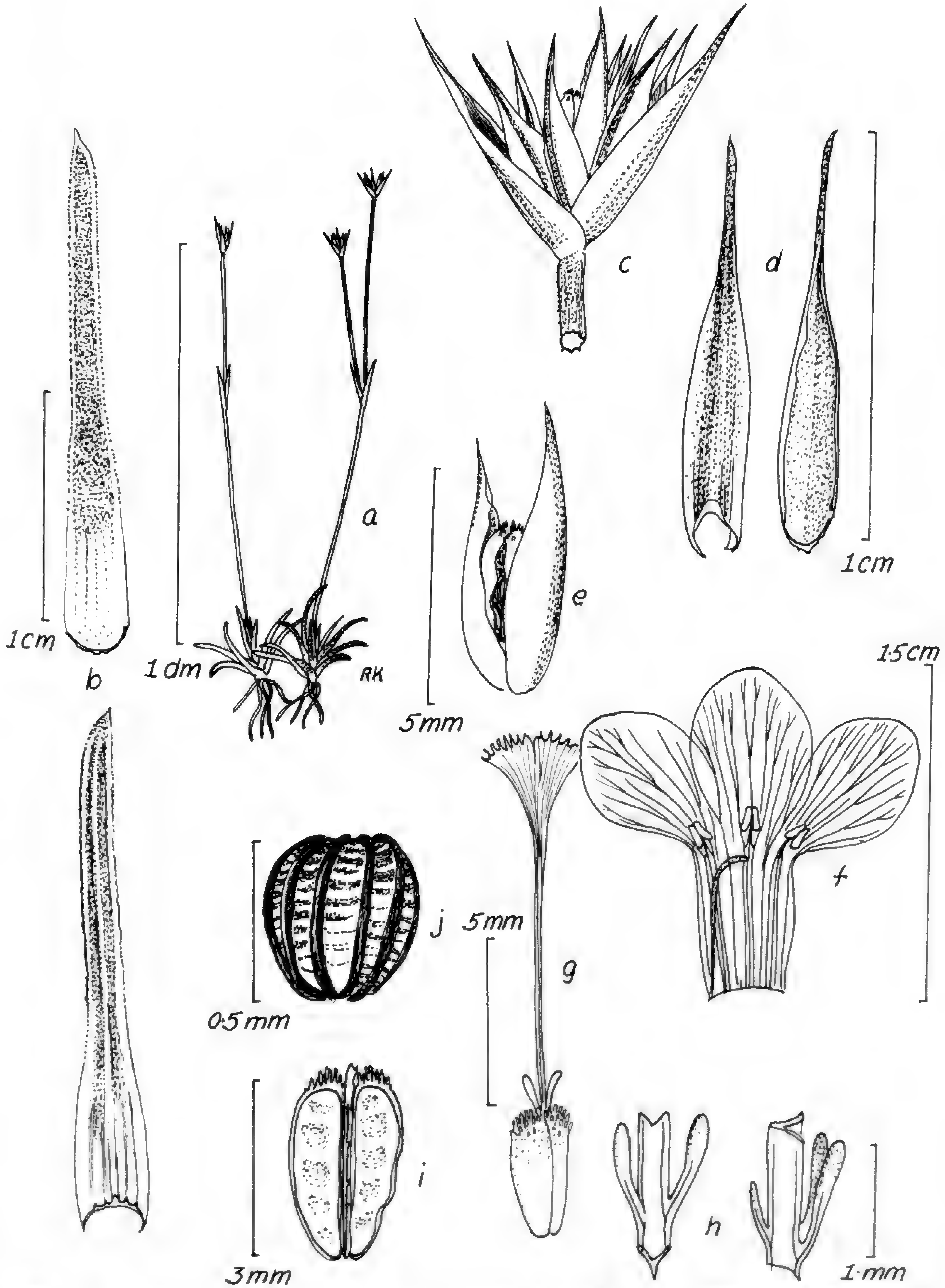

FIGURE 18. *Abolboda acicularis* var. *granularis* (*Steyermark, Berry & Delascio 130352*; *Wurdack & Adderley 43295*).—a. Habit.—b. Adaxial view of leaf (above), abaxial view of leaf (below).—c. Spike.—d. Abaxial view (left) and adaxial view (right) of spike bract.—e. Lateral sepals and capsule.—f. Spread corolla, stamens.—g. Gynoecium.—h. Two views of stylar base.—i. Capsule opened so as to show inner view of columella, septa of 2 locules.—j. Seed.

ciniate-fimbriate; ovary apex thickened, crested with tubercles and papillae. Capsule oblong-obovoid, 3–3.5 mm long, the valves very thickened at the tuberculate, incurved tips. Seeds subglobose or asymmetrically broadly obovoid, ca. 0.5 mm long, coarsely longitudinally 10–11-ribbed, the intervals finely transversely corrugated.

Distribution. Infrequent in low-elevation (100–400 m) white sand savanna, from Territorio Federal Amazonas in Venezuela westward into Vaupés, Colombia.

Additional specimens examined. COLOMBIA. VAUPÉS: Puerto Inirida, *Garcia-Barriga 20.824* (US); Araracuara, *Maguire & A. Fernandez P. 44126* (GH, NY, US); Cerro Yapoboda, *Schultes & Cabrera 14381* (NY, US); Araracuara, *Duivenvoorden 213* (VDB). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Santa Cruz, *Foldats 3685* (NY); Chapezon, laja, *Liesner & Carnevali 22923* (MO, VDB); Sabana Venado, Caño Pimichín, *Maguire & Wurdack 35594* (NY, US); N Cerro Vinilla SSW Ocamo, *Steyermark et al. 130352* (VDB, VEN), *130369* (VDB, VEN); Sabana Venado, Caño Pimichín, *Wurdack & Adderley 43295* (NY, US).

Several differences in character between this and variety *acicularis* can tempt one to distinguish the two as species. Among these characters are, for variety *granularis*, a coarser indument, a different leaf apex, a tendency for the scape to branch, and development of erect, rather than reflexed, stylar appendages from the style base rather than upstyle. However, my studies of the floral characters are as yet too limited for such a decision.

16. Abolboda ciliata Maguire & Wurdack, Mem. New York Bot. Gard. 10: 17, fig. 2. 1958. TYPE: Venezuela. Territorio Federal Amazonas: 5 km W of Cumbre camp, 1,900 m, Cerro de la Neblina, 6 Jan. 1954, *Maguire, Wurdack & Bunting 37132* (holotype, NY; isotype, US). Figure 19.

Densely caespitose perennial, the rosettes from ascending branches to 9 cm long, these densely cloaked by imbricate, chaffy spirals of old leaf bases, the roots spongy-thickened. Leaves fairly uniform in a rosette, the principal ones stiffly ascending to spreading, usually recurved apically, 2.5–10 cm long, their dilated clasping bases thin, to 8 mm broad, broadly scarious-bordered, long-ciliate or fimbriate-lacerate, the backs medially with 7 nerves, narrowing 2–3 cm from base to elongate-linear, stiff blades, these with convex, strongly nerved abaxial surfaces and involute, distantly scabrid or ascending ciliate margins, thickest toward apex, often in cross section triangular or lunate, the tips blunt with 1(–2) eccentric, short, stiff spinules. Scapes stiffly ascending or erect, 19–55 cm long, terete, 1–1.3 mm thick, multicostulate, papillose to scabrid apically and at base enfolded by oblong-elliptic, erect, imbricate bracts to 3 cm long, these with broad, scarious borders, the convex backs apically strongly keeled and costate, the central costa excurrent as a green, blunt-tipped mucro; scape bracts 1 pair, below, at, or just above, midscape, unequal or subequal, erect, strongly conduplicate, oblong-linear, 3.5–5 cm long, the convex backs strongly ribbed, the midcosta excurrent as a strong blunt mucro or cusp, the broad borders pale, scarious, entire; spike solitary and terminal, broadly turbinate, ca. 1.5 cm long, 4–5(–6)-flowered, all bracts fertile, lanciform, navicular, the lowest ca. 1.5 cm long, the ones above progressively slightly shorter, all with chaffy, broad, pale borders and medially thickened, their convex backs green or maroon, multiribbed, apically with strong, scaberulous, thickened, blunt-tipped cusps; sepals 2, navicular-curvate, 8–10 mm long, medially thickened, the keel narrow but firm, entire or papillate; corolla 12–13 mm long, the obovate lobes blue-violet, slightly shorter than the tube; staminodia 2–3, filiform-clavate; stamens with anthers ca. 1 mm long, the thecae with divaricate bases and longer than the short, flat filaments; gynoecium 8–9 mm long, the style base flattened, with 2 recurved appendages 2–3 mm above base, the 3rd appendage not evident. Capsule 4–5 mm long, broadly ellipsoid, the valves much thickened apically, with a dense crest of papillae and tubercle. Seeds few per locule, asymmetrically short-cylindric or wedge-shaped, 1 mm long, dark brown to nearly black with 20–22 strong, narrow, strongly papillate ribs.

Distribution. Frequent in high (1,900–2,200 m) boggy-rocky meadows and clearings in shrub, so far known only from along the summits of the Neblina Massif in Territorio Federal Amazonas and (presumably) bordering Brazil.

Additional material examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Neblina 2.5–3.5 km NE Pico Phelps, *V. A. Funk 6261* (US, VDB); Vale de Titírico N of Pico Phelps, *Kral & Brewer-Carias 71916* (F, MO, NY, US, VDB, VEN); Neblina, 4–6 km NE Cumbre Camp, *Maguire & Wurdack 42145* (F, K, NY), *42390* (NY, US), *42420* (NY); Neblina, ridge, Brazil–Venezuela border, *Plowman & Thomas 13592* (F, NY, VDB); Headwaters Canón Grande, Neblina, *Steyermark 104017* (NY); Neblina, *Steyermark & Luteyn 129826* (MO, VDB, VEN).

This distinctive species may occur with *Abolboda neblinae* or *A. paniculata*, but its morphological affinities are with taxa of lower elevations,

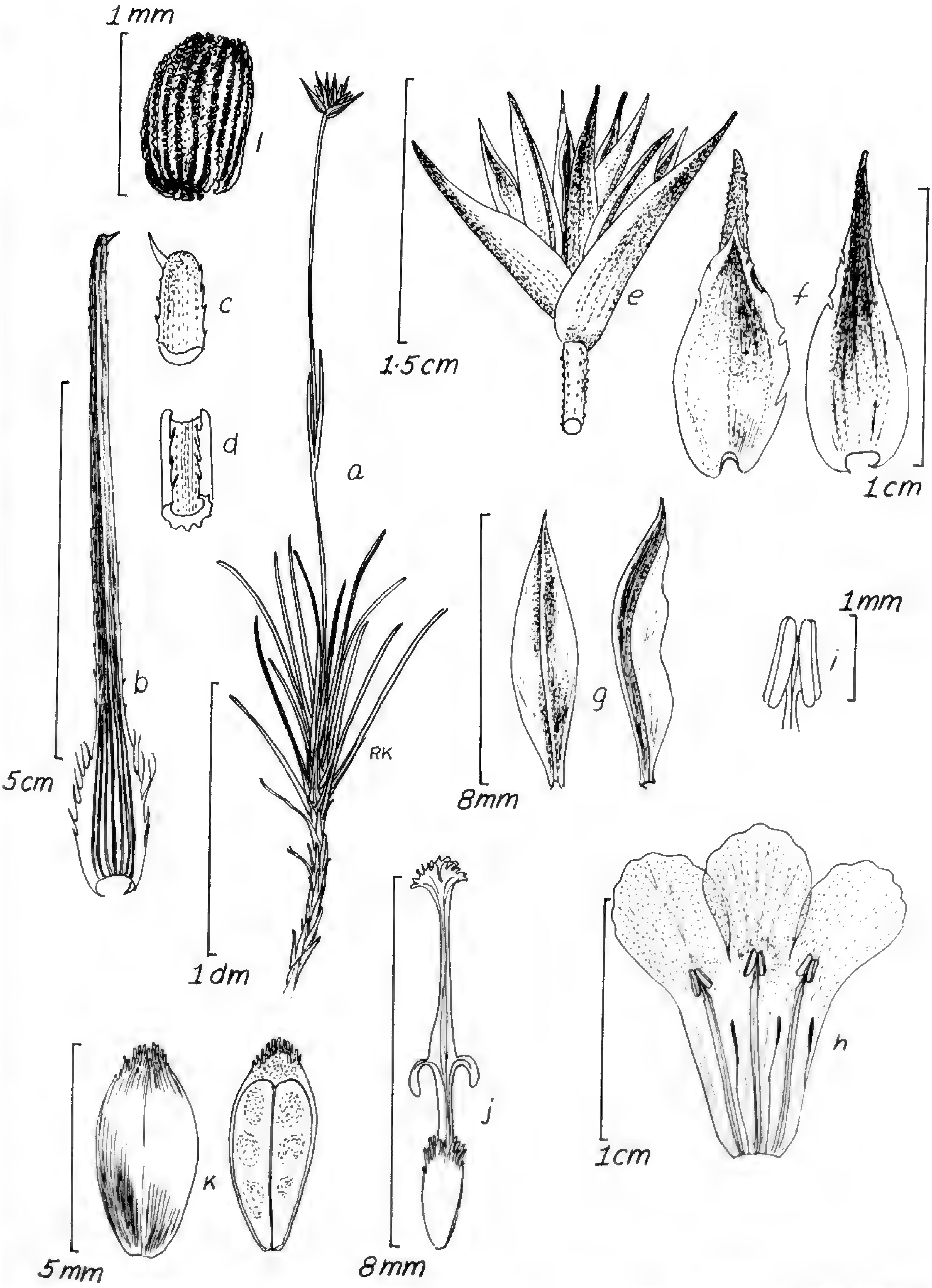

FIGURE 19. *Abolboda ciliata* (*Steyermark & Luteyn 129826*; *Kral 71926*).—a. Habit.—b. Leaf, abaxial side.—c. Leaf tip.—d. Leaf blade, sector at midblade, adaxial side.—e. Spike.—f. Fertile bract, midspike.—g. Lateral sepals, abaxial view (left), side view (right).—h. Spread corolla with stamens, staminodes.—i. Stamen.—j. Gynoecium.—k. Capsule (left); adaxial view of capsule valve (right).—l. Seed.

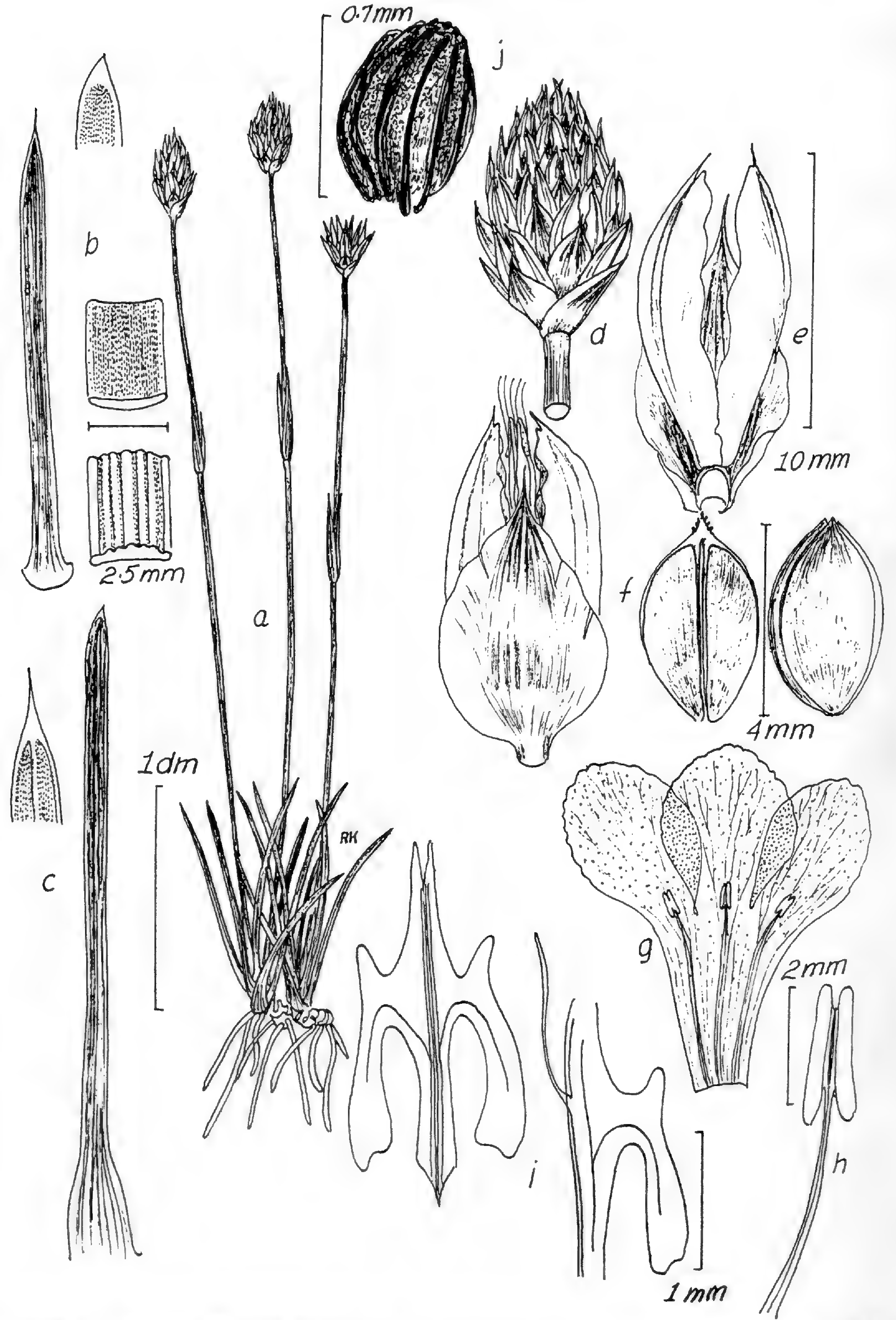

FIGURE 20. *Abolboda poarchon* var. *poarchon* (*Hatschbach 40099*).—a. Habit.—b. Leaf, abaxial side (left), apex (top); adaxial surface at midblade (middle), abaxial surface at midblade (below).—c. Leaf, abaxial apex (left); abaxial view of blade (right).—d. Spike.—e. Lateral sepals, inner view, showing fertile bract in background (above);

particularly *A. ebracteata.* No other species has leaf bases that are long-ciliate.

17. Abolboda poarchon Seub. in C. Martius, Fl. Bras. 3(1): 223. 1871. TYPE: Brazil. Minas Gerais: campis ascensus Chapada do Paranán, *Martius 1728* (lectotype, M; phototype, NY).

17a. Abolboda poarchon Seub. var. **poarchon.** Figure 20.

A. chapadensis Hoehne, Com. Lin. Telegr., Bot., pt. 5: 11. 1915. TYPE: Brazil. Mato Grosso: Campo úmido, cabeceiras do Rio Taquara-ussu, Mar. 1911, *com Rondon 3597* (lectotype, R; phototype, US).

A. chapadensis Hoehne var. *pauciflora* Hoehne, Com. Lin. Telegr. Bot., pt. 5: 12. 1915. *A. poarchon* Seub. var. *pauciflora* (Hoehne) Hoehne, Indice Bibliogr. e Numérico Pl. Colhidas Com. Rodon: 144. 1951. TYPE: Brazil. Mato Grosso: Coxim, June 1911, *com Rondon 3595* (lectotype, R; phototype, US).

Coarse to slender, glabrous, stout-rhizomatous perennial, the stems contracted or short-caudiciform, solitary or tufted on or along a coarse knotty rhizome, the roots spongy-thickened. Leaves erect to ascending, often excurved, stiff, (6–)10–25 cm long, compressed but firm, narrowed gradually or abruptly from dilated, pale, clasping and strongly convex-backed, multicostate bases to variously elongated, linear to linear-triangular blades 2–4 mm wide, these abruptly acute to acuminate to subulate-aristate at tip, at midblade usually lingulate, with incrassate, thickened-rounded edges, these pale and wirelike (actually from a thickened margin strongly curved inward), the surfaces rich green or anthocyanic, adaxially concave or rarely level, relatively smooth except at scabridulous apex marginally, abaxially slightly to very convex, often coarsely multinerved. Scapes stiffly erect to ascending, pale green or with tints of red or purple, terete, distally 1.5–2.1 mm thick, sometimes striate longitudinally, rarely sulcate, from scarious-bordered, erect, basal bracts, the scape bracts in 1 pair, slightly to very unequal, conduplicate, erect, oblong-linear, (2–)3–5 cm long, the convex medial zone ribbed, mostly deep green or marked with purple, apically acute, the borders broad, pale, scarious, the midrib excurrent as a cusp or mucro, also sometimes aristate; spike solitary, highly variable in shape, size, and pigmentation, from narrowly turbinate to obovate, ellipsoid or ovoid (this to some extent determined by age of spike), 1.5–3 cm long, the flowers several to many, all but the lowest (or even this) fertile, the lowermost bracts broadly ovate and usually slightly longer, 9–13 mm, the apex acuminate-aristate, the borders broad, scarious, pale or marked with purple bands, the medial zone strongly thickened, dark green or green and purple, coarsely few-costate, the central costa usually broadest and pale; sepals 2, viewed from side elliptic-oblong, incurved, conspicuously exserted, 10–16 mm long, with broad, pale, scarious borders, the medial area thickened, the keel thin but firm, pale-cartilaginous, broad, short-spinulose at the retuse sepal tip, the sepal sides at keel base usually longitudinally banded with brown, purple, or green, the keel itself mostly papillate-ciliate or denticulate at least distally; corolla 14–16 mm long, blue or violet-blue, the broadly obovate lobes 5.5–6.5 mm long; staminodia not evident; anthers 2–2.5 mm long, narrowly oblong, deeply emarginate and sagittate, on slender filaments to 5 mm long; gynoecium nearly as long as corolla, the slender style base deeply triquetrous, with 3 appendages, the laterals reflexed, clavate, basally with acute or oblong auricles, the median appendage usually filamentous and suberect. Capsule valves uniformly firm, the body broadly ellipsoid, ca. 4 mm long, the slightly thickened valve tips short-acuminate, papillate; seeds ovoid to ellipsoid or subprismatic, 0.7–0.8 mm long, dark brown to nearly black, coarsely and irregularly longitudinally ribbed, the intervals broad and nearly smooth.

Distribution. Moist to wet rocky campos, campinas, savannas and savanna bogs, edges of gallery forest and stream banks, 400–1,300 m, Amazonian and planaltan Brazil, from Amazonas, Pará, and Mato Grosso south through the planalto to Minas Gerais; Paraguay; Surinam(?).

Additional specimens examined. BRAZIL. AMAZONAS: Transamazon Hwy., 9 km W Rio dos Pombos, *Calderon et al. 2548* (INPA, NY, US, VDB); Transamazonica km 350 e 400, E Humaitá, *Cid Ferreira 5897* (INPA, NY, VDB). BAHIA: Rio Piau 150 km SW Barreiras, *Irwin et al. 14740* (F, GH, MO, NY, US). DISTRITO FEDERAL: Chapada da Contagem, *Irwin & Soderstrom 5236* (F, NY), ca. 1.5 km W antenas de Radiobrasil, *Kirkbride 4734* (VDB). GOIÁS: ca. 15 km N Curumba de Goiás, *W. R. Anderson 10443* (F, K, MO, NY, US); *W. Gardner 3486* (F, GH, K, NY); Serra dos Pyreneos, *Glaziou 22233* (F, K, MO); Pinanhas, *Hatschbach 40099* (MO, NY, US, VDB); 30 km N Veadeiros, *Irwin et al. 24507* (NY); ca. 20 km N Veadeiros, *Irwin et al. 12627* (F, GH, K, MO, NY—this set a mix with *A. pulchella*); 30 km N Veadeiros, *Irwin et al. 24507* (NY); 20 km N Alto

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fertile bract, outer view, showing exserted lateral sepals (diagonally below).—f. Capsule (right); inner view of one valve (left).—g. Spread corolla and stamens.—h. Stamen.—i. Two views of stylar appendages.—j. Seed.

do Paraíso, *Irwin et al. 32126* (F, NY, US); 12–20 km N Alto Paraiso, *King & Bishop 8837* (US—extremely puzzling material consisting of 2 plants, the taller with no scape bracts on one of the two scapes, the other a lower plant with one bractless scape, but with a pair directly subtending spike); Jataí to Milho Verde, *Kral & Wanderley 75004* (SP, VDB); 5 km N Alto Paraíso, *Kral & Wanderley 75856* (SP, VDB); Pirineus, *Macedo 3700* (MO, NY, US). MATO GROSSO: 6 km S Xavantina, *Argent et al. 6450* (U); San Antonio de Levenger, *Hatschbach et al. 36096* (US, VDB); Xavantina–Cachimbo Road, *Hunt & Ramos 5663* (K, NY, VDB); 84 km N Xavantina, *Irwin et al. 16400* (F, GH, MO, NY, VDB); 23 km S Agua Boa, *Kral & Wanderley 75213* (SP, VDB); 6 km S Xavantina, *Richards R677* (U); Xavantina–São Felix Rd., *de Santos et al. 1693* (NY, U). MINAS GERAIS: Cachoeira do Campo, *Glaziou 20520* (F); 27 km SW Diamantina, *Irwin et al. 21947* (F, GH, MO, US); Cerro do Cabral, *Kral & Wanderley et al. 72639, Wanderley & Kral et al. 790* (SP, VDB); 5–7 km N Grão Mogul, *Kral & Wanderley 75434* (SP, VDB); Boa Vista to Extracçao, *Melo-barreto 9657* (F); Serra do Espinhaço, *Hatschbach & Pelanda 27764* (VDB); Joaquim Felecio, Serra do Cabral, *Stannard et al. SPF 35902, CFCR 6297* (CFCR, K, SPF, VDB). PARA: Serra do Cachimbo, *Alvarenga, Jardim Bot. do Rio de Janeiro 90.585* (US); Ariramba, *Black et al. 57-19611* (NY); campo Piranema, *P. S. Goeldi, Herb. Mus. Paraensis 15061* (US); Obidos, Jaramacarú R, *Egler 277* (US); Serra do Cachímbo, *Pires et al. 6185* (NY). PARAGUAY. Cerro Torin–Sierra de Amambay, *T. Rojni 4066* (GH). SURINAM. (?) "Surinam, coll. *Focke*" (MO—a depauperate, possibly mislabeled, specimen).

Abolboda poarchon var. *poarchon*, by far the most abundant and wide-ranging of the two varieties treated here, is also the most highly variable. Typically, it forms large clumps or clones by means of branching rhizomes. The plants of grassy wet campos usually have more erect, elongate-linear leaves and scapes reaching nearly to a meter; those of more exposed sites or at higher elevations are lower with shorter leaves that are more spreading and also frequently setaceous-tipped. Additionally, the plants of high elevations and of more exposed sites have much more anthocyanin. This is produced in large quantity on the dorsal areas of sepals and bracts, making the inflorescence quite handsome. It flowers later in the day than does either its other variety or *A. pulchella*, with which it frequently associates.

17b. Abolboda poarchon Seub. var. **intermedia** (Lyman B. Smith & Downs) Kral, comb. nov. *A. pulchella* Humb. & Bonpl. var. *intermedia* Lyman B. Smith & Downs, Arq. Bot. Estado São Paulo, nov. ser., Vol. 4, fasc. 2: 26. 1966. TYPE: Brazil. Minas Gerais: Carandai–Brejao, 28 Nov. 1946, *A. P. Duarte 682* (holotype, US; isotype, RB). Figure 21.

Strongly clonal, glabrous perennial, the rosettes from slender, spreading or ascending rhizomes and forming a localized "turf," the roots coarse, the rhizomes more slender than in the type variety. Leaves of new rhizomes and shoots scalelike, spiral, variously triangular, 5–15 mm long, subulate-tipped, grading upstem to progressively narrower and more close-set ones of the principal rosette, these ascending to spreading or recurved, 20–60(–70) mm long, the sheaths broadly clasping, pale, thin, except for the ca. 5 raised costae, narrowing abruptly to linear or linear-triangular blades, these mostly 2–3 mm wide, firm, slightly lingulate (rarely plane), broadly or narrowly acute, the margin thick, entire or rarely with a few denticles or tubercles apically, green to greenish brown or maroon, the adaxial surface level or slightly concave, not evidently nerved, the abaxial surface convex, faintly to conspicuously broadly raised-nerved. Scapes usually 1 per rosette, erect, stiff, 15–40(–50) cm high, slightly compressed to variously few-costate or bluntly angulate, ca. 1(–1.5) mm broad or thick, medially with 1 pair of erect, conduplicate, equal or unequal scape bracts 2–3 cm long, these convex-backed with broad, green, low-costate medial areas, broad, pale, scarious, entire borders, and subulate-aristate tips; spikes solitary, mostly narrowly ovoid, aging narrowly turbinate or ellipsoid, 1.5–2 cm long, (2–)4(–7)-flowered, often at tip with 1–2 sterile florets; spike bracts all fertile or the lowermost empty, in any case ovate, ca. 9 mm long, those upspike slightly longer, to 10.5 mm long, all with broad green to maroon multicostulate convex backs with broad, thin borders and short-acuminate, then aristate, tips; sepals 2(–3), the laterals lanciform, subequal, navicular, 11–12 mm long, the curvate medial zone with a strong entire keel, this comprising the narrowly acuminate apex, the inner sepal when present thinner, lanciform but less keeled, ca. 9 mm long; corolla deep bright blue, 18–20 mm long, the lobes broadly ovate, ca. 10 mm long, erose-margined; staminodia not evident; anthers oblong, yellowish or pale, ca. 2–2.5 mm long, deeply emarginate and sagittate, the slender, flattened filaments attached 3–3.5 mm below corolla sinus; gynoecium ca. 14–15 mm long, the slender style 11–12 mm long, the 3 appendages set 1.5 mm or more above ovary summit, reflexed, the laterals claviform, ca. 1.5 mm long, the median one filamentous, longer, the stigma infundibular, lacero-fimbriate, bright blue-violet. Capsule ovoid, ca. 4 mm long, the thickened valves smooth, broadly acute at tip. Seeds irregularly ovoid to subprismatic or turbinate, deep brown to nearly black, 0.6–0.7 mm long, sculpted as in the type variety.

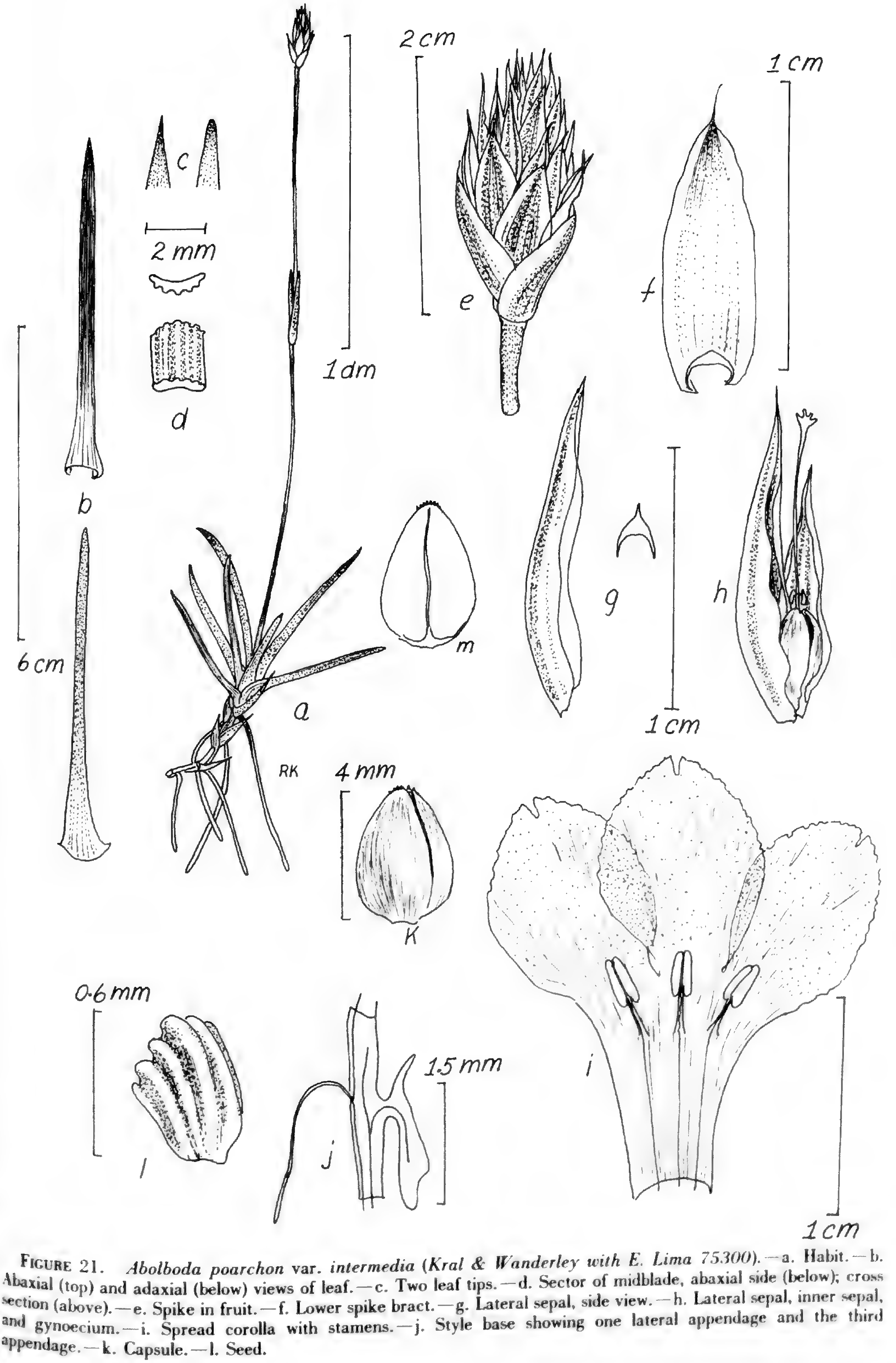

FIGURE 21. *Abolboda poarchon* var. *intermedia* (*Kral & Wanderley with E. Lima 75300*).—a. Habit.—b. Abaxial (top) and adaxial (below) views of leaf.—c. Two leaf tips.—d. Sector of midblade, abaxial side (below); cross section (above).—e. Spike in fruit.—f. Lower spike bract.—g. Lateral sepal, side view.—h. Lateral sepal, inner sepal, and gynoecium.—i. Spread corolla with stamens.—j. Style base showing one lateral appendage and the third appendage.—k. Capsule.—l. Seed.

Distribution. Wet, often rocky, campos, 400–1,200 m, often associated with *Abolboda pulchella* and *A. poarchon* var. *poarchon* in the Brazilian planalto from Goiás and Minas Gerais to São Paulo.

Additional material examined. BRAZIL. GOIAS: 30 km W of Jataí, 21 Sep. 1988, *Kral & Wanderley 75005* (SP, VDB); by BR 050, 10 km S Cristalina, 12 Oct. 1988, *Kral & Wanderley 75300* (SP, VDB); by BR 050, 92 km S of Cristalina, *Kral & Wanderley 75340* (SP, VDB); Jataí to Goiania, *Maguire et al. 57001* (NY, US). MINAS GERAIS: Carandaí–Brejão, *Duarte 682* (US); Serra do Espinhaço, Gouveia, *Hatschbach & Pelanda 27764* (US).

As mentioned above, this plant is most remarkable in the field and almost invariably is associated with *Abolboda pulchella* and *A. poarchon* var. *poarchon.* One is struck by the finer, lower habit of both *A. pulchella* and *A. poarchon* var. *intermedia,* and by the fact that they are both morning bloomers while nearby plants of *A. poarchon* var. *poarchon* bloom later in the day. In the overall perspective, in leaf character, in the larger number of flowers, in stylar appendages, bracts, and seeds, the affinities of variety *intermedia* are distinctly with *A. poarchon* rather than with *A. pulchella,* thus necessitating a varietal-level transfer. Interestingly, typical *A. poarchon* has leaf tips noticeably serrulate-denticular or papillate, and its lateral sepals are often either tuberculate or tuberculate-ciliate to denticulate, particularly apically. These characters are either less-developed or are entirely lacking in variety *intermedia.*

18. Abolboda grandis Griseb., Linnaea 21: 281. 1848. TYPE: Surinam. Joden-Savanna, Cordonpad, *Kegel 1131* (holotype, GOET).

18a. Abolboda grandis Griseb. var. **grandis.** Figure 22.

A. grandis Griseb. var. *minor* Spruce ex Malme, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26 (Afd. 3, no. 19): 14. 1901. TYPE: Brazil. Amazonas: "Prope Barra, Prov. Río Negro," July 1851, *Spruce 1654* (holotype, K; isotypes, BM, NY).

Solitary or tufted, glabrous perennial, the stems short and stout-caudiciform, sometimes with ascending branches, the roots spongy-thickened. Rosette leaves several to many, erect to spreading, mostly linear-lorate, 8–35 cm long, 8–15(–17) mm wide, the sheath base pale, clasping, lingulate, to 5 mm broad, upward strongly convex-backed and multicostate, variously narrowing, then dilating to the blade, this flat or lingulate (concave), mostly elliptic-linear or linear-oblanceolate, deep green, multinerved, the nerves more raised abaxially, the border broad, pale, hyaline, this apically involute, converging to form a conic-subulate, sharp tip. Scapes terete, 1–4 or more from a shoot, axillary to inner (upper) shoot leaves, (20–)30–80 cm high, 1.2–2 mm thick, sheathed at base by 2–3 involute, oblong, acute to acuminate basal bracts to 3 cm long, the surface dull green, low-costate or striate; scape bracts (1–)2(–3) pairs, erect, oblong or elliptic-oblong, conduplicate, 1.5–3 cm long, their rounded backs green or tinged with red, strongly nerved, broadly scarious-bordered, their tips acute, the midzone excurrent as a strong mucro or cusp; spikes broadly ovoid to subglobose or hemispheric, 1.5–3 cm long, several-flowered, the bracts conspicuously shorter than the sepals they subtend, all fertile or (rarely) the lowermost sterile, nearly subequal, (5–)6–9(–10) mm long, broadly ovate, strongly convex, the dorsal areas broad, green or anthocyanic, strongly ribbed, the borders broad, pale red or near white, the midrib usually excurrent as a mucro; lateral sepals subequal, broadly lanciform but rounded-conduplicate, strongly curved outward, 12–15 mm long, the keel sharp but broad and firm, entire or minutely scaberulous, excurrent as a short-sharp mucro; inner sepal sometimes present, ecarinate, spathulate, to ½ as long as the laterals; corolla ca. 20 mm long, the lobes slightly shorter than the tube, broadly obovate, blue-violet; staminodia lacking; anthers oblong, 2.5 mm long, the thecae parallel, the slender filaments ca. 3 mm long; gynoecium ca. 15 mm long, the triquetrous style base with 3 appendages, the laterals ca. 2.5 mm long, reflexed, spathulate, flattened distally inside, the central appendage shorter, erect or recurved, linear, the stigma infundibular, densely fimbriate. Capsule ovoid, 6–8 mm long, the valves thickened at the bifid-toothed acuminate tips. Seeds angulately broadly obovoid to subglobose, ca. 1 mm long, sometimes broader than long, dark, with several strong, wavy, longitudinal ribs and slightly lower, variously transverse connecting ridges, thus appearing reticulate.

Distribution. Acidic, usually arenaceous and peaty soils, in full sun or shade, of caatinga, savanna, or shrub, mostly in gallery forest edges, at low to medium, rarely high, elevations (25–1,900 m), Amazonian Brazil north to Surinam, west into southern Colombia.

Representative material examined. BRAZIL. AMAZONAS: Plato da serra Aracá, 18 Jan. 1984, *I. L. do Amaral 1624* (K); Manaus–Caracaraí Rd., km 140, 27 Sep. 1973, *Berg et al. P18166* (INPA, U, US); Manaus, *C. Chagas INPA 1789* (US); Rio Uatuma, 13 Aug. 1979, *Cid et al. 287* (F, INPA, NY, VDB); Igarapé das Lajes, 9 Aug. 1983, *Cid 4286* (INPA, NY, VDB); Cachoeira

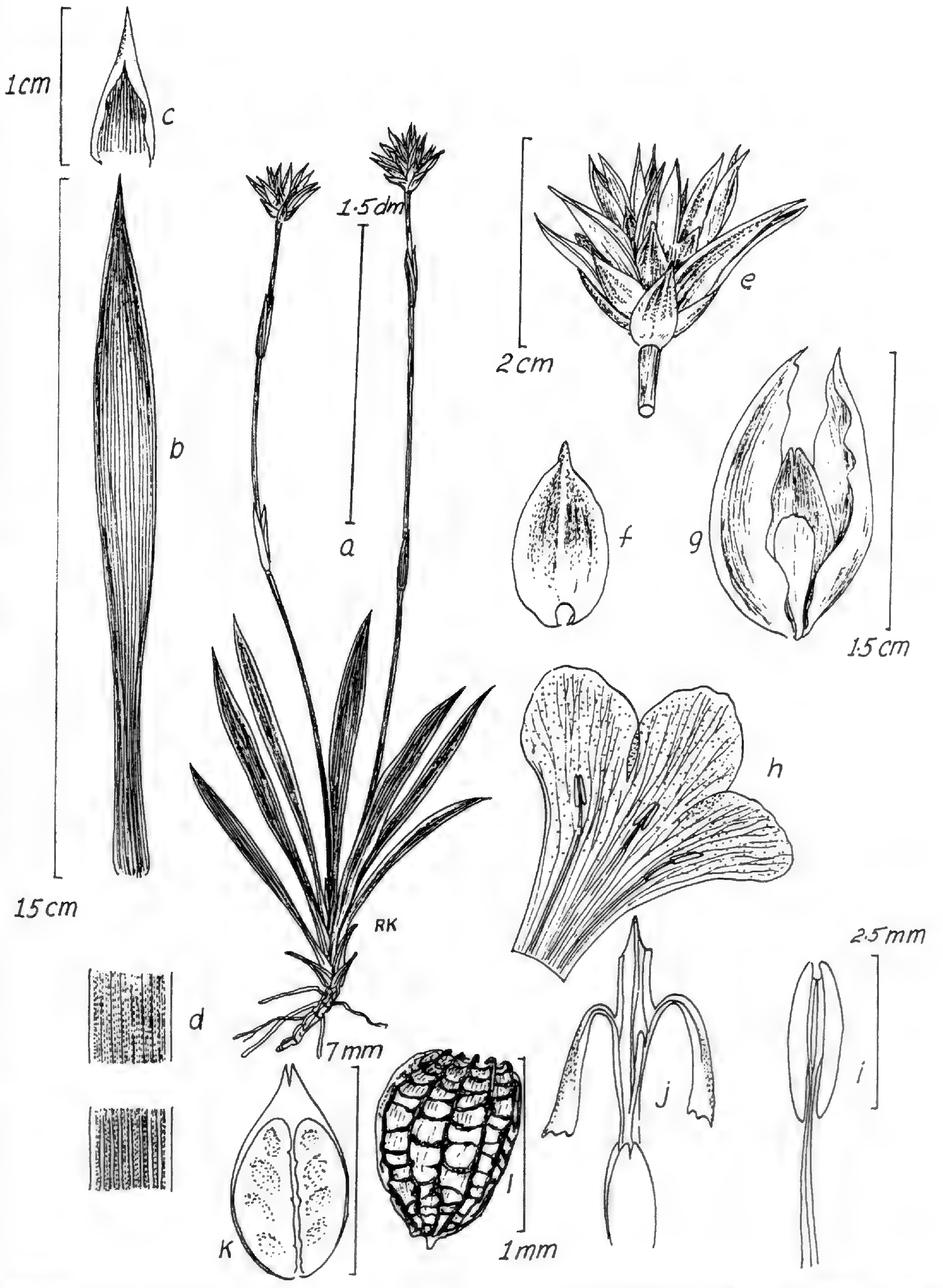

FIGURE 22. *Abolboda grandis* var. *grandis* (*Clark 7018*; *Prance et al. 28883*).—a. Habit.—b. Leaf.—c. Leaf tip.—d. Sector of midblade, adaxial side (above), abaxial side (below).—e. Spike.—f. Fertile bract.—g. Sepals and enclosed ripe capsule.—h. Spread corolla, stamens.—i. Stamen.—j. Stylar base and appendages.—k. Capsule valve, inner view.—l. Seed.

do Passarinho, 13 June 1927, *Ducke s.n.* (US); km 130, Manaus–Caracaraí Rd., *Gentry 12947* (MO, NY); Falls of Tarumá, *Killip & Smith 30164* (US); Basin of Rio Negro–Rio Cuieras, *Prance, Coêlho & Monteiro 14822* (F, GH, K, NY, US); Rio Cuieras 2 km below mouth of Rio Brançinho, *Prance et al. 1791* (GH, MO, US); Rio Xie, Cachoeira Cumati, 29 Nov.–7 Dec. 1947, *Schultes & Lopez 9213* (NY); Wasserfall das Taurumu, Manãos, Mar. 1912, *Ule 8827* (K); Obidos, *Egler 433* (US); Alto Tapajos, 14 July, 1959, *Egler & Raimundo 89A* (MG, US). RORAIMA: 6 km ao S do equador na Br 174, *Cordeiro et al. 79* (INPA, NY, VDB). COLOMBIA. VAUPES: Río Piraparana, cuenca Río Apaporis, *Garcia-Barriga 14277* (US); Río Vaupés, Cerro de Circasia, *Garcia-Barriga 15038* (GH, US); Puerto Colombia, *Maguire et al. 41867* (US); Rio Xie, Cachoeira Cumatí, *Schultes & Lopez 9213* (US); Cachivera Palaito, *Schultes & Cabrera 13179* (GH, US); San Filipe and vic., *Schultes et al. 18009* (GH); Cerro Kañenda, 10 Nov. 1952, *Schultes & Cabrera 18386* (GH); Raudal de Yuruparí, *Schultes & Cabrera 19722* (GH); Mitu and vic., Río Vaupés at Circasia, *Zarucchi 2046* (GH, K, MO, US). GUYANA. Canister Falls, Demerara Co., *Abraham 301* (K, NY); Kaieteur savanna, *Jenman 1020* (NY); Amatuk Falls, Potaro River, *Jenman 7480* (K, NY); Mt. Membaru, *Maas & Westra 4270* (NY). SURINAM. Sanderij, *Essed 111* (K, U); N of Berlijn, *Heyligers 102* (U); Tafelberg, *Kramer et al. 3256* (U); Zanderij I, airport, *Lanjouw & Lindeman 259* (NY, U); Coppenam River headwaters, *Maguire 24176* (F, GH, K, NY, U); "Surinam," *Miquel 1850* (K); Tafelberg, Savanna I, *Maguire 24215* (F, GH, MO, NY, U, US). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: base of Cerro Cucuy, *Baldwin 3233* (US); Yavita, *Bunting et al. 3745* (F); "Cabeza de Manteco," "Raudal Manteco," *Guanchez & Melgueiro 3433* (MYF, VDB); Macizo Aracamuni, *Huber & Medina 5912* (US, VEN); 9 km NE of San Carlos, *Liesner 3918* (MO, NY); Cerro Aracamuni, summit, *Liesner & Delascio 21955* (MO, VDB); Cerro Sipapo, 1,600 m, *Maguire & Politi 28206* (NY); sabanita E of Maroa, *Maguire & Wurdack 35687* (K, NY); Pimichin, *Maguire et al. 36382* (NY, US—noted by Maguire as a possible hybrid between *A. angustifolia* and *A. grandis*); 8–10 km N of San Carlos, 21 Apr. 1984, *Plowman 13704* (F); ad flum. Guainía, ostium flumenensis Casiquiare, *Spruce 3545* (GH); 30 km SSW Ocamo, *Steyermark et al. 130357* (MO). BOLIVAR: punta meridional del Auyan-tepui al Norte y el Uiapan-tepui al Sur, *Huber et al. 9900* (MYF, NY, VDB, VEN—a borderline morphology with var. *rigida*); 3 km S of El Puaji, *Liesner & Holst 18798* (MO, VDB); 15.5 km E of Icabaru, *Steyermark et al. 117794* (NY).

This widespread variety is comparatively homogeneous over most of its range except for the area of northern Amazonian Brazil transitional to the Guayana Highlands. Here, in parts of Amazonas and Territorio Roraima in Brazil and contiguous Bolívar and Territorio Federal Amazonas in Venezuela, intermediates can be found that are very difficult to place because they grade into the typically highland *Abolboda grandis* var. *rigida*. A more detailed description of the problem is given below. Typically *A. grandis* var. *grandis* is a lower plant with leaves tending more to a linear-lorate pattern, with scapes much more slender, scape bracts shorter, spikes smaller and of a broader outline, and with tips of capsule valves distinctly and sharply bidentate.

18b. Abolboda grandis var. **rigida** Malme, Bull. Torrey Bot. Club 58: 326. 1931. *A. rigida* (Malme) Steyermark, Fieldiana Bot. 28: 105. 1951, non Gleason, 1929. TYPE: Venezuela. Territorio Federal Amazonas: Brocchinia Hills, summit of Mount Duida, 4,500 ft., 4 Jan. 1929, *G. H. H. Tate 586* (holotype, NY; phototypes, F, NY). Figure 23.

A. pervaginata Malme, Ark. Bot. 25A(12): 16. 1933. TYPE: Brazil. Pará: lugares umidos, Campos Ariramba, meio Rio Trombetas, 4 Dec. 1910, *Ducke 11352* (lectotype, S; isolectotypes, MG, RB, US).

A. grandis var. *guayanensis* Maguire, Mem. New York Bot. Gard. 10: 8. 1958. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Sipapo (Paraque), Campo Grandé, 1,500 m, 8 Dec. 1948, *Maguire & Politi 27561* (holotype, NY; isotypes, NY, US).

Similar to *Abolboda grandis* but overall a coarser and taller plant, the rosettes solitary or tufted from a stout caudex, or often from stiff and stout crown branches, the roots spongy-thickened. Principal leaves fairly uniform, broadly linear to triangular-linear or lorate, stiffly spreading to erect, 15–60 cm long, 10–20 mm wide, tapering above midblade and involute to form a subulate tip, the margins with an entire, pale or violaceous, thin, hyaline border, the adaxial surface dark to pale green, narrowly multiveined, the abaxial surface with the nerves more raised, often anthocyanic. Scapes 1 to several, 50–110 cm long, subterete or sometimes sulcate-angulate, low-striate, pale green or variously tinged with red or purple, apically 1.5–3(–4) mm thick, invested at base by 2–3 erect, scarious, lance-oblong, subulate-tipped bracts to 3–4 cm long, the pairs of scape bracts (1–)2–3(–4), erect, lance-oblong, conduplicate, those of a pair subequal, the lowest pair usually largest, 3–5 cm long, all with strongly rounded backs, medially multicostate, with broad, scarious, pale borders sharply contrasting with the darker green or anthocyanic dorsal areas, the apex short-subulate or cuspidate; spikes mostly ovoid or cylindric-ovoid, rarely obovoid, 1.8–4 cm long, the bracts and sepals as in the species but proportionally longer; bracts (6–)6.5–9 mm long, with green anthocyanic dorsal areas, the lateral sepals 1.2–2 cm long, the broad, curved keels often distantly

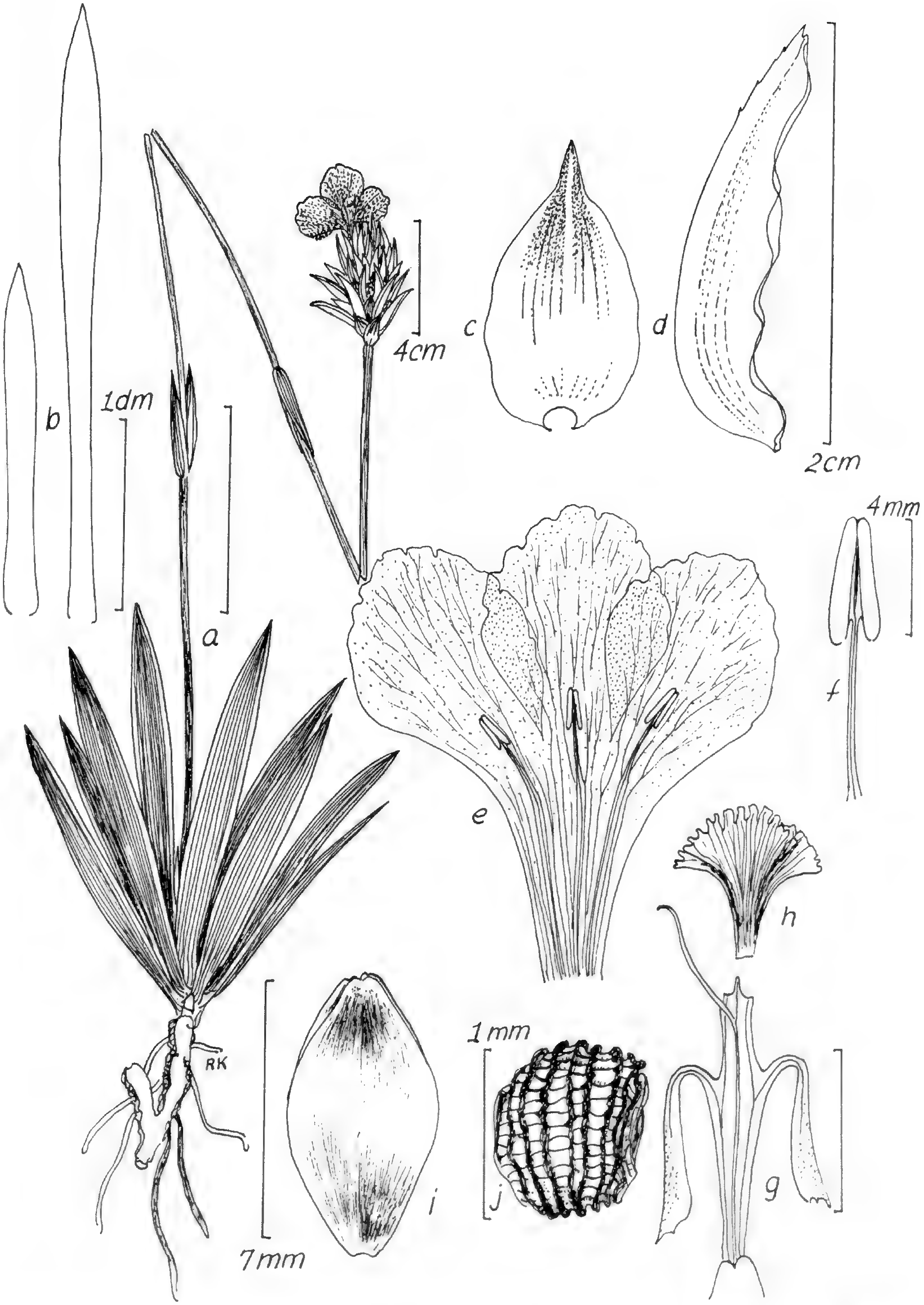

FIGURE 23. *Abolboda grandis* var. *rigida* (*Maguire & Politi 27561*; *Tate 586*).—a. Habit.—b. Two extremes of leaf outline.—c. Fertile bract.—d. Lateral sepal.—e. Spread corolla and stamens.—f. Stamen.—g. Style base and appendages.—h. Stylar apex and stigmas.—i. Capsule.—j. Seed.

low-lacerate; corolla 3–3.5 cm long, the lobes broadly obovate, ca. as long as the tube, violet-blue; staminodia not evident; stamens with anthers oblong, 4–4.5 mm long, the locule bases slightly divergent, the filaments 5–6 mm long, flattened; gynoecium 3–3.5 mm long, the strongly triquetrous style base producing 4–5 mm above the ovary a pair of reflexed, claviform, obliquely truncate lateral appendages ca. 4 mm long, the reduced appendage above or slightly below, filamentous, often erect, the stigma lobed-infundibular, with lobe edges fimbriate. Capsule ellipsoid, subtrigonous, 6–7 mm long, the valve tips shallowly round-lobed apically. Seeds dark red-brown, longitudinally coarsely ribbed as in the species, ca. 1 mm long, pyramidal or variously quadrate and faceted, the cross-ribs numerous and slightly lower and finer, thus seed surface reticulate.

Distribution. Wet, acidic savanna bog, gallery forest edges, rocky shrubby summits of tepuis and high bogs, at medium to high elevations (600–2,000 m), Surinam west to Territorio Federal Amazonas, Venezuela, and south into northern Amazonian Brazil (to Pará).

Representative specimens examined. BRAZIL. AMAZONAS: Serra Aracá, 12 Feb. 1984, *Prance et al. 28988* (NY, VDB), *28883* (NY, US, VDB); Manaus-Caracari, km 130, 25 May 1974, *Rodrigues et al. 9283* (F, INPA). PARA: região do Ariramba, 30 May 1957, *Black et al. 57-19806* (IADN, NY); E of Faro, 27 Aug. 1907, *Ducke 8530* (US); Obidos, *Egler 433* (US). RORAIMA: Serra Parima S of Auraris, 10 Feb. 1969, *Prance et al. 9816* (INPA, K, NY, US); summit Serra Parima, 30 July 1974, *Prance et al. 21565* (INPA, K, MO, NY, U, US). COLOMBIA. AMAZONAS: opposite Maroa, 12 Oct. 1957, *Maguire et al. 41867* (NY—material difficult to place with either variety). GUYANA. ATKINSON: St. Cuthbert's Trail, 12 Jan. 1969, *U. G. Bio. 106* (NY); Kaieteur plateau, 7 Mar. 1962, *Cowan & Soderstrom 1061* (K, NY, US); Kaieteur Savanna, *Jenman 1019* (K, NY); Mt. Membaru, 12 Nov. 1979, *Maas & Westra 4270* (K, NY, U, US); Mt. Aymatoi, *Maas et al. 5681* (US); Kaieteur Plateau, *Maguire & Fanshawe 23148* (F, GH, MO, NY, U, US); Partang Savanna, *Maguire & Tillett 43817* (K, NY); Membaru Creek, *Pinkus 223* (GH, MO, NY, US). SURINAM. prope Jodensavanne, *Heyligers & Knoppe 3223* (U); Zanderij I, *Lanjouw & Lindeman 259* (U); W of Zanderij I, *Lindeman 6518* (F, GH); Lobin savanna, *Teunissen-LBB 15180* (U). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: between Yavita and Pimichín, *Bunting et al. 3745* (K, NY, U, VDB); Serrania Parũ, *Cowan & Wurdack 31146* (NY, US), sector centro-norte, *Huber 4335* (K, MYF, NY, VDB); plateau of Duida, *Liesner 18161* (MO, VDB, VEN); Cerro Sipapo, *Maguire & Politi 28702* (K, NY, US), middle east drainage, *28354* (NY); Cerro Duida, *Maguire et al. 29623* (NY, U); summit Cerro Guanay, *Maguire 31702* (NY); Cerro Guaiquinima, *Maguire 32958* (US); 1 km E of Maroa, *Maguire & Wurdack 36424* (F, NY, US); Duida, Brocchinia Hills, *Steyermark 58181* (F, NY); Sierra Parima, *Steyermark 107514* (F, NY, MO); Cerro Duida, cumbre, *Steyermark et al. 126382* (NY); Duida, Savanna Hills, *Tate 1041* (NY); Yavita, *L. Williams 13910, 13951* (F, US—these and material collected by Williams from Maroa comprising difficult transitional morphs); Río Siapa just below Raudal Gallineta, *Wurdack & Adderley 43539* (GH, NY, US). BOLIVAR: S base Auyan-tepui, *Davidse & Huber* (MO, MYF); hacia Icabaru, *Huber & Alarcon 7892* (NY); Macizo Guaiquinima, *Huber 9354* (MYF, VDB); Serranía Guanay, *Huber 10954* (MYF, NY, VDB); 25 km ENE of Canaima, *Huber 12108* (MYF, VDB); El Puaji, *Liesner 19412* (MO, VDB, VEN); Cerro Guaiquinima, N Valley, *Maguire 32921* (NY, US); Cerro Pitón, *Maguire & Steyermark 53666* (NY); Sierra Pakaraima, *Steyermark 107264* (MO, NY); Meseta Jaua, *Steyermark et al. 109420* (F, K, NY).

After a sustained effort to distinguish variety *guayanensis* Maguire from variety *rigida*, I had to give up. What I found was a series of specimens from the highlands of northern Brazil and southern Venezuela that were proportionally taller, coarser, with larger floral parts (thus spikes), and with considerably more anthocyanic pigmentation than that for most *A. grandis* var. *grandis*, a plant normally of lower elevations. But what has been described as two varieties from the uplands is an inextricable mix of morphologies, thus forcing me, however interesting the extremes, to consider all these as parts of one variety, with the oldest available name for them being variety *rigida*.

19. Abolboda macrostachya Spruce ex Malme, Bih. Kongl. Svenska Vetensk-Akad Handl. 26: Afd. 3. 19: 15. 1901. TYPE: Venezuela. Territorio Federal Amazonas: "prope Esmeralda, ad flumen Orinoco, Dec. 1853," *R. Spruce 3229* (lectotype, S; isolectotypes, BM, P, K, NY).

19a. Abolboda macrostachya var. **macrostachya**. Figure 24.

A. macrostachya Spruce ex Malme var. *angustior* Maguire, Mem. New York Bot. Gard. 10: 10, fig. 3i–n. 1958. TYPE: Venezuela. Territorio Federal Amazonas: Sabana Venado, Caño Pimichín, Río Guainía, 140 m, 23 Nov. 1953, *Maguire, Wurdack & Bunting 36342* (holotype, NY; isotypes, GH, NY, VEN).

Stiff, smooth perennial, often robust, usually tufted, from a simple or branched-caudiciform, thick (to 2 cm) rhizome, the roots spongy-thickened. Rosette leaves numerous and fairly uniform, spirally imbricate at base, spreading or ascending, primarily lorate-linear or linear-triangular, highly variable in size, 7–35 cm long, (4–)6–20 mm wide, firm but flattened, narrowing gradually above a clasping, broad, multinerved, convex base to the blade, this flat, lingulate or involute, at apex narrowly acute to acuminate, the margins there con-

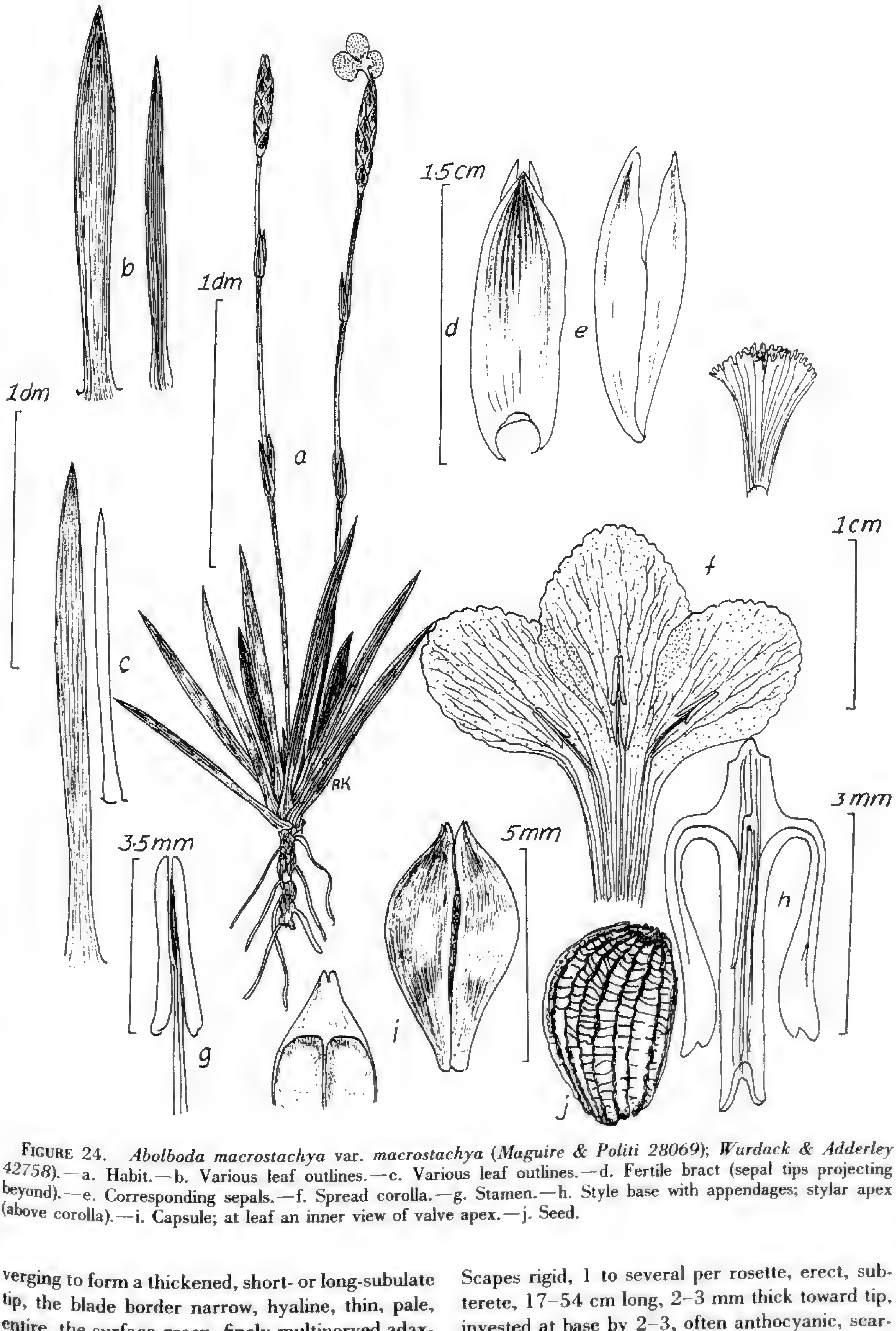

FIGURE 24. *Abolboda macrostachya* var. *macrostachya* (*Maguire & Politi 28069*); *Wurdack & Adderley 42758*).—a. Habit.—b. Various leaf outlines.—c. Various leaf outlines.—d. Fertile bract (sepal tips projecting beyond).—e. Corresponding sepals.—f. Spread corolla.—g. Stamen.—h. Style base with appendages; stylar apex (above corolla).—i. Capsule; at leaf an inner view of valve apex.—j. Seed.

verging to form a thickened, short- or long-subulate tip, the blade border narrow, hyaline, thin, pale, entire, the surface green, finely multinerved adaxially, more coarsely nerved and darker abaxially. Scapes rigid, 1 to several per rosette, erect, subterete, 17–54 cm long, 2–3 mm thick toward tip, invested at base by 2–3, often anthocyanic, scarious-bordered, chaffy, lance-oblong bracts to 4 cm long; scape bracts commonly 2, rarely 1 or 3 pairs, the lowest pair slightly longer, lance-ovate or broadly lance-oblong, those of a pair subequal, 1–1.8 cm long, conduplicate-rounded, at apex acute to acuminate, with the costa short-excurrent, the dorsal area green or anthocyanic, striately multinerved; spikes 1 per scape, multiflowered, cylindric, ellipsoid or lance-cylindric, 3.5–8 cm long, 8–10 mm thick, the bracts tightly spirally imbricate, all fertile, or the lowermost sterile (rarely), and slightly larger, most bracts ovate-oblong, 1.4–1.6 cm long, acute, the backs strongly convex with ovate, strongly nerved, deep green or variously anthocyanic dorsal areas, producing a short, subapical, erect, blunt mucro, the border broad, hyaline, pale or suffused with pale purple; sepals 2, elliptic-lanciform, strongly and sharply folded, 15–17 mm long, their narrowly acute tips projecting slightly beyond the tip of subtending bract, their keels broad, curved, entire, firm; corolla 2.0–2.5 cm long, blue-violet, the spreading lobes broadly obovate to reniform or suborbicular, shorter than the tube; staminodia not evident; anthers narrowly oblong, white aging yellow, the thecae slightly divergent below, deeply sagittate, 3–3.5 mm long, on filaments 3.5–4 mm long; gynoecium over 2 cm long, the slender triquetrous base producing 3 recurved appendages 5–6 mm up from ovary summit, the laterals narrowly flabellate-clavate, ca. 3–3.5 mm long, the central shorter and filamentous. Capsule firm-valved, obovoid, 6–7 mm long, slightly acuminate, a lustrous pale brown. Seeds obovoid to variously angulate-isodiametric, ca. 1 mm long, longitudinally irregularly coarsely dark-ridged, with many lower, transverse connecting ridges, the pattern thus reticulate.

Distribution. Locally abundant in moist to wet, mostly low-elevation savanna or at edges of gallery forest therein (50–200 m, occasionally in Territorio Federal Amazonas up to 1,250 m), southern Venezuela west into southeastern Colombia and south into Amazonian Brazil.

Additional material examined. BRAZIL. AMAZONAS: rd. to Igarapé Preto, 2 July 1979, *Calderon et al. 2742* (INPA, K, MO, NY, US, VDB); Humaitá–Jacarecanga, 21 June 1982, *Teixeira et al. 1266* (INPA, NY, VDB). RORAIMA: caatinga com Barcella, 30 Apr. 1974, *J. M. Pires et al., Herb. Ipean 14.489, 14.460* (GH, NY, US). COLOMBIA. VAUPES: Yapoboda, 10 Dec. 1943, *P. H. Allen 3205* (GH, MO, US); Cerro Kañenda, 2–4 Nov. 1952, *Garcia-Barriga 15055* (US); savanna, Guranjuda, *Garcia-Barriga et al. 16028* (GH, NY, US); Cacagual, *Maguire et al. 36285* (NY), *36287* (NY); Araracuara, 6 Sep. 1959, *Maguire & A. Fernandez P. 44178* (GH, NY, US); Puerto Colombia opp. Maroa, *Maguire et al. 41855* (NY); Yapoboda, *Schultes & Cabrera 14242* (US); Cerro Kañenda, *Garcia-Barriga 15055* (GH), *Schultes & Cabrera 18361* (COL, GH, US, VDB); savanna of Yapoboda, *Schultes et al. 18494* (GH, US); Río Paraná Pichuna, *Schultes & Cabrera 19905* (GH, US), *20053* (GH); Mitu, Río Kubiyū, *Zarucchi et al. 1132* (GH, US), *2010* (GH, K, VDB). VICHADA: Parque Nacional Natural "El Tuparro," *Zarucchi & Barbosa 3541* (MO, VDB). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Esmeralda, *Croizat 127* (GH, MO, NY, US); Yapacana, *Holt & Blake 757* (GH, US); Cucuri, *Davidse et al. 17047* (MO); Cucurital de Yagua, Caño Yagua, *Davidse et al. 17398* (MO, VDB); Santa Cruz, Río Atabapo, *Foldats 3682* (NY); "Cerro la Trampa," Rio Autana, *Guanchez & Melgueiro 3540* (MARNR, MYF, VDB); 10 km W of Manapiare, *Huber 1238* (GH, US, VEN); Cerro Yapacana, *Huber 1644* (US); Canaripo, *Huber 1927* (GH, U, US); Yapacana Savanna III, *Huber 2014* (K, NY); sabana N laguna de Yagua, *Huber 2569* (NY); SE de Carmelitas, *Huber 2681* (MYF, VDB); 30 km SE de la confluencia Orinoco–Ventuari, *Huber & Tillett 2782* (K, NY, U, US); savanna III, Yapacana, *Huber 2996* (US); Maroa, *Huber 3405* (K, NY); sabanita N del medio Caño Canamé, *Huber et al. 3754* (NY); Cerro Cucurito, *Huber 3874* (NY); alto Caño Yagua, *Huber 4849* (NY); 10–12 km W de Esmeralda, *Huber 5055* (NY); ribera izquierda (S) del Río Guayapo medio, *Huber & Tillett 5512* (US, VEN); 2 km al W de San Antonio del Orinoco, *Huber & Tillett 5416* (US, VEN); 5 km al S de Laguna Yagua, *Huber & Tillett 5482* (US, VEN); Yapacana Savanna III, *Kral & Huber 70713* (MARNR, NY, VDB); Cerro Morocoto, *Level L.11* (NY, US); Cerro Sipapo, *Maguire & Politi 27957* (F, K, NY, US), *28043* (NY); Yapacana Savanna III, *Maguire et al. 30467*; Cerro Moriche, *Maguire et al. 30888* (NY), *30990* (NY); Cerro Duida, *Maguire & Wurdack 34697* (GH, NY); Yapacana Savanna III, *Maguire et al. 36600* (NY, US—paratype of var. *angustior*), *Maguire et al. 30472* (NY, U), *Maguire et al. 36598* (NY), *Maguire et al. 41446* (NY); Esmeralda Savanna, *Steyermark 57838* (F, NY, US); cerro Vinilla, SSW Ocamo, *Steyermark et al. 130387* (MO); Yapacana, *Thomas & Rogers 2606* (NY); 15 km above Guarinumo, *Wurdack & Adderley 42981* (GH, US); Sabana de Moyo, *Wurdack & Adderley 43684* (GH); 20 km above San Fernando, *Wurdack & Adderley 42758* (NY, US); 2 km below mouth of Atabapo, *Wurdack & Adderley 42708* (NY); 5 km below Guarinumo, *Wurdack & Adderley 42850* (NY); Sabana de Moyo, *Wurdack & Adderley 43664* (NY). BOLIVAR: morichal 2 km E of Río Orinoco between Río Horeda and Cerro Gavilan, *Wurdack & Monachino 39957* (F, GH, K, NY, U).

A review of *Abolboda macrostachya* var. *macrostachya* and many duplicates of the variety *angustior* (most of these cited above) shows that the characters used to distinguish the two all blend.

19b. Abolboda macrostachya var. **robustior** Steyermark, Fieldiana Bot. 28: 104. 1951. TYPE: Venezuela. Bolívar: Gran Sabana NW Kavanayen at 1,220 m, 26 Oct. 1944, *Steyermark 57349* (holotype, F; isotype, VEN). Figure 25.

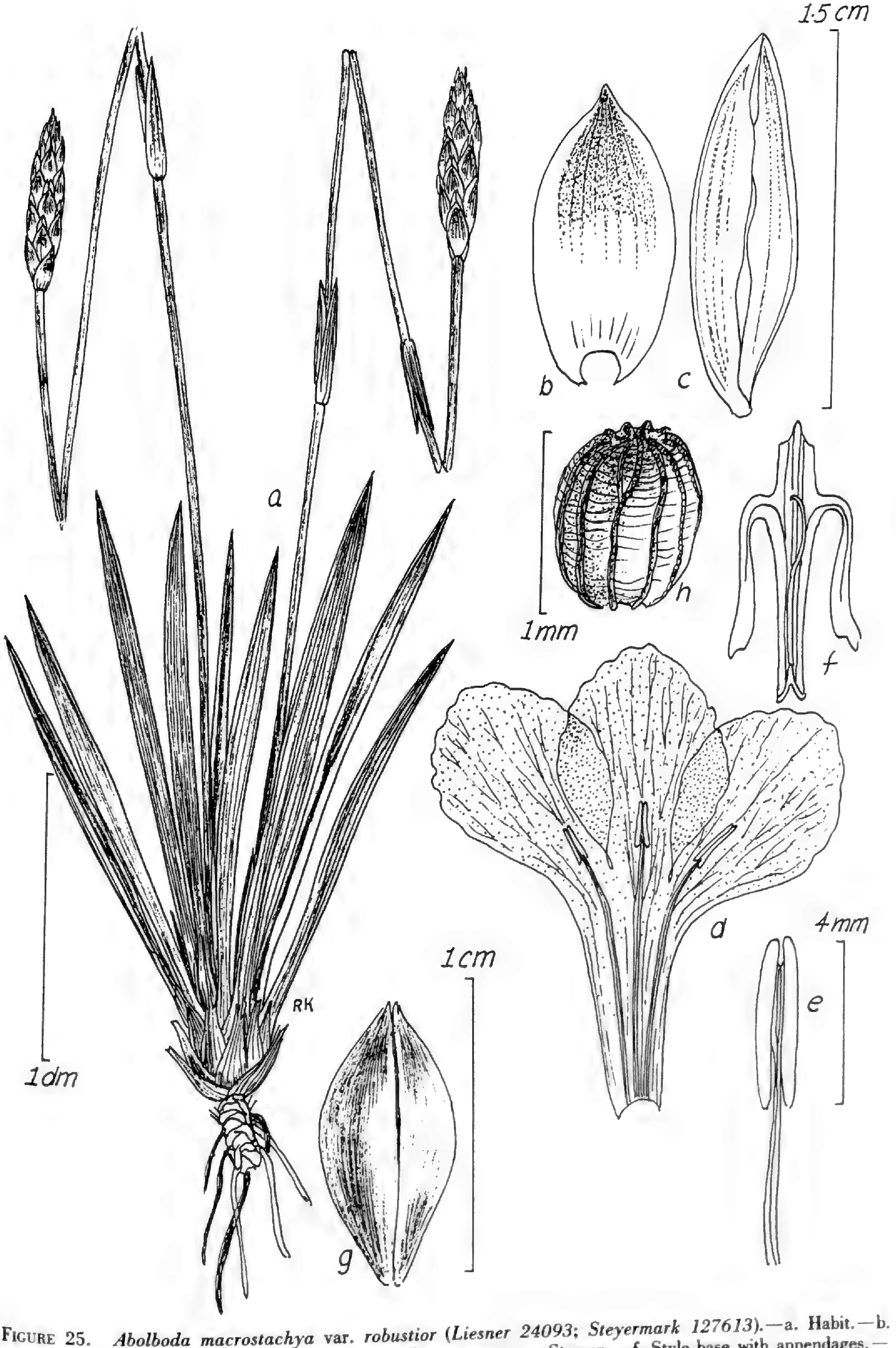

FIGURE 25. *Abolboda macrostachya* var. *robustior* (*Liesner 24093*; *Steyermark 127613*).—a. Habit.—b. Fertile bract.—c. Lateral sepal pair.—d. Spread corolla, stamens.—e. Stamen.—f. Style base with appendages.—g. Capsule.—h. Seed.

A. rigida Gleason, Bull. Torrey Bot. Club 58: 17. 1929. TYPE: "British Guiana," *Schomburghk 146.S.* (lectotype, K—specimen at right on type sheet; specimen at left is *A. grandis* var. *rigida* Malme).

A. excelsa Malme, Ark. Bot. 25A(12): 16. 1933. TYPE: Venezuela. Bolívar: "In Sumpfen, Río Cuquenan, Februar 1910," *E. Ule 8545* (lectotype, K; isolectotypes, L, MG).

As in variety *macrostachya* but typically far more robust, the rosettes solitary or tufted, the stems caudiciform, simple or branched, thick, to 1 dm long, erect or ascending, 1–2 cm thick, naked at base, above cloaked in chaffy old leaf bases and appearing sub-bulbous, the roots spongy-thickened. Leaves several to many per rosette, spreading to ascending, stiff, mostly linear, 15–45 cm long, 10–25 mm wide, compressed, flat or lingulate or infolded, the base broadly clasping, to 25 mm wide, strongly multinerved on the convex backs, abruptly or gradually constricted above for up to 1 dm, thence broadening to an elliptic-linear or linear-triangular blade, above middle narrowing gradually, the narrow, pale, hyaline borders converging to form a subulate, sharp point, the surfaces pale, bright green or glaucous, multinerved, with nerves stronger on abaxial surface. Scapes rigid, 1–several per rosette, axillary, terete or sometimes angulate-sulcate, fistulose, 60–120 cm long, distally 3–4.2 mm thick, smooth, often strongly suffused with purple; scape bracts 1(–2) pairs, 4–6.5 cm long, those of a pair erect, subequal, lance-oblong, conduplicate, the rounded backs strongly multinerved, the medial area green or purplish, the border broad, pale (or rarely deep purple), thin, converging to acute or acuminate tip, the midrib excurrent as a short cusp or mucro; spikes solitary and terminal, mostly cylindric-ellipsoid, 4–7(–10) cm long, 1–1.5 cm thick, multiflowered, all bracts fertile and erect (or the lowermost sterile), broadly to narrowly ovate, 1.4–2 cm long, the lower ones slightly longer, all with strongly rounded, multiribbed, deep green or purplish pigmented backs, the thin, hyaline borders broad, converging apically to an acute or short-acuminate tip, the medial area raised distally and sometimes short-excurrent as a low mucro or short cusp; sepals 2, navicular, lance-elliptic in side view, 1.6–2.3 cm long, the tips conspicuously exserted, the thickened medial area produced to a narrow, thin but firm, entire keel, the sides longitudinally low-nerved, the nerves often anthocyanic; corolla bright blue or violet-blue, 3–4 cm long, the lobes ca. as long as the tube, broadly obovate to suborbicular; staminodia usually not evident, when present filamentous; anthers narrowly oblong, 3.5–4 mm long, yellow, on filaments 4–5 mm long; stylar appendages as in the type variety. Capsule obovoid-ellipsoid, 9–10 mm long, the thickened valve tips narrowly bifid. Seeds variously obovoid-angulate and faceted, sometimes isodiametric, ca. 1 mm long, with several straight or irregular coarse ribs longitudinally, these connected by narrow alveolae.

Distribution. Common to frequent in rapateaceous savanna bog, clearings in shrub or edges of gallery forest therein, in sandy, acidic wet sites at medium to high elevations (600–1,900 m), from eastern Guyana westward across southern Venezuela to Cerro Sipapo in Territorio Federal Amazonas, and probably (but without records presently) southward from Bolívar, Venezuela, into contiguous northern Brazil.

Additional material examined. GUYANA. Pakaraima Mts., Mt. Aymatoi, 15 Oct. 1981, *Maas et al. 5692* (NY, U); Samwarakna-tipu, 10 Nov. 1951, *Maguire & Fanshawe 32521* (NY); upper Mazaruni River, *Pinkus 223* (F). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Sipapo, 15 Dec. 1948, *Maguire & Politi 27682* (NY), 25 Dec. 1948, *27910* (GH, NY), 1 Jan. 1949, *28112* (NY), *28117* (F, K), 6 Jan. 1949, *28176* (NY, US). BOLIVAR: Guiaquinima-tepui, 11 May 1987, *Aymard C. 5977* (MO, PORT); Río Aponguao, cruce con carretera El Dorado–Sta. Elena, *Burandt et al. V1052* (MO, UCOB); Cerro Auyan, Jan. 1949, *Cardona 2614* (NY, US); 24 km S La Ciudadella, *Davidse et al. 4768* (MO); cabaceras Río Waiparu, *Fernandez 2050* (MYF, VDB); 20 km al N Kama-Maru, 4 abr. 1985, *Holst et al. 2226* (MO); Parupa, *Huber et al. 7217* (MYF, VDB); entre San Francisco de Yuruani y Chirimata, 21 June 1983, *Huber & Alarcon 7544* (MYF, VDB); 8–10 km SSE San Ignacio de Yuruani, *Huber & Febres 9188* (MYF, NY, VDB); 15 km N "Paso Pacheco," *Huber 9223* (NY); ca. 40 km NE Uriman, *Huber et al. 9915* (MYF, NY, VDB); 10 km SW Wadakapiapue-tepui, *Huber 11964* (MYF, VDB); Salto Carapo, *Huber 12406* (MYF, VDB); 2 km E Kavanayen, *Kral 72093* (MO, NY, US, VDB); El Puaji, *Liesner 19356* (MO, VDB, VEN); 15 km WSW Karaurin-tepui, Quebrada Tanuan, *Liesner 24093* (MO, VDB); Ilu-tepui, *Maguire 33356* (NY), *33528* (NY); 140 km S El Dorado, Rio Aponguao, *Rutkis 545* (VEN); Uarama-tepui, NE Luepa, *Steyermark & Nilsson 594* (NY); mesa between Ptari-tepui and Sororopan-tepui, *Steyermark 60243* (F); Auyan-tepui, *Steyermark 93502* (F, K, NY, US); cabeceras Río Aponguao, Arauta-paru, *Steyermark & Dunsterville 104114* (NY); valley of Río Cama at km 199.9 S of Río Cama, *Steyermark 111318* (F, NY, U); 50 km N Sta. Elena, *Steyermark & Liesner 127613* (MO, VDB).

This variety is perhaps easily confused in Territorio Federal Amazonas with the type variety, because variety *macrostachya* can be very robust in some of the low-elevation savanna along the Orinoco and its tributaries. However, such large individuals typically have very short scape bracts, and the tips of their lateral sepals do not project as far beyond subtending bract tips. In variety *robustior*, the usual case is for the scapes to be much more elongate, thicker, and the habit in general to be much more coarse, with a greater degree of purple or red pigmentation in scapes, bracts, and often leaves. This increased purple pigmentation of foliage and other parts in higher-elevation species and varieties, in contrast to less of it in species and varieties of lower elevations, seems to occur throughout the genus.

Gleason, in examining the type of his *Abolboda rigida* (*Schomburghk 146.S*) at K, did not note that the material is a mixture. The right-hand specimen must be what he refers to as "*A. rigida*," particularly in that he gives correct dimensions for *A. macrostachya* var. *robustior* spikes; the left-hand specimen, actually the more ample example, is material fitting the description of Malme for his *A. rigida*, which is now *A. grandis* var. *rigida*. The degree to which these authors relied on one or both of these examples on the single sheet is unclear.

20. Abolboda linearifolia Maguire, Mem. New York Bot. Gard. 10: 14. 1958. TYPE: Venezuela. Territorio Federal Amazonas: Yapacana Savanna III, 125 m, 31 Dec. 1950, *Maguire, Cowan & Wurdack 30468* (holotype, NY; isotypes, GH, NY, US). Figure 26.

Smooth perennial from a scaly, variously elongate, sparingly branched rhizome 3–6 mm thick, the roots spongy-thickened. Rosettes few-leaved, terminal at rhizome tips, the principal leaves 11–36 cm long, the sheaths thin, with convex, multicostate backs, narrowing ± abruptly from a broadly clasping base to 10 mm wide into narrowly linear, erect or ascending blades 2–3 mm wide, these compressed but firm, apically abruptly rounded to acute, mucronate or short-subulate, the margins forming a narrow hyaline border, the upper surface slightly concave or plane, finely striate-nerved, the lower surface coarsely 3–5-ribbed longitudinally. Scape erect, usually 1 per rosette, 20–25 cm long, 1.5–2.3 mm thick distally, there terete or with a few broad ribs; scape bracts 1 pair, subequal, at ½–⅔ way up scape, erect, lance-oblong, 1–2 cm long, the tips acute to subulate-spinulose, the borders broad, scarious, pale, the convex backs firm, coarsely nerved; spikes narrowly cylindric-ellipsoid, solitary and terminal, 2.5–5.5 cm long, 6–8 mm thick, many-flowered, the erect bracts all fertile, oblong-ovate, 12–15 mm long, broadly acute, with broad, pale scarious borders, the convex backs multiribbed and usually anthocyanic or deep green medially; sepals 2 or 3, the laterals elliptic-lanceolate, 10–12 mm long, the firm keel broadly alate, the apex narrowly rounded, the inner sepal oblong, scarcely keeled, mostly scarious, ca. 7–8 mm long; corolla ca. 2 cm long, bright blue, the broadly elliptic lobes ca. 1 cm long, spreading; anthers lance-oblong, ca. 3 mm long, yellowish, on filaments ca. 2.5 mm long; style ca. 2 cm long, the triquetrous base with 3 appendages, the laterals pendulous, irregularly claviform, acute, ca. 2.5 mm long, the central appendage reduced and slightly above the laterals. Capsule ca. 5 mm long, the valves elliptic, thickened and deeply notched apically. Seeds nearly isodiametric, ca. 0.7 mm long, coarsely reticulate, the longitudinal ribs slightly stronger and spiral.

Distribution. Locally abundant in low-elevation, mostly white sand savanna (50–200(–400) m) from Territorio Federal Amazonas, Venezuela, west into southeastern Colombia (Vaupés) along the Río Orinoco, Río Negro, and tributaries. Probably also in contiguous Brazilian savannas.

Additional material examined. COLOMBIA. VAUPES: Puerto Inírida, Río Inírida, 14 ago. 1975, *Garcia-Barriga 20831* (GH, US), *20855* (GH); W of Río Guainía N of Boca de Casiquiare, 5 Feb. 1980, *Liesner & Clark 9111* (MO, VDB). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: cerro Chipital, E cerro Chipital, *Guanchez 1087* (TFAV, VDB); Cerro Yapacana, *Huber 1599* (NY, US); bajo Ventuari, *Huber 4858* (NY); Yapacana Savanna I, Jan. 1951, *Maguire et al. 30789* (GH, NY—paratype); Pimichín, Nov. 1953, *Maguire et al. 36381* (NY—paratype), *36382* (NY—annotated as a possible hybrid between *A. grandis* and *A. macrostachya*); Yapacana III, *Maguire et al. 36622* (NY, US—paratype); Caño Hechimoni above mouth Río Siapa, *Maguire et al. 37642* (NY—paratype); Yapacana savannas, Sep. 1957, *Maguire et al. 41495* (GH, NY); Sabana Pacimoni, Oct. 1957, *Maguire & Wurdack 41680* (F, K, NY, US); Yavita, Jan. 1942, *L. L. Williams 14045* (F, US); 5 km below Guarinumo, June 1959, *Wurdack & Adderley 42855* (NY).

The comparatively blunt-tipped, uniformly linear leaf blades and the rhizome character distinguish this from the closely related *Abolboda macrostachya*. Some of the narrower-leaved extremes of *A. macrostachya* (described as *A. macrostachya* var. *angustior*) may indeed be products of gene exchange between the two species. However, I believe these are mostly separable on the basis of a distinct taper of leaf blade and a stouter rootstock in *A. macrostachya*, in contrast to the lack of taper of leaf blade and a narrow rootstock in *A. linearifolia*.

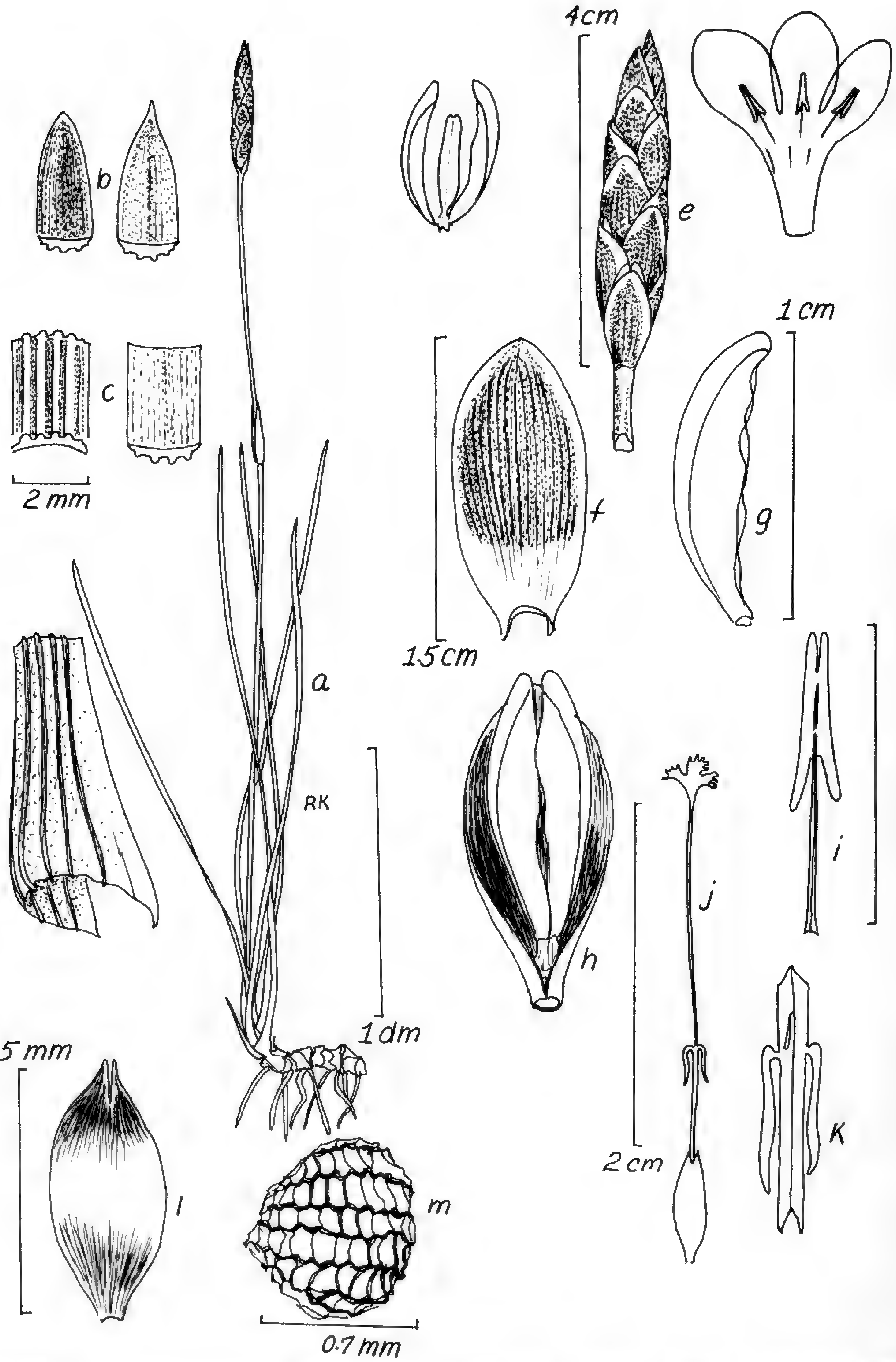

FIGURE 26. *Abolboda linearifolia* (*Maguire, Cowan & Wurdack 30468*).—a. Habit.—b. Leaf tip, two sorts.—c. Abaxial (left) and adaxial (right) views of a sector of leaf midblade.—d. Leaf base.—e. Spike and upper scape (middle); calyx (at left) showing 3 sepals; spread corolla, stamens (at right).—f. Fertile bract.—g. Lateral sepal.—h. Inner view to show relative position of sepals within fertile bract.—i. Stamen.—j. Gynoecium.—k. Enlarged view of stylar base with appendages.—l. Capsule, external view of one valve.—m. Seed.

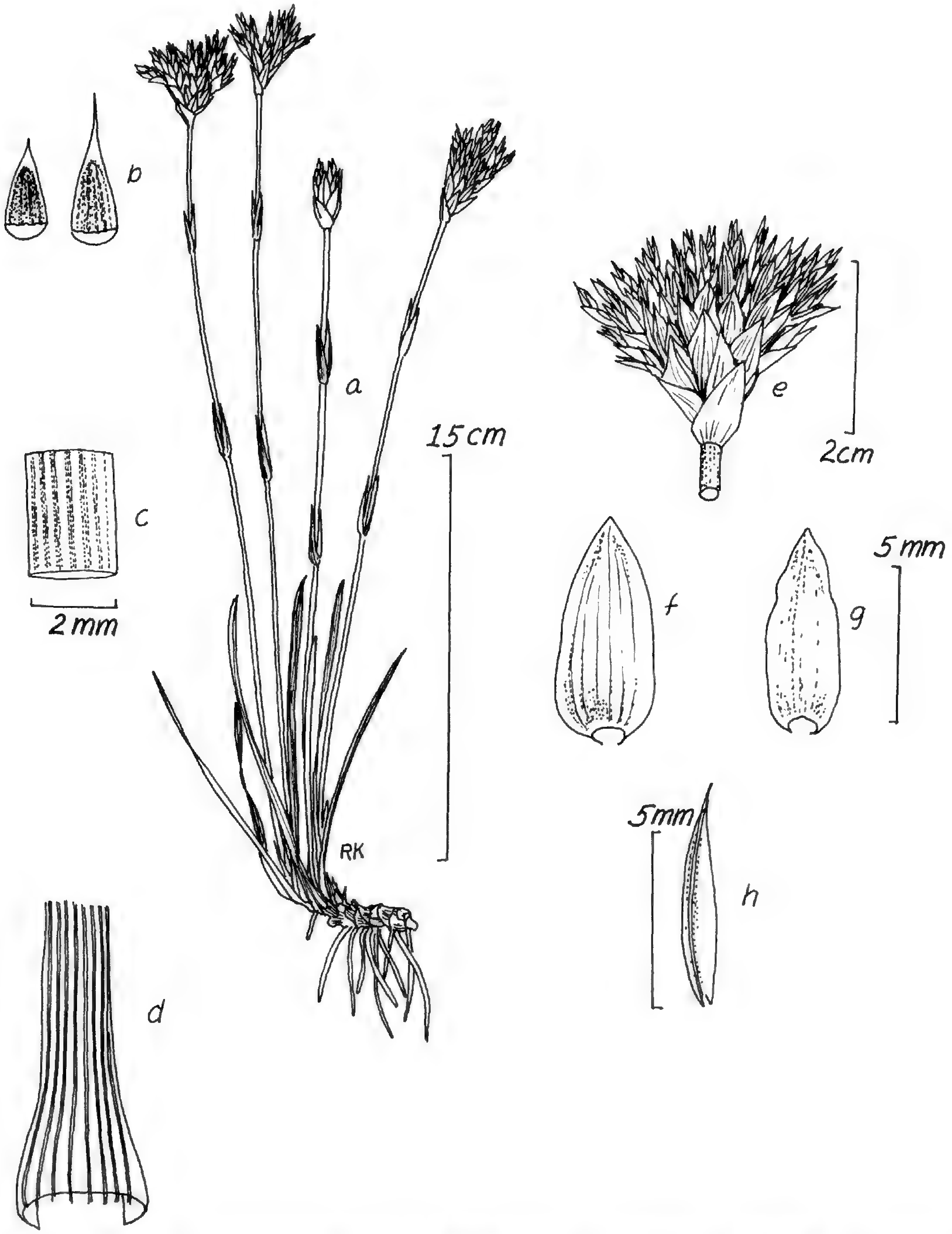

FIGURE 27. *Abolboda* ×*glomerata* (*Maguire & Wurdack 35593*).—a. Habit.—b. Leaf tips.—c. Sector of leaf at midblade, abaxial side.—d. Leaf base.—e. Inflorescence.—f. Lower inflorescence bract.—g. Spike bract, abaxial side.—h. Lateral sepal.

21. **Abolboda ×glomerata** (Maguire) Kral, stat. nov. *Abolboda glomerata* Maguire, Mem. New York Bot. Gard. 10: 14. 1958. TYPE: Venezuela. Territorio Federal Amazonas: Sabana Venado, left banks of Caño Pimichín above Puerto Pimichín, affluent Río Guainía, 140 m, 14 Apr. 1953, *Maguire & Wurdack 35593* (holotype, NY; isotype, US). Figure 27.

Glabrous perennial from a stout horizontal rhizome ca. 6 mm thick, the roots spongy-thickened. Leaves few, stiff, spreading-ascending, 5–10 cm long, the stramineous, thin, multicostate sheaths ca. 5 mm wide at clasping base, narrowing to linear, firm blades, 2–2.5 mm wide, these narrowed abruptly to acute, mucronate or subulate apices, the margins rather thin but with narrow, pale, cartilaginous, wirelike borders, the adaxial surface flat or slightly concave, finely nerved, the abaxial surface coarsely nerved and usually convex, both sides dull green. Scapes stiffly erect or ascending, 16–27 cm high, yellow green, distally 15–23 mm thick, terete or somewhat angled, coarsely costate to striate; scape bracts 2 pairs, erect, lance-oblong, subequal, 1–2 cm long, involute, the tips subulate to acute, the borders broad, pale, scarious; inflorescence a narrowly to broadly turbinate or ellipsoid fascicle of spikes, ca. 2 cm long, the individual spikes mostly lanceoloid or ellipsoid-cylindric; lower inflorescence bracts (involucre) broadly to narrowly ovate, 8–15 mm long, those above within the spikes numerous, progressively shorter, in spikes 1–2 cm long, these bracts ascending, ovate, 5–8 mm long, acute, with strongly nerved, convex, green or purple-tinged median areas and somewhat keeled apically, subtending lanceolate, thin, lateral sepals ca. 6–8 mm long, these with tips acuminate-subulate, with backs carinate, the keel strong, entire, excurrent, the sides thin, pale; flower parts other than sepals not developed.

Distribution. Known only from the type locality and not collected since.

It is suggested that these plants, while abundant according to record, are genetic anomalies, possibly the result of chance hybridization between *Abolboda linearifolia* and *A. macrostachya* var. *macrostachya*. As no floral structure other than sepals is developed in the spikes, it can only be assumed that reproduction is strictly vegetative, clonal either by rhizome or by a toppling and rooting of scapes within the inflorescence.

Achlyphila Maguire & Wurdack, Mem. New York Bot. Gard. 10(2): 12, fig. 1a–m. 1960. TYPE: *A. disticha* Maguire & Wurdack.

1. **Achlyphila disticha** Maguire & Wurdack, Mem. New York Bot. Gard. 10(2): 12. 1960. TYPE: Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, 2,000 m, 14 Dec. 1957, *B. Maguire, J. J. Wurdack & C. K. Maguire 40402* (holotype, NY; isotypes, US, VEN). Figures 28, 29.

Stiff, slender, papillose-scabrid perennial herb from branched, slender, horizontal, short-internoded, branched rhizomes to 3 mm thick, the roots slender-fibrous. Leaves distichous, stiff, erect or ascending, imbricate-based, the lowest scalelike, gradually longer upstem, the longest at or toward scape base, lance-linear, 8–12 cm long, their bases completely sheathing the compressed internodes, these laterally compressed, 2–3 mm wide, strongly nerved; blades with bases strongly open-sheathing, the sheaths strongly infolded, scabrous-keeled, equaling or longer than the blades, with broad, scarious borders, these converging gradually to a strong, scarious, blunt-tipped ligule 2–4 mm long; blades linear-triangular, laterally compressed, 2–3 mm wide at junction with ligule and tapering evenly to subterete, incrassate, setaceous tips, the margins strongly thickened and strongly papillose-tuberculate, the surfaces transversely rugulose-papillose, pale yellow-green. Scapes terminal, laterally compressed, 7–15 cm long, ca. 3 mm wide, narrowly elliptic in cross section, the narrow hard edges papillose-tuberculate, the pale green surfaces finely papillose. Inflorescence terminal, mostly narrowly turbinate, 3–6 cm long from base to bract tips, the bracts and flowers essentially distichously arranged, with primary and secondary peduncles erect or ascending, occasionally excurved; bracts as in foliage leaves but shorter, the lowest erect and slightly shorter or slightly longer than the rest of the inflorescence, thus 4–6 cm long, producing from axils either a fascicle of 3–4 pedicels subtended by a lanciform, scarious-bordered secondary bract or 2–3 pedicels and an opposing short (to 1 cm long) laterally compressed, costate internode and a bract, this subtending 2–3 pedicels subtended by an opposing yet shorter bract (prophyll?); pedicels stiff, erect or somewhat excurved to ascending, 1–3 cm long, linear-claviform; flowers subregular, the sepals lanciform, spirally imbricate, the laterals external, 1.5–1.7 cm long, with thickened dorsal areas crested by a broad, rounded, tuberculate-papillate keel and with broad, scarious, strongly involute borders, these converging-overlapping at sepal tip, this with a scarious-bifid apex, the costa excurrent as a stiff, scaberulous cusp; inner sepal similar to the laterals but less spreading and shorter; petals 3, distinct to base and unclawed, obovate to rhombic, 1.2–1.4 cm long, yellow, the apex narrowly rounded, the margins undulate or sinuate; staminodia lacking; stamens opposing petals and hypogynous, the anthers tetrasporangiate and bilocular, at anthesis broadly lanciform, 2.5–3 mm long, the apex shallowly notched, the base with locules widely divergent along a broadened, thin connective, sagittate, there joined to the slender tip of a broad-based, somewhat flattened filament 5–5.5 mm long; ovary oblong-trigonous, ca. 3.5 mm long; style ca. 2 mm long,

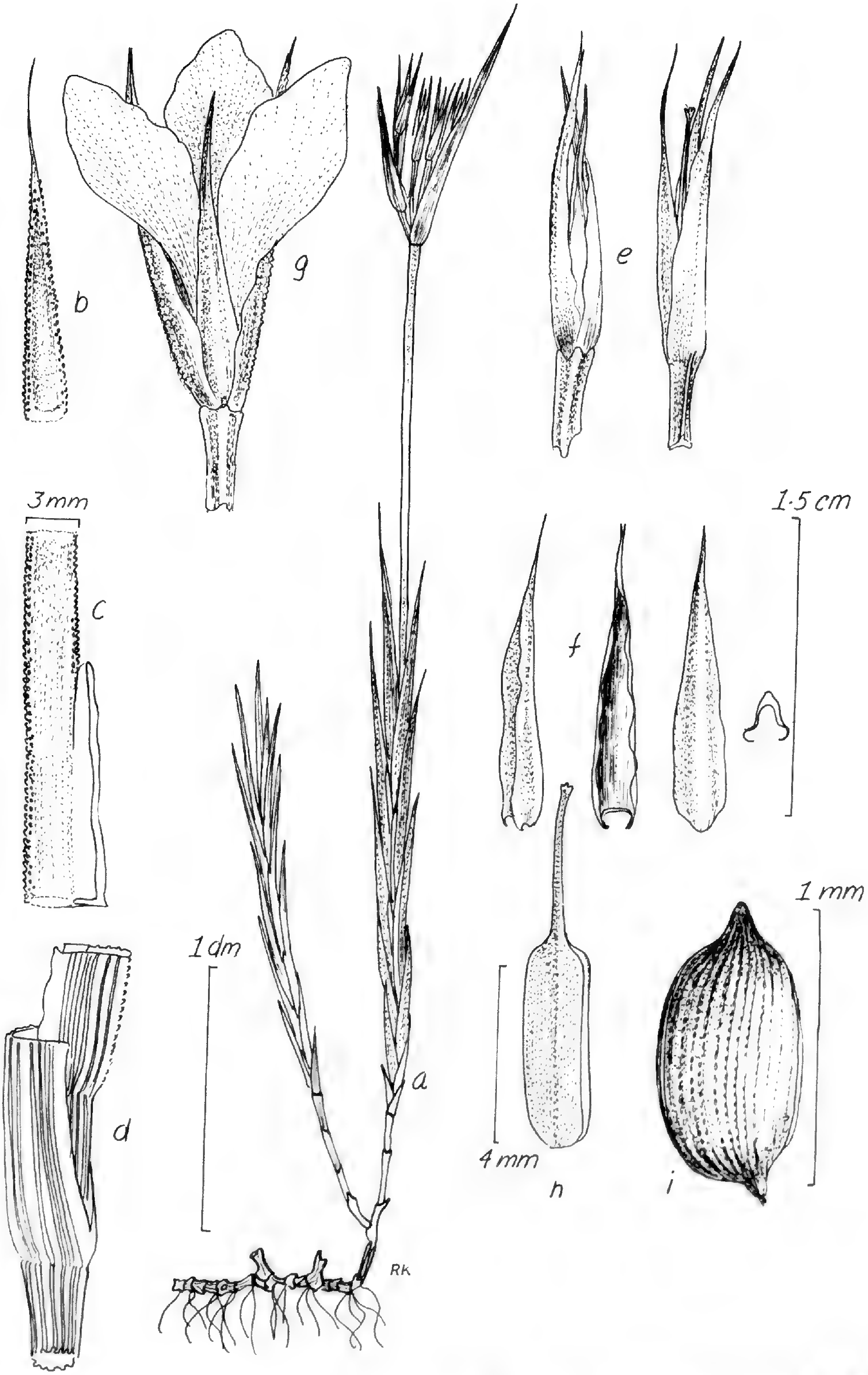

FIGURE 28. *Achlyphila disticha* (*Kral 71924*).—a. Habit.—b. Leaf tip.—c. Leaf at junction of blade and sheath, side view.—d. Two nodes with blades cut away above base.—e. Two views of fruiting calyx.—f. Lateral (left), inner (middle), and outer (right) views of a lateral sepal.—g. Flower.—h. Capsule.—i. Seed.

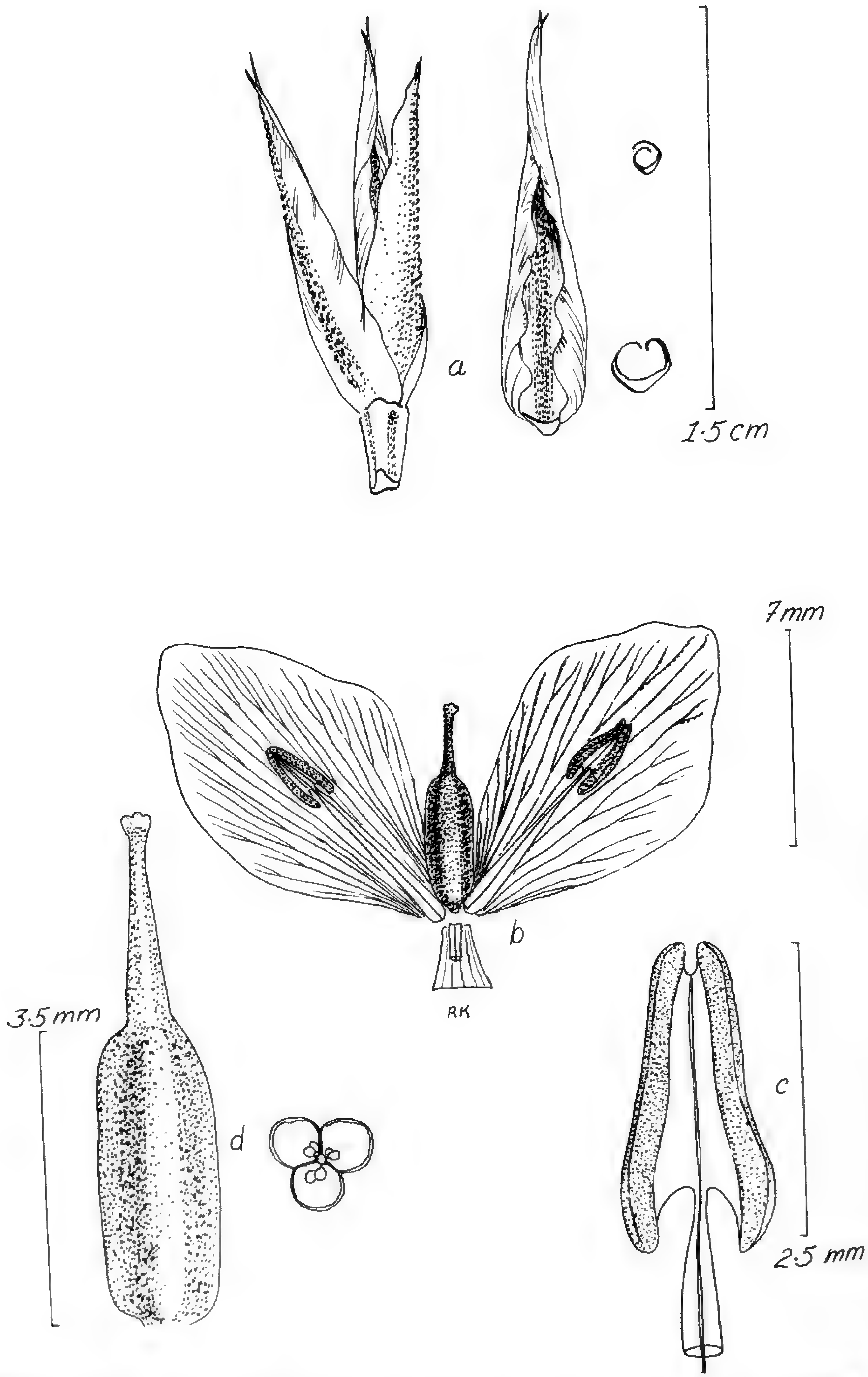

FIGURE 29. *Achlyphila disticha* (*Kral 71924*).—a. At left, mature calyx; at right, an inner view of a lateral sepal.—b. Spread flower showing relative positions and dimensions of petals, stamens, and gynoecium.—c. Enlarged view of anther at anthesis.—d. Side view of capsule with persistent style (left); diagram of cross section of young capsule (right).

stiffly erect, tapering-linear, with a short, capitate, shallowly 3-lobed stigma. Capsule ca. 4.5–5 mm long, oblong-trigonous, dull brown, the placentation axile along 2 approximate placental lines per locule, the valves later falling free. Seeds ovoid to subglobose, 0.9–1.0 mm long, with a short, bluntly conic apiculus and with several slightly spiral, longitudinal, minutely papillate ribs, the intervals marked by numerous, low, transverse short connections.

Distribution. Abundant locally in peaty, moist to wet, rocky shrub bogs, summit elevations along Cerro Neblina, Territorio Federal Amazonas, Venezuela (ca. 800–2,300 m), thus, along a common border with Brazil (this as yet undocumented).

Additional material examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: near E escarpment of upper Cañón Grande basin , 2,000 m, 14 Dec. 1957, *Maguire et al. 42386* (NY—paratype); Valle de Titírico, N of Pico Phelps, Neblina Massif, by rocky but wet ridges, ca. 2,300 m, 1 Dec. 1984, *Kral 71924* (F, GH, MO, NY, SP, US, VDB, VEN); Camp III, Neblina and Massif, NW Plateau (arm) 13.5 km ENE of Cerro de la Neblina Base Camp, 1,750–1,850 m, on ridge, 16–18 Feb. 1984, *Liesner 16049* (MO, NY, VDB, VEN).

This is the monotypic genus whose discovery led anatomists and morphologists to treat Abolbodaceae and Xyridaceae as one family, because it possesses characters intermediate to both. Its general floral organization is the most primitive in the family except for the lack of staminodia. It is the only xyridaceous genus in which the stamens are distinct from the petals. The elongate stems with their equitant and distichous, strongly ascending and imbricate leaves form plates of leaves similar to some of the more "primitive" xyris, which likewise have a completely axile placentation, namely species such as *X. ptariana*, *X. witsenioides*, *X. xiphophylla*, all of which have a similar distribution and ecology.

Aratitiyopea Steyermark & Berry, Ann. Missouri Bot. Gard. 71: 297. 1984. TYPE: *Aratitiyopea lopezii* (Lyman B. Smith) Steyerm. & Berry. Figure 30.

Robust perennial from a trailing or repent rhizome to 2 m long and to 1.5 cm thick, the rhizomal nodes numerous and annular, the reddish brown internodes short-cylindric, the roots slender-fibrous. Outer part of rhizome densely cloaked by spirally imbricate scales (the scales being remnants of old leaf bases), passing gradually into a sprawling or ascending leafy shoot. Leaves spirally imbricate, numerous and crowded toward shoot apex, the principal ones spreading or ascending, lorate-linear, ligulate, the longer ones downstem, 20–40 cm long, 20–40 mm broad, strongly compressed, narrowly acute to slenderly acuminate, upstem proportionately gradually shortening and with broader outline, more spreading, more broadly acute, all blades with thin, entire, subscarious and often crisped margins, and smooth, deep-lustrous-green, finely nerved surfaces; leaf bases broadly clasping, and here a lustrous pale to deep brown, immediately above this somewhat constricted, thence upblade gradually broadening, thence from midblade to tip evenly narrowing to blade apex; inner (upper) foliage leaves ringing a dense, subcapitate, chaffy-involucrate head, this convex mass hemispheric, of many bracts subtending flower clusters and ringing the complex, the outer bracts broadest, mostly 5–7 cm long, lanciform, ecarinate and sharply acute, the inner ones directly subtending flowers narrower, ca. as long, all distinctly paler than the foliage leaves, mostly with red-purple, entire borders and tips, the center paler, cream with flecks of red, appearing pale pink, the surfaces smooth, finely striate-nerved. Sepals 3, comparable to inner bracts in outline and length, the outer (lateral) 2 infolded inequilaterally, their bases spirally imbricate, the keel sharp and usually anthocyanic, entire; inner sepal ecarinate but with a median sharp, narrow costa. Corolla salverform, actinomorphic, pale purple, 7–10 cm long from base to tip of lobes, the tube narrowly cylindric, dilated over the broad ovary, at apex abruptly broadening to 3, ascending to spreading-recurved oblong, lingulate, broadly rounded or shallowly retuse lobes 1.5–2.2 cm long; stamens 3, epipetalous, arising just below the base of each lobe, the filaments erect, slender, flattened, the anthers golden, narrowly oblong-linear, 4–5 mm long, the anther apex slightly emarginate, the connective producing a median apiculus, the base shallowly auriculate. Ovary dorisventrally compressed, greenish, obovate, trilocular with 3 locules and 6 placentae, the slender style ca. 8 cm long, below triangled and producing at each angle at very base 3 appendages, these at their callused, subtruncate bases doubled back and terminating in narrowly to broadly flabellate, unevenly crenate, thin tips which touch the ovary summit; stylar apex 3-branched, producing 3 connivent, bristly-hairy, broad stigma lobes. Ripe fruit thin-walled, greenish, dorsiventrally compressed, oblong-ellipsoid to obovoid, 1.2–1.4 cm long, the apex obscurely 3-lobed, in profile subtruncate or broadly rounded, the slightly depressed center produced to a short-broad apiculus (very base of style). Seeds numerous, broadly ellipsoid to subglobose, mostly subsymmetric, pale brown to deep brown,

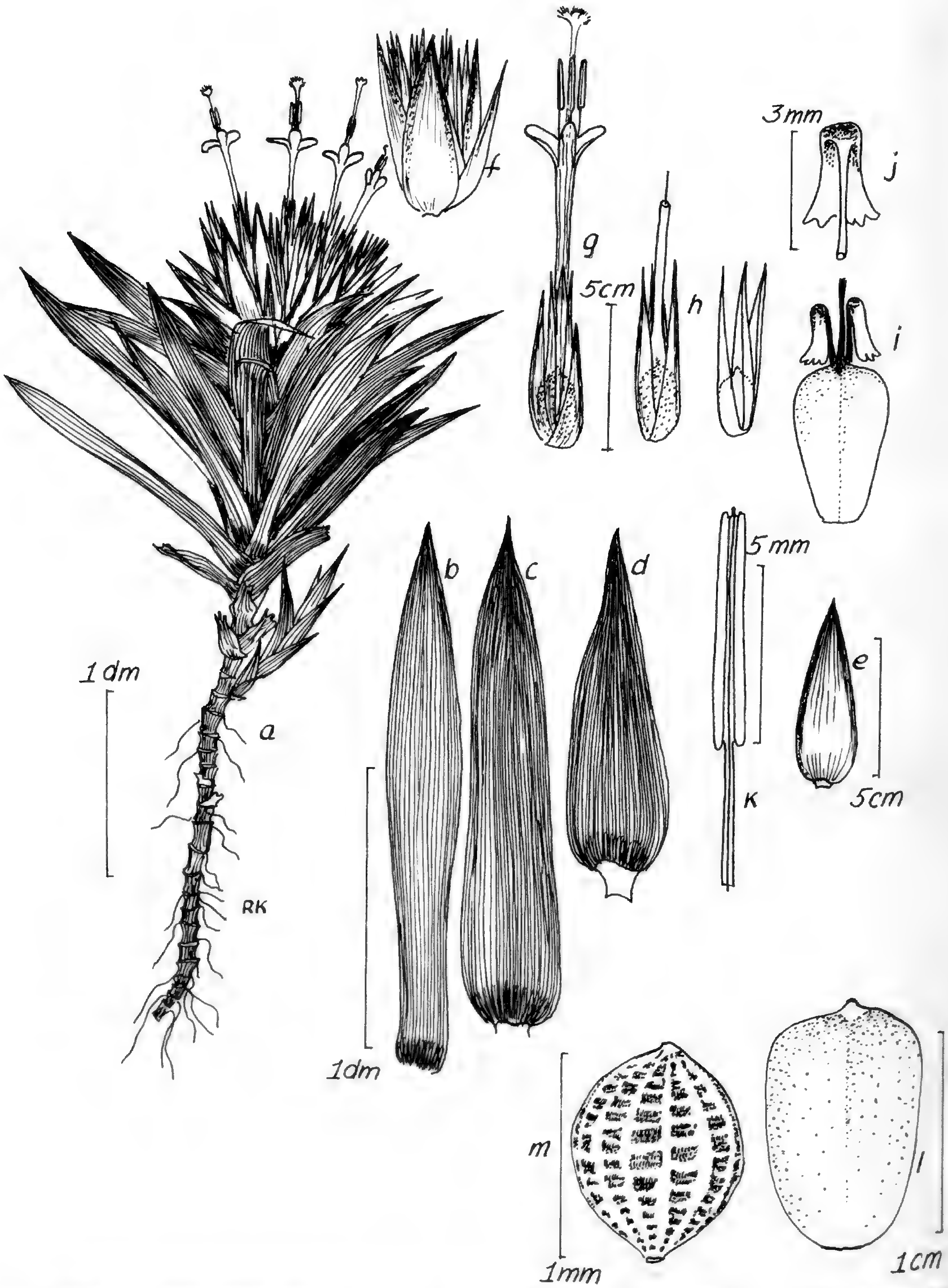

FIGURE 30. *Aratitiyopea lopezii* var. *lopezii* (*Maguire & Politi 27742*).—Habit.—b. Principal foliage leaf, upper stem.—c. Uppermost principal leaf.—d. Foliage leaf directly subtending involucre.—e. Outer bract of flower cluster.—f. Flower cluster.—g. Flower at anthesis, subtended by two inner bracts.—h. Calyx with enclosed floral base (outer view, left); calyx with enclosed ovary (inner view, right).—i. Gynoecial base, showing appendages at stylar base.—j. Appendage, inner view.—k. Anther, with portion of filament apex.—l. Capsule.—m. Seed.

longitudinally with 12–14 strong ribs, and numerous lower cross-ribs in the intervals, thus reticulate-alveolate.

KEY TO VARIETIES OF *ARATITIYOPEA LOPEZII*

1a. Larger leaves 20–40 cm long, 2–4 cm wide; heads 3–7 cm across base, 7–15 cm broad, 7–10 cm high; floral bracts 5–7 cm long, red-purple with paler median zones; sepals ca. as long, roseate-bordered; corollas (fide *Steyermark & Berry*) pale purple .... 1a. *A. lopezii* var. *lopezii*

1b. Larger leaves 10–18 cm long, 1.5–2.5 cm wide; heads 2–3 cm across base, 4–7 cm broad, 4–5 cm high; floral bracts 3–4 cm long, purple outside, yellowish to purple inside; sepals ca. as long, pinkish or pinkish-bordered; corollas white or near white .... 1b. *A. lopezii* var. *colombiana*

1a. **Aratitiyopea lopezii** (Lyman B. Smith) Steyerm. & Berry var. **lopezii**, Ann. Missouri Bot. Gard. 71: 297, fig. 1A–K. 1984. *Navia lopezii* Lyman B. Smith, Bot. Mus. Leafl. 15: 40. 1951. TYPE: Brazil. Amazonas: Cerro Dimiti, upper Rio Negro basin, on rocks, 800 m, 12–19 May 1948, *Schultes & Lopez 9956* (holotype, *US-1985318*; isotype, *US-1985319*). Figure 30.

See genus description and key.

Distribution. Territorio Federal Amazonas of southwestern Venezuela, northwestern Brazil, and southeastern Colombia (Vaupés), usually on wet, open or shaded, rocky faces, 250–1,600 m.

Additional material examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Avispa, *Dunsterville & Dunsterville*, Dec. 1972 (US); Cerro Avispa, Río Siapa, *Dunsterville & Dunsterville s.n.* (US); Cerro Sipapo, lower N escarpment, Nov. 1948, *Maguire & Politi 27497* (US); spray of waterfalls, Caño Profundo, Jan. 1949, *Maguire & Politi 28276* (US); Cerro Aratitiyope, ca. 90 km SSW de Ocamo, 24–28 fev. 1984, *Steyermark et al. 130088* (MO, US), *130289* (MO); Río Siapa just below Raudal Gallipeta, July 1959, *Wurdack & Adderley 43564* (US).

The discussion of the species given by Steyermark & Berry (1984) appears largely to be based upon *Aratitiyopea lopezii* var. *lopezii*, the widest-ranging and most-collected of the two varieties. For some reason, the authors did not include information on the variety *colombiana* (Lyman B. Smith) Steyerm. & Berry in their article, but simply made the transfer from *Navia* (Bromeliaceae). Doubtless this was because of the paucity of material available. From the few examples I have available on loan (three sheets at US, all from Cerro Isibukuri by Río Kananari in Vaupés, Colombia, two (one the type) collected 4 August 1951, and one the following year (23–25 January), these could be from the same population. Differences between the two varieties appear to be largely quantitative. The habit is the same, but the rhizome of variety *colombiana* is narrower; the leaves of variety *colombiana* are similarly shaped but smaller, as are involucral bracts and sepals. The colors (as given by Schultes & Cabrera, the collectors of the Vaupés material) appear to be different from those of the type variety, as bracts are described as "purple-brown" or "purple inside and out." Bract color on the type specimen is given as "purple outside, pinkish or yellowish inside." Flowers (none available on the material) are described as white on the type label, "whitish" on one of the paratypes.

A later and more detailed, field-oriented survey of the two varieties may show a running together of the two. In any case, this species should be cultivated, as it is without question (even from one who has seen only color slides of it) the most beautiful of the Xyridaceae yet found. From examination of specimens without flowers and from viewing the color photographs, it is easy to see how these plants were first placed in the Bromeliaceae.

1b. **Aratitiyopea lopezii** (Lyman B. Smith) Steyerm. & Berry var. **colombiana** (Lyman B. Smith) Steyerm. & Berry, Ann. Missouri Bot. Gard. 71: 299. 1984. *Navia lopezii* var. *colombiana* Lyman B. Smith, Bot. Mus. Leafl. 16: 195. 1954. TYPE: Colombia. Vaupés: Río Kananari, Cerro Isibukuri, piedra de arenisca, 250 m, 4 Aug. 1951, *R. E. Schultes & I. Cabrera 13342* (holotype, US; isotypes, GH, COL).

See key to varieties and discussion under variety *lopezii*.

Distribution. Shaded and sunny, wet, rock outcrops, Vaupés, southeastern Colombia, 250–700 m.

Additional material examined. COLOMBIA. VAUPES: Río Kananari, Cerro Isibukuri, 4 ago. 1951, *Schultes & Cabrera 13393* (US); Río Kananari, Cerro Isibukuri, base of mountain, 23–25 Jan. 1952, *Schultes & Cabrera 15078* (US).

Orectanthe Maguire, Mem. New York Bot. Gard. 10: 2–3. 1958. TYPE: *Abolboda sceptrum* F. Oliver.

Coarse, smooth, perennials 0.5–2 m high; stems either short, stout, producing dense basal rosettes, or lax, decumbent, elongate and cloaked by higher, looser spirals of leaves. Leaves polystichous, narrowly panduriform, 5–40 cm, firm, bases dilated, clasping with a broad, maroon or red-brown patch, blades variably linear, lingulate to flat, finely multinerved, apically sharply subulate, margins thin, entire, aging lacerate. Scapes 1–several from axils of upper leaves, fistulose, terete, 0.2–2 m, to 2 cm thick at base; spikes burrlike, multiflorous, hemispheric to broadly turbinate or globose, 5–10 cm broad across spreading sepal tips; outer bracts in 1(–2) whorls of 3, often empty, floral bracts much shorter than sepals, ovate to broadly lanceolate. Sepals 3, subequal, lanciform-navicular, acuminate, the laterals with broad curved keel, the third thinner and without keel; petals connate, unequal, forming a spreading-recurved, yellow (rarely reddish), two-lipped corolla to 6 cm long, limb about as long as recurved tube and throat, trilobed, upper lobe largest, broadest, forming a hood, the lower 2 spreading outward, forward, slightly down and forming the lower lip; staminodes none; stamens 3, adnate to upper corolla tube, filaments longer than anthers, anthers ca. 1 cm long; placentation axile; style elongate, apically curved, with terminal, patelliform, papillose, later fimbriolate, stigma; stylar appendages linear, firm, doubled back to form an inverted "U," arising from ovary summit around style base and 2–2.4 cm long. Capsule ovoid to obovoid, trilobed, 1.5–2 cm, valves thick, tips shallowly bilobed; seeds numerous, irregularly curvate-triangular, 2–4 mm, edged with a broad wing around embryo, 1 edge forming a narrow, ascending, thumblike lobe, surface finely curved-striate, lustrous brown. Two species of northern South America.

Distribution. Southwestern Guyana across southern Venezuela into Territorio Federal Amazonas and southward into contiguous Brazil, on the Roraima sandstones, usually in boggy pockets among rocks and in full sun, at medium to high elevations (500–2,700 m).

KEY TO SPECIES OF *ORECTANTHE*

1a. Stem contracted, caudiciform, erect; leaves in dense basal rosette; outer cephalar bracts mostly with flowers, thus directly subtending lateral sepals; scapes mostly solitary, mostly longer than stem .... 1. *O. sceptrum*
1b. Stem elongate, lax, often decumbent, or sprawling to 1.5 m or more; leaves in long, high spiral, not forming a distinct basal rosette; outer cephalar bracts empty; scapes 2 or more, shorter than stem .... 2. *O. ptaritepuiana*

1. Orectanthe sceptrum (F. Oliver) Maguire, Mem. New York Bot. Gard. 10(1): 3. 1958. *Abolboda sceptrum* F. Oliver, Trans. Linn. Soc. London, Bot. 2: 286. 1887. TYPE: Guyana. Roraima summit, *im Thurn 312* (holotype, K; isotype, US). Figures 31, 32.

Orectanthe sceptrum (F. Oliver) Maguire subsp. *occidentalis* Maguire, Mem. New York Bot. Gard. 10: 5. 1958. TYPE: Venezuela. Territorio Federal Amazonas: SE escarpment, Cerro Huachamacari, *Maguire et al. 30140* (holotype, NY).

Robust, glabrous, sometimes glaucous, Yucca-like perennial, rosulate herb, (2–)4–15(–20) dm tall from a thick caudex, the roots coarse, fibrous, the stem erect or ascending, stout, to 2 cm thick, either short or elongating to 3 dm, simple or from branch buds of a rosette base. Leaves firm, spirally imbricate in tight or loose spirals, those of elongating shoots and branches ascending to spreading in loose spirals, those of flowering portion in flatter tight spirals, thus forming a rosette, the former type mostly linear and more lax, those of rosettes usually gladiately linear-triangular or lanceolate, spreading to erect, (5–)10–30(–40) cm long, blades flat, apically narrowly acute to acuminate, involute at tips to a callused point, the margins forming a deep red-brown, thin but firm and sharp entire border, this aging to be upwardly jagged, toward base usually somewhat constricted, then flaring to the broadly sheathing (1–6 cm wide) base and with a broad, brown to castaneous patch, the leaf bases persisting several seasons as a tight, chaffy, stubbly shingling on the stem. Scapes usually solitary at stem apex, less often 2 or few from axillae of rosette leaves, mostly erect, fistulose, terete, cloaked at base by 2–several, erect, short, involute sheath leaves and there 1–2 cm thick, overall tinted with red-purple or brown, rarely with 1–2 narrowly linear subscarious bracts toward base; spikes headlike, solitary and terminal, multiflorous, in bud ovoid, during and after anthesis with parts more spreading, broadly turbinate to broadly ovoid, but usually globose to hemispheric, 5–10 cm high, nearly as broad across the sepal tips; outer (involucral) bracts of 1 (rarely 2) series of 3, ovate to lanceolate, leathery-chaffy, rigid, 2–6 cm long, 7–15 mm wide, finely nerved, acute, entire, yellow-green or anthocyanic; flowers rigid-based and tightly imbricate, each consisting of 1 adaxial, appressed, lance-ovate bracts ca. ½ as long as sepals and 3 erect, subequal, connivent sepals to ca. 6 cm long, all imbricate in 1 flat spiral; lateral sepals lanceolate, to 6 cm long, chaffy, strongly folded, narrowly acute, subequilateral with a strong, broad, flat entire keel, the inner sepal adaxial, lanceolate but ecarinate, thinner, the borders narrowly involute but thin, apically more inrolled to a subulate tip;

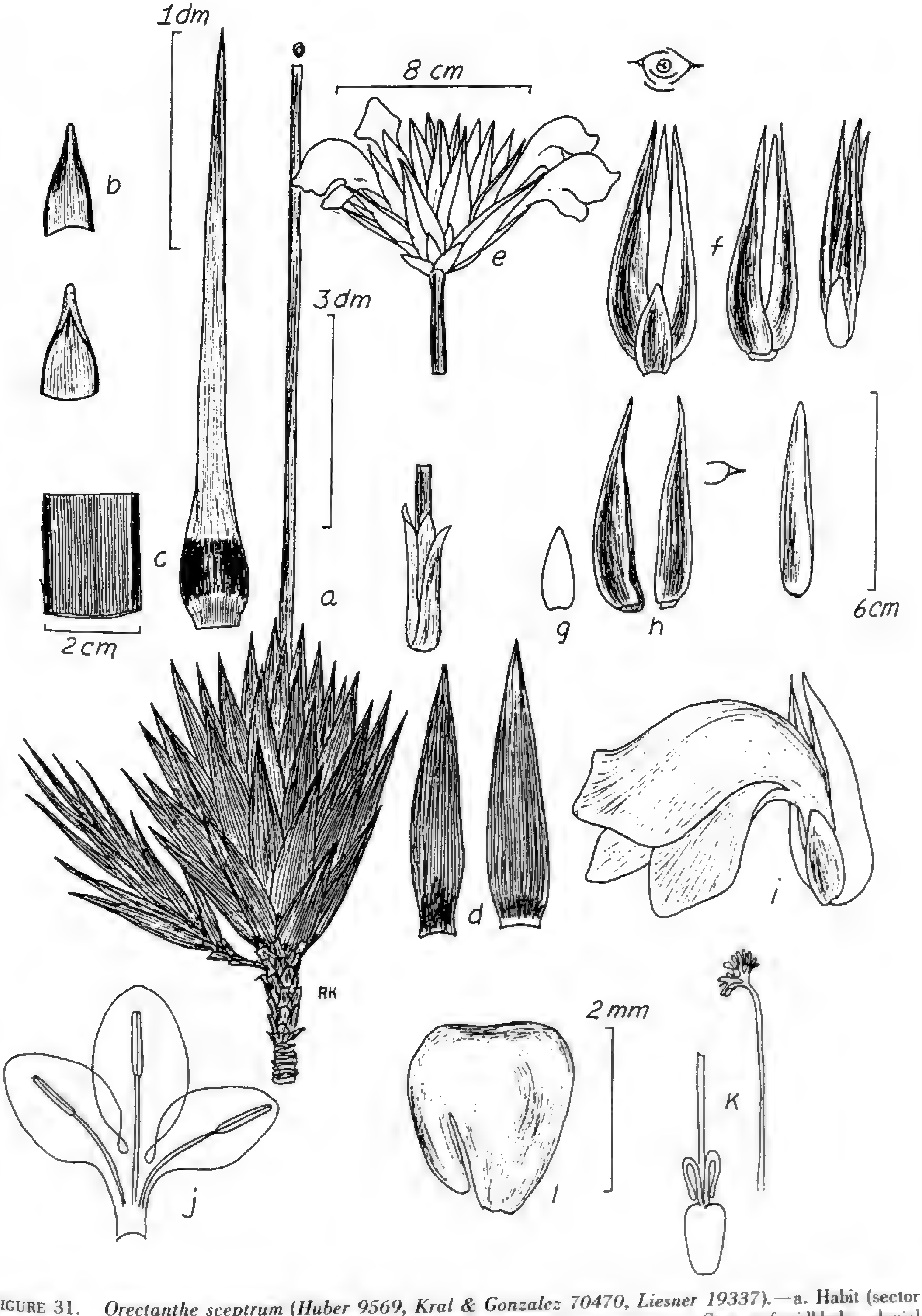

FIGURE 31. *Orectanthe sceptrum* (*Huber 9569, Kral & Gonzalez 70470, Liesner 19337*).—a. Habit (sector of upper scape removed).—b. Two leaf tips, abaxial side (above), adaxial side (below).—c. Sector of midblade, adaxial side (left) and abaxial view of entire blade (right).—d. Some shorter rosette leaves (below) and basal bracts of scape (above).—e. Flowering inflorescence.—f. Abaxial view of floral bract and calyx (left); inner view of calyx (middle); oblique view of floral bract and calyx (right).—g. Floral bract.—h. Lateral sepals (left); inner sepal (right).—i. Flower, natural posture.—j. Ideal view of spread corolla, stamens.—k. Ideal view of gynoecium.—l. Seed.

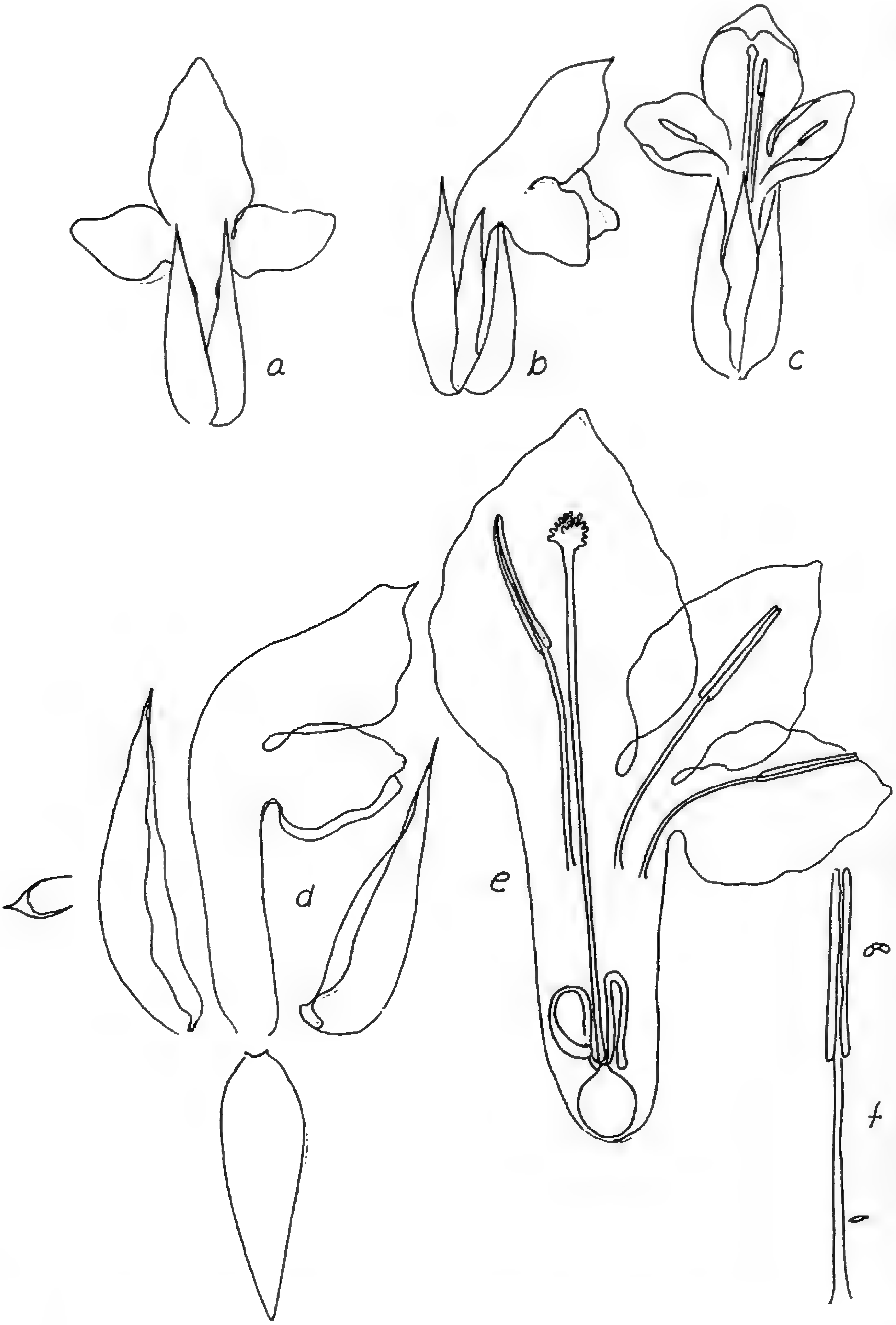

FIGURE 32. *Orectanthe sceptrum* (*Huber 9569*).—a–c. Inside (left), lateral (middle), and oblique (right) views of flower, scale omitted.—d. Exploded flower, corolla viewed from side.—e. Flower opened so as to show spread corolla, stamens, gynoecium.—f. Stamen.

corolla large for a xyrid, 6–8 cm long, zygomorphic, yellow, rarely purple, the lobes longer than the erect tube, broadly ovate, the upper one spreading and excurved, its margins spreading, the laterals spreading and directed downward (see figure); staminodia lacking; anthers oblong-linear, basifixed, 10–11 mm long, on slender filaments 15–25 mm long, arising midway down corolla tube; style erect, 30–35 mm long, terete, briefly recurved apically to produce a glandular-fimbriolate oblique stigma pad, the ovary summit around its base producing 3 linear reflexed firm appendages

20–24 mm long, these disarticulating just above base to leave 3 nubs at the capsule apex; capsule thick-valved, ovoid, 15–20 mm long, lustrous, brown, the narrowed valve tips each with 2 thickened short lobes, these forming a 6-lobed "annulus" around the appendaged fruit apex. Seeds numerous, irregularly curvate-triangular, 2–4 mm long, edged with a broad wing around embryo, 1 edge forming a narrow, ascending, thumblike lobe, the surface finely curved-striate, lustrous brown.

Distribution. Through the Guayana Highlands, in boggy rocky savanna atop Roraima sandstones, at medium to high elevations (500–2,700 m) from southwestern Guyana and contiguous Brazil westward across Bolívar through southern Territorio Federal Amazonas, Venezuela.

Representative material examined. BRAZIL. RORAIMA: *Ule 8559* (K). GUYANA. Mt. Roraima, Oct. 1884–Jan. 1885, *Mt. Roraima Expedition, Set C, no. 312* (K—a single small rosette); Roraima, Nov.–Dec. 1931, *Abbensetts 37* (K—base with 3 scapes); Roraima, N ridge escarpment, Mar. 1978, *Edwards, K. E. R. 106* (K); Imbaimadai Savannas, Oct. 1951, *Maguire & Fanshawe 32254* (NY, US); Mt. Ayanganna, *Maguire & Bagshaw 40567* (K, NH); Summit Roraima, *McConnell & Quelch 668* (K); Roraima Escarpment, Oct. 1973, *Persaud 83* (K, NY); Mt. Ayanganna, Aug. 1960, *Tillett & Boyan 45097* (K, NY, US—several scapes per stem). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Camp III, Neblina, NW plateau, Feb. 1984, *Liesner 15991* (MO); Cerro Marahuaca, *Liesner 24764* (MO); Cerro Sipapo, West Peak, Dec. 1948, *Maguire & Politi 2777* (GH, NY); Sipapo, Jan. 1949, *Maguire & Politi 28106* (NY), *28451* (NY); Cerro Sipapo, North Mountain, *Maguire & Politi 28569* (K, NY, U, US); Sipapo, South Escarpment, *Maguire & Politi 28645* (NY); South Basin, *Maguire & Politi 28678* (NY); Cerro Huachamacari, *Maguire et al. 29822, 30079, 30213* (all NY); Cerro Neblina, *Maguire et al. 37303* (NY, US); Neblina, W Savannas, *Maguire & Wurdack 42166, 42418* (NY); Cerro Marahuaca, *Maguire et al. 65563* (MO); Planicie de Zuloaga, Neblina, *Steyermark 103824* (NY); Cerro Marahuaca, cumbre, *Steyermark et al. 124394* (MO), *125981* (NY), *129486* (MO); Mt. Duida, *Tate 398* (NY). BOLIVAR: Aprada Tepuy, ago.–sept. 1953, *Bernardi 936* (NY); Auyan-tepui, *Bogner 1000* (K); Matahui-tepui, *Castillo 2284* (UCV, VDB); El Pauji, *Holst & Liesner 2323* (MO); Murisipan-tepui, *Holst et al. 2930* (MO); Chimantá, *Huber & Colella 8953* (NY, VDB, VEN); Kukenan-tepui, *Huber 9470* (NY); Ilu-tepui, *Huber 9526* (K, NY); Aprada-tepui, 30 km E Uriman, *Huber 9569* (NY—corolla lavender-rose), *9571* (NY—corolla pale yellow); Uei-tepui, *Huber 10043* (MARNR, MYF, NY, VDB); Kavanayen, *Lasser 1826* (NY); El Pauji, *Liesner 19337* (MO, VDB, VEN); Tereke-Yuren, W edge, *Liesner et al. 21099* (MO, VDB); Kukenan tepui, *Liesner 23173* (MO, VDB); 15 km WSW Karaurin tepui, *Liesner 24102* (MO); Ilu-tepui, Mesa Grande, *Maguire 33342*; Kavanayen, *Maguire 33680* (MO); NE Luepa, *Steyermark & Nilsson 597* (NY); Mt. Roraima, Emerald Swamp, *Steyermark 58861* (F, GH, US—some plants with 4 scapes); Ptari-tepui, SW shoulder, *Steyermark 59787* (F, GH, NY); mesa between Ptari-tepui and Sororopan-tepui, *Steyermark 60144* (F); Chimantá, Apr. 1953, *Steyermark 74999* (F—plants with 8 scapes but leaves as in *O. sceptrum*); Chimantá Massif, *Steyermark 75885* (F); Auyan-tepui, cumbre, *Steyermark 93689* (K, NY); Cerro Jaua, cumbre, 24 feb.–7 mar. 1974, *Steyermark et al. 109435* (NY); Cerro Guanacoco, cumbre, *Steyermark et al. 109742* (NY); Cerro Roraima, cumbre, *Steyermark et al. 112453* (F); Chimantá, *Steyermark et al. 128355* (MO); Camarca/Barai/Tepui, *Steyermark et al. 131999* (MO, US, VDB, VEN).

Orectanthe sceptrum is a highly variable species as to size, leaf dimensions, and bract character. In the western part of the range are many morphs corresponding to what Maguire called subspecies *occidentalis*, a lower plant with nonglaucous foliage and shorter cephalar bracts; in the eastern part of the range the plants are mostly taller, with the longer range of involucral bracts and cephalar bracts, and with the foliage tending toward glaucousness (subsp. *sceptrum*). However, these intergrade to the extent that it is difficult to assign even varietal rank. In the eastern part of the range, and adding to the problem, *O. ptaritepuiana* may be hybridizing with *O. sceptrum*, as some specimens there appear to be intermediate as to bract and scape.

2. **Orectanthe ptaritepuiana** (Steyerm.) Maguire, Mem. New York Bot. Gard. 10(1): 5. 1958. *Abolboda ptaritepuiana* Steyerm. Fieldiana Bot. 28: 104. 1951. TYPE: Venezuela Bolívar: Ptari-tepui, *Bonnettia roraimae* forest on SW-facing shoulder, 2,000–2,200 m, 2 Nov. 1944, *Steyermark 59760* (holotype, F; isotype, GH). Figure 33.

Stems elongate, often to 15 dm or more, densely leafy but the leaves ascending in high spirals, the growth often sprawling, often branched, erect only toward tips, the leaf blades without red-brown border or this indistinct; scapes 2–several, as in *Orectanthe sceptrum*, but distinctly shorter than the leafy portion of the stem; involucre of 3 sterile, lanciform bracts distinctly longer than the inner (cephalar) bracts and up to 6 cm long. Flowers, fruit, and seed as in *O. sceptrum*.

Distribution. Boggy, rocky open sites, seeps on high cliffs and ledges, southwestern Guyana, westward into southeastern Bolívar, Venezuela, and (probably) southward into contiguous Brazil at 500–2,700 m.

Additional material examined. GUYANA. Summit Mt. Wokomung, July 1989, *Boom & Samuels 9087* (NY, VDB); Mt. Ayanganna, *Tillett et al. 45125* (NY). VENEZUELA. BOLIVAR: Cerro Guaiquinima, *Cardona 967*

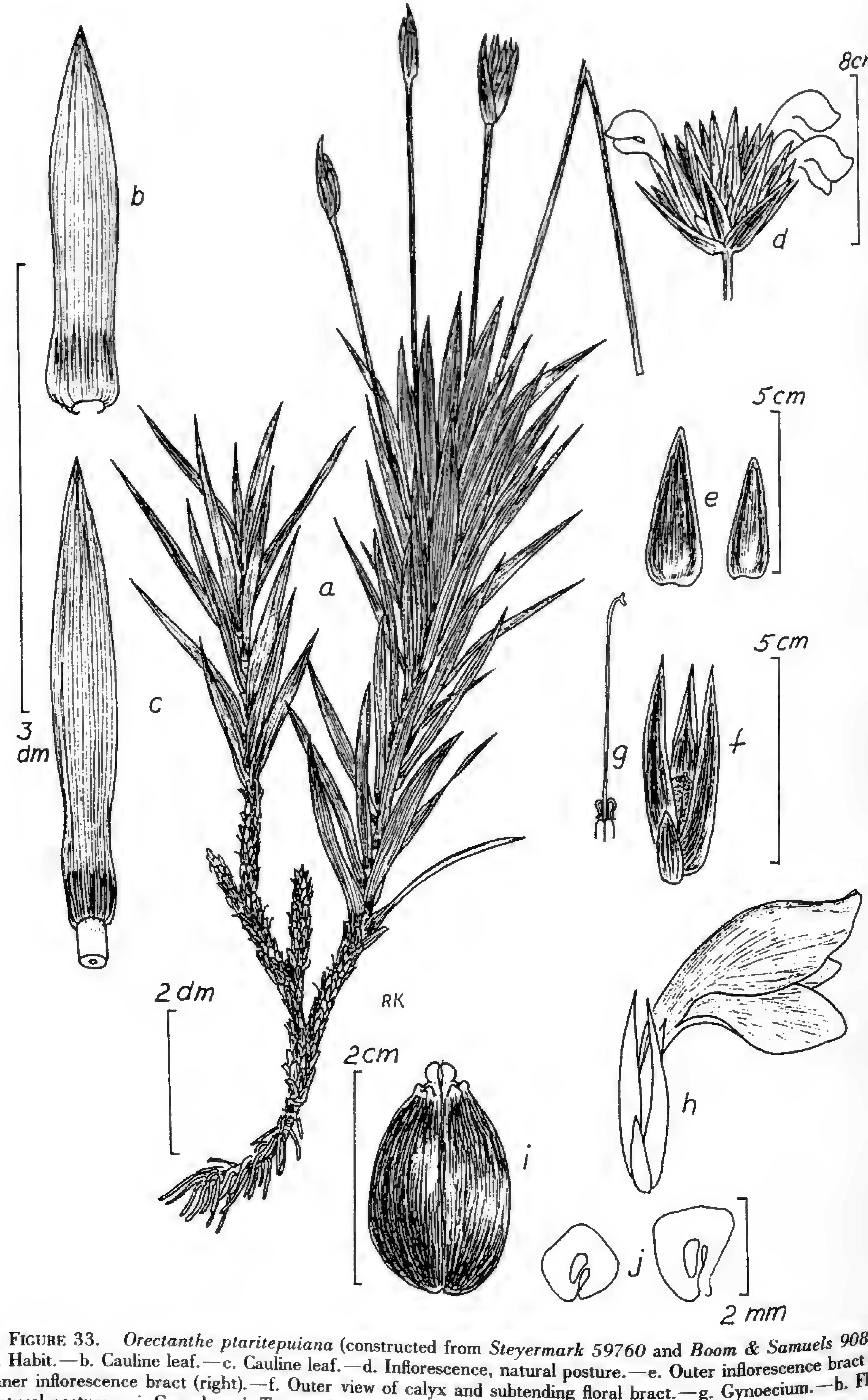

FIGURE 33. *Orectanthe ptaritepuiana* (constructed from *Steyermark 59760* and *Boom & Samuels 9087*).—a. Habit.—b. Cauline leaf.—c. Cauline leaf.—d. Inflorescence, natural posture.—e. Outer inflorescence bract (left); inner inflorescence bract (right).—f. Outer view of calyx and subtending floral bract.—g. Gynoecium.—h. Flower, natural posture.—i. Capsule.—j. Two seeds, showing size range.

(US); Murisipan-tepui, summit, *Holst et al. 1926* (MO); Auyan-tepui, *Huber et al. 8829* (NY, VDB, VEN); Chimantá Massif, *Huber et al. 8889* (NY, VDB, VEN); Uei-tepui, *Huber 10043* (MFV, VDB); Cerro Guaiquinima, *Maguire 31761* (NY), *32786* (NY, US), *32823* (NY), *32979* (NY), *33022* (NY), *33035* (NY); Ilu-tepui, Gran Sabana, *Maguire 33431 33467* (NY); frontier between Territorio do Rio Branco, Brazil, and Bolívar, Serra do Sol, cumbre, *Maguire 40413* (NY); Chimantá Massif, Torono-tepui, *Steyermark & Wurdack 523* (F, K, NY), *905* (NY), *1221* (F, NY, US); Abacapa-tepui, *Steyermark 74927* (NY); Apacará-tepui, *Steyermark 75885* (F, NY); Cerro Venamo, *Steyermark & Dunsterville 92759* (GH, US); Ptari-tepui, *Steyermark 93715* (NY); Auyán-tepui, *Steyermark 93903* (F, NY, US); Chimantá, *Steyermark et al. 128848* (MO); Camarcaibarai-tepui, SW shoulder, *Steyermark et al. 132020* (MO); Chimantá Massif, *Wurdack 34234-A* (NY).

As mentioned under the discussion of *Orectanthe sceptrum,* there are intergrades between it and *O. ptaritepuiana* sufficient to tempt one to treat the two as subspecies of a common species. It remains to be explained how the dramatic extremes described by Steyermark and Maguire originated. This calls for comparative cultivation of these extremes and other experimental approaches that would demonstrate the true relationship between them. For now, it is probably best to retain the two as species.

CONCLUSIONS

In the taxonomic treatment above, four of the five genera of Xyridaceae are presented. Emphasis is given to the morphological taxonomy and to the keys in which critical differences between the genera and species are set forth. Evolutionary relationships are implied only by the circumstantial evidence given. On that basis, it may be postulated that the ancestral stock from which the existing genera arose was (1) a rhizomatous perennial (2) with polystichous, spirally arranged leaves, (3) scapose (4) flowers in bracteate racemes, (5) with sepals and petals distinct and equal, (6) the stamens 6 and distinct, and (7) the ovary superior, tricarpellate, and with axile placentation. This sort of plant probably existed in what is now called the Guayana Highlands, the most ancient part of the New World surface geography, and from it one branch led to *Achlyphila* and *Xyris* (which share a common pollen type), and the other branch led to *Aratitiyopea* and *Abolboda,* culminating in *Orectanthe.*

As mentioned in the preface, this introductory approach to the Xyridaceae is but the first part of a work that will conclude with a treatment of the known species of New World *Xyris.* This will be the last of my work with the family Xyridaceae.

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REVISION OF *COSMIBUENA* (RUBIACEAE)[1]

Charlotte M. Taylor[2]

ABSTRACT

Cosmibuena is distinguished by its epiphytic habit, interpetiolar stipules that are also partially fused intrapetiolarly, and salverform white corollas. Four species are recognized: *C. grandiflora* (Ruíz Lopez & Pavón) Rusby, *C. macrocarpa* (Bentham) Walpers, *C. matudae* (Standley) L. O. Williams, and *C. valerii* (Standley) C. M. Taylor, comb. nov. (= *Hillia valerii* Standley).

Cosmibuena Ruíz Lopez & Pavón is a genus of four species of characteristically epiphytic shrubs found throughout the moist and wet continental Neotropics. Its species are easily recognized by their succulent stems and leaves, salverform white corollas with relatively long tubes, and cylindrical woody capsules that contain numerous small glabrous seeds with thin membranaceous wings.

Species of *Cosmibuena* can be confused with those of *Hillia* Jacquin, a more speciose genus with a similar morphological aspect and geographic range (Taylor, 1989). *Hillia* can be separated from *Cosmibuena* by: their seeds, which are similar in size and form but bear a tuft of brown "trichomes" (deeply fimbriate seed wings; Robbrecht, 1988) 1–3 cm long attached at one end, in contrast to the "glabrous" seeds (with entire or only slightly fimbriate wings) in *Cosmibuena*; and by their stipules, which are interpetiolar in contrast to both interpetiolar and partially fused intrapetiolarly in *Cosmibuena*. These genera can usually also be separated by the stigmas, which are bilobed, densely papillose, and held above the anthers in *Cosmibuena,* in contrast to subcapitate, bilobed, or linear, less densely papillose, and held above or below the anthers in *Hillia*.

Several additional characteristics that have been used to separate these genera are less useful. *Hillia* has been distinguished from *Cosmibuena* by the presence of raphides in its tissues, in contrast to their absence in *Cosmibuena* (Verdcourt, 1958); however, raphides are present in all species of *Cosmibuena*. Steyermark (1974) distinguished *Hillia* from *Cosmibuena* by the lack of a marginal wing on its seeds in contrast to a well-developed wing in *Cosmibuena*, but *Hillia* seeds show at least a thin marginal wing while those of *Cosmibuena* are variable. In his key to genera Standley (1938) separated these taxa based on the persistent calyx of *Hillia* in contrast to the deciduous calyx of *Cosmibuena*, although in his text he described the calyx of *Hillia* as absent or having the lobes "caducous"; Schumann (1891) and Wernham (1916) contrasted the caducous calyx of *Hillia* with the persistent calyx of *Cosmibuena* for this same distinction. Actually, persistence of the calyx limb varies in both genera and among individuals of some species, or the calyx limb may not develop at all, as in several species of *Hillia*. Standley (1938) also distinguished these two genera by the presence of a well-developed calyx tube in *Cosmibuena*, in contrast to a completely divided calyx limb (when present) in *Hillia*; however, that distinction does not apply to *C. valerii* (Standley) C. M. Taylor, which has a completely divided calyx limb. Dwyer (1980) separated these genera in Panama based in part on width of the leaf blades, but this distinction is invalidated here by the inclusion of *C. valerii*, which has narrow leaves, and was never useful outside of Panama, where species of *Hillia* with larger leaves are found.

TAXONOMIC HISTORY

Cosmibuena was originally described by Ruíz Lopez & Pavón (1794) in their *Prodromus*. The name commemorates Cosme Bueno (1711–1798), a professor of medicine, mathematics, and cos-

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mology at the University of San Marcos in Lima (Steele, 1964), and was originally applied to a species of *Hirtella* Linnaeus (Chrysobalanaceae). However, in their subsequent *Flora*, Ruíz Lopez & Pavón (1802) applied the name to a different species, a succulent member of the Rubiaceae they had previously treated in the *Prodromus* as *Cinchona grandiflora*. Ruíz Lopez & Pavón now treated the rubiaceous species under a new, illegitimate name, *Cosmibuena obtusifolia*. Their use of *Cosmibuena* in the first sense was followed by most nineteenth-century authors, who therefore placed their rubiaceous species in *Buena* Pohl (e.g., Bentham & Hooker, 1873; de Candolle, 1830; Bentham, 1839, 1844). Unfortunately, *Buena* Pohl is an illegitimate later homonym of *Buena* Cavanilles, which is rubiaceous but does not include the species of Ruíz Lopez & Pavón. Their species and its congeners were subsequently transferred from *Buena* Pohl to Ruíz Lopez & Pavón's second (1802) illegitimate *Cosmibuena* by Klotzsch (1846) and Schumann (1891). By this time *Cosmibuena* in its first sense had been relegated to synonymy and thus practically, though not formally, rejected, although it still existed for purposes of priority. Thus, the rubiaceous plants lacked a legitimate name for more than a century. This problem was recognized but not addressed by Standley (1921), who used the name *Cosmibuena* in all of his works (Standley, 1921, 1930, 1931a, b, 1938). The conservation of *Cosmibuena* in Ruíz Lopez & Pavón's second, rubiaceous sense finally resolved this situation (Monachino, 1949; Lanjouw et al., 1956).

The first treatment of the entire genus was presented by de Candolle (1830), who recognized three species, one of which is today treated in *Ladenbergia*. Subsequent outlines of the genus were presented by Klotzsch (1846), Bentham & Hooker (1873), and Schumann (1891). Aside from these works, treatments of individual species have been presented in regional floras, notably by Standley (1921, 1931a, b, 1938), Standley & Williams (1975), Dwyer (1980), Croat (1978), and Steyermark (1974). *Cosmibuena* has not been treated comprehensively since de Candolle's work, although Monachino (1949) presented a perceptive conspectus of the genus that has been followed by more recent authors (Standley & Williams, 1975; Dwyer, 1980).

RELATIONSHIPS OF *COSMIBUENA*

Cosmibuena has been classified by most workers in the tribe Cinchoneae of the subfamily Cinchonoideae (Schumann, 1891; Bremekamp, 1966; Robbrecht, 1988; Lorence, 1990; Andersson & Persson, 1991). Twentieth-century authors (Bremekamp, 1966; Robbrecht, 1988; Kirkbride, 1982) cite a lack of raphides as a characteristic of this tribe and subfamily, but most have apparently overlooked the presence of raphides in *Cosmibuena* (e.g., Bremekamp, 1966; Robbrecht, 1988; Lorence, 1990). Based on its raphides, Kirkbride (1982) removed *Cosmibuena* to the previously monogeneric Hillieae of the subfamily Rubioideae. Bremekamp (1966) originally removed *Hillia* from the Cinchoneae based on its raphides and "comose" seeds, which are unique in the family. *Cosmibuena* has "glabrous" seeds, but this character was discounted by Kirkbride in favor of similarities of habit and general aspect.

Some species of *Hillia* are similar to those of *Cosmibuena*, as discussed above. However, *Cosmibuena* shares with *Ladenbergia* and other genera of Cinchoneae several features not found in *Hillia*, including intrapetiolarly partially fused stipules and stigma morphology. The combinations of characters found in these genera suggest that the similarity of habit and morphology between *Hillia* and *Cosmibuena* may be convergent, and that raphides may not be a reliable tribal character (Robbrecht, 1988; Andersson & Persson, 1991). A detailed analysis of the relationship between these genera depends on a modern study of *Hillia* currently underway (Taylor, 1989, in prep.).

Separation of *Cosmibuena* and *Hillia* was clearer before the discovery of *Cosmibuena valerii* (Standley) C. M. Taylor. Previously, in addition to the characters discussed in the introduction, these genera could be separated by their corolla aestivation, which was imbricate in *Cosmibuena* in contrast to convolute in *Hillia*; flower number, which was 3–11 in a cymose arrangement in *Cosmibuena*, in contrast to solitary (with one clearly derived exception, Taylor, 1989) in *Hillia*; the development of a tubular calyx limb in *Cosmibuena*, in contrast to a completely divided or (frequently) absent calyx limb in *Hillia*; and interpetiolarly and partially intrapetiolarly fused stipules in *Cosmibuena*, in contrast to only interpetiolar stipules in *Hillia*. However, *Cosmibuena valerii* has convolute corolla aestivation, solitary flowers, a completely divided calyx limb, partially intrapetiolarly fused stipules, elliptic, flattened, densely papillose stigmas, and "glabrous" seeds. This species is here classified in *Cosmibuena* based on its seed, stigma, and stipule characters. Convolute and imbricate corolla aestivation are both found in the Cinchoneae (Robbrecht, 1988), and thus the distinction between these conditions seems less important than some other features. Number of flowers is variable within genera of Rubiaceae and within species, and again seems unreliable, as does development of a tubular calyx limb. In contrast, "comose" seeds are unique in the family, intrapetiolarly fused stipules are rare (Robbrecht, 1988) and style and stigma characters appear to be more important than previously recognized (Bremer et al., 1990). Detailed study of the relationships among the species of *Cosmibuena* will be presented later (Taylor, in prep.).

MORPHOLOGY

HABIT, STEMS, AND VESTURE

Plants of *Cosmibuena* are erect succulent shrubs or trees. They are usually epiphytes, although occasionally they may be terrestrial. The branches are often a meter or more in length and flexuous. The stems are quadrate and green when young, usually becoming terete and covered with smooth gray-brown bark. The stems, leaves, and stipules become gray-green when dry, with the exception of *C. valerii*, which becomes a distinctive red-brown similar to many members of *Psychotria* L. subg. *Psychotria*. The plants are glabrous throughout, with the exception of the puberulous abaxial leaf surfaces of some individuals of *C. grandiflora* (Ruíz Lopez & Pavón) Rusby from Colombia and adjacent areas. Raphides are found in all parts of all species, but are most evident in the stipules, ovaries, and abaxial surfaces of the leaf veins.

LEAVES

The leaves are isophyllous with succulent, entire, usually elliptic or obovate blades borne on short stout petioles. The caducous stipules are fused interpetiolarly and partially intrapetiolarly as well. The interpetiolar portion is generally ligulate to obovate, and rounded to obtusely angled at the apex. The stipules are initially green, changing to pale green and then white when they are ready to fall, or in *C. valerii*, frequently red turning red-brown when ready to fall.

FLOWERS

The inflorescences are terminal, with cymes of 3–11 flowers produced in one to two whorls, or flowers solitary (in *Cosmibuena valerii*). The stout peduncles are usually reduced, and the equally stout pedicels relatively short. Inflorescence bracts are usually lacking, or when present are similar in form to the stipules and caducous. The terminal flower of a cyme is generally a few millimeters larger in calyx, corolla, anthers, and stigma than the subtending flowers, which are similar to each other in size. The flowers are homostylous and apparently protandrous, with the general morphological features correlated with sphingid moth pollination (Haber & Frankie, 1989). The duration of a single flower is not known.

The calyx limb is tubular and may be truncate or shallowly to completely divided into 4–7 triangular lobes. This calyx limb may be persistent on the developing fruit, caducous at anthesis, or show any intermediate condition. The presence or persistence of the calyx limb does not appear to be consistent within a single species, and certainly not within the genus.

The corollas are salverform with relatively long slender tubes and four to seven elliptic lobes; the number of lobes may vary within a species. The corollas are white or pale green externally when fresh, or (in *C. valerii*) tinged with rose-pink on the surfaces exposed in bud. They change in all species to cream, yellow, or brown when old. The corolla is thickly carnose and glabrous throughout, or the internal surface of the tube and bases of the lobes may be papillose. Aestivation is imbricate with three lobes external, or convolute as in *C. valerii*. The imbricate lobes may appear convolute unless examined carefully, and have been described as convolute by previous authors (e.g., Schumann, 1891; Steyermark, 1972), and even as convolute with the direction variable (Bentham & Hooker, 1873).

The stamens are inserted near the apex of the corolla tube and are usually equal in number to the corolla lobes. The free portions of the filaments are generally about equal in length to the anthers, which are bithecal and dehiscent by a longitudinal slit. The anthers are usually included or may be slightly exserted in more southerly populations of *Cosmibuena grandiflora*.

The slender, straight, white style arises from inside an annular disk and extends just beyond the apex of the corolla tube. It is frequently pilose in the upper ⅓–½, more densely so distally and frequently most densely so at the stigma attachment. The two stout white stigmas are elliptic, flattened, and densely papillate adaxially. The inferior ovary is turbinate to cylindrical with axile placentas that bear numerous vertically imbricated ovules.

FRUIT

The mature capsules are cylindrical, brown, woody, and often spotted with conspicuous white lenticels. Dehiscence is septicidal and basipetal, with the valves then loculicidally dehiscent. The old valves often unroll but remain attached to the plant after the seeds are dispersed, with the fibrous exocarp and mesocarp separating from the papery endocarp.

The seeds are strongly flattened, with a small elliptic embryo ca. 1–2 mm long surrounded by a narrowly rhombic, papery or membranaceous wing that is frequently erose or fimbriate, but never comose or pilose. The seeds are apparently dispersed by wind.

TAXONOMIC TREATMENT

The present treatment includes four species of *Cosmibuena. Cosmibuena grandiflora* is morphologically variable and widely distributed in moist middle to montane regions from Peru to Costa Rica; most of the names published in the genus are synonyms of this species. It is replaced from Nicaragua to Mexico by *C. matudae* (Standley) L. O. Williams. *Cosmibuena macrocarpa* (Bentham) Walpers is found from Costa Rica to Peru in wet forest and coastal formations. *Cosmibuena valerii* is restricted to wet montane forests of Costa Rica and Panama.

This treatment is based on fieldwork in Costa Rica and on study of herbarium specimens from A, AAU, CAS, CR, DS, DUKE, F, GB, GH, MO, NY, UCR, US, and W. Haber's personal collection in Monteverde, Costa Rica (designated in specimen citations as "Haber"). Plants of *Cosmibuena* are fleshy, and about 0–10% reduction in size of soft parts can be expected in dried material; measurements of such parts given here should be adjusted accordingly.

Cosmibuena Ruíz Lopez & Pavón, Fl. Peruv. 3: 2. 1802, nom. cons. TYPE: *Cosmibuena obtusifolia* Ruíz Lopez & Pavón, nom. illeg., typ. cons. [= *Cosmibuena grandiflora* (Ruíz Lopez & Pavón) Rusby]. Not *Cosmibuena* Ruíz Lopez & Pavón, Fl. Peruv. Prodr. 10. t. 2, f. 1–8. 1794, nom. rej.

Buena Pohl, Pl. Bras. Icon. Descr. 1: 8, t. 8. 1826, nom. illeg. TYPE: *Cosmibuena grandiflora* (Ruíz Lopez & Pavón) Rusby. Not *Buena* Cav., Anales Hist. Nat. 2: 278, t. 23. 1800.

Erect, succulent, unarmed, glabrous or rarely puberulent, usually epiphytic shrubs or small trees with raphides. *Leaves* isophyllous, petiolate, entire, without domatia; stipules interpetiolar and also fused intrapetiolarly for ¼–⅔ of their length, membranaceous to subcoriaceous, caducous or those subtending flowers frequently persistent until anthesis in *C. valerii*, the interpetiolar portion oblanceolate to obovate with numerous parallel veins arising from the base. *Inflorescences* terminal, pedunculate, cymose with 1–2 whorls or reduced to a solitary flower; bracts similar to stipules and caducous or apparently sometimes lacking; bracteoles usually lacking or when present 2 per flower, similar to bracts but smaller; flowers pedicellate, perfect, actinomorphic, nocturnal, fragrant, apparently protandrous; *calyx* limb persistent or deciduous, green, membranaceous to coriaceous, truncate or shallowly to completely divided into (4–)5–6(–7) subequal to unequal lobes; *corolla* salverform with slender long tube, carnose, white becoming cream, yellow, or brown when old, externally glabrous and sometimes tinged with green or red, internally glabrous or frequently papillose near mouth of tube, the lobes (4–)5–6(–7), aestivation imbricate with 3 lobes external, or convolute in *C. valerii*; *stamens* equal in number to corolla lobes, inserted near apex of tube, the filaments about equal in length to anthers, the anthers bithecal, yellow, narrowly oblong, acute at base and apex, mostly to completely included, basifixed or attached near base and between extended ends of thecae, dehiscent by a longitudinal slit; disk annular; *ovary* bilocular, inferior, the ovules numerous, vertical, imbricate, on axile placentas; *style* slender, straight, usually equal to corolla tube; stigmas 2, elliptic-ovate, stout, densely papillose on adaxial surface. *Fruit* capsular, cylindrical, woody, dark brown, smooth or with scattered white lenticels, septicidally and basipetally dehiscent, the valves then loculicidally and basipetally dehiscent by a slit in the septum; seeds pale brown, elliptic, flattened, surrounded by a narrowly rhombic, papery to membranaceous, entire to irregular or somewhat erose marginal wing.

Four species, southern Mexico to Peru, Bolivia, and southern Brazil.

KEY TO THE SPECIES OF *COSMIBUENA*

1a. Leaves 1–4.2 cm wide, obovate, obtuse to broadly rounded at apex, thickly coriaceous; plants drying red-brown, old stipules red; flowers solitary; corolla tube and outside of lobes often pink to red in bud; calyx limb divided to base; capsules usually smooth .... 4. *C. valerii*

1b. Leaves 2.4–16 cm wide, elliptic to obovate, obtuse to broadly rounded or acute at apex, coriaceous to subcoriaceous; plants drying green or gray-green, old stipules white to pale green; flowers (2–)3–8(–9) in 1–2 whorls; corolla tube and outside of lobes pale green to white in bud; calyx limb partially lobed to truncate, with a tube 1–11 mm long; capsules frequently lenticellate.

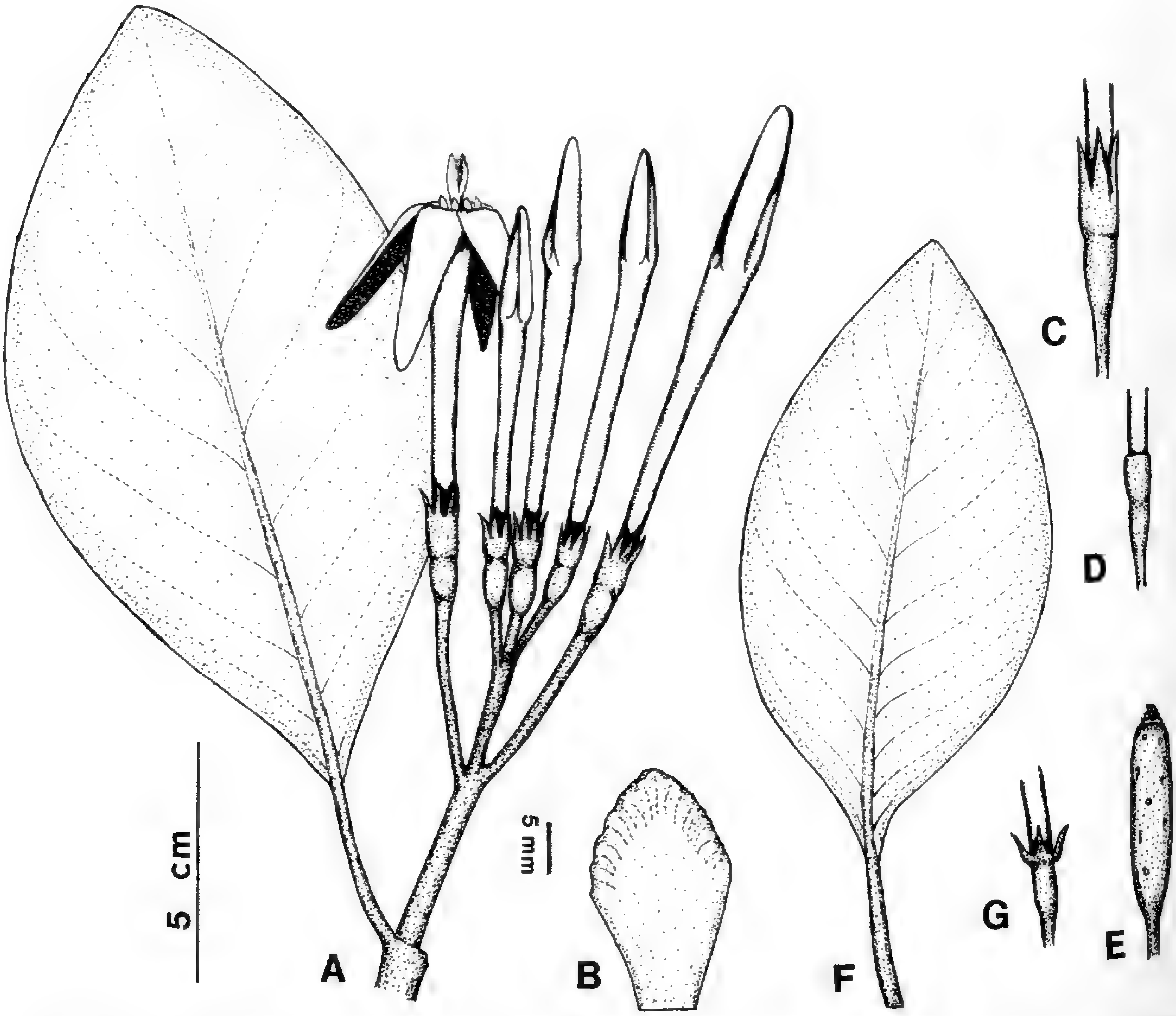

FIGURE 1. A–E. *Cosmibuena grandiflora* (Ruíz Lopez & Pavón) Rusby.—A. Habit.—B. Stipule.—C. Calyx limb.—D. Calyx limb.—E. Capsule. Calyx limb of A shows the "typical" form, those of C and D show variants, (C from Colombia, D from Panama). F, G. *Cosmibuena matudae* (Standley) L. O. Williams.—F. Leaf.—G. Calyx limb. A, B, from *Hutchinson et al. 6037* (F); C, from *Cuatrecasas 23788* (F); D, from *Duke 6193* (F); E, from *Williams 17010* (F); F, from *Molina 26038* (F); G, from *Moreno 9950* (MO). A, C–G to same scale.

2a. Capsules 73–112 mm long; seeds 7–9 mm long including wing; leaves coriaceous, obovate, obtuse to broadly rounded at apex; secondary veins usually straight, acutely angled with the midrib ______ 2. *C. macrocarpa*
2b. Capsules 40–65 mm long; seeds 5–6 mm long including wing; leaves subcoriaceous to coriaceous, elliptic to broadly elliptic, acute at apex; secondary veins straight to usually curved, acutely angled to usually nearly perpendicular to the midrib.
  3a. Calyx limb truncate to lobed, the lobes shorter than or equal to the tube; leaf blades 3.6–16 cm wide, with secondary veins (3–)4–6 pairs; southern Nicaragua to Bolivia and Peru ______ 1. *C. grandiflora*
  3b. Calyx limb lobed, the lobes longer than the tube; leaf blades 3–8 cm wide, with secondary veins (6–)7–9 pairs; southern Mexico to Nicaragua __ 3. *C. matudae*

1. Cosmibuena grandiflora (Ruíz Lopez & Pavón) Rusby, Bull. New York Bot. Gard. 4: 368. 1907. *Cinchona grandiflora* Ruíz Lopez & Pavón, Fl. Peruv. 2: 54, t. 198. 1799. *Cosmibuena obtusifolia* Ruíz Lopez & Pavón, Fl. Peruv. 3: 3. 1802, nom. illeg. *Buena obtusifolia* (Ruíz Lopez & Pavón) DC., Prodr. 4: 356. 1830, nom. illeg. TYPE: Peru. Huánuco: ad Pozuzo et San Antonii de Playa Grande, *Ruíz Lopez & Pavón s.n.* (holotype, MA not seen; isotypes, B destroyed, photos (neg. # 240) F.) Figure 1A–E; Steyermark, 1974: fig. 24.

Cinchona longiflora Mutis ex Steudel, Nomencl. Bot. ed. 1, 1: 196. 1821, nom. nud.
Cosmibuena triflora (Benth.) Klotzsch in Hayne, Getreue Darstell. Gew. 14: subt. 15. 1846. *Buena triflora*

Benth., J. Bot. (Hooker) 3: 216. 1841. TYPE: Guayana. Falls of the Río Quitaro, 1838, *Schomburgk 553* (holotype, K not seen, photo (neg. # NS 3195) NY; isotypes, G not seen, fragment F).

Cosmibuena latifolia (Benth.) Klotzsch ex Walp., Repert. Bot. Syst. 6: 69. 1846. *Buena latifolia* Benth., Pl. Hartw. 191. 1845. *Cosmibuena obtusifolia* var. *latifolia* (Benth.) Hooker f. ex Monach., Phytologia 3: 65. 1949. *Cosmibuena grandiflora* var. *latifolia* (Benth.) Steyerm., Mem. New York Bot. Gard. 23: 296. 1972. TYPE: Colombia. Cundinamarca: inter pagos Villega et Guaduas, *Hartweg s.n.* (holotype, K not seen, photo (neg. # NS 3197) NY).

Cosmibuena quinqueflora Klotzsch in Hayne, Getreue Darstell. Gew. 14: subt. 15. 1846. TYPE: Venezuela. Mérida: Mérida, Nov. 1844–1845, *Moritz 407* (holotype, B not seen, destroyed, photos (neg. # 242) F; isotype, P).

Cosmibuena skinneri (Oersted) Hemsley, Biol. Cent.-Amer., Bot. 2: 12. 1881. *Buena skinneri* Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 4: 48. 1853. TYPE: Nicaragua. Masaya: toppen af Vukanen Masaya, 2,000–3,000 ft. [654–968 m], Jan. 1848, *Oersted 11134* (holotype, C not seen, photos (neg. # 22790) A, F; isotype, US).

Cosmibuena gardenioides Wernham, J. Bot. 51: 321. 1913. TYPE: Colombia. Cauca: *Lehmann 1955* (holotype, K not seen).

Cosmibuena arborea Standley, Contr. U.S. Natl. Herb. 17: 447. 1914. TYPE: Colombia. Cauca: Cauca Valley, near Espejuelo, 1,000 m, Jan. 1906, *Pittier 985* (holotype, US; isotypes F, US).

Cosmibuena ovalis Standley, Contr. U.S. Natl. Herb. 18: 137. 1916. TYPE: Panama. Coclé: vicinity of Ola, 100–350 m, 7–9 Dec. 1911, *Pittier 5074* (holotype, US, photo (without number) F; isotype, NY).

Epiphytic or terrestrial, glabrous or sometimes pubescent, to 12 m tall, drying green or grayish green; stems rounded to subquadrate; bark smooth, becoming gray to grayish brown. *Leaf* blades elliptic to broadly so, 6.5–19.5 cm long, 3.6–16 cm wide, acute at apex, acute to cuneate at base, subcoriaceous to coriaceous, glabrous throughout or hirtellous or pilosulous abaxially along midrib in some plants from Colombia and adjacent Venezuela and Ecuador; secondary veins (3–)4–6 pairs, acutely angled to nearly perpendicular to midrib, usually curving, sometimes rather well marked, not prominulous, the distal 1–2 veins sometimes looping to interconnect; petioles 5–40 mm long, glabrous or sometimes sparsely to moderately hirtellous or pilosulous; stipules connate intrapetiolarly for ca. ¼–⅔ of their length, membranaceous to subcoriaceous, pale green to white at dehiscence, the interpetiolar portion oblanceolate to obovate, 8–30 mm long, rounded to obtusely angled. *Flowers* 3–5(–9) in 1–2 whorls; peduncles 6–30(–40) mm long; internode (when present) 5–20 mm long; bracts usually none, or when present oblanceolate, 10–18 mm long, membranaceous; pedicels 5–30 mm long; *calyx* limb 4–15 mm long, the tube 4–8(–11) mm long, truncate to sinuous or lobed, the lobes 5–6, ligulate to narrowly triangular, 0–4(–7) mm long, rounded to acute; *corolla* white throughout or flushed with pale green externally, the tube (47–)58–90(–100) mm long, the lobes 5–6(–7), narrowly to broadly elliptic-oblong or ovate, (9–)15–35(–41) mm long, 6–20 mm wide, broadly angled to rounded; *anthers* 5–6(–7), 10–18 mm long, with the thecae extending ca. 1–3 mm below filament attachment, the apices included or occasionally exserted for 1–3 mm; disk annular, 1–2 mm high; *ovary* elliptic to cylindrical, 5–10 mm long; *style* 1–2 mm shorter than to 1–3 mm longer than corolla tube, glabrous or more frequently sparsely to densely pilose in distal 1–3 cm; stigmas 4–7 mm long, frequently unequal in length by 1–2 mm. *Capsules* 40–65 mm long, 6–13 mm diam., crowned by a beak ca. 2–4 mm long, frequently lenticellate; *seeds* including wings 5–6 mm long, 1–2 mm wide.

Phenology. Collected in flower throughout the year, in fruit January–April and July–December.

Habitat and distribution (Fig. 2). Southern Nicaragua to Bolivia and Peru, in moist to wet thickets, forests, and on banks at (0–)500–2,200 m.

Selected specimens examined. Bolivia. LA PAZ: Mapiri, *H. H. Rusby 2103* (F, GH, NY, US). Brazil. TERRITORIO DO AMAZONAS: Manaus–Caracaraí Highway, BR 174 Km 168, *G. T. Prance et al. 22680* (NY, US). TERRITORIO DO RORAIMA: upper plateau and summit of Serra Tepequem, *G. T. Prance et al. 4413* (F, GH, NY). Colombia. ANTIOQUIA: Amalfi, vereda "El Oso" 13–16 km from Amalfi toward Medellín, Cordillera Central, 6°54′N, 75°08′W, *J. Betancur et al. 896* (MO—2 sheets). CAUCA: Cali, *Lehmann BT 1171* (A, F, GH, NY). CHOCO: Río San Juan Palestina, Quebrada de las Sierpes, *J. Cuatrecasas & L. Willard 26048* (US). CUNDINAMARCA: Cordillera Oriental, S side of Guavio River, 22 km NE of Gachala, Caño Castalia, Station 90, *M. L. Grant 10544* (NY). META: Quebradablanca, near bridge on road from Bogotá to Villavicencio, *T. Plowman et al. 4277* (F, GH). NORTE DE SANTANDER: Balcones, head of Quebrada de Miraflores 7 km NNW of Convención, 8°31′N, 73°22′W, *F. R. Fosberg 21407* (NY, US). SANTANDER: Río Surata valley between El Jaboncillo and Surata, *E. P. Killip & A. C. Smith 16424* (F, GH, NY, US). TOLIMA: Mariquita, *J. Linden 5257* (F). VALLE: Cordillera Occidental, eastern slope, El Saladito, *J. Cuatrecasas 23788* (F, US). Costa Rica. ALAJUELA. Upala, Dos Ríos, 2.5 km NW of Finca La Palma, 10°55′N, 85°20′W, *G. Herrera 1071* (DUKE). GUANACASTE: road from ICE project at Santa Cruz to Vista de Mar, *L. D. Gómez & G. Herrera 23668* (MO). PUNTARENAS: Monteverde, San Luis valley, *W. Haber & E. Bello 2911* (CR, Haber); Parque Nacional Corcovado, along Ollas trail near station, 8°29′N, 83°34′W, *B. Hammel & J. Trainer 17126* (CR). SAN JOSE: basin of the Río El General, *A. F. Skutch & M. Barrantes 5155* (CR, US). Ecuador. BOLIVAR–CAÑAR–CHIMBORAZO–GUAYAS BORDER REGION: foothills of W Cordillera near Bucay

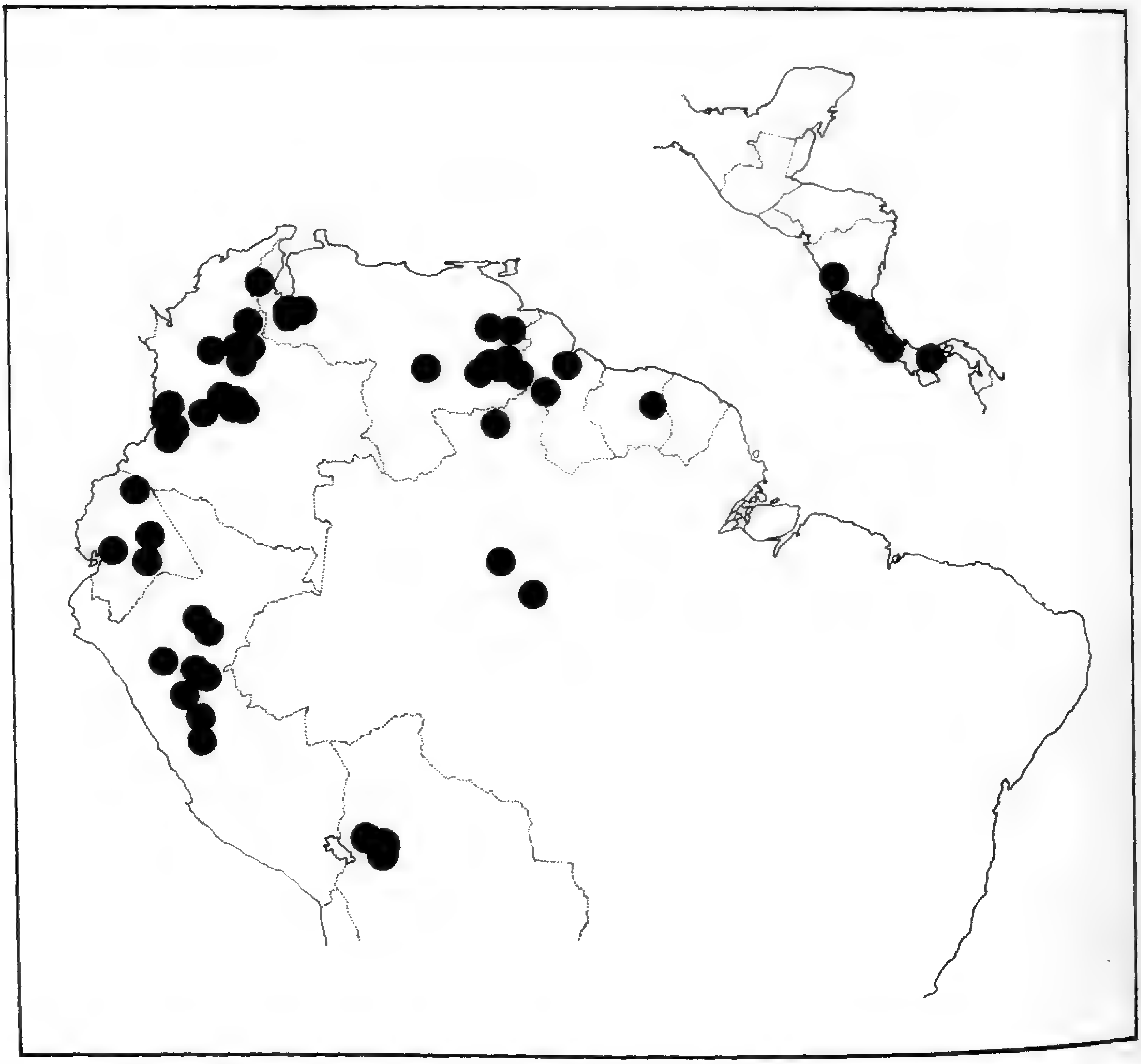

Figure 2. Distribution of *Cosmibuena grandiflora* (Ruíz Lopez & Pavón) Rusby in Central and South America.

village, *W. H. Camp E-3825* (MO, NY). CARCHI: along Lita–Salinas road, *H. van der Werff et al. 9578* (MO). MORONA–SANTIAGO: along Río Palora 1–4 km upstream from Arapicos, *H. Lugo S. 6087* (GB, MO). NAPO: Reserva Biológica Jatún Sacha, ca. 8 km ESE of Puerto Misahuallí, 1°04′S, 77°37′W, *J. S. Miller et al. 2212* (MO). PASTAZA: Tenneco oil well "Garza," ca. 35 km NW of Montalvo, 1°49′S, 76°42′W, *V. Zak & S. Espinoza 4561* (MO). Guyana. ESSEQUIBO: Karietur Plateau, *B. Maguire & D. B. Fanshawe 23226* (A, F, MO, NY, US). Nicaragua. MASAYA: top of Volcán Masaya, *Oersted 11134* (US). Panama. CHIRIQUI: Sabana de la Tortuga, between El Boquete and Caldera, *H. Pittier 3309* (US). COCLE: S of El Valle de Antón, *P. H. Allen 2798* (F). Peru. HUANUCO: distrito Padre Luyando, provincia Leoncio Prado, Saipai, *A. Gutierrez R. 71* (F, MO, NY, US). JUNIN: provincia Chanchamayo, road to San Vincente, S of San Ramón along Río Tulumayo between Kms 5 and 8, 11°15′S, 75°15′W, *B. Stein & C. Todzia 2352* (MO, NY). SAN MARTIN: provincia Mariscal Cáceres, distrito Tocache Nuevo, Quebrada Luis Salas, 5 km NE of Puerto Pizana, *J. Schunke V. 6667* (GH, MO). UCAYALI: provincia Coronel Portillo, lower Boquerón del Padre Abad, *P. C. Hutchison et al. 6037* (F, GH, NY). Surinam. SARAMACCA: Lely Mountains, 5°N, 55°W, *J. C. Lindeman 660* (MO). Venezuela. BARIÑAS: distrito Bolívar, near La Soledad, 8°50′N, 70°32′W, *H. van der Werff & R. Ortiz 6042* (MO, NY). BOLIVAR: Río Chicanan, Cerro Pitón, Cordillera Epicara, *B. Maguire et al. 53574* (F, MO, NY, US). TERRITORIO DELTA AMACURO: downstream from Yarakita River, Río Amacura, Sierra Imataca, *J. A. Steyermark 87428* (F, NY). ZULIA: S of Perija, between the hill that goes toward Pishikakao and Pishikakao, following the Río Vikay-kuna (a tributary of the Río Tumuriasa), *J. A. Steyermark et al. 105758* (NY).

Cosmibuena grandiflora is distinguished by its short, stout capsules and tubular calyx limb with the lobes shorter than the tube or completely lacking. It has frequently been confused with *C. matudae*; the distinctions between them are outlined under the latter species.

Cosmibuena grandiflora has also been confused with *C. macrocarpa*, but these species differ in capsule length and diameter. In addition, they are easily separated by leaf shape and venation pattern in the northern portion of their shared range, although they may be difficult to distinguish on this basis in southern Colombia, Ecuador, and Peru. The various collections (unnumbered and unidentified as to locality) of "*Cinchona grandiflora*" and "*Cosmibuena obtusifolia*" made by Ruíz Lopez and Pavón in Peru actually include both *Cosmibuena grandiflora* and *Cosmibuena macrocarpa.* The two species are never mixed on a single sheet and are probably not from the same site. Among the specimens seen, *Cosmibuena grandiflora* predominates, and this species is also figured in the illustration that accompanied the description of *C. obtusifolia.* Ruíz Lopez and Pavón's material was undistributed for many years, although the illustrations for their *Flora*, with *Cosmibuena* depicted in its second, rubiaceous sense, were widely distributed (Steele, 1964). Thus, the illustration must be given weight not only in the authors' interpretation of *Cosmibuena* but also in subsequent applications of this name, including the conservation of the generic name (Lanjouw et al., 1956). Steyermark (1974) considered all of Ruíz Lopez and Pavón's material to represent one species and annotated this material accordingly. However, some of the material collected by Ruíz Lopez and Pavón represents *C. macrocarpa*, and is excluded from the type material cited here. The confusion of these two species by Ruíz Lopez and Pavón may have been responsible for the origin of their epithet "obtusifolia," which contrasted with the illustration to which it was applied.

Cosmibuena grandiflora varies throughout its geographic range in the persistence and degree of lobing of its calyx limb, in its leaf and style pubescence, and in the size of its capsules. None of these features shows any correlation with other morphological characters, and most show little or no geographic pattern.

The calyx limb of *Cosmibuena grandiflora* is usually persistent on the fruit, or may be deciduous either at anthesis, with the corolla after anthesis, or during fruit development; this characteristic shows no correlation with geographic range. In contrast, the calyx lobes vary in shape and size, with some geographic pattern evident in this variation. Plants from Costa Rica and Panama usually have truncate to sinuous calyx limbs, but sometimes show short (1–5-mm-long) lobes that are separated by truncate portions of the limb; this shape is also seen on occasional individuals from northern and northeastern South America. In most South American plants the calyx limb is lobed for half or more of its length, and the shape of the lobes varies widely from rounded to more frequently acute. Some South American plants have a calyx limb that is lobed to about the middle, similar to that of *C. matudae.*

Pubescence is encountered on the leaves and petioles of some plants from Colombia, western Venezuela, and northern Ecuador, but glabrous plants occur in the same range and only glabrous plants are found elsewhere. Both pubescent-styled and glabrous-styled individuals occur throughout the range of the species, with no apparent geographic pattern except that the most densely pilosulous styles are found on plants from Costa Rica and Panama.

The diameter of the mature capsules and thus the proportional width varies throughout the geographic range, but no pattern is evident.

Steyermark separated *Cosmibuena grandiflora* var. *latifolia* based on its rounded calyx lobes and the pubescence of its petioles and abaxial leaf midribs. However, as discussed above, pubescent-leaved and glabrous-leaved individuals are found sympatrically in western South America, and this feature appears to be no more than sporadic variation. This leaf pubescence appears to have been the principal character used by Steyermark; the calyx lobes actually vary widely in size and shape among the pubescent-leaved individuals, and several specimens annotated by Steyermark have strongly acute lobes.

The name *Cosmibuena skinneri* was applied to Central American specimens of *C. macrocarpa* by Monachino (1940). His usage was followed by later authors, but the type of this name clearly represents *C. grandiflora.*

2. **Cosmibuena macrocarpa** (Benth.) Klotzsch ex Walp., Repert. Bot. Syst. 6: 69. 1846. *Buena macrocarpa* Benth., Bot. Voy. Sulphur 104. t. 38. f. 1–14. 1845. Not *Buena macrocarpa* Wedd., J. Linn. Soc., Bot. 11: 187. 1869. TYPE: Colombia. Nariño: Island of Gorgona, *Hinds 353* (holotype, K, photo (neg. # NYBG NS 3196) NY). Figure 3; Dwyer, 1980: fig. 27; Croat, 1978: fig. 518.

Cosmibuena gorgonensis Wernham, J. Bot. 51: 321. 1913. TYPE: Colombia. Nariño: Island of Gorgona, *Barclay 919* (holotype, K).

Cosmibuena paludicola Standley, Contr. U.S. Natl. Herb. 18: 137. 1916. TYPE: Panama. Colón: vicinity of Viento Frío between Playa Damas and Viento Frío, in mangrove formation along beach near sea level, 7–8 Aug. 1911, *Pittier 4107* (holotype, US (# 679204), photos (without number) F (# 613829); isotypes, GH, NY).

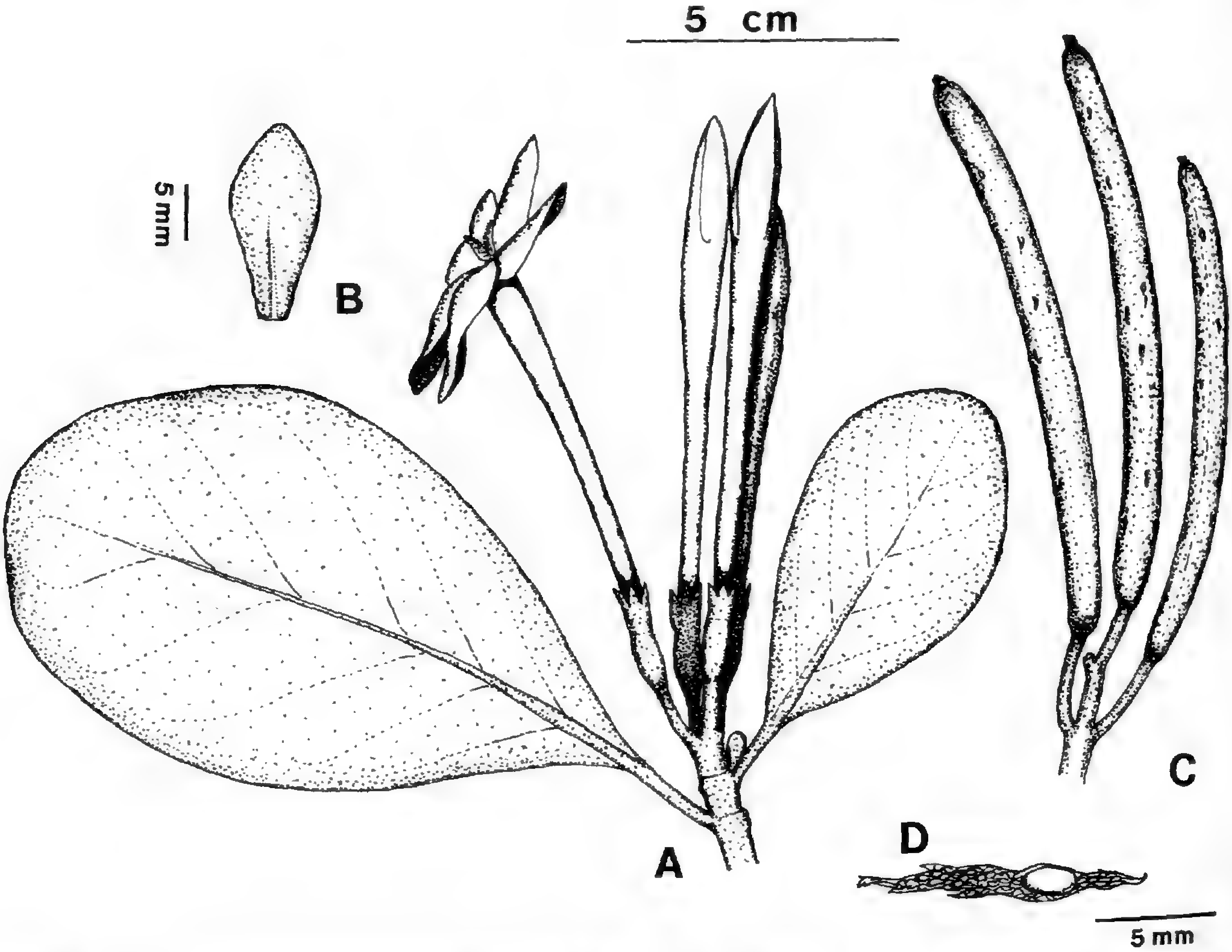

FIGURE 3. *Cosmibuena macrocarpa* (Bentham) Walpers.—A. Habit.—B. Stipule.—C. Capsules.—D. Seed. A, from *Foster 1912* (GH); B–D, from *Croat 5057* (F). A, C to same scale.

Epiphytic or terrestrial, glabrous or puberulous, to 12 m tall, drying green or grayish green; stems quadrate to subterete; bark smooth, becoming gray-brown. *Leaf* blades obovate, 5.5–15 cm long, 2.4–8 cm wide, obtuse to broadly rounded at apex or somewhat angled in plants from southern Colombia to Peru, acute to attenuate at base, coriaceous, glabrous throughout or rarely puberulous abaxially along midrib on young leaves; secondary veins 4–6 pairs, acutely angled with midrib, usually straight, not well marked, not prominulous, the distal 1–2 veins sometimes looping to interconnect; petioles 5–18(–25) mm long, glabrous; stipules connate intrapetiolarly for ca. ⅔ of their length but later separating, membranaceous, pale green to white at dehiscence, the interpetiolar portion obovate, 6–20 mm long, broadly rounded. *Flowers* 3–8 in 1–2 whorls; peduncles 5–30 mm long; internode (when present) 5–30 mm long; bracts obovate to ligulate, 6–11 mm long, broadly rounded, membranaceous; pedicels 9–16 mm long, elongating somewhat in fruit; *calyx* limb 1.5–9 mm long, the tube (1–)2–5 mm long, lobed, the lobes 5, deltoid to narrowly triangular, 0.5–4 mm long, acute; *corolla* white throughout or flushed with pale green externally, the tube 58–93 mm long, the lobes 5, elliptic to oblong, 18–30 mm long, 6–20 mm wide, frequently slightly unequal, obtuse to rounded; *anthers* 5, 13–15 mm long, the thecae extending ca. 1–2 mm below filament attachment, the apices included; disk annular to slightly lobed, ca. 1–2 mm high; *ovary* cylindric, 6–13 mm long; *style* 1–2 mm longer than tube, pilose in upper 1–3 cm; stigmas 6–9 mm long, frequently unequal in length by 1–2 mm. *Capsules* 73–112 mm long, 7–8 mm wide, crowned by beak ca. 2 mm long, frequently lenticellate; *seeds* including wings 7–9 mm long, 2–3 mm wide.

Phenology. Collected in flower December–February and May–October, in fruit in February, April–May, and September–October.

Habitat and distribution (Fig. 4). Costa Rica to Peru, in coastal and inland wet forests at 0–500 m.

Selected specimens examined. COLOMBIA. ANTIOQUIA: vicinity of Pararando Grande W of Mutata, near Chocó border, *A. Gentry & H. León 20259* (MO). CHOCO: Río San Juan near Tado, *A. Gentry & M. Fallen 17771* (MO, NY). NARIÑO: Gorgonilla Island, *E. P. Killip & H. García 33069* (A, F). VALLE: Costa del Pacífico, Río Naya, abajo de Punto Merizalde en el brazo de Ají Chiquito, *Cuatrecasas 14301* (F, US). COSTA RICA. ALAJUELA: 8

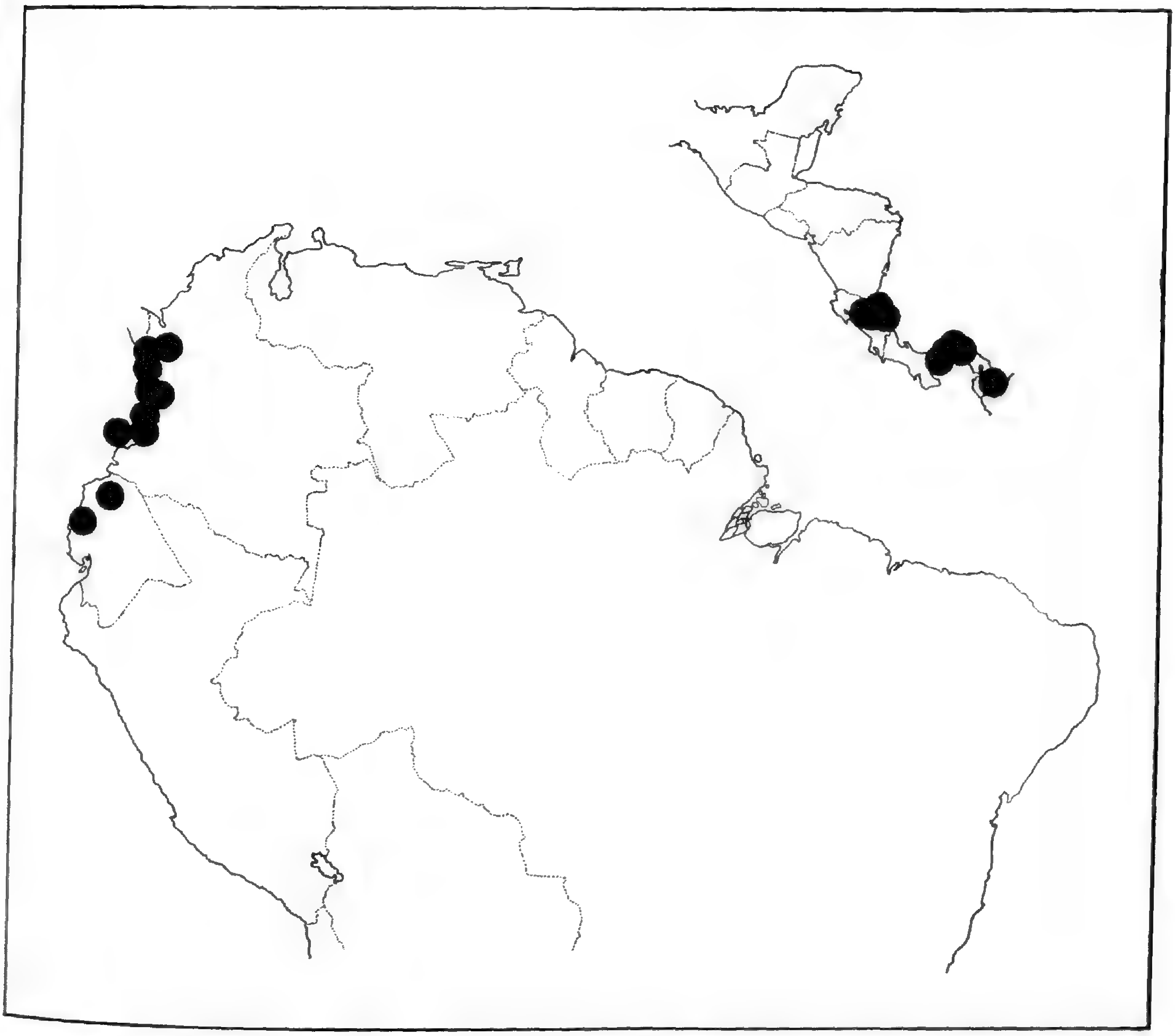

FIGURE 4. Distribution of *Cosmibuena macrocarpa* (Bentham) Walpers in Central and South America.

km SW of San Isidro, lower valley of the Río Peñas Blancas, village of San Miguel, *W. Haber 1476* (Haber). GUANACASTE: Río Chiquito de Tilarán, Río Negro Valley, 10°22'N, 84°52'W, *E. Bello & W. Haber 5863* (Haber). HEREDIA: Finca La Selva, the OTS field station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, *B. E. Hammel 8620* (DUKE), *13364* (DUKE). LIMON: Parque Nacional Tortuguero, Estación Cuatro Esquinas, Laguna T, 10°31'N, 83°30'W, *R. Robles 1312* (CR). SAN JOSE: confluence of the Ríos Sucio and Hondura, Parque Nacional Braulio Carillo, *J. Gómez-Laurito 6577* (CR). ECUADOR. ESMERALDAS: near Lita on the Ibarra–San Lorenzo railroad, *M. T. Madison et al. 5143* (MO). IMBABURA: Lita, *M. Acosta Solís 2468* (F). MANABI: road from Chone to El Carmen, at Flavio Alfaro, 0°24'S, 79°55'W, *L. Holm-Nielsen & J. Jaramillo 27928* (NY). PANAMA. COCLE: vicinity of El Valle, *P. H. Allen 758* (F, GH, US). COLON: Barro Colorado Island, *W. N. Bangham 473* (A, F, US), *T. B. Croat 5057* (F, NY). PANAMA: 3 mi. de la Carretera Interamericana en la carretera a Cerro Campana, *M. D. Correa & R. L. Dressler 997* (CR), *1032* (F). SAN BLAS: Nusagandi, along continental divide on El Llano Cartí road, 9°19'N, 78°15'W, *G. de Nevers 3613* (CAS).

Cosmibuena macrocarpa is distinguished by its long slender capsules. It has been confused with *C. grandiflora* and *C. valerii*; their distinction from *C. macrocarpa* is discussed under the treatments of the former two species.

Cosmibuena macrocarpa was mistakenly combined with *C. skinneri* (Oersted) Hemsley, a synonym of *C. grandiflora*, by Monachino (1940), who was followed by Croat (1978) and Dwyer (1980). It was also apparently confused with *C. grandiflora* by Ruíz Lopez & Pavón; this confusion is discussed under the treatment of *C. grandiflora*.

The label data of one specimen (*Kvist & Asanza 40401*, MO) indicate that in Ecuador the leaves of this species are macerated and mixed with water, and this mixture drunk to relieve vomiting caused by various diseases.

3. Cosmibuena matudae (Standley) L. O. Williams, Fieldiana, Bot. 31: 45. 1965. *Hillia*

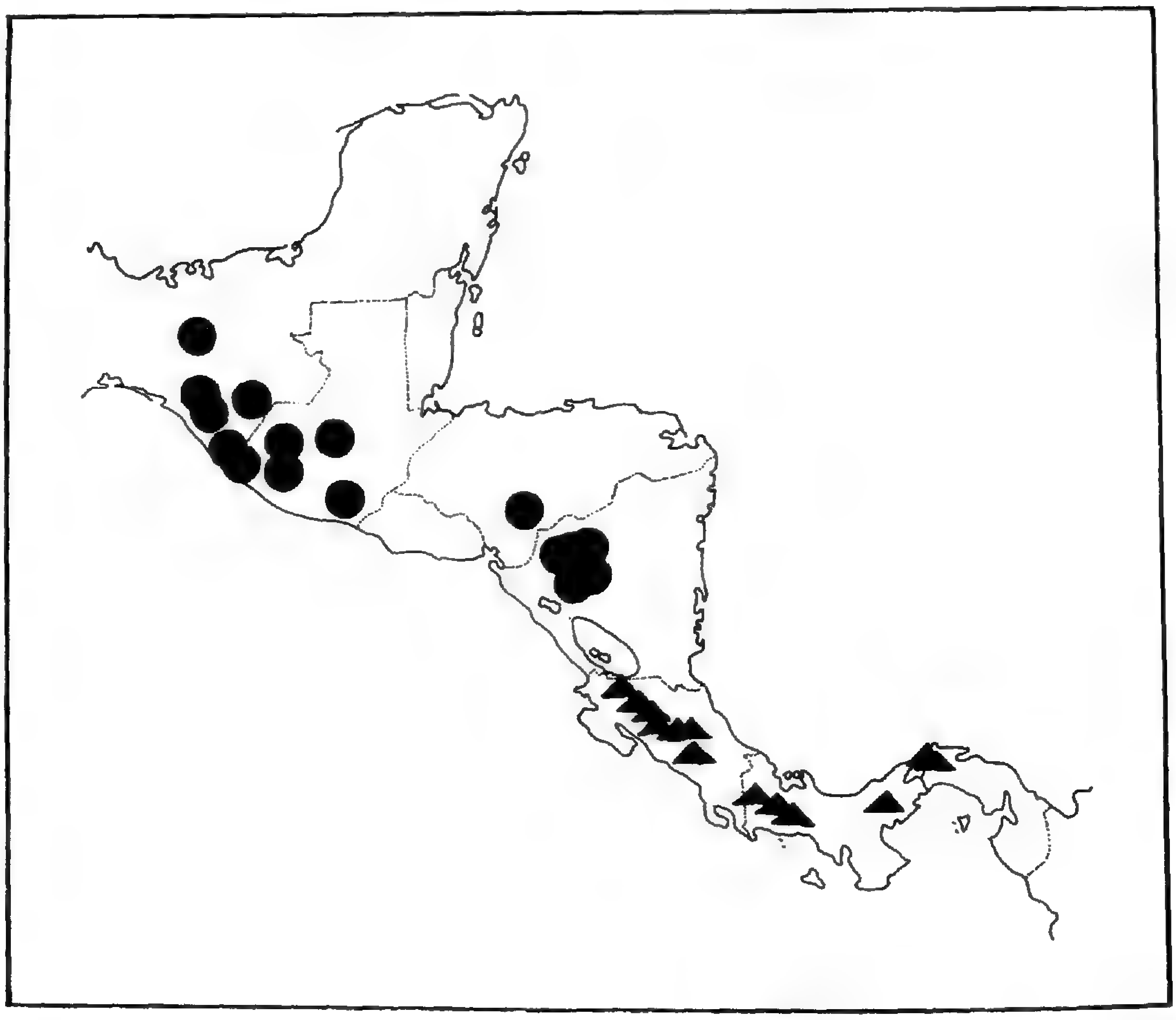

FIGURE 5. Distribution of *Cosmibuena matudae* (Standley) L. O. Williams (circles) and *C. valerii* (Standley) C. M. Taylor (triangles) in Central America and southern Mexico.

matudae Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 51. 1940. TYPE: Mexico. Chiapas: Volcán de Tacaná, 2,000–4,038 m, Aug. 1938, *E. Matuda 2327* (holotype, F (# 980255), photo (neg. # CNHM 52425) F (# 1631431); isotypes, A, NY, US (# 2216160)). Figure 1F, G; Standley & Williams, 1975: fig. 15.

Cosmibuena holdridgei Monach., Phytologia 3: 64. 1949. TYPE: Guatemala. Barillas to Tokija, July 1948, *L. R. Holdridge s.n./Monachino 519* (holotype, NY (# 3187) not seen, photo (neg. # CNHM 53087) NY; isotype, NY not seen, photo (neg. # CNHM 53088) NY).

Epiphytic or terrestrial, glabrous, to 16 m tall, drying green or grayish green; stems rounded to subquadrate; bark smooth, becoming gray to grayish brown. *Leaf* blades elliptic, 6.5–13 cm long, 3–8 cm wide, acutely angled at apex, acute to cuneate at base, subcoriaceous to coriaceous, glabrous throughout; secondary veins (6–)7–9 pairs, acutely angled with midrib, usually straight, usually well-marked and prominulous at least on abaxial surface, the distal 1–2 veins sometimes looping to interconnect; petioles 1–3 cm long, glabrous; stipules connate intrapetiolarly for ca. ¼–½ of their length, membranaceous to subcoriaceous, pale green to white at dehiscence, the interpetiolar portion oblanceolate to obovate, 15–30 cm long, rounded to broadly angled. *Flowers* (2–)3(–4) in one whorl; peduncles 5–15 mm long; bracts usually none or when present oblanceolate, 5–18 mm long, membranaceous; pedicels 6–15(–25) mm long; *calyx* limb 7–13 mm long, the tube 2–3(–5) mm long, deeply lobed, the lobes 5–6, narrowly triangular, 5–8 mm long, acute; *corolla* white throughout or flushed with pale green externally, the tube (40–)60–82 mm long, the lobes 5, elliptic-oblong, (10–)25–35 mm long, 6–20 mm wide, broadly angled to rounded; *anthers* 5, 15–18 mm long, the thecae extending ca. 1–3 mm below the filament attachment, the apices included or usually exserted for 1–3 mm; disk annular, 1–2 mm high; *ovary* elliptic to cylindric, 5–10 mm long; style 1–2 mm shorter than to 1–2 mm longer than corolla tube, glabrous or sparsely pilose in distal 1–3 cm; stigmas 4–7 mm long, frequently unequal in length by ca. 1 mm. *Capsules* 28–65 mm long, 6–13 mm diam., crowned by a beak ca. 2–5 mm long, frequently lenticellate; *seeds* including wings 5–6 mm long, 1–2 mm wide.

Phenology. Collected in flower May–October, in fruit October–January.

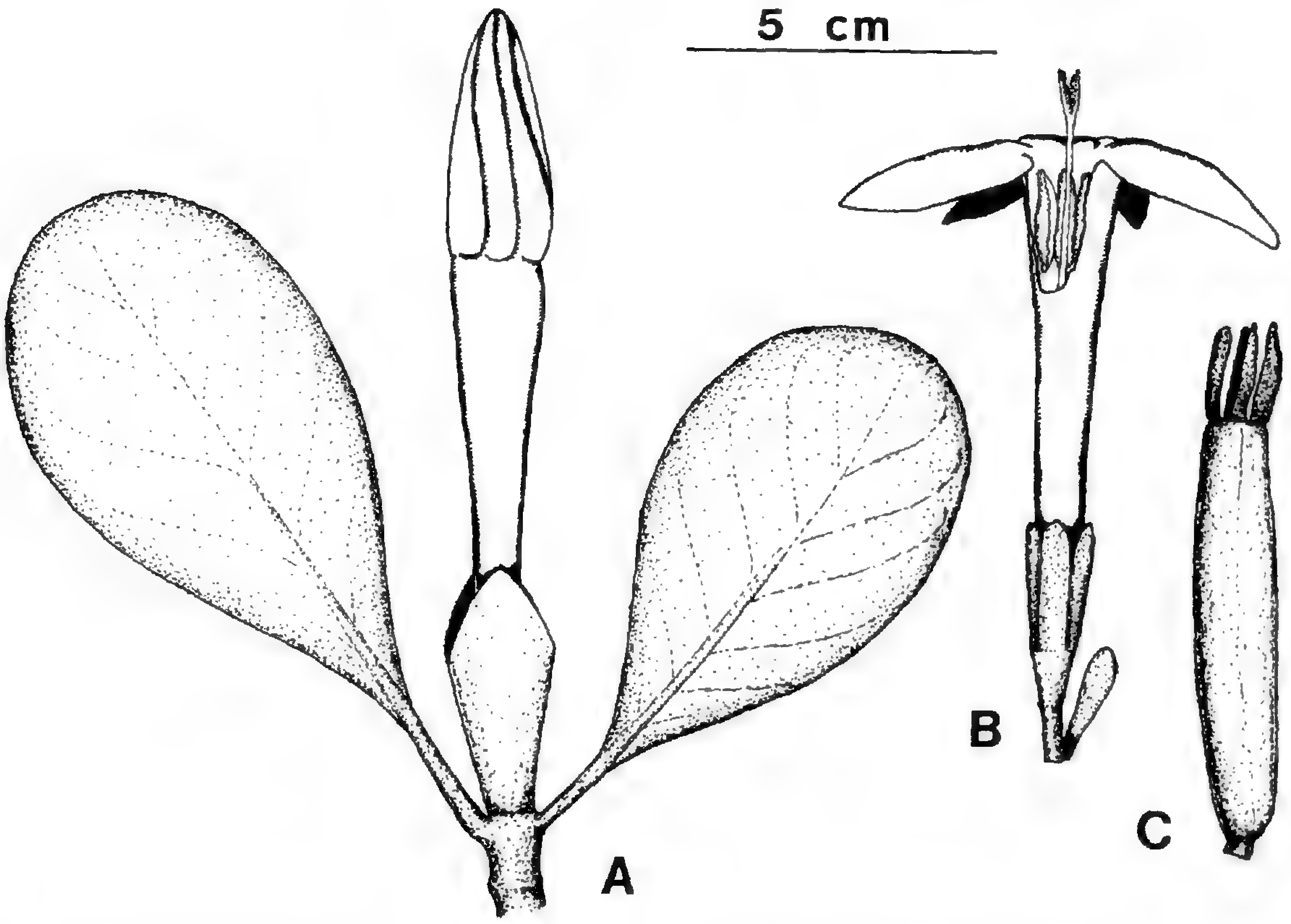

FIGURE 6. *Cosmibuena valerii* (Standley) C. M. Taylor.—A. Habit.—B. Flower, partially opened, with bract.—C. Capsule. A, B, from *Taylor 511* (F); C, from *Williams et al. 28318* (F). A–C to same scale.

Habitat and distribution (Fig. 5). Southern Mexico to Nicaragua, in wet thickets, banks, and forest at 1,200–2,500 m.

Selected specimens examined. GUATEMALA. ALTA VERAPAZ: ca. 10 km N of Cobán, *L. O. Williams et al. 42069* (F). CHIQUIMULA: upper slopes of Montaña Tajurán, vicinity of El Barriol, *J. A. Steyermark 30823* (F). HUEHUETENANGO: between Ixcan and Finca San Rafael, Sierra de los Cuchumatanes, between Cerro Chiblac and Finca San Rafael, *J. A. Steyermark 49471* (F). QUEZALTENANGO: above Mujulia, between San Martín Chile Verde and Colombia, *J. A. Steyermark 85538* (F). HONDURAS. MORAZAN: Mt. Uyuca, *L. O. Williams 17010* (F, GH, MO, US, WIS). MEXICO. CHIAPAS: E base of Cerro Tres Picos near Cerro Bola, SW of Colonia Agrónomos Mexicanos, Villa Corzo, *D. E. Breedlove & R. Thorne 30069* (MO, NY). NICARAGUA. JINOTEGA: along Hwy. 3, 1.9 km NW of Aranjuez road entrance, 13°02′N, 85°56′W, *W. D. Stevens 9166* (MO). MATAGALPA: along road to La Fundadora, ca. 5 km N of Santa María de Ostuma, Cordillera Central de Nicaragua, *L. O. Williams et al. 27760* (F, G, NY, US).

Cosmibuena matudae is distinguished by its relatively short, stout capsules and its calyx limb with the lobes longer than the tube. It is similar to *C. grandiflora*; the latter species can also be separated by its calyx limb with the tube longer than the lobes. These two species have generally complementary geographic ranges and appear to be closely related.

4. **Cosmibuena valerii** (Standley) C. M. Taylor, comb. nov. *Hillia valerii* Standley, J. Wash. Acad. Sci. 16: 164. 1928. TYPE: Costa Rica. San José: vicinity of La Palma on the road to La Hondura, 1,500–1,700 m, 17–18 July 1923, *Maxon & Harvey 8092* (holotype, US (# 11817760), photo (without number) F). Figure 6.

Hillia ligulifolia Dwyer, Ann. Missouri Bot. Gard. 67: 216. 1980. TYPE: Panama. Veraguas: 6–7 km W of Santa Fe on road past agricultural school, 935 m, 17 Feb. 1974, *M. Nee 9812* (holotype, MO (# 2244248); isotype, MO (# 2244247)).

Hillia chiriquiensis Dwyer, Ann. Missouri Bot. Gard. 67: 216. 1980. TYPE: Panama. Chiriquí–Bocas del Toro border: N of San Félix at province border, on Cerro Colorado copper mine road, 1,613–1,774 m, 3 May 1975, *Mori & Kallunki 5810* (holotype, MO (# 2259027); isotype, MO (# 2259026)).

Epiphytic or terrestrial, glabrous, to 15 m tall, drying reddish brown; stems quadrate to subterete; bark smooth, becoming brown. *Leaf* blades obovate, 3–9.8 cm long, 1–4.2 cm wide, obtuse to usually broadly rounded at apex, acute to attenuate at base, thickly coriaceous, glabrous; secondary veins 4–7 pairs, acutely angled with the midrib, usually straight, sometimes well marked, not prominulous, the distal 1–2 veins often looping to interconnect; petioles 5–20 mm long, glabrous; stipules connate intrapetiolarly for ca. ⅔ of their length but later separating, membranaceous, red at dehiscence, the interpetiolar portion obovate, 16–42 mm long, broadly rounded. *Flowers* solitary; peduncles 0–5 mm long; bracts often none, or when present broadly triangular, 2–11 mm long, membranaceous, rounded; *calyx* limb divided to base, the lobes 5, triangular to narrowly ligulate, 4–17 mm long, obtuse to rounded; *corolla* white throughout or flushed with pink or red externally, the tube 47–75 mm long, the lobes 5, elliptic to oblong, 17–31 mm long and usually unequal, 10–18 mm wide, rounded; *anthers* 5, 12–15 mm long, with the thecae extending ca. 2–3 mm below the filament attachment, the apices included; disk annular to slightly lobed, ca. 1 mm high; *ovary* cylindric, 6–17 mm long; *style* 2–5 mm longer than corolla tube, glabrous; stigmas 6 mm long, subequal in length. *Capsules* 40–98 mm long, 8–10 mm diam., crowned by a beak ca. 1–2 mm long, usually not lenticellate; *seeds* including wings 5–6 mm long, 1–2 mm wide.

Phenology. Collected in flower January–February, May–November, in fruit November–March and May–September.

Habitat and distribution (Fig. 5). Costa Rica and western Panama; wet montane forest, 774–2,300 m.

Selected specimens examined. COSTA RICA. ALAJUELA: La Palma de San Ramón, *A. M. Brenes 3827* (CR, F, NY), *5512* (CR, F, NY). CARTAGO: near La Sierra, ca. 25 km S of Cartago, *L. O. Williams et al. 28138* (F, GH, NY, US). GUANACASTE: Parque Rincón de la Vieja, Hacienda Santa María, sendero desde el Mirador en la falda del Volcán Santa María, 10°48′N, 85°19′W, *G. Herrera 652* (DUKE), *1382* (DUKE). HEREDIA: Tres Marías, Volcán Barba, *L. R. Holdridge 6675* (CR, F, NY). PUNTARENAS: ca. 3.5 km NE of Monteverde in the Peñas Blancas Trail, *R. L. Wilbur et al. 15804* (F). SAN JOSE: vicinity of La Palma on road to La Hondura, *J. Utley & K. Utley 2583* (CR, F, NY). PANAMA. BOCAS DEL TORO–CHIRIQUI BORDER: N of San Félix at province border, on Cerro Colorado copper mine road, *S. Mori & J. Kallunki 5810* (MO), *5934* (GH). CHIRIQUI: Cerro Colorado, along road to copper mine, 34.1 km beyond bridge over the Río San Félix near town of San Félix, 13.1 km beyond turnoff to Escopeta, *T. Croat 37256* (NY). PANAMA: vicinity of Cerro Jefe, near tower, *T. Antonio 4731* (NY). VERAGUAS: NW of Santa Fe 10.8 km from the Escuela Agrícola Alto de Piedras on road to Calovébora, *Mori 6707* (US).

Cosmibuena valerii is distinguished by its solitary flowers, calyx limb divided to the base, and red-brown color when dried. It has been confused with *Hillia tetrandra* Swartz and *H. maxonii* Standley; these two species can be distinguished by their four-lobed corollas, linear stigmas held well below the anthers, interpetiolar stipules, and comose seeds. *Cosmibuena valerii* has also been confused with *C. macrocarpa*; this latter species can be distinguished by its long slender capsules, imbricate corolla aestivation, and calyx limb with a well-developed tube.

Apparently neither Standley nor Dwyer saw fruits of *Cosmibuena valerii*, the seeds of which clearly lack trichomes, although the solitary flowers and completely lobed calyx limb do suggest *Hillia* rather than *Cosmibuena*. The placement of this species in *Cosmibuena* is problematic, as discussed in the introduction.

The calyx lobes of this species vary in length, shape, and persistence, but these characters show no geographic pattern or correlation with other features.

The illustration presented by Dwyer (1980: fig. 48) of "*Hillia chiriquiensis*" does not represent *Mori & Kallunki 5810*, as stated, but rather *H. panamensis* Standley. In practice, Dwyer applied the epithet "*chiriquiensis*" to specimens of *H. panamensis*, but the type collection he cited represents *Cosmibuena valerii*. The Latin and English descriptions he presented for his new species describe the flowers as green and funnelform, the calyx lobes as twice as wide as long (in the Latin description only), and the leaves as rounded at the apex; these descriptions do not satisfactorily fit any species of *Hillia* or *Cosmibuena* known from Panama.

EXCLUDED SPECIES

Cosmibuena acuminata Ruíz Lopez & Pavón, Fl. Peruv. 3: 3. t. 236. 1802. *Cinchona acuminata* (Ruíz Lopez & Pavón) Poiret, Encycl. Suppl. 4: 640. 1816. *Buena acuminata* (Ruíz Lopez & Pavón) DC., Prodr. 4: 356. 1830. TYPE: Peru. Chicoplaya, *J. Tafalla s. n.* (holotype, MA not seen; isotypes, F). = *Hillia parasitica* Jacquin.

Cosmibuena dichotoma (Ruíz Lopez & Pavón) G. Don, Gen. Hist. 3: 479. 1834. *Cinchona dichotoma* Ruíz Lopez & Pavón, Fl. Peruv. 2: 53. t. 197. 1794. *Ladenbergia dichotoma* (Ruíz Lopez & Pavón) Klotzsch in Hayne, Getreue Darstell. Gew. 14: subt. 15. 1846. TYPE: Peru. Chicoplaya, *J. Tafalla s. n.* (holotype, MA not seen). = *Joosia dichotoma* (Ruíz Lopez & Pavón) Karsten.

Cosmibuena ochracea Endl., Iconogr. Gen. Pl. t. 90. 1839. TYPE: Brazil. Minas Gerais: ad Tabara, 1839, *Martius 708* (holotype, W not seen; isotype, NY). = *Ladenbergia hexandra* (Pohl) Klotzsch.

Cosmibuena rhizophorae Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 178. 1940. TYPE: Colombia. Valle: Buenaventura Bay, mangrove swamp, 13 Apr. 1939, *E. P. Killip 34972* (holotype, F; isotype, US). = *Hillia maxonii* Standley.

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Numbered Collections of *Cosmibuena* Examined

Specimens are listed alphabetically by principal collector. The numbers in parentheses correspond to the number of the species in the text. Types are in boldface. All collections cited in the text are included here, along with additional collections of all species not cited in the text.

André, E.-F. 1976 (1). Anonymous (St. George Expedition) 580 (2). Acosta Solís, M. 2468 (2). Allen, P. H. 758 (2); 2798 (1). Antonio, T. 4731 (4).

Bailey, L. H. 279 (2). Bang, M. 2055 (1). Bangham, W. N. 473 (2). Barclay, A. S. 3741 (1). Betancur, J. 896 (1). Breedlove, D. 20277 (3); 24978 (3); 29633 (3); 30069 (3); 30864 (3); 31044 (3); 32287 (3); 32658 (3); 52306 (3); 55734 (3); 58089 (3). Brenes, A. M. 1911 (4); 3827 (4); 4924 (4); 5512 (4); 22012 (4). Burger, W. 9729 (4); 10259 (4).

Cabrera R., I. 3269 (2). Camp, W. H. E-3825 (1). Carrasquilla, L. 2108 (4). Chacón, I. A. 1931 (4). Churchill, H. 3958 (4). Contreras, R. 19 (2). Core, E. L. 1075 (1). Correa, M. D. 1032 (2). Croat, T. B. 5057 (2); 6326 (2); 6554 (2); 7833 (2); 11965 (2); 12285 (2); 12444 (2); 37256 (4); 54720 (1); 67042 (4); 67455 (2). Cuatrecasas, J. 14301 (2); 15287 (1); 23788 (1); 26048 (1); 28824 (1).

Danforth, R. E. 5 (1). D'Arcy, W. G. 6162 (2). Davidse, G. 31506 (1). de la Cruz, J. S. 1318 (1). de Nevers, G. 3613 (2); 6696 (4). Devia, W. 318 (1). Dryander, E. 2626 (1). Dryer, V. J. 506 (4); 705 (4); 1079 (4); 1552 (4). Duke, J. A. 6008 (2); 6193 (1); 11574 (2). Dwyer, J. D. 7773 (2).

Ebinger, J. E. 917 (2).

Fassett, N. C. 25488 (1). Fendler, A. 296 (2). Fernandez, A. 378 (2). Folsom, J. 4722 (4). Fosberg, F. R. 21407 (1). Foster, R. 1912 (2); 1225 (2). Fuchs, H. P. 22066 (2).

García, H. 20577 (1). Gentry, A. 5761 (2); 6114 (2); 13606 (2); 15341 (1); 17771 (2); 20259 (2); 35686 (2); 40715 (2); 53396 (2). Gómez, L. D. 23668 (1); 23984 (1). Gómez L., J. 5822 (4); 6577 (1). Grant, M. L. 9751 (1); 10544 (1). Grayum, M. H. 7754 (4). Gutiérrez R., A. 47 (1); 71 (1).

Haber, W. 409 (1); 548 (4); 614 (1); 1476 (2); 1929

(4); 1973 (4); 2911 (1); 5305 (4); 5863 (4); 5952 (1); 7381 (4); 7964 (1). Hall, J. S. 7944 (3). Hammel 8620 (2); 13364 (2); 15256 (4); 17090 (2); 17126 (1). Hampshire, R. J. 140 (4). Haught, O. 5580 (2). Hayes, S. 142 (2); 683 (2); 871 (2). Heinrich, J. E. 382 (3). Herrera 652 (4); 1071 (1); 1382 (4); Higgins, J. E. 400 (2). **Hinds 353 (2).** Hitchcock, A. S. 17619 (1). Hoffmann, C. 717 (1). Holdridge, L. R. 2254 (1); 6675 (4). Holm-Nielsen, L. 27928 (2). Holton, I. F. 22 (1); 439 (1). Hutchison, P. C. 6037 (1).

Johnston, I. M. 1598 (2). Juncosa, A. 1667 (2).

Kenoyer, L. A. 559 (2). Killip, E. P. 16424 (1); 33069 (2); 34816 (1). Knight, D. H. 8 (2). Koie, M. 4850 (2). Krukoff, B. A. 10418 (1). Kvist, L. P. 40401 (2); 40421 (1).

Lao, E. A. 15 (2). Lehmann BT 355 (1); BT 1171 (1); 8873 (2). Lent, R. W. 1836 (4); 2842 (4). Liesner, R. 15496 (4); 20300 (1). Lindeman, J. C. 660 (1). Linden, J. 1170 (1); 1257 (1); 5257 (1). Lumer, C. 1335 (4). Lugo, M. 50 (1). Lugo S., H. 6039 (1); 6087 (1). Luteyn, J. L. 419 (4); 4465 (4).

Maas, P. J. M. 7486 (1). McPherson, G. 7120 (4); 9552 (4). Madison, M. T. 5143 (2). Maguire, B. 23226 (1); 32511 (1); 40034 (1); 40082 (1); 53574 (1); 53710 (1); 53736 (1). Marcano B., L. 31-981 (1); 65-981 (1). **Matuda, E. 2327 (3)**; 15472 (3). **Maxon, W. R. 8092 (4).** Miller, J. S. 2212 (1). Molina, A. 11045 (3); 20876 (3); 22874 (3); 26038 (3); 31606 (3). **Monachino, J. V. 109 (3).** Moreno, P. P. 9550 (3). **Mori, S. 5810 (4)**; 5934 (4); 6707 (4). **Moritz 407 (1).** Mutis, J. 2241 (1); 4596 (1).

Nee, M. 9812 (4). Neill, D. 2326 (3).

Oersted, A. S. 11134 (1).

Pérez A., E. 2554 (1). **Pittier, H. 985 (1)**; 3309 (1); **4107 (2); 5074 (1).** Plowman, T. 4177 (1). Poveda, L. J. 769 (4). Prance, G. T. 4413 (1); 22680 (1); 28410 (1). Primack, R. 274 (4).

Robles, R. 1312 (2). Rodrigues, W. 4382 (1). Rodríguez, J. 10189 (1). Rubio, D. 690 (2). Ruíz L., H. 7184 (2). Rusby, H. H. 2103 (1).

Sánchez V., P. E. 98 (2); 118 (2). Sandwith, N. Y. 166 (1). Salvoza, F. M. 951 (2). **Schomburgk 553 (1).** Schunke V., J. 4105 (1); 6667 (1). Shattuck, O. 863 (2). Silvestre A. 78 (2). Skutch, A. F. 2974 (1); 5155 (1). Smith, A. P2283 (4). Solomon, J. 9376 (1); 14939 (1). Spruce, R. 4179 (1). Standley, P. A. 10943 (3); 50151 (4); 85538 (3). Stein, B. 2352 (1). Stevens, W. D. 9166 (3); 11292 (3); 11505 (3); 22577A (3). Steyermark, J. A. 105 (1); 4695 (1); 30815 (3); 30823 (3); 49471 (3); 87428 (1); 88859 (1); 89044 (1); 92875 (1); 103735 (1); 105758 (1); 117541 (1). Sytsma, K. J. 3963 (2).

Taylor, C. M. 511 (4); 2888 (4); 9737 (1). Thompson, S. A. 4701 (2). Tillett, S. S. 45481 (1). Todzia, C. 1935 (4). Tonduz 12440 (4). Triana 148 (1); 1818 (1); 1857 (2).

Utley, J. 394 (4); 2583 (4).

Weberbauer 3502 (1); 4713 (1). Werff, H. van der 6042 (1); 9578 (1). Wilbur, R. L. 15804 (4); 18632 (4); 20385 (4); 22001 (4); 22498 (4); 23797 (4); 24544 (4); 29522 (4); 29580 (4). Williams, Ll. 11413 (1); 11427 (1). Williams, L. O. 17010 (3); 23594 (3); 27760 (3); 27822 (3); 28138 (4); 29249 (3); 42069 (3). Woodson, R. E., Jr. 1738 (2). Woodworth, R. H. 711 (2).

Zak, V. 4561 (1). Zamora, N. 609 (4).

NOTES ON *ALOPHIA* (IRIDACEAE) AND A NEW SPECIES, *A. VERACRUZANA*, FROM VERA CRUZ, MEXICO[1]

Peter Goldblatt[2] *and Thad M. Howard*[3]

ABSTRACT

Alophia veracruzana is a new species of this American genus of Iridaceae subfamily Iridoideae. Closely related to the widespread *A. drummondii*, it differs in its pale to dark lilac-blue perianth with white to yellow markings, secund flower, and more or less erect inner tepals with lightly raised marginal areas bordering a smooth median zone. The generic characters of *Alophia* lie exclusively in its stamens and style, and the genus is defined by pandurate, nearly latrorse anthers, and deeply, but incompletely divided style branches with slender, ascending-recurved, terminally stigmatic style arms. The relationships of *Alophia* within tribe Tigridieae are uncertain, and its suggested affinities with *Tigridia* (Tigridiinae) seem unlikely. Despite a similar and derived karyotype with $n = 14$, and comparable forked style branches, the pollen grains of *Alophia* are not bisulcate as they are in all other Tigridiinae.

Among the many and mostly weakly differentiated genera of tribe Tigridieae of Iridaceae subfamily Iridoideae (Goldblatt, 1990), *Alophia* Herbert (synonym *Eustylis* Engelm. & Gray) comprises four species, distinguished on the basis of their pandurate anthers (Figs. 1B, 2B, 3B) with marginal sporangia and broad connective, and nearly terete style branches that are erect below and deeply divided into slender, ascending-recurved tubular arms stigmatic only at the apices (Figs. 1C, D, 2B, 3B). Vegetatively, species of *Alophia* can usually be distinguished by their rhipidial spathes (the paired opposed bracts enclosing the umbellate flower cluster), which are markedly unequal and long-attenuate. In addition the margins of the outer spathes are free and not even contiguous below. The bulbous rootstock and plicate leaves, the major synapomorphies for Tigridieae, differ in *Alophia* hardly, if at all, from most other genera of the tribe.

AFFINITES OF *ALOPHIA*

The immediate affinities of *Alophia* are uncertain. Historically, it has sometimes been included in *Tigridia* Juss. (e.g., Shinners, 1964) or considered closely related to this Central and South American genus (Goldblatt, 1974, 1982), which also has filiform, partly or often completely divided style branches (Molseed, 1970). *Tigridia* differs in having united or partly united filaments, more or less linear, extrorse anthers, usually held almost at right angles to the filament column, and style branches usually divided to the base into filiform, spreading style arms. In addition, in most species of *Tigridia* there is a mucro in the angle between the style arms of each style branch (Molseed, 1970). Species such as *T. molseediana* Ravenna and *T. martinezii* (Calderón, 1987), however, have suberect style branches divided only in their upper third and ascending anthers like *Alophia* and the monotypic *Fosteria* Molseed. The latter differs from *Tigridia* largely in the style branches, which in addition to being suberect and only partly divided, are ciliate, and presumably stigmatic, throughout (Molseed, 1968).

Together with these two genera and *Cobana* Ravenna and *Sessilanthera* Molseed & Cruden, *Alophia* was tentatively assigned to subtribe Tigridiinae (Goldblatt, 1982), based on their apparently shared derived polyploid karyotype with $x = 14$, in addition to the filiform and deeply divided style branches, and, except for *Alophia* (Goldblatt & Le Thomas, in prep.), united filaments and bisulcate pollen. Bisulcate pollen is now known to

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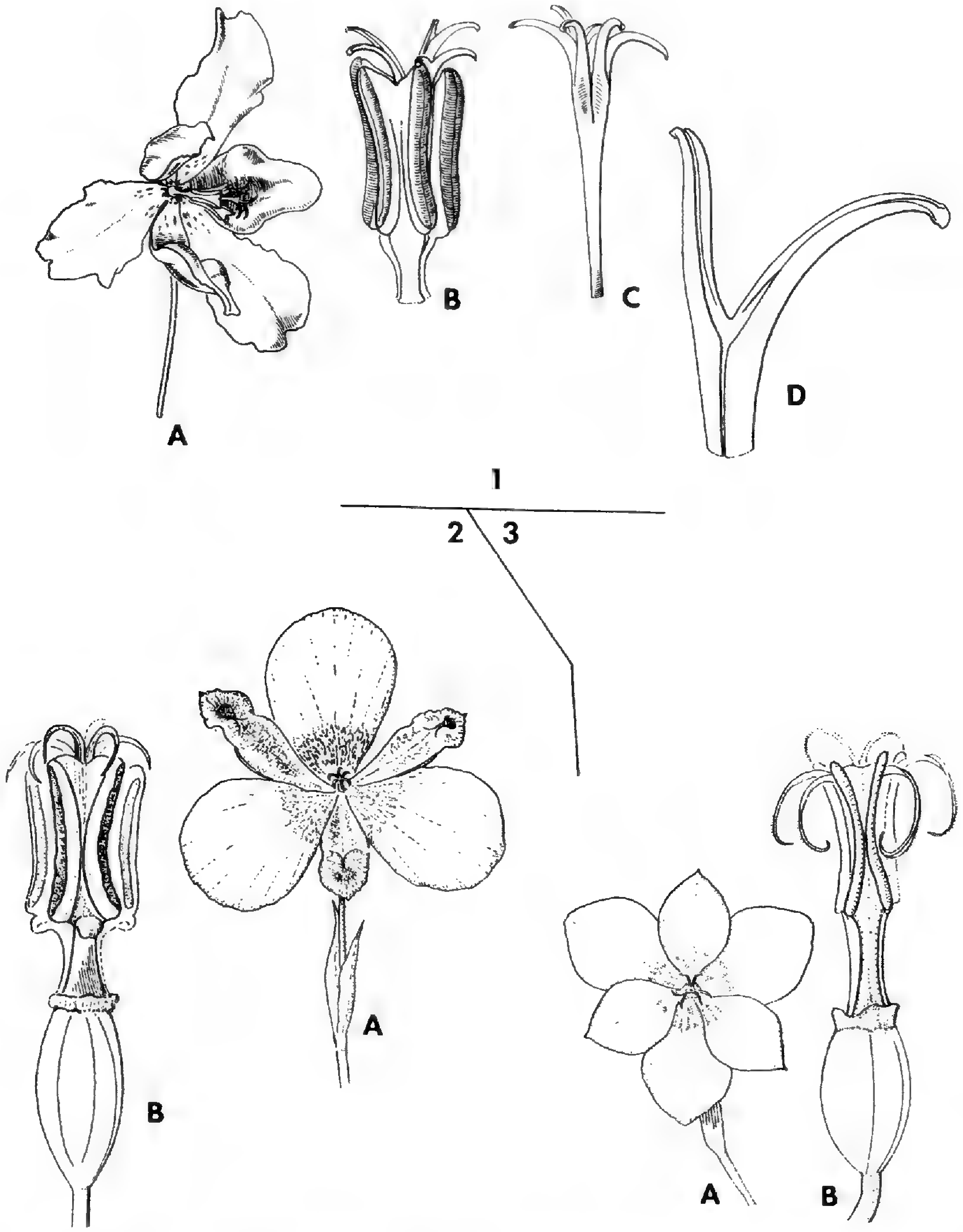

FIGURES 1–3. 1. *Alophia veracruzana*.—A. Whole flower.—B. Stamens and style branches.—C. Entire style.—D. Single style branch showing adaxial channeling and broadened stigmatic apices of individual arms. 2. *Alophia drummondii*.—A. Whole flower.—B. Stamens and style branches. 3. *Alophia silvestris*.—A. Whole flower.—B. Stamens and style branches. Whole flowers all full size, stamens and style branches, ×4, detail of style branch, D, × 10.

occur also in some Cipurinae (Rudall & Wheeler, 1988), another subtribe of Tigridieae. Moreover, one South American species of *Tigridia* from Peru (Kenton & Heywood, 1984) has been found to be diploid, $n = 7$, so that the tetraploid state is presumably not apomorphic for the subtribe.

Alophia shares some striking similarities with the monotypic Mesoamerican *Ainea* Ravenna (1979). Its style is virtually identical with that of *Alophia* (Goldblatt & Henrich, 1991), and the unusually long stamens also have a broad connective and lateral sporangia. However, unlike *Alophia*, the anthers are linear, not pandurate, and after anthesis they collapse inward in circinnate fashion. Like *Alophia*, *Ainea* has sulcate pollen grains and free filaments. The flowers of *Ainea* are unusual in their inner tepals, which are reduced in size and either oblong or obovate with a long central cusp. In either case, the inner tepals have raised marginal areas comparable with those of *Alophia veracruzana* and *A. drummondii*. So strong is the resemblance in critical taxonomic characters that *Ainea* and *Alophia* may be closely related, perhaps even congeneric, a possibility that needs to be explored.

Cardiostigma (*Sphenostigma*) *hintonii* (R. Foster) Ravenna also has a style similar to that of *Alophia* and *Ainea* (Goldblatt & Henrich, 1991), but the resemblance goes no further, and *C. hintonii* probably does not have a particularly close relationship to *Alophia* or *Ainea*.

Little attention has been paid to the broad connective condition in Iridaceae, and although it seems intuitively to be apomorphic, the character is distributed in two of three genera of Maricaeae and several species of *Cypella*, possibly the basal genus of Tigridieae. Thus, a broad connective is probably synapomorphous for the clade that includes Mariceae and Tigridieae (see Goldblatt, 1990) but plesiomophic for *Ainea* and *Alophia*, although the pandurate shape in *Alophia* seems unique. There no longer seems any reason to place *Alophia* in Tigridiinae. The shared polyploid base number is almost certainly convergent, and *Alophia* does not have either the united filaments or bisulcate pollen grains that are apomorphic for Tigridiinae. Beyond a possible close relationship with *Ainea*, the affinities of *Alophia* seem more uncertain than ever.

DISTRIBUTION AND SPECIES REVIEW

Alophia occurs across a wide portion of temperate and tropical America. The most well known and widespread species, *A. drummondii* (Graham) R. Foster (synonyms *Eustylis purpurea* (Herbert) Engelm. & Gray, *E. punctata* (Herbert) Ravenna), extends from the southern United States (Arkansas, Louisiana, Oklahoma, and Texas) to southern Mexico (including Vera Cruz, Chiapas, and Tabasco) (Goldblatt, 1974; Henrich & Goldblatt, 1992). The species, or one closely related to it, also occurs in Guyana (cf. *Maas et al. 1774*, U). This seems to have slightly smaller flowers, filaments united in the lower half, and style branches that are shorter and do not arch over the stamens. A second species, the smaller-flowered *A. silvestris* (Loesener) Goldblatt (synonyms *Nemastylis bequaertii* Standley, *A. rotacea* Ravenna), is restricted to Central America, where it extends from southern Mexico to Costa Rica. A third species, *A. medusa* (Baker) Goldblatt (basionym *Chlamydostylis medusa* Baker), apparently poorly known, occurs in Goiás, central Brazil. It is particularly distinctive in its large flowers and spathes (tepals 2.5–3 cm long, inner spathes 6 cm), a conspicuous band of glandular tissue in the median of the inner tepal limbs, and terete leaves. To these the new *A. veracruzana* can now be added. This has a restricted distribution in northeastern Mexico, currently known only from Vera Cruz.

One species, *Alophia intermedia* Ravenna (1964) (known to us only from the description) from Sinaloa in western Mexico, may be misplaced in the genus. It reportedly has pendent lilac-violet flowers with a yellow center, connate filaments, pandurate anthers, and deeply forked style branches, the arms of which are 14–15 mm long. In the article in which he described *A. intermedia*, Ravenna (1964) included *A. triflora* in *Alophia*, a species now regarded as conspecific with *Tigridia meleagris* (Molseed, 1970). Examination of the type of *A. intermedia*, not available to us, is necessary before its status and generic position can be assessed.

Alophia veracruzana seems most closely related to *A. drummondii*, which it resembles in the size and general form of the flower (Figs. 1A, 2A). *Alophia drummondii* is normally a taller plant, and the flowers are violet to red-purple with the well-differentiated tepal claws marked cream to yellow and densely speckled throughout with dark red-purple. The major difference between the two species lies in the shape of the inner tepals. In *A. drummondii*, the inner tepals are narrower than the outer tepals, and the limbs are sharply bent at the base (Fig. 2A). The edges of the lower part of the inner tepal limbs are closely pinched together below where they are whitish to yellow and arched over the median lower part of the limb. This fold covers a narrow median zone of stalked glandular, presumably nectariferous tissue. The distal part of the outer tepal limb is dark red-purple and ascending. *Alophia veracruzana* (Fig. 1A) lacks a clear distinction of tepal claw and limb, and the inner tepals, as wide as the outer and with lightly undulate margins, have no nectariferous band.

SYSTEMATICS

Alophia veracruzana Goldblatt & Howard, sp. nov. TYPE: Mexico. Vera Cruz: sandy roadside south of Alvarado, cultivated Missouri Botanical Garden, June 1990, *Goldblatt & Howard 9070* (holotype, MEXU; isotypes, K, MO). Figure 1.

Plantae 25–30 cm altae, bulbis anguste ovoideis, tunicis atrobrunneis, foliis 4–5, laminis plicatis, 5–8 mm latis, rhipidiis 4–5 florum, spatha interiore 32–38 mm longa, floribus lilacinis tepalis interioribus maculis albis vel luteis notatis, tepalis obovatis obscure unguiculatis, exterioribus 17–20 mm longis, ca. 10 mm latis, interioribus 16–19 mm longis, ca. 10 mm latis, staminibus atropurpureis, filamentis ca. 2 mm longis infra contiguis, antheris anguste panduratis, latrorsis, ca. 4 mm longis, 1.1 mm latis infra, ca. 2 mm supra.

Perennial geophyte 25–30 cm high. *Bulbs* narrowly ovoid, the scales dark brown. *Leaves* 4–5, laminate except the uppermost ± entirely sheathing and elaminate, blades plicate, mostly about as long to slightly longer than the stems, the lower 2–3 inserted below the ground, the upper two inserted well above ground, the lower of these near the base and the upper near the midline and shortest, narrowly lanceolate (to almost linear), 5–8 mm at the widest, apices attenuate. *Stem* terete, generally with one branch produced in the upper third, subtended by the sheathing leaf. *Inflorescences* rhipidia, single and terminal, usually 4–5-flowered; *spathes* green, attenuate, the apices generally dry and light brown, unequal, the inner 32–38 mm long, the outer about ⅔ as long. *Flowers* secund, the pedicels about ⅔ as long as the inner spathe, curved outward at the apex; *perianth* actinomorphic, pale to dark lilac-purple (rarely whitish), paler toward the center and lightly flecked toward the margins with darker purple, the inner tepals with undulate margins and each with a pair of large white to yellow marks near the base of the limbs, with a weak spicy-sweet scent; *tepals* free, ± obovate, claws weakly differentiated and spreading outward, outer tepals 17–20 mm long, the limbs spreading, ca. 10 mm wide, inner tepals 16–19 mm long, ca. 10 mm wide, the limbs held at ± right angles to the claws and with the lower lateral areas raised and the median portion recessed. *Stamens* dark purple, filaments ca. 2 mm long, broader and contiguous below, narrow in the upper half; *anthers* coherent at their bases, with a broad narrowly pandurate connective narrowest in the middle ⅔, weakly ascending, ca. 4 mm long, 1.1 mm wide at the base, nearly 2 mm at the apex, sporangia marginal and nearly latrorse; pollen yellow, broadly sulcate. *Ovary* narrowly obovoid, ca. 4 mm long, exserted from the spathes; *style* ca. 5.5 mm long, dividing opposite the middle of the anthers into three thickened branches, the branches erect, ca. 1.5 mm long, each dividing into two long ascending-recurved arms, these ca. 3 mm long, tubular, stigmatic apically, arching over the anthers. *Capsules* obovoid-oblong, trigonous and truncate, 14–24 mm long; *seeds* 1.8–2.0 × 1.3–1.5 mm, obovoid-pyriform, narrowest at the micropylar end, the chalazal end concave, lightly rugose, yellow-brown. *Chromosome number* $2n =$ 28 (*Goldblatt & Howard 9070*).

Flower Phenology and Compatibility

As in all Tigridieae, the fugacious flowers last only one day. Flower buds appear the day before flowering, and the tepals enlarge to their full size during the night. Early in the day the outer tepals unfold, but until 7 A.M. the inner tepals remain closed over the style and stamens. The inner tepals begin to separate at about 8 A.M., and by 9 A.M. they have spread sufficiently to allow access to the style and stamens; by this time the anthers have dehisced, revealing the bright yellow pollen. At about 10 A.M. the inner tepals reach their full open position. The tepals begin to collapse at about 2:30 P.M., and by 3:30 P.M. are closed together. Like its relative *A. drummondii*, *A. veracruzana* is self-compatible. Self-fertilization often occurs in one or two flowers of a rhipidium with resultant capsule and seed production. As the stigmas are not in contact with the anthers while the flowers are open, pollination presumably occurs after the flowers collapse, when the parts of the flowers are pushed together by the inward-falling tepals. Outcrossing is presumably the normal mode of reproduction for the species in view of the colorful and fragrant perianth. The occasional selfing presumably serves to ensure seed production in the absence of insect-mediated pollination. Plants of *A. veracruzana* can be raised from seed to flowering in a single growing season. Seeds sown in late fall in the greenhouse in St. Louis grew to flowering size in about six months.

Karyology and Pollen Morphology

Chromosome number in *Alophia veracruzana* is $2n = 28$. Four long chromosomes, one pair submetacentric and the other acrocentric, contrast markedly from the 12 remaining much smaller pairs. The karyotype accords with that of the tetraploid members of Tigridiinae (Goldblatt, 1982; Kenton & Heywood, 1984).

The pollen grains have a single broad sulcus as long as the grains when fully expanded (Goldblatt & Le Thomas, in prep.) and resemble those of *A. drummondii* (Goldblatt, 1974). The grains of *Alophia* thus correspond with those of the majority of Tigridieae excluding Tigridiinae (*Tigridia*, *Fosteria*, *Sessilanthera*, and *Cobana*—Molseed, 1970; Ravenna, 1974), which have bisulcate grains.

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CHROMOSOME NUMBER IN *TICODENDRON* (FAGALES, TICODENDRACEAE)

Neil Snow[1] *and Peter Goldblatt*[2]

ABSTRACT

The chromosome number of *Ticodendron incognitum* is reported for the first time as $2n = 26$, and the phylogenetic significance of this number within Fagales is discussed.

After exhaustive collaboration among several authors (Hammel & Burger, 1991) the monotypic family Ticodendraceae was described (Gomez-Laurito & Gomez P., 1991) to accommodate the Mesoamerican tree *Ticodendron incognitum* Gomez-Laurito & Gomez P. (1989). Evidence from wood anatomy (Carlquist, 1991), leaf anatomy (Hickey & Taylor, 1991), floral anatomy and morphology (Tobe, 1991), pollen (Feuer, 1991), and sieve element characters (Behnke, 1991) strongly suggests its inclusion in Fagales. We report for the first time the chromosome number of *Ticodendron incognitum* as $2n = 26$ and discuss the possible phylogenetic significance of this number within Fagales.

MATERIALS AND METHODS

Root tips were collected at approximately 9:30 A.M. from a single specimen growing in the greenhouses at the Missouri Botanical Garden (Voucher: *Hammel & Rivera 17834*, MO). After pretreatment with aqueous 1-bromonaphthalene for 4 hours, the tips were fixed in 3:1 ethanol (95%)–glacial acetic acid. After hydrolysis in 10% HCl for 7 minutes at 70°C, root tips were squashed in FLP orcein (Jackson, 1973).

DISCUSSION

The diploid number of $2n = 26$ and small, relatively uniform chromosomes of *Ticodendron incognitum* corroborate the results cited above that indicate the distinctness of this taxon from other families of Fagaceae.

The Fagales (sensu Cronquist, 1981) have base numbers $x = 8, 11, 12, 13$, and 14 (Raven, 1975). In Fagaceae $x = 12$ predominates, occurring in *Castanopsis, Cyclobalanopsis, Fagus, Castanea, Lithocarpus, Pasania,* and *Quercus* (Mehra & Hans, 1969; Raven, 1975; Morawetz & Samuel, 1989), while *Trigonobalanus* has $x = 21$ or 22 (Hou, 1971; Soepadmo, 1972). *Colombobalanus* and *Formanodendron,* segregated from *Trigonobalanus* by Nixon & Crepet (1989), remain uncounted in the family. *Nothofagus,* which may merit its own family (Nixon, 1982), has $x = 13$ (Armstrong & Wylie, 1965; Ono, 1977). Within Betulaceae *Carpinus, Ostrya,* and *Ostryopsis* form a distinct, evidently paleodiploid group with $x = 8$ (Raven, 1975; Löve & Löve, 1982); *Betula, Alnus* (Raven, 1975), and *Dusckechia* (Kovanda, 1984; Pashuk, 1987) have $x = 14$; *Corylus* may have $x = 14$ (records of $2n = 28$ require confirmation), but there are records of $n = 11$ in the genus as well (e.g., Löve & Löve, 1982). The monogeneric Balanopaceae appear to have $x = 20$ (Morawetz & Samuel, 1989) (the single count of $n = 21$ in *B. australina* (Goldblatt, 1979) may be erroneous).

Clearly, $x = 13$ is infrequent in Fagales. Our count of $2n = 26$ from a single plant suggests $x = 13$ for Ticodendraceae, so within the order *Ticodendron* shares this number only with *Nothofagus*, a genus from which it is distinct.

Although Raven (1975) proposed $x = 7$ as basic for Fagales, a plausible scenario for chromosomal evolution can be suggested based on $x = 8$. Assuming $x = 8$, presumed base number in the closely related Hamamelidales as well (Goldblatt & Endress, 1977; Morawetz & Samuel, 1989), for the early members of Fagales, dysploid reduction to $x = 7$, followed by a doubling to 14 and subsequent reduction to 13, 12, and 11 seems to us the most reasonable explanation for change within extant members of the order. The base number $x = 13$,

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common to *Ticodendron* and *Nothofagus*, was most likely achieved independently from $x = 14$, a hypothesis supported by significant differences in wood anatomy (Carlquist, 1991), reproductive morphology (Tobe, 1991), leaf architecture (Hickey & Taylor, 1991) and other features. We note, however, the comment by Tobe (1991: 141) that *Nothofagus* is the best candidate in comparing Fagaceae with *Ticodendron*, which is at least superficially similar in a number of important characters.

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THE GENUS *CYBIANTHUS* SUBGENUS *CONOMORPHA* (MYRSINACEAE) IN GUAYANA[1]

John J. Pipoly III[2]

ABSTRACT

A taxonomic treatment of the species in *Cybianthus* subg. *Conomorpha* occurring in the Guayana Floristic Province is presented. Twenty-one species are described and illustrated, and their phylogenetic relationships are discussed. The distribution and ecology of each species are provided. A key to the subgenera of *Cybianthus* occurring in Guayana is presented, as is a key to the species within subgenus *Conomorpha*. Of the 21 species described, seven are new to science, one is transferred from subgenus *Weigeltia*, and one is transferred from subgenus *Cybianthus*. The new taxa include: *Cybianthus fabiolae*, *C. huberi*, *C. julianii*, *C. plowmanii*, *C. wurdackii*, *C. holstii*, and *C. maguirei*. The species concept of *Cybianthus guyanensis* is amplified to include *C. multipunctatus* as a subspecies, and the new combination, *C. guyanensis* subsp. *multipunctatus*, is made. Five additional binomials are lectotypified.

RESUMEN

Se presenta un tratamiento taxonómico de las especies del género *Cybianthus* subgénero *Conomorpha* procedentes de la Provincia Florística Guayanesa. Se describen y se ilustran veintiún especies y se discuten su parentezco, distribución geográfica y ecología. Se presenta una clave para los subgéneros de *Cybianthus* de la Guayana, y una para las especies dentro del subgénero *Conomorpha*. De las veintiún especies descritas, siete son nuevas para la ciencia, una se transfiere del subgénero *Weigeltia*, y otra se transfiere del subgénero *Cybianthus*. Los nuevos taxa incluyen: *Cybianthus fabiolae*, *C. huberi*, *C. julianii*, *C. plowmanii*, *C. wurdackii*, *C. holstii*, y *C. maguirei*. El concepto de *Cybianthus guyanensis* se amplifica para incluir a *C. multipunctatus* como subespecie, y la nueva combinación, *C. guyanensis* subsp. *multipunctatus*, se publica. Cinco binomiales adicionales son lectotipificados.

Cybianthus Martius is the second largest genus of Myrsinaceae in the Neotropics, after *Ardisia* Swartz, the latter containing nearly 200 species. As here interpreted, *Cybianthus* contains 150 species in 10 subgenera. During the course of my work on the genus, it became apparent that an integral part of any *Flora Neotropica* monograph would involve detailed study of the Guayanan species, particularly those of *Cybianthus* subg. *Conomorpha* (A. DC.) Agostini. The subgenus had been revised by Agostini (1971) in his dissertation, but in 1978 he gave me his file on the genus and suggested I pursue a monograph.

While revising subgenus *Conomorpha*, I dis-

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covered my concept of phylogenetic relationships within the subgenus and among the subgenera differed substantially from that of Agostini (Pipoly, 1987). The specimens collected by Steyermark, Huber, Holst, and the various collectors who participated in the Cerro de la Neblina expeditions provided material and ecological data that nearly doubled the amount of information available to Agostini. Fieldwork allowed me to observe sympatry, separation of species by abrupt changes in life zone, and sexual lability (dioecy and various combinations of polygamy in the same population), which had caused taxonomic confusion when studied only in the herbarium. Were it not for the wealth of new collections and field studies of populations, the reliance on relative lengths of the free portions of the filaments to separate many species by Agostini (1971) could not have been replaced by more practical characters, and phylogenetic analysis would have been precluded.

The present treatment is a precursor to my contribution to the *Flora of the Venezuelan Guayana*. Because the abbreviated format of the *Flora* does not allow discussions of ecology, morphology, and the description of novelties outside the territorial limits established therein, it became necessary to present a more comprehensive treatment prior to its publication.

MORPHOLOGY

In this treatment, morphological terms follow Lindley (1848) and Pipoly (1987).

HABIT AND ARCHITECTURE

All species of *Cybianthus* subg. *Conomorpha* are terrestrial shrubs or trees to 5 m tall with positively geotropic roots. All species of the subgenus except *C. fabiolae* exhibit Rauh's Model (Hallé et al., 1978), which is characterized by a monopodial, rhythmically growing, readily distinguishable trunk, which develops tiers of branches morphogenetically identical to itself. All branches are orthotropic and monopodial, with lateral (axillary) inflorescences that do not affect shoot development. As in most tropical trees exhibiting Rauh's Model, branching in members of subgenus *Conomorpha* is exclusively sylleptic. The sylleptic branches are easily recognized by the absence of basal bud-scales and the elongate hypopodium (an elongate portion of the stem below the prophylls). In subgenus *Conomorpha*, all species have sylleptic branches (sensu Hallé et al., 1978) that possess two ephemeral prophylls on the hypopodium, except *C. apiculatus*, in which they are persistent, leaflike, and petiolate. It is the only species in the genus known thus far with persistent prophylls.

While I had earlier (Pipoly, 1987) doubted the possibility of finding Aubréville's Model (Hallé et al., 1978) within the genus, I observed it in the field in *Cybianthus fabiolae* Pipoly. Aubréville's Model is characterized by a monopodial, rhythmically growing trunk with tiers of branches morphogenetically distinct from it. The branches grow rhythmically, but are modular, developing as complexes that are plagiotropic and sympodial by apposition. In these complexes, the terminal meristem is displaced by an axillary one, but continues its growth in a rhythmic manner, producing extremely short internodes, thus remaining as a "short shoot." The sylleptic branch axis is at first oriented obliquely upward, but is progressively displaced downward, eventually in a plane perpendicular to the axis. Inflorescence production is lateral and occurs only in the axils of recently developed leaves of the short shoot. The inflorescence is sylleptically produced, senescent after fruit fall, and does not influence leaf or shoot production. The architectural dynamics of this model result in the characteristic "*Terminalia* branching" first described by Fisher (1977), with the exception that the progressive downward bending of branches was not observed. Whether this notable exception to modular dynamics is attributable to the small branch size and insignificant fruit weight in *C. fabiolae*, or some other morphogenetic or environmental factor, is unknown.

Unlike previous architectural studies in the genus (Pipoly, 1987), the present study did not reveal a direct correlation between sexual lability and architectural reiteration. It seems possible that this phenomenon might occur in *C. quelchii*, based on polygamy observed in some collections (e.g., *Tillett et al. 45609*), but it has not been observed in the field. Bayonet reiteration (Hallé et al., 1978), caused by destruction of the apical meristem of the trunk, was seen in *C. quelchii* on Serra Aracá, but the individual was not in flower, precluding study of consequential effects on sexual expression. In populations of *C. fabiolae* studied on Mt. Ayanganna, riverine reiteration (sensu Hallé et al., 1978), presumably produced by stress as a result of overshadowing by other trees, resulted in the production of an orthotropic shoot in the distal portion of an otherwise plagiotropic branch. Because the reiterative shoot was not in flower, the only concrete variation was the notable elongation of internodes and saplinglike leaf morphology. Further study of these populations is necessary to establish whether

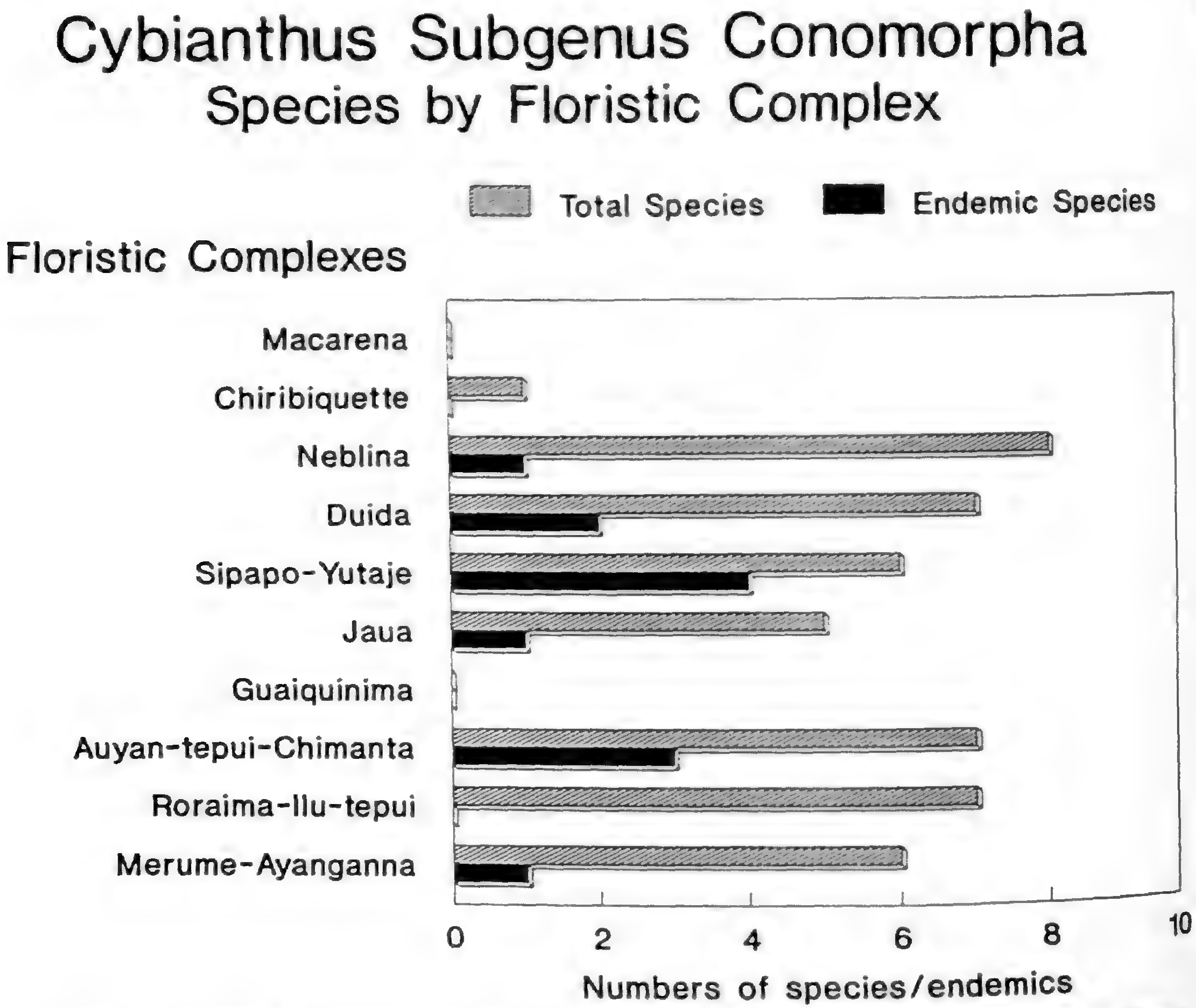


FIGURE 1. Species of *Cybianthus* subgenus *Conomorpha* (A. DC.) Agostini, found in the Guayana Floristic Province: total species vs. endemics per floristic complex (sensu Maguire, 1979). Complexes listed from top to bottom proceed from west to east across South America. Note that Chiribiquette and Macarena complexes belong to the Trans-Río Negro, Colombian Guayana Subprovince; Neblina, Duida, Sipapo-Yutajé, Jaua, and Guaiquinima complexes belong to the Río Caroní-Río Negro Subprovince; Auyán-tepui-Chimantá, Roraima-Ilú-tepui, and Merume-Ayanganna complexes belong to the Guyana-Pakaraima-Venezuelan Gran Sabana Subprovince.

exploration is needed in the Macarena, Chiribiquette, and Guaquinima complexes to determine if the low representation of subgenus *Conomorpha* is biogeographically significant, or if it is merely a collecting artifact.

TAXONOMIC CONCEPTS AND NOTES ON KEYS

My species concept follows that of Wiley (1978, 1981), who defined a species as follows: "An evolutionary species is a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." My subspecies concept (Pipoly, 1987) defines a subspecies as follows: "groups of populations within a single lineage of ancestor-descendant populations that show variation by unique combinations of plesiomorphies, or homoplasic apomorphies, correlated with biogeography and/or ecology. This rank is primarily used to convey information regarding variation in the life histories of these populations and character state differences hypothesized to be the result of this variation. The subspecific rank in no way attempts to predict speciation events."

The keys are artificial and designed to expedite identification of herbarium specimens. The numbers appearing before the taxa refer to the respective position of the species in the key, and any correlation with phylogenetic relationship is coincidental. Quantitative and qualitative data presented in keys and descriptions for floral parts and bracts were taken from organs rehydrated from herbarium specimens by boiling in water. Measurements from these range from 10% to 15% greater than those measurements taken directly from dried material. Data regarding stem diameters, inflorescence rachises, pedicels, leaf, and fruit shape were taken from dried herbarium specimens.

A description of the genus *Cybianthus* and a key to its subgenera are provided below. This description, along with that of subgenus *Conomorpha,* includes features found in the taxon as a whole, including those species occurring outside the Guayana Florisic Province.

Cybianthus Martius, Nov. Gen. Sp. Pl. 3: 87. 1831, nom. cons. TYPE SPECIES: *Cybianthus penduliflorus* Martius, Nov. Gen. Sp. Pl. 3: 87. 1831.

Terrestrial or epiphytic, monoaxial or polyaxial shrubs or trees to 15 m tall. Architectural development by Rauh's Corner's, or Aubréville's Models (Hallé et al., 1978). Roots positively geotropic or diageotropic. Branchlets glabrous, glandular-granulose, dendroid- and stellate-tomentose, furfuraceous- or ferrugineous stipitate-lepidote. Leaves sessile or petiolate, alternate, subopposite or pseudoverticillate, the venation camptodromous or acrodromous, the petioles canaliculate, pulvinate, or absent. Inflorescence axillary, a simple, condensed or spicate raceme (the flowers sessile to subsessile), a panicle with racemose branches, or an indeterminate umbel. Flowers functionally unisexual or bisexual, 3–6(–7)-merous. Staminate flowers with pistillode conic, lageniform, turbinate or irregularly shaped, vestigial, hollow or bearing sterile placenta, rarely absent. Pistillate flowers with staminodes morphologically similar to the stamens but reduced in size, at times producing abortive pollen. Calyx patelliform, crateriform, cotyliform, or cupuliform, the lobes imbricate, valvate, or somewhat contorted, basally connate ⅕–⅔ their length, abaxially glabrous, glandular-granulose, or with translucent or ferrugineous lepidote scales, adaxially glabrous. Corolla cupuliform, campanulate, rotate or subrotate, the lobes basally connate ⅕–¾ their length, abaxially glabrous, glandular-granulose along the margins, or with ferrugineous lepidote scales, adaxially glabrous or glandular-granulose. Stamens adnate to corolla tube at least ⅔ their length, the filaments variously connate to form a tube, the staminal tube adnate to the corolla tube or at times developmentally fused with it (the stamens thus appearing epipetalous), bearing fleshy lobes alternate with the anthers or not, the anthers ovate, widely ovate, or triangular, basifixed or dorsifixed, apically acute, rounded, emarginate or minutely apiculate, basally cordate, erect or dorsally recurved, dehiscent by confluent apical pores or by wide to narrow longitudinal slits; pollen tricolporate, psilate; pistil obnapiform, umbonate, or turbinate, the ovary glabrous or sparsely to densely translucent glandular-lepidote, the style glabrous, the stigma capitate, capitate-lobate or punctiform, the placenta free-central, carnose, umbonate to subglobose, the ovules campylotropous, (1–)2–5(–7), uni- or biseriate. Fruit drupaceous, 1(–2)-seeded, the endosperm translucent, nonstarchy, the embryo small, linear, flexuous, erect or curved, longitudinal or transverse, the cotyledons not well developed.

A neotropical genus of 150 species, *Cybianthus* is a conspicuous element of the Guayana Highland, inhabiting tepui summit savannas, gallery, talus slope, lowland igapó, várzea, moist and wet forest formations throughout the Guayana Shield. Its species may always be found near watercourses, and many apparently sympatric species are separated ecologically by life zone rather than elevation.

The genus is cladistically defined by the unique glandular granules at the corolla lobe and tube junction (Pipoly, 1987). For practical purposes of identification, the combination of axillary racemes, spikes or racemose panicles, and filaments that are shorter than the corolla, connate at least ¼ their length, and adnate to the corolla at least ⅓ its length allows for easy recognition.

In the Guayana Highland, there are 40 species in five subgenera. A key to the subgenera of the Guayana Floristic Province is provided below.

KEY TO SUBGENERA OF *CYBIANTHUS* IN GUAYANA

1a. Corolla cupuliform to campanulate; anthers longer than wide, usually distally recurved in anthesis, mostly apically acute or minutely apiculate.
  2a. Branchlets and calyx ferrugineous stipitate-lepidote; calyx lobe margin glabrous (except in *C. apiculatus*); abaxial corolla surface mostly glabrous along the margin .... I. *Conomorpha*
  2b. Branchlets and calyx stellate and/or dendroid tomentose; calyx lobe margin glandular-ciliate; abaxial corolla surface always glandular-granulose along the margin .... II. *Laxiflorus*
1b. Corolla rotate to subrotate; anthers wider than long, always erect, apically rounded or emarginate.
  3a. Petioles abruptly swollen basally; anthers versatile, longitudinally dehiscent .... III. *Weigeltia*
  3b. Petioles not abruptly swollen basally or absent; anthers basifixed, poricidally dehiscent.
    4a. Leaves apically mucronate, the petioles absent, the margins scarious, the venation acrodromous, the bases au-

riculate; staminal tube merely adnate to the corolla tube ____ IV. *Grammadenia*

4b. Leaves apically not mucronate, the petioles present, the margins opaque, the venation camptodromous, the bases attenuate, acute or cuneate; staminal tube developmentally fused to the corolla tube, the stamens thus appearing epipetalous ______ V. *Cybianthus*

I. **Cybianthus** Martius subg. **Conomorpha** (A. DC.) Agostini, Acta Biol. Venez. 10: 150. 1980. *Conomorpha* A. DC., Trans. Linn. Soc. London, Bot. 17: 102. 1834; *Conomorpha* sect. *Euconomorpha* Miquel, Stirp. Surinam. Select. 111. 1850; *Conomorpha* subg. *Euconomorpha* (Miquel) Mez, in Engler, Pflanzenr. IV, 236: 254. 1902. TYPE SPECIES: *Cybianthus oblongifolius* (A. DC.) Agostini (lectotype, selected by Agostini, Acta Biol. Venez. 10: 151. 1980).

Conomorpha sect. *Aconomorpha* Miquel in Martius, Fl. Bras. 10: 304. 1856. TYPE SPECIES: *Conomorpha heterantha* Bentham (lectotype, selected by Agostini, Acta Biol. Venez. 10: 151. 1980).

Terrestrial shrubs or trees. Bark smooth or fissured, brown or beige, rarely with significant amounts of cork (*C. quelchii*). Trunk distinguishable, leptocaulous, the growth dynamics following Rauh's or rarely (*C. fabiolae*) Aubréville's Architectural Model. Branchlets thin to moderately thick, terete or ridged, densely to moderately covered with ferrugineous stipitate-lepidote scales, the scales at times appressed, rarely glabrescent (*C. quelchii*, *C. apiculatus*). Leaves alternate, petiolate, covered with ferrugineous stipitate-lepidote scales, often glabrescent above; petioles canaliculate, marginate, or rarely winged. Inflorescence axillary, racemose, spicate or paniculate, the panicles with racemose branches, rarely a solitary flower; inflorescence bract small, lanceolate, early caducous; rachis erect or lax, straight or rarely tortuous, ferrugineous stipitate-lepidote; floral bracts deltate, lanceolate or ovate, ferrugineous stipitate-lepidote, inserted at the base of the pedicel; pedicels terete, at times clavate in fruit, erect, apically recurved, pendent, or nodding, at times accrescent in fruit, rarely absent. Flowers unisexual, rarely bisexual, dimorphic, (3–)4–5(–6)-merous, the plants dioecious or rarely polygamous; calyx cotyliform, cupuliform, crateriform, or patelliform, the lobes valvate, the margin entire, rarely crenulate or erose; corolla campanulate to cupuliform, rarely subrotate (*C. apiculatus*), or deeply rotate (*C. crotonoides*), the lobes erect or reflexed, valvate or imbricate, ferrugineous stipitate-lepidote or glabrous without, at times with a narrow line of glandular granules along the margin, glandular-granulose within, epunctate or the punctations conspicuous, not prominent, brown or translucent, the margins entire or rarely crenulate, glabrous or rarely glandular-granulose; staminodes resembling stamens but reduced in size, the tube conspicuous or inconspicuous, adnate to the corolla, lobate or elobate, the anthers ovate or triangular-ovate, usually recurved distally, rarely erect, the apex acute or apiculate, rarely rounded, the apiculum dorsally, rarely proximally recurved or erect, the base cordate, dorsifixed from near base to subversatile, the connective punctate or not; pistillode conic to lageniform, rarely absent, translucent-lepidote, hollow; pistil obnapiform, rarely conic, the ovary globose, lobed or with an apical apophysis (*C. huberi*, *C. holstii*), the style short, the stigma capitate-lobate, 2–3-lobed or punctiform; placenta cupuliform or cotyliform, the ovules 2–4. Fruit subglobose, 1(–2)-seeded.

Cybianthus subg. *Conomorpha* contains 38 species, 21 of which have been collected in the Guayana Highland. All species are readily distinguishable by their autapomorphic ferrugineous stipitate-lepidote scales (Pipoly, 1987), which are always present on the branchlets.

KEY TO SPECIES OF *CYBIANTHUS* SUBGENUS *CONOMORPHA*

1a. Leaves mostly less than 3 cm long (rarely to 3.5 cm in *C. huberi*), up to 2 cm wide.

2a. Inflorescence 2(–3)-flowered, at times 1-flowered; leaves smooth above; anthers rounded to emarginate apically.

3a. Trunk orthotropic, the branches plagiotropic; leaves chartaceous, apically obtuse to rounded, the margins flat; petioles 2–4 mm long; calyx chartaceous; pedicels 5–10 mm long ______ 1. *C. fabiolae*

3b. Trunk and branches orthotropic; leaves coriaceous or cartilaginous, apically acute or abruptly acuminate, the margins revolute; petioles 5–10 mm long; calyx coriaceous; pedicels 0–4.5 mm long.

4a. Leaves coriaceous, apex abruptly acuminate; flowers sessile; calyx deeply crateriform, 1.9–2.4 mm long ______ 2. *C. huberi*

4b. Leaves cartilaginous, apex acute; flowers on pedicels 3–4.5 mm long; calyx cotyliform, 0.8–1.2 mm long ______ 3. *C. julianii*

2b. Inflorescence 4–9-flowered; leaves scrobiculate above; anthers apiculate to cuspidate apically.

5a. Leaf blades nitid above; flowers carnose; staminate corolla 2.7–2.9 mm long; pistillate corolla 1.9–2.2 mm long; stamens 1.6–1.7 mm long, the free portion of the filaments flat, less than 0.1 mm long; staminodes 1.0–1.3 mm long, the free portion of the filaments flat, 0.1–0.2 mm long; stigma capitate, 2-lobed …… 4. *C. steyermarkianus*

5b. Leaf blades dull above; flowers coriaceous; staminate corolla 2.0–2.3 mm long; pistillate corolla 2.4–2.8 mm long; stamens 1.4–1.5 mm long, the free portion of the filaments terete, 0.1 mm long; staminodes 1.8–2.1 mm long, the free portion of the filaments terete, 0.2–0.3 mm long; stigma not capitate, 3–4-lobed …… 5. *C. wurdackii*

1b. Leaves mostly 3.1–24 cm long, (1.5–)2.1–8.5 cm wide.

6a. Inflorescence paniculate or spicate.

7a. Inflorescence paniculate.

8a. Branchlets 5–12 mm diam.; leaves coriaceous.

9a. Branchlets stiff, not subsucculent, the bark creamish white; inflorescence a simple panicle, the branches racemose; leaf apices acuminate.

10a. Branchlets terete, prominently furrowed, moderately adpressed-lepidote, without lenticels; leaves smooth above, the margins flat; pedicels 2–3 mm long; calyx patelliform, coriaceous, the lobes oblate to suborbicular; corollas 3.0–3.5 mm long, apically cucullate …… 6. *C. plowmanii*

10b. Branchlets angular, densely lepidote, prominently lenticellate; leaves scrobiculate above, the margins revolute; pedicels 0.5–1.0 mm long; calyx cupuliform, carnose, the lobes ovate-triangular to deltate; corollas 2.3–2.7 mm long, apically flat …… 7. *C. amplus*

9b. Branchlets subsucculent, the bark yellowish brown; inflorescence tripinnately paniculate; leaf apices rounded, obtuse, truncate, or emarginate …… 8. *C. quelchii*

8b. Branchlets 2–3 mm diam.; leaves membranaceous to chartaceous.

11a. Leaves to 5(–6) cm wide, abruptly acuminate apically; petioles canaliculate, marginate only distally; inflorescence to 8 cm long; pedicels erect.

12a. Leaf margin revolute; calyx cotyliform, carnose; corolla carnose …… 9. *C. punctatus*

12b. Leaf margin flat; calyx subcupuliform, chartaceous; corolla chartaceous …… 14. *C. guyanensis*

11b. Leaves 5–7 cm wide, apically acute; petioles marginate along entire length; inflorescence 8–15 cm long; pedicels curved upward …… 10. *C. cardonae*

7b. Inflorescence spicate.

13a. Flowers subsessile (pedicels 0.2–0.6 mm long); calyx deeply cupuliform, carnose, the lobes proximally curved; corolla lobes not keeled.

14a. Leaves pustulate above; inflorescence (2–)6–16 cm long; corolla lobe apex flat; anthers erect …… 11. *C. lepidotus*

14b. Leaves smooth above; inflorescence 0.8–1.0 cm long; corolla lobe apex cucullate; anthers distally recurved …… 12. *C. sipapoensis*

13b. Flowers sessile; calyx crateriform, coriaceous, the lobes erect to spreading; corolla lobes prominently keeled.

15a. Leaves membranaceous 6–9.5 cm long, (1.5–)2.2–3.5 cm wide, scrobiculate above; petioles 1.2–1.5 cm long; corolla coriaceous; anthers proximally recurved, the apex apiculate, glabrous; pistil sessile …… 13. *C. holstii*

15b. Leaves coriaceous, 2.5–3.5(–4) cm long, 1.2–1.9 cm wide, smooth above; petioles 0.5–1.0 cm long; corolla carnose; anthers erect, the apex rounded, glandular-papillate; pistil on a carnose disc …… 2. *C. huberi*

6b. Inflorescence racemose.

16a. Staminate corolla 2–2.5 mm long; staminate calyx 0.7–1.1 mm long; pistillate calyx 0.8–1.2 mm long.

17a. Leaves elliptic, 7–20 cm long, apices acuminate; corolla membranaceous or chartaceous; fruit 4–7 mm diam. when dried.

18a. Branchlets 2–3 mm diam., the bark beige; leaves smooth above, the margins flat; petioles 0.5–2.0 cm long; pedicels to 1 mm long; corolla campanulate; fertile and sterile anthers strongly recurved dorsally, the apical portion of the sterile anthers tightly twisted …… 14. *C. guyanensis*

18b. Branchlets 3.5–4.5 mm diam., the bark reddish brown; leaves pusticulate above, the margins revolute; petioles 2–3 cm long; pedicels 2–3.5 mm long; corolla rotate, the lobes reflexed, perpendicular to the tube in anthesis; fertile and sterile anthers slightly recurved dorsally, the apical portion of the sterile anthers straight …… 15. *C. roraimae*

17b. Leaves obovate-spathulate, 4–5 cm long, apices obtuse to rounded; corolla carnose, glandular-granulose within; fruit 7–8 mm diam. …… 16. *C. breweri*

16b. Staminate corolla 2.5–3.7 mm long; staminate calyx 1.1–1.5 mm long; pistillate calyx 1.1–1.7 mm long.

- 19a. Calyx cotyliform; corolla glabrous or glandular-ciliate along the margins; staminal tube conspicuous, chartaceous or carnose, opaque.
  - 20a. Leaves membranaceous, long-acuminate apically, smooth above; petioles (1–)1.3–1.7(–2.3) cm long; pedicels 0.6–1.0 mm long; calyx without scales, the margin glandular-ciliate; corolla lobe apex cucullate; staminal tube carnose, costate, elobate, the free portion of the filaments as long as the anthers; fruit 4–7 mm diam. .... 17. *C. apiculatus*
  - 20b. Leaves chartaceous to coriaceous, rounded to acute apically, pustulate above; petioles 0.5–1.1 cm long; calyx sparsely lepidote, the margin glabrous; corolla lobe apex flat; staminal tube chartaceous, terete, bearing lobes to 0.1 mm long alternating with the filaments, the free portion of the filaments shorter than the anthers; fruit 3–3.5 mm diam. .... 18. *C. agostinianus*
- 19b. Calyx cupuliform; corolla glandular-granulose along the margins; staminal tube inconspicuous, membranaceous, hyaline.
  - 21a. Leaves smooth above, the margins flat; petioles 0.1–0.2 cm long; inflorescence tortuous; staminate corolla 3.5–3.7 mm long, pistillate corolla 2.7–3.5 mm long .... 19. *C. spathulifolius*
  - 21b. Leaves scrobiculate or pusticulate above, the margins revolute; petioles 0.9–1.3 cm long; inflorescence straight; staminate corolla 2.5–3.0 mm long, pistillate corolla 1.9–3.3 mm long.
    - 22a. Leaves pustulate above, moderately lepidote below, the scales not overlapping; pedicels erect, less than 1 mm long; calyx lobes longer than broad; staminate corolla 2.7–3.0 mm long, pistillate corolla 3.0–3.3 mm long, the lobes flat; free filaments shorter than the anthers; fruit verruculose, 6–8 mm diam. .... 20. *C. maguirei*
    - 22b. Leaves scrobiculate above, densely lepidote below, the scales overlapping; pedicels nodding, 1–3 mm long; calyx lobes broader than long; staminate corolla 2.5–2.7 mm long, pistillate corolla 1.9–2.0 mm long; free filaments longer than the anthers; fruit smooth, 4.5–5.0 mm diam. when dried .... 21. *C. crotonoides*

1. Cybianthus fabiolae Pipoly, sp. nov. TYPE: Guyana. Cuyuni-Mazaruni Region No. VIII, Mazaruni Subregion No. VIII-2: Mt. Ayanganna, summit of E plateau, 5°24′N, 59°57′W, 1,350–1,380 m, elfin forest on cliffs dominated by *Bonnetia roraimae*, 11 Mar. 1987 (pist. fl, fr), *Pipoly, Gharbarran, Samuels & Chin 11120* (holotype, US; isotypes, AAU, B, CAY, COL, F, FDG, G, GH, L, MO, NY, P, VEN). Figure 2.

Quoad filamenta staminum tubi manifeste punctata, antheras non apiculatas suberectas vel ventraliter recurvatasque, folia obovato-spathulata, ad *C. dussium* valde affinis, sed ab ea pedicellis gracilibus 4–10 (non crassis, 1.5–2.5) mm longis inflorescentisque reductis (1–)2-floris (non racemosis, plus quam 3-floris) praeclare differt. Species haec allopatricos *C. steyermarkiano* et *C. wurdackii* simulans, sed ab eis filamentis punctatis (non epunctatis) Aubrevillei (nec Rauhii) architectura statim distinguitur.

Treelet to 2.5 m tall, 2 cm diam.; trunk monopodial, orthotropic, the growth rhythmic, the branching pseudoverticillate, the branches modular, with rhythmic growth, plagiotropic by apposition (Aubréville's Model); branchlets terete, 1.5–2.0 mm diam., densely lepidote at first, glabrescent, with only scattered scales persistent. Leaves broadly obovate-spathulate, chartaceous, 1.3–2.0 cm long, 0.9–1.2 cm wide, apex obtuse to rounded, base cuneate, slightly decurrent on the thin petiole, midrib depressed on the upper surface, prominent below, nerves 5–7 pairs, inconspicuous above, somewhat conspicuous below on older leaves, prominently black punctate above, densely lepidote at first, but glabrescent above, moderately lepidote below, the scales not impressed, the margin entire, punctate, flat; petiole canaliculate, 0.2–0.4 cm long, densely lepidote. *Staminate inflorescence:* a reduced, 2-flowered raceme (appearing umbelliform) or at times 1-flowered; rachis, pedicels, and calyces densely stipitate-lepidote, the margins often overlapping; peduncle 0.5–1.5 cm long; floral bracts lanceolate, 1.0–1.5 mm long, 0.3–0.5 mm wide, apex acute, densely lepidote below, the margin entire; pedicel terete, 5–10 mm long. Flowers pendent, 4–5-merous; calyx patelliform, chartaceous, 0.7–1.1 mm long, the tube 0.1–0.3 mm long, the lobes subdeltate, 0.6–0.8 mm long, 0.7–1.0 mm wide, apex acute, densely stipitate-lepidote without, the margins of the scales overlapping, glabrous within, the margin glabrous, subentire to crenulate; corolla subcotyliform, chartaceous, 2.1–2.3 mm long, the tube 0.3–0.6 mm long, the lobes erect, slightly concave, narrowly ovate, 1.6–1.8 mm long, 0.9–1.1 mm wide, apex rounded, sparingly glandular-granulose within and along margin only at apex, sparingly lepidote without apically, prominently black punctate and punctate-lineate without,

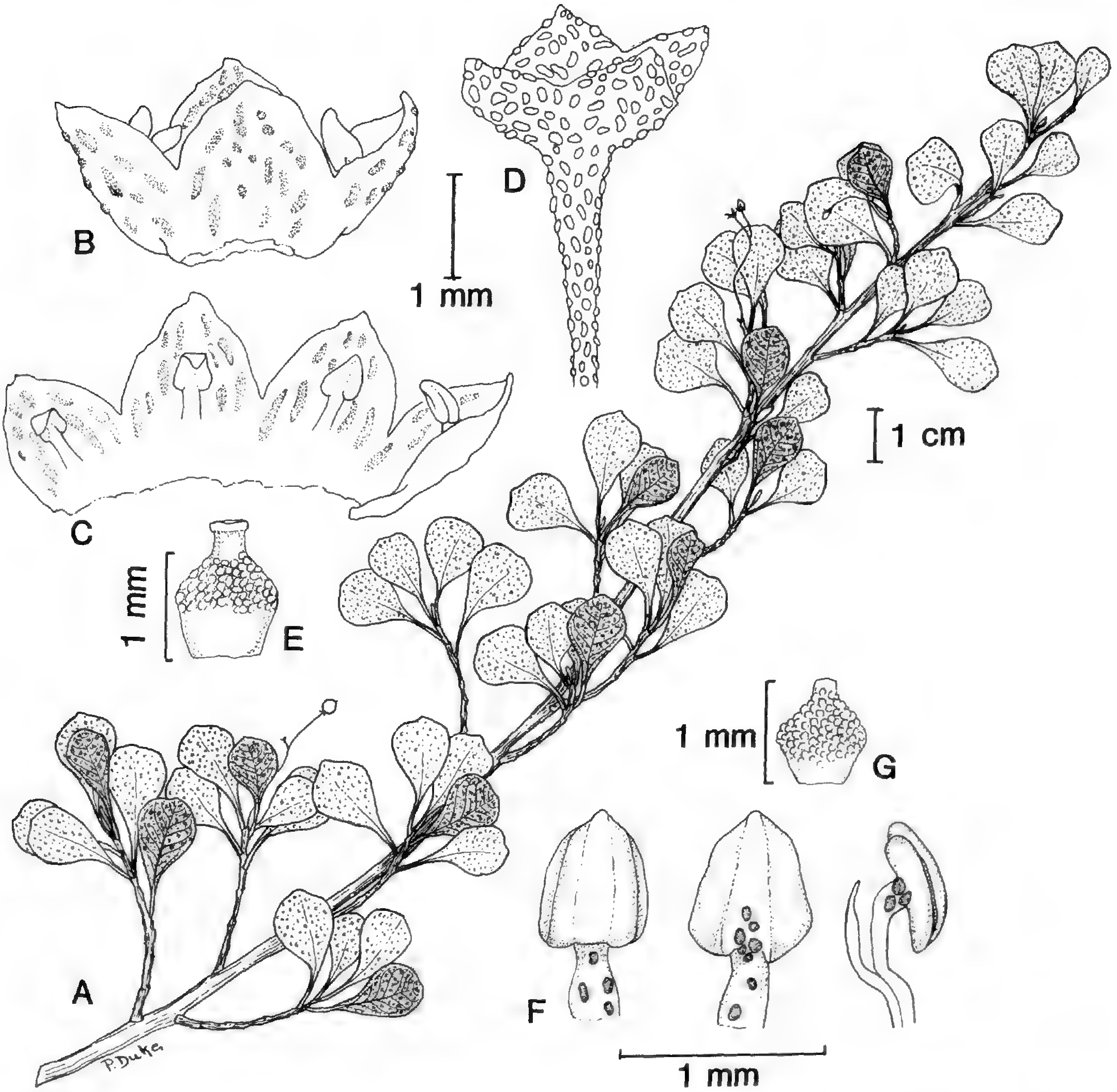


FIGURE 2. *Cybianthus fabiolae* Pipoly.—A. Habit, showing short shoots.—B. Staminate corolla.—C. Opened pistillate corolla, showing suberect to proximally recurved anthers.—D. Pistillate calyx.—E. Pistil.—F. Anther, ventral, dorsal, and lateral views, showing punctate filaments and connective.—G. Pistillode, showing punctiform stigma. (A, C, D, and E, from the holotype; B and F, from *Pipoly et al. 11112.*)

the margin regular, entire; stamens 1.6–1.9 mm long, the tube inconspicuous, membranaceous, 0.4–0.5 mm long, the apically free filaments 0.5–0.7 mm long, flat, prominently punctate, the anthers suberect to proximally recurved, ovate, 0.7–0.9 mm long, 0.5–0.6 mm wide, apex truncate to emarginate, base cordate, subversatile, the connective prominently black punctate; pistillode globose, 1.0–1.1 mm long, the ovary 0.7–0.8 mm long, 0.8–0.9 mm wide, densely translucent glandular-lepidote, the style 0.3–0.4 mm long, glabrous, stigma punctiform. *Pistillate inflorescence:* a reduced, 2-flowered raceme (appearing umbelliform), 1.5–2.0 cm long, axis sparingly lepidote; peduncle 1.0–1.5 mm long; floral bracts ovate, 0.7–1.0 mm long, 0.4–0.5 mm wide, sparingly lepidote adaxially; pedicels terete, 5.0–5.5 mm long, densely lepidote. Flowers pendent, 4- or 5-merous; calyx subcotyliform, chartaceous, 0.7–0.9 mm long, the tube 0.2–0.3 mm long, the lobes widely ovate to deltate, 0.6–0.8 mm long, 0.6–1.0 mm wide, apex rounded, sparingly lepidote without, glabrous within, punctations dark brown, not prominent, the margin entire to crenulate; corolla subcotyliform, chartaceous, 1.9–2.0 mm long, the tube 0.5–0.6 mm long, the lobes broadly ovate, 1.5–1.6 mm long, 1.3–1.5 mm wide, apex rounded, sparingly glandular-granulose within apically, sparingly lepidote medially at apex without, prominently black punctate and punctate-lineate without, the margin somewhat irregular, entire; staminodes 1.5–1.8 mm long, the tube inconspicuous, membranaceous, 0.7–0.9 mm long, glabrous, the apically free filaments flat, 0.4–0.5 mm long, conspicuously punctate, the anthers erect to ventrally recurved, deltate, 0.4–0.5 mm long and wide, apex truncate to emarginate, base cordate, subversatile, the connective prominently black punctate dorsally; pistil obnapiform, 1.4–1.5 mm long, the ovary 0.9–1.0 mm long, 0.9–1.2 mm diam., densely glandular-lepidote, the style 0.1-0.2 mm long, glabrous, epunctate, the stigma capitate, 3–4-lobed, the placenta deeply cupuliform, the ovules 2–3, deeply imbedded. Fruit globose, ca. 5 mm long, 3 mm diam., the exocarp thin, prominently black punctate-lineate.

Distribution. Endemic to the elfin and scrub forest on the uppermost slopes and summit of Mt. Ayanganna, Guyana, at 1,350–1,380 m elevation.

Ecology. *Cybianthus fabiolae* occurs in thickets in zones between *Bonnetia roraimae* forests and large rock outcrops. The treelets grow on hummocks and rarely exceed 2.5 m in height. The flowers and fruit are pendent beneath the leaf rosettes, and no odor was detected.

Paratypes. GUYANA. CUYUNI-MAZARUNI REGION, NO. VIII, MAZARUNI SUBREGION VIII-2: Mt. Ayanganna, upper cliffs of E flank, 1,380 m, 11 Mar. 1987 (stam. fl), *Pipoly et al. 11112* (FDG, NY, US), *11117* (B, CAY, FDG, NY, P, PH, TEX, US), (fr) *11135* (CAY, F, FDG, L, NY, PH, US), on E flank above Thompson Camp, 1,370 m, 8 Aug. 1960 (pist. fl, fr), *Tillett et al. 45056* (F, FDG, NY, US, VEN).

Cybianthus fabiolae is unique within *Cybianthus* because its morphogenesis follows Aubréville's Model (Hallé et al., 1978). This architectural model is defined by a monopodial, orthotropic trunk with rhythmic growth, producing pseudoverticillate tiers of branches that are modular, with plagiotropic growth by apposition. In this type of growth, the terminal meristems are evicted by sylleptic branches, which function as short shoots because no elongation occurs. The short shoots produce rosettes of leaves, and the small, axillary inflorescences are pendent beneath them. *Cybianthus fabiolae* can most readily be confused with *C. wurdackii*, but can immediately be distinguished from it by the architectural model, the punctate filaments, the emarginate or truncate anthers, the subcotyliform corolla, umbelliform inflorescence, and long pedicels.

I dedicate this species to my wife, Fabiola Monje-Pipoly, whose patience, hard work, enthusiasm, and moral support were a constant source of encouragement during our residence in Guyana.

2. Cybianthus huberi Pipoly, sp. nov. TYPE: Venezuela. Bolívar: Dtto. Cedeño, Serranía Guanay, NE sector, headwaters of Río Paraguaza, 1,700 m, 5°55′N, 66°23′W, 20–28 Oct. 1985 (pist. fl, fr), *Huber 11005* (holotype, VEN; isotypes, MO, NY). Figure 3.

Quoad inflorescentias spiciformias reductasque, calyces crateriformes, corollarum lobos abaxaliter carinatos erectos ad apicem cucullatos, *C. holstii* arcte affinis, sed illa ab hac laminis coriaceis (non membranaceis) staminodiorum tubi conspicui (nec inconspicui) lobulis filamentis alterans praeditis (nec destitutis) filamentis glandulosis (nec eglandulosis) fructibusque 5.5–10 (nec 4.0–4.5) mm diametris statim cognoscitur.

Shrub to 3 m tall; branchlets terete, ca. 3 mm diam., densely appressed-lepidote. Leaves obovate, coriaceous, (2.5–)3.0(–3.5) cm long, 1.2–1.9 cm wide, abruptly acuminate apically, the acumen 0.3–0.7 cm long, cuneate basally, the blade decurrent on the petiole, smooth and glabrous above at maturity, epunctate, midrib depressed above, prominently raised below, nerves inconspicuous, the margin revolute; petioles canaliculate and prominently marginate, 5–10 mm long, densely lepidote, the scales overlapping. *Staminate inflorescence:* unknown. *Pistillate inflorescence:* a 2-flowered spike or a solitary flower; peduncle 1.0–1.2 cm long; floral bracts chartaceous, deltate, 0.8–1.1 mm long and wide, the apex acute, densely lepidote abaxially, the margin entire; pedicels absent. Flowers 4-merous, sessile, 2.7–3.0 mm long; calyx deeply crateriform, coriaceous, 1.9–2.4 mm long, the tube 1.3–1.6 mm long, the lobes very broadly triangular, 0.5–0.9 mm long, 1.1–1.4 mm wide, acute, medially keeled, prominently brown punctate, lepidote along the margins, the margins irregular, entire; corolla cupuliform, carnose, 2.3–2.7 mm long, the tube 0.4–0.6 mm long, the lobes oblong, erect, keeled medially, 1.9–2.1 mm long, 0.4–0.6 mm wide, apically rounded and cucullate, glabrous and prominently orange punctate without, glandular-granulose within the margin entire, glandular-granulose; staminodial tube conspicuous, carnose, 0.5–0.7 mm long, bearing lobes alternate with the filaments to 0.1 mm long, the tube and filaments eglandular, the apically free filaments less than 0.1 mm long, the anthers subsessile, erect, ovate, 0.9–1.1 mm long, 0.6–0.7 mm wide, apex rounded and rufous glandular-papillate, dorsifixed ca. ¼ from base, the connective prominently punctate dorsally; pistil above a carnose disc, obnapi-

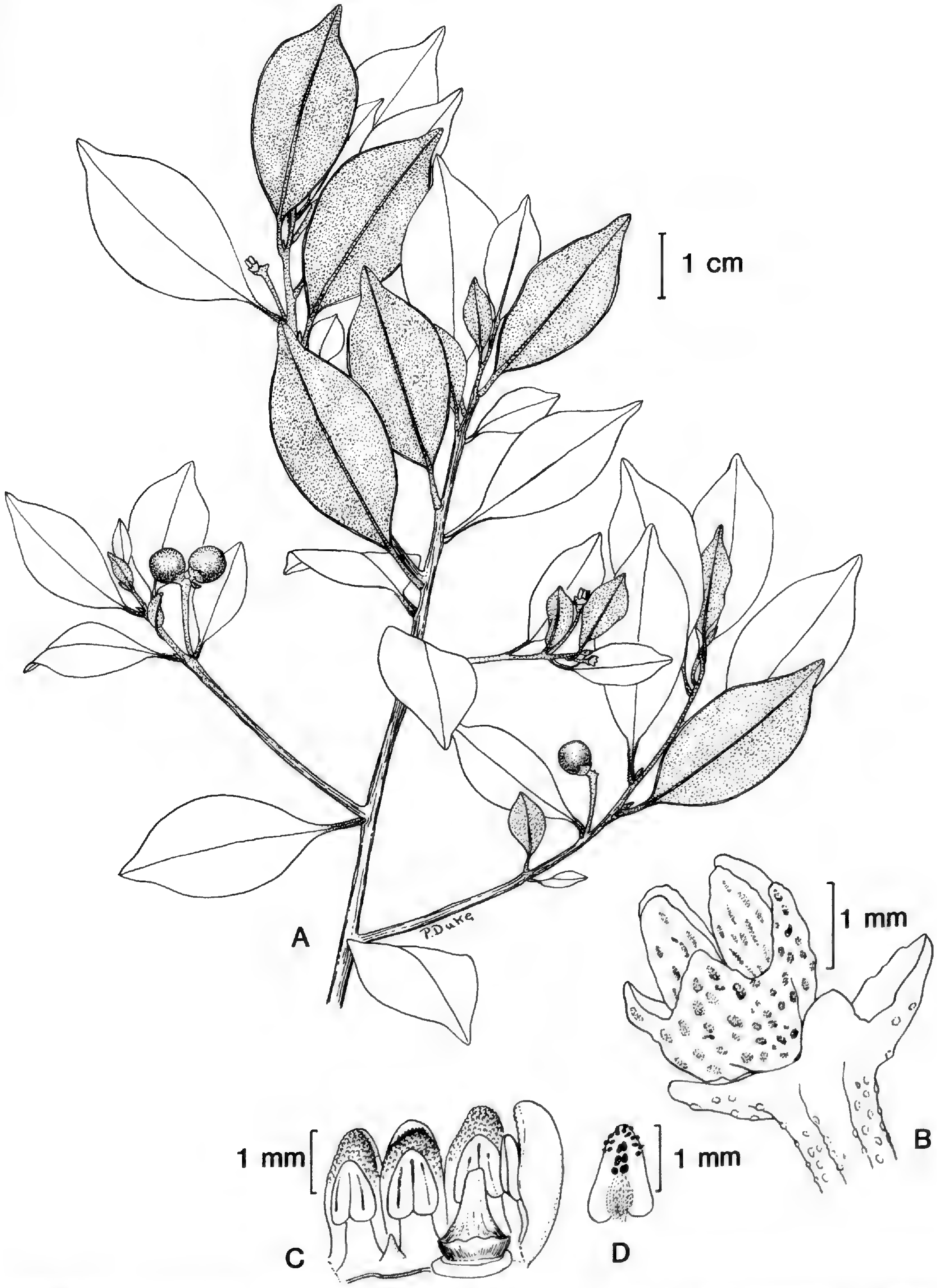


FIGURE 3. *Cybianthus huberi* Pipoly.—A. Habit.—B. Inflorescence, with one flower removed.—C. Opened pistillate flower, showing cucullate corolla lobes, and apophysate ovary with disc below.—D. Dorsal view of sterile anther, showing punctate connective and glandular-papillate thecae. (From the holotype.)

form, the ovary 4-lobed, deeply costate, with an upper apophysate rim, 1 mm long, 1.3 mm diam., glabrous, the style truncate, prominently punctate, the stigma punctiform. Fruit depressed-globose, 0.5–1.0 cm long and in diam., black at maturity, the exocarp thin.

Distribution. Known only from the type, from Serranía Guanay, at 1,700 m elevation.

Ecology. *Cybianthus huberi* is a scrub forest species growing near low, inundated areas and small watercourses.

Cybianthus huberi is unique within the genus because of its pistil on a carnose disc and, within subgenus *Conomorpha*, by its rufous-papillate anthers. Its reduced spike, crateriform calyces, carinate corolla lobes, and apically apophysate ovary are synapomorphies with *C. holstii*. However, *C. huberi* may be easily separated from *C. holstii* by coriaceous (not membranaceous) leaves, the conspicuous lobate (not inconspicuous, elobate) staminodial tube, subsessile anthers (not on short, apically free filaments), pistil on a disc (not sessile), and larger fruit.

This species is dedicated to Otto Huber, friend and preeminent authority on the vegetation of the Guayana Highland and neotropical savannas. His collections and their accompanying detailed ecological data have greatly increased our understanding of the Guayana flora.

3. **Cybianthus julianii** Pipoly, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Atabapo, Cerro Marahuaca, cumbre, central portion of SE mesa, along Quebrada Yekuana, tributary of Río Negro, 3°40′30″N, 65°26′20″W, 2,560 m, 10–12 Oct. 1983 (fr), *Steyermark 129448* (holotype, VEN; isotypes, MO, NY). Figure 4.

Ob laminas plicatas secus marginem revolutas subtus dense lepidotas *C. crotonoideo* arcte similis, sed ab ea laminis cartilagineis (non coriaceis) inflorescentiis uni- vel bifloris (non racemis largis), calycis lobis suborbicularibus ad apicem obtusis (non ovatis ad apicem rotundatis) fructibusque luteis (non atris) praeclare distat.

Shrub to 1.5 m tall; branchlets terete, 2–3 mm diam., appressed-lepidote. Leaves elliptic to oblanceolate, cartilaginous, 2.6–3.1 cm long, 0.8–1.4 cm wide, apically acute to subacuminate, prominently pellucid punctate above and below, densely lepidote below, the scales not overlapping, the midrib depressed above, prominently raised below, the leaf plicate, the margin revolute; petioles canaliculate, 0.5–0.7 cm long, densely appressed-lepidote. *Staminate inflorescence:* unknown. *Pistillate inflorescence:* a 2-flowered raceme or solitary flower, 1.0–2.0 cm long, densely lepidote; peduncle 0.5–0.7 mm long; floral bracts linear-lanceolate, 1.9–2.5 mm long, 0.3–0.5 mm wide, apex acute, densely lepidote above and below, the margin entire, glabrous; pedicels terete, erect, 3.0–4.5 mm long. Fruiting calyx cotyliform, coriaceous, 0.8–1.2 mm long, the tube less than 0.1 mm long, the lobes very broadly ovate to suborbicular, 0.8–1.2 mm long and wide, apex rounded to obtuse, densely and prominently black punctate, lepidote, the margin crenulate; corolla unknown. Fruit yellow, globose, 2–3 mm long and in diam. when dried.

Distribution. Known only from the type, collected on Cerro Marahuaca, Amazonas, at 2,560 m.

Ecology. *Cybianthus julianii* occurs at the margins of boggy areas on the summit of Cerro Marahuaca.

Cybianthus julianii is unique within the genus because of its cartilaginous leaves and yellow fruits. Within subgenus *Conomorpha*, it appears to be most closely related to *C. crotonoides*, from which it is easily separated by its cartilaginous (not coriaceous) leaves, 2(not many)-flowered inflorescence, calyx lobes suborbiculate (not deltate) and apically obtuse (not acute), and the yellow (not black) fruit. *Cybianthus julianii* also bears a superficial resemblance to *Cybianthus laetus* of Colombia, Peru, and Bolivia, a poorly understood taxon known only from eight gatherings. From *C. laetus*, *C. julianii* is readily distinguished by its terete (not subterete) branchlets, leaves 2.6–3.1 (not 3–8) cm long, inflorescence 1–2 (not 2–3) cm long, pedicels 3.0–4.5 (not 0.9–1.5) mm long, calyx coriaceous (not carnose), 0.8–1.2 (not 1.2–1.8) mm long, and fruit yellow (not black), 2–3 (not 5–8) mm long and in diam. It is hoped that more collecting on Cerro Marahuaca will result in collection of the flowering specimens needed for a detailed phylogenetic analysis.

The species is dedicated to the late Julian Steyermark.

4. **Cybianthus steyermarkianus** (Agostini) Agostini, Acta Biol. Venez. 10: 156. 1980. *Conomorpha steyermarkiana* Agostini, Acta Bot. Venez. 2: 283. 1967. TYPE: Venezuela. Bolívar: Cerro Auyán-tepui, cumbre, 2,100 m, without date, (stam. fl), *Cardona 2723* (holotype, VEN; isotype, NY). Figure 5.

FIGURE 4. *Cybianthus julianii* Pipoly.—A. Habit, showing two-flowered racemes. (From the holotype.)

Shrub to 4 m tall; branchlets terete, 2.5–3 mm diam., densely lepidote, at times glabrescent. Leaves suborbicular, obovate, or elliptic, stiffly coriaceous, (1.2–)1.5–2.5 cm long, 1.0–1.7 mm wide, apically rounded to obtuse, basally acute to obtuse, decurrent on the petiole, nitid and scrobiculate, densely lepidote when young, glabrescent above, densely to sparingly lepidote below, midrib depressed above, prominent below, nerves 6–12 pairs, the margin prominently revolute, often inrolled; petioles canaliculate, 0.5–1.0 cm long, densely or sparingly lepidote. *Staminate inflorescence:* a simple, erect raceme, 5–9-flowered, 0.7–3 cm long, the axis and pedicels densely lepidote; peduncle 0.3–1.5 cm long; pedicels 1.5–3.5 mm long; floral bracts narrowly elliptic, 1.0–1.5 mm long, 0.4–0.6 mm wide, apically acute, densely lepidote adaxially, the margin entire. Flowers pendent, 4-merous; calyx cupuliform, 0.9–1.2 mm long, the tube 0.2–0.3 mm long, the lobes triangular, carnose, 0.7–0.8 mm long, 0.6–0.7 mm wide, tapering to a rounded apex, sparingly lepidote without, inconspicuously pellucid or orange punctate, the margin entire, lepidote; corolla campanulate, 2.7–2.9 mm long, the tube 0.8–0.9 mm long, the lobes elliptic, broadly elliptic or ovate, carnose, 2.0–2.2 mm long, 1.2–1.4 mm wide, apically rounded, glabrous, sparingly lepidote without, pellucid or orange punctate; stamens 1.6–1.7 mm long, adnate 1.2–1.4 mm to the corolla tube, the tube 0.8–1.4 mm long, inconspicuous, elobate, the apically free filaments less than 0.1 mm long, the anthers erect, dorsifixed near the base, ovate, 0.5 mm long, 0.4–0.5 mm wide, apex apiculate, base cordate, the connective pellucid or orange punctate; pistillode clavate, 1.2–1.4 mm long, hollow, translucent glandular-lepidote, the style elongate, the stigma punctiform. *Pistillate inflorescence:* a simple, erect raceme, 5–9-flowered, 0.7–3 cm long, the axis and pedicels densely lepidote; peduncle 0.3–1.5 cm long; pedicels 1.5–3.5 mm long; floral bracts narrowly elliptic, 1.0–1.5 mm long, 0.4–0.6 mm wide, apically acute, densely lepidote adaxially, the margin entire. Flowers pendent, 4-merous; calyx cupuliform, 0.9–1.2 mm long, the tube 0.2–0.3 mm long, the lobes triangular, carnose, 0.7–0.8 mm long, 0.6–0.7 mm wide, tapering to a rounded apex, sparingly lepidote without, inconspicuously pellucid or orange punctate, the margin entire, glabrous, lepidote; corolla campanulate, carnose, 1.9–2.2 mm long, the tube 0.4–0.5 mm long, the lobes elliptic to broadly elliptic, 1.6–1.7 mm long, 0.9–1.1 mm wide, the apex obtuse, rounded or attenuate to a rounded tip, glabrous, sparingly lepidote outside, pellucid or orange punctate; staminodes 1.0–1.3 mm long, adnate 0.6–0.8 mm to the corolla tube, the tube 0.4–0.7 mm long, elobate, the apically free filaments 0.1–0.2 mm long, the anthers erect, dorsifixed near the base, ovate, 0.5–0.6 mm long, 0.4–0.5 mm wide, apex apiculate, base cordate, the connective pellucid or orange punctate; pistil obnapiform, 1.2–1.4 mm long, the ovary 0.6–0.7 mm long and in diam., densely glandular-lepidote, the style elongate, 0.5–0.6 mm long, ca. 0.2 mm diam., glabrous, epunctate, the stigma capitate, 2-lobed; the placenta cotyliform, the ovules 3, naked. Fruit not seen.

Distribution. Endemic to the tepuis of the Chimantá Massif, located in the eastern portion of the state of Bolívar, from 2,000 to 2,300 m elevation.

Ecology. *Cybianthus steyermarkianus* grows in cracks along the upper edges of narrow, deep canyons (zanjones) and in rocky outcrops near the edge of savannas on the summits of the tepuis of the Chimantá Massif. It is subject to high winds and rain in the evening hours, and high levels of sunlight and radiation during the day.

Specimens examined. VENEZUELA. BOLIVAR: Dtto. Piar, Macizo del Chimantá, N sector, Abacapa-tepui, NW summit, 2,125–2,300 m, 13 Mar. 1953 (fr), *Steyermark 74934* (BM, F, MO, NY, US, VEN); Acopán-tepuí, sector NE, headwaters of Río Yunek, 1,950 m, 8–11 Feb. 1985 (stam. fl), *Pipoly et al. 7187* (F, MO, NY, PH, TEX, US, VEN), *7162* (MO, NY, US, VEN); summit, Apacará-tepui, 2,450–2,500 m, 26 June 1953 (pist. fl, fr), *Steyermark 75899* (NY, US, VEN), S base of upper cliffs of Apacará-tepui, 2,200 m, 30 Jan.–1 Feb. 1983 (stam. fl), *Steyermark et al. 128435* (F, MO, MYF, NY, US, VEN), 30 Jan.–1 Feb. 1983 (stam. fl), *Huber & Steyermark 6990* (MO, NY, VEN); Aprada-tepui, 2,460–2,500 m, 25 Feb. 1978 (fr), *Steyermark et al. 115888* (MO, NY, VEN); Chimantá-tepui, Río Tirica, Caño Grillo, 7–9 Feb. 1983 (ster.), *Steyermark et al. 128920* (MO, NY, VEN); NW cumbre, Churi-tepui (Muru-tepui), 2,300–2,350 m, 3 Feb. 1953 (stam. fl), *Wurdack 34299* (NY); S-central section, wide valley between the NE border of Torono-tepui and the central section of Chimantá-tepui, 2,100 m, 11–15 Feb. 1985 (stam. fl), *Pipoly et al. 7293* (MO, MYF, NY, TEX, US, VEN); Torono-tepui, summit, 2,165–2,180 m, 9 Feb. 1955 (fr), *Steyermark & Wurdack 660* (BM, F, MO, NY, US, VEN), summit, N-facing slopes above Caño Mojado, 2,030–2,150 m, 21 Feb. 1955 (pist. fl), *Steyermark & Wurdack 1035* (NY, VEN).

Cybianthus steyermarkianus is most closely related to *C. wurdackii*, an apparently sympatric species, but is easily separated by its epunctate, revolute-inrolled leaf margins, branchlets 2.5–3 (not 3–3.5) mm diam., nitid (not dull) upper leaf surface, and carnose (not coriaceous) flowers. For a discussion of ecological differences, see *C. wurdackii.*

5. **Cybianthus wurdackii** Agostini ex Pipoly, sp. nov. TYPE: Venezuela. Bolívar: Macizo del Chimantá, Churi(Muri)-tepui, NW summit, 2,250–2,300 m, 26 Jan. 1953 (stam. fl), *Wurdack 34240* (holotype, VEN; isotypes, COL, F, NY, S, US). Figure 6.

Quoad filamenta anthera breviora, folia parva obovata vel late elliptica, species haec sympatrico *C. steyermarkiano* praeclare affinis sed florum staminatorum corolla 2.0–2.2 (non 2.7–2.9) mm longa, extusque lepidota (nec glabra), staminibus 1.4–1.5 (nec 1.6–1.7) mm longis et tubo staminali conspicuo (nec inconspicuo) statim separabilis.

Treelet to 3 m tall; branchlets terete, 3.0–3.5 mm diam., densely lepidote at first, glabresent, the bark smooth, not ridged. Leaves obovate-spathulate, coriaceous, 1.5–2.4 cm long, 0.8–1.4 cm wide, apex obtuse to rounded, rarely appearing

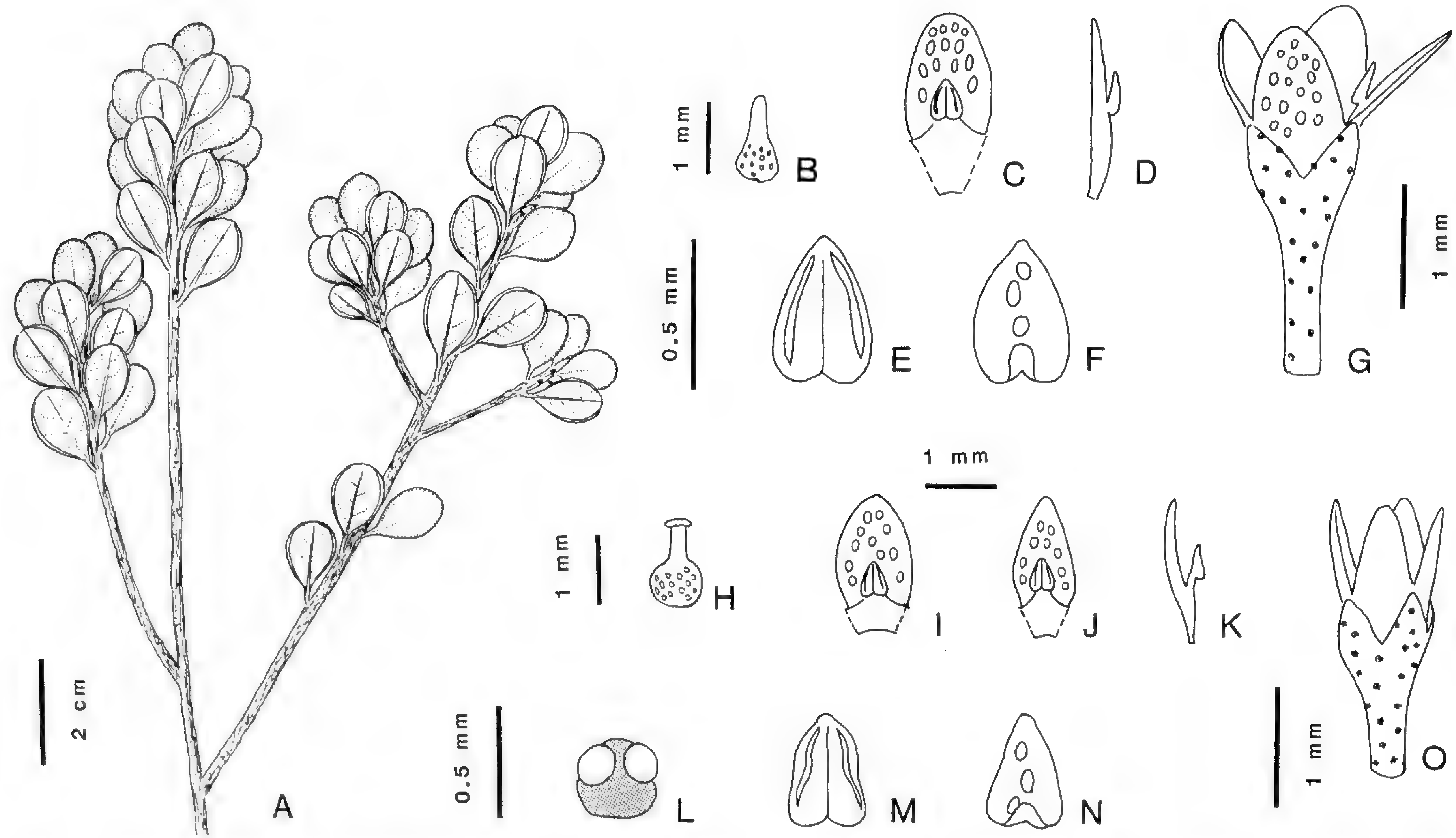


FIGURE 5. *Cybianthus steyermarkianus* (Agostini) Agostini.—A. Habit.—B. Pistillode.—C. Ventral view, pistillate corolla lobe.—D. Lateral view, pistillate corolla lobe.—E. Anther, ventral view.—F. Anther, dorsal view, showing punctate connective.—G. Staminate flower.—H. Pistil, showing capitate stigma.—I, J. Staminate corolla lobes, ventral view.—K. Staminate corolla lobes, lateral view.—L. Placenta, showing naked ovules.—M. Sterile anther, ventral view.—N. Sterile anther, dorsal view, showing punctate connective.—O. Pistillate flower. (A–G, from holotype; H–O, from *Steyermark 75899*.)

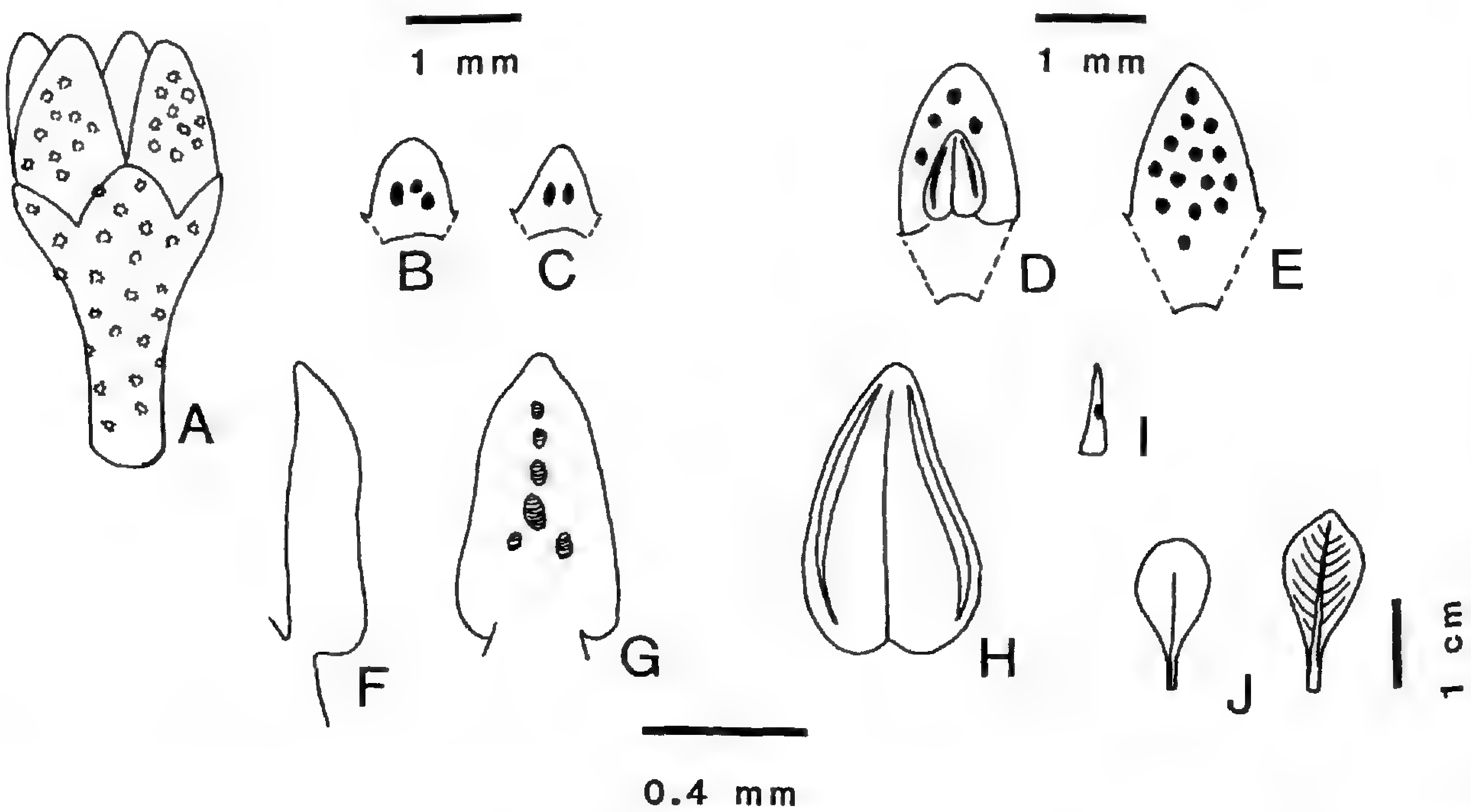


FIGURE 6. *Cybianthus wurdackii* Agostini ex Pipoly.—A. Staminate flower.—B, C. Staminate calyx lobes, showing punctations.—D, E. Staminate corolla lobe, ventral and dorsal views.—F. Anther, lateral view.—G. Anther, dorsal view, showing punctate connective.—H. Anther, ventral view, showing dehiscence slits.—I. Pistillode.—J. Leaf, adaxial and abaxial views. (From the holotype.)

subacute, base cuneate, slightly decurrent on the petiole, midrib depressed above, prominently raised below, nerves 6–8 pairs, inconspicuous above and below, upper surface wrinkled, at first densely lepidote, then scrobiculate and sparingly lepidote, densely lepidote below, the scales sunken, not overlapping, inconspicuously pellucid punctate, except prominently so beneath the margin, the margin entire, revolute; petioles canaliculate, 0.3–0.7 mm long, densely lepidote. *Staminate inflorescence:* a 4–7-flowered raceme, 1.0–2.0 cm long, the peduncle, rachis, and pedicels densely lepidote; peduncle 0.6–0.8 mm long; floral bracts ovate, 0.5–1.0 mm long, 0.2–0.4 mm wide, apex acute, densely lepidote adaxially, the margin entire; pedicels terete, 1.5–1.8 mm long. Flowers 4-merous, nodding; calyx cupuliform, coriaceous, 0.8–1.0 mm long, the tube 0.1–0.2 mm long, the lobes ovate to broadly ovate, 0.7–0.9 mm long, 0.5–0.7 mm wide, apex obtuse, rarely rounded, somewhat cucullate medially and keeled, sparingly lepidote without, glabrous within, conspicuously black punctate, the margin entire, glabrous; corolla cupuliform, coriaceous, 2.0–2.3 mm long, the tube 0.6–0.7 mm long, the lobes ovate, 1.3–1.4 mm long, 1.0–1.2 mm wide, apex rounded, sparingly lepidote without, glabrous within, conspicuously black punctate, the margin entire, glabrous; stamens 1.4–1.5 mm long, the tube conspicuous, chartaceous, 0.7–0.8 mm long, without lobes, the apically free filaments 0.1 mm long, epunctate, terete, the anthers erect, ovate, 0.7–0.8 mm long, 0.4–0.5 mm wide, apex apiculate to cuspidate, the apiculum erect, base cordate, the connective prominently punctate dorsally; pistillode conic, 0.8–0.9 mm long, glabrous, prominently black punctate. *Pistillate inflorescence:* a 4–9-flowered raceme, 1.0–1.6 mm long, peduncle, rachis, and pedicels densely lepidote, the scales not overlapping; peduncle 0.3–0.6 mm long; floral bracts ovate, 0.7–1.5 mm long, 0.9–1.0 mm wide, apex obtuse, keeled, densely lepidote adaxially; pedicels terete, 3.0–3.5 mm long. Flowers 4-merous, nodding at first, then erect in fruit; calyx deeply cupuliform, coriaceous, 1.2–1.5 mm long, the tube 0.5–0.6 mm long, the lobes widely ovate to suborbicular, 1.1–1.2 mm long and wide, apex obtuse, somewhat cucullate, medially keeled, sparingly lepidote, with three conspicuous black punctations, the margins entire, glabrous; corolla deeply cupuliform, coriaceous, 2.4–2.8 mm long, the tube 0.9–1.0 mm long, the lobes suborbicular to widely ovate, 1.4–1.8 mm long, 1.6–2.0 mm wide, dorsally reflexed, somewhat concave, moderately lepidote without, glabrous within, the margin entire, glabrous; staminodes resembling stamens but larger, 1.8–2.1 mm long, the tube 0.9–1.0 mm long, the apically free filaments terete, 0.2–0.3 mm long, the anthers ovate to deltate, 0.6–0.7 mm long and wide; pistil obnapiform, 1.8–2.1 mm long, the ovary 1.1–1.2 mm long, 1.3–1.4 mm diam., prominently black punctate, glabrous, the style 0.7–0.9 mm long, epunctate, glabrous, the stigma 3–4-lobed, not capitate, the placenta cotyliform, with 3–4 naked ovules. Fruit depressed-globose, 4–6 mm long, 6–8 mm wide, the exocarp thin, prominently punctate.

Distribution. Endemic to the Auyán-tepui-Chimantá Floristic Complex (Maguire, 1979) in eastern Bolívar.

Ecology. *Cybianthus wurdackii* is restricted to the heavily shaded, moist bottoms of zanjones. It is sympatric with *C. steyermarkianus,* which thrives in the small shrub islands on the summits, frequently bordering the canyons.

Paratypes. VENEZUELA. BOLIVAR: Dtto. Piar, Kamarkaibaray-tepui, E of Auyán-tepui, 2,400–2,500 m, 25–26 Mar. 1987 (stam. fl), *Delascio 13146* (MO, VEN); Ptari-tepui, summit, 2,360–2,420 m, 23 Feb. 1978 (pist. fl), *Steyermark et al. 115657* (MO, NY, VEN), 2,300 m, 26 Mar. 1987 (pist. fl, fr), *Holst 3600* (MO, US, VEN); Macizo del Chimantá, NE section, central portion of Murey-(Eruoda-)tepui, 2,500 m, 24 Feb. 1978 (stam. fl), *Steyermark et al. 115785* (MO, VEN), 15–17 Mar. 1986 (pist. fl, fr), *Huber 11590* (MYF, NY, VEN); Sarven-tepui, 1,750–1,850 m, 19 Jan. 1953 (stam. fl), *Wurdack 34189* (NY, US, VEN).

Cybianthus wurdackii seems to be most closely related to *C. steyermarkii.* However, *C. wurdackii* is easily recognized by its smaller, lepidote staminate corolla, shorter staminodes, a conspicuous staminal tube, and leaves that are dull above and merely revolute along the margin.

The species is dedicated to John Wurdack of the Smithsonian Institution, explorer of the Guayana and preeminent authority on the systematics of neotropical Melastomataceae.

6. Cybianthus plowmanii Pipoly, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Río Negro, Cerro de la Neblina, Venezuelan–Brazilian border, vic. Camp 6, on ridge 3.5 km W of Pico Zuloaga, 0°53′N, 65°56′W, 2,000 m, 13–15 Apr. 1984 (stam. fl), *Thomas & Plowman 3048* (holotype, VEN; isotypes, F, MO, NY, US). Figure 7.

Quoad folia supra dense atro-punctata, laminarum nervulos utrinque conspicuos, inflorescentiam paniculatam ad *C. amplum* valde affinis sed ab ea corollae lobis plicatis (nec planis) ad apicem cucullatum (nec planum) asymmetricis (nec symmetricis) manifeste atro- (nec brunneo-) punctatis, antherisque ad apicem apiculatos (nec acutos) atque ventraliter (nec dorsaliter) curvatis facile cognoscitur.

Shrub or tree to 8 m tall; branchlets terete, 0.7–1.2 mm diam., stiff, the bark creamish white, prominently furrowed, without lenticels, moderately adpressed-lepidote, at times glabrescent. Leaves oblanceolate to obovate, coriaceous, (5.5–)9.3–24 cm long, (4.5–)5.5–7.5(–8.5) cm wide, apically acuminate, the acumen subacute, 0.3–1.8 cm long, the base cuneate, decurrent on the petiole, costa depressed above, prominently raised below, secondary nerves prominent above and below, nitid above, pallid below, the surface smooth above, with scattered appressed-lepidote scales below, not conspicuously punctate, the margin essentially flat, regular, entire; petioles prominently marginate, thick, (1.4–)1.8–2.5 cm long, 2–4 mm diam., lepidote at first, early glabrescent. *Staminate inflorescence:* a panicle, rarely appearing almost racemose, (1.5–)3.5–5.5 cm long, the rachis densely lepidote; bracts linear-lanceolate, 1.1–1.5 mm long, 0.3–0.5 mm wide, plicate, apically acuminate, the margin entire, glabrous; pedicels 2.1–3.0 mm long. Flowers 4-merous, erect; calyx patelliform, coriaceous, 1.2–1.3 mm long, the tube 0.2–0.3 mm long, the lobes widely ovate to suborbicular, 1.0–1.1 mm long and wide, apex obtuse to rounded, lepidote, medially thick and rugose without, densely and prominently black punctate, the margin irregular, entire; corolla campanulate, carnose, 3.0–3.5 mm long, translucent, the tube 0.9–1.1 mm long, the lobes widely ovate, asymmetric, reflexed at anthesis, 2.0–2.4 mm long, 1.4–1.6 mm wide, plicate, obtuse to rounded apically, cucullate, minutely red lepidote and glandular-granulose within, basally red lepidote and glandular-granulose near the margin without, veins 4, black, conspicuous, prominently black punctate without apically, the margin entire, glandular-granulose; stamens 2.7–3.0 mm long, the tube conspicuous, carnose, 1.2–1.3 mm long, translucent, epunctate, elobate, the apically free filaments 1.0–1.2 mm long, flat, the anthers ovate, erect, 1.4–1.6 mm long, 0.8–0.9 mm wide, apiculate, the apiculum ventrally recurved perpendicular to the anther, the base cordate, glabrous, the connective prominently black punctate, the slits extremely wide, not confluent; pistillode conic, 1.2–1.3 mm long, 0.5 mm diam., the ovary translucent-lepidote. *Pistillate inflorescence:* paniculate, at times poorly formed, appearing racemose in fruit; 3.5–8.0 cm long, the rachis densely lepidote; floral bracts linear-lanceolate, 1.1–1.3 mm long, 0.5–0.6 mm wide, sparsely lepidote, plicate, early caducous, the margin entire, glabrous; pedicel erect, (1.0–)2.0–3.0(–4.0) mm long, moderately punctate, terete, thickening in fruit. Flowers 4-merous; calyx patelliform, coriaceous, 1.0–1.2 mm long, the tube short, 0.1–0.2 mm long, the lobes appearing free, suborbicular, 0.7–0.8 mm long, 1.2–1.3 mm wide, apex rounded to obtuse, essentially glabrous, medially thick and rugose, prominently black punctate, the margin irregular, entire, lepidote; corolla rotate, 3.0–3.2 mm long, the tube 0.5–0.7 mm long, the lobes highly reflexed at anthesis, touching the pedicels,

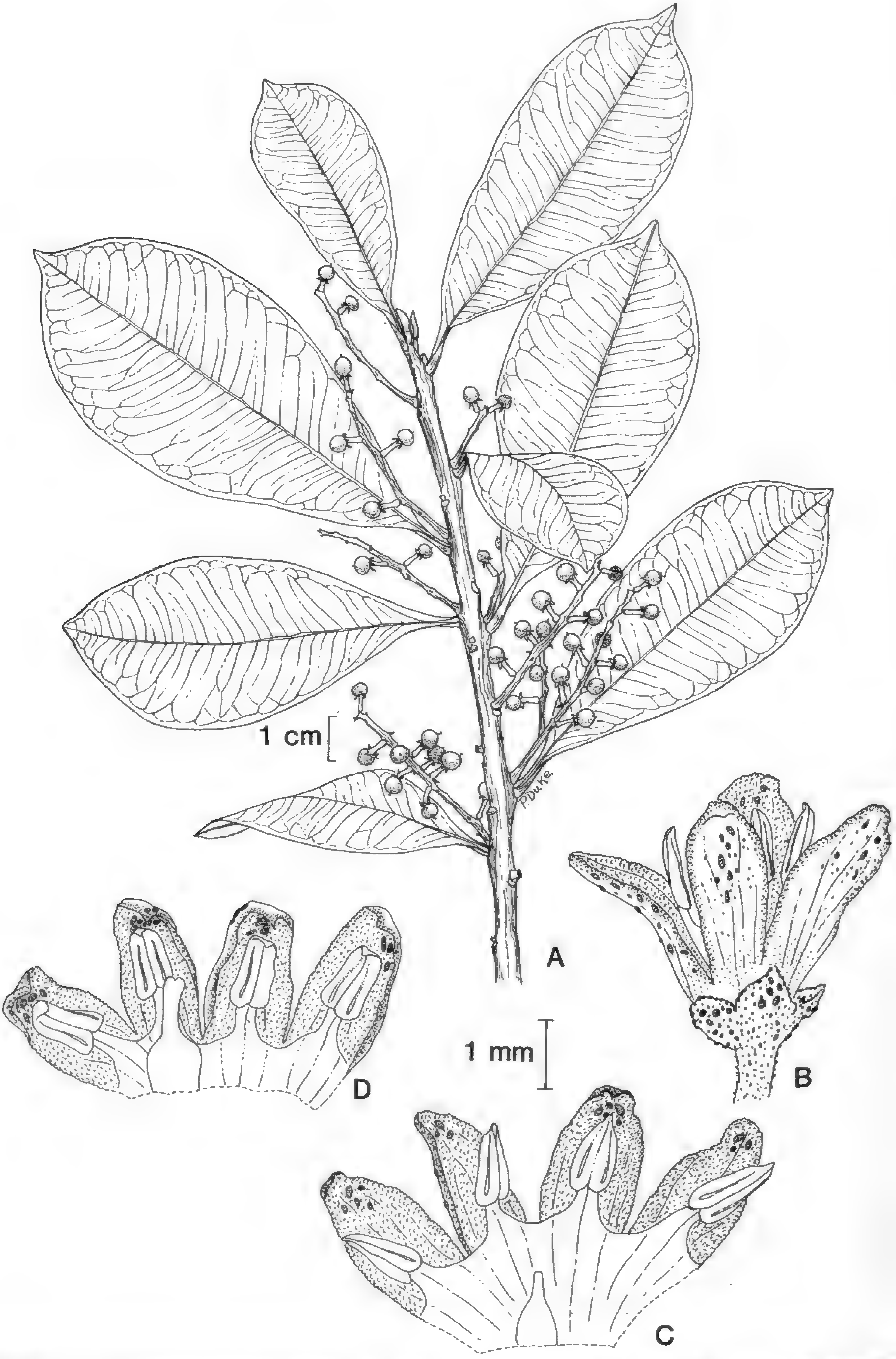


FIGURE 7. *Cybianthus plowmanii* Pipoly.—A. Habit.—B. Staminate flower, showing plicate corolla lobes, calyx, and corolla punctations and erect anther with proximally recurved apiculum.—C. Opened staminate flower, showing cucullate corolla lobes and punctations.—D. Opened pistillate flower, showing pistil with 2-lobed stigma. (A, from *Thomas & Plowman 3048*; B and C, from holotype; D, from *Thomas & Plowman 3069*.)

ovate, 2.5–2.8 mm long, 1.7–1.8 mm wide, asymmetric, apically cucullate, minutely red lepidote and glandular-granulose within, basally red lepidote and glandular-granulose near the margin without, the veins 4, conspicuous, prominently black punctate apically without; staminodes 2.6–2.9 mm long, the tube prominent, carnose, 0.8–1.0 mm long, translucent, the apically free filaments 0.8–1.0 mm long, the anthers dorsifixed ca. ⅓ from base, erect, narrowly ovate, 1.0–1.2 mm long, apiculate, the apiculum ventrally recurved, perpendicular to anther, base nearly cordulate, appearing obtuse, the connective darkened, epunctate but with a prominent translucent callosity and appearing verrucose; pistil obnapiform, 2.0–2.2 mm long, the ovary terete, 1.0–1.2 mm long, 1.3–1.5 mm wide, glabrous, black punctate, the style terete, ca. 0.9 mm long, epunctate, the stigma capitate, 2-lobed, the placenta bilobed, bearing 2 deeply imbedded ovules. Fruit depressed-globose, ca. 0.5–0.8 cm long, 0.7–1.0 cm diam., prominently punctate, verrucose, exocarp thin.

Distribution. Restricted to cloud and scrub forests of Cerro de la Neblina and the environs of Serra Aracá, the latter a satellite tepui in Amazonas, Brazil, at elevations to 2,000 m.

Ecology. Cybianthus plowmanii occurs on outcrops in exposed areas, in small shrub islands. It appears to be locally common, but the populations are few and infrequently encountered.

Paratypes. VENEZUELA. AMAZONAS: Depto. Río Negro, Cerro de la Neblina, Venezuelan–Brazilian border, vic. Camp 6, on ridge 3.5 km W of Pico Zuloaga, 2,000 m, 13–15 Apr. 1984 (fr), *Thomas & Plowman 3060* (F, NY, US, VEN), (pist. fl), *3069* (F, US, VEN), Camp VII, 29 Nov. 1984 (pist. fl), *Anderson 13386* (MICH, NY, VEN), S slopes of Cañon Grande, 1,900 m, 29 Nov. 1984 (pist. fl), *Croat 59409* (MO, VEN), E escarpment, Caño Grande below Cumbre Camp, 1,200–2,200 m, 27 Dec. 1957 (fr), *Maguire et al. 42533* (F, NY—3 sheets, US, VEN), 1,730–1,850 m, 31 Jan. 1985 (fr), *Nee 30663* (MO, NY, US, VEN). BRAZIL. AMAZONAS: Rio Cuieras, 50 km upstream, farm of Sr. Caldez, [near Serra Aracá], 3 Apr. 1974 (fr), *Campbell et al. P21820* (INPA, MG, NY, US).

Cybianthus plowmanii is most easily confused with *C. amplus* in the western limit of Guayana. However, the terete branchlets, flat leaf margins, branchlets without lenticels, asymmetric, plicate, and apically cucullate corolla lobes with prominent black punctations easily distinguish *C. plowmanii* from *C. amplus*.

Preliminary data obtained from phylogenetic analysis (Pipoly, unpublished) reveals that *C. peruvianus*, *C. amplus*, and *C. plowmanii* form a clade defined by staminal and staminodial tube longer than the corolla tube. From there, *C. peruvianus* and *C. plowmanii* form a clade defined by asymmetric corolla lobes. *Cybianthus peruvianus* is defined by its unique linear-lanceolate anthers, while *C. plowmanii* is distinguished by its plicate corolla lobes. *Cybianthus amplus* is defined by its angulate, lenticellate branchlets.

7. **Cybianthus amplus** (Mez) Agostini, Acta Biol. Venez. 10: 151. 1980. *Conomorpha ampla* Mez in Engler, Pflanzenr. IV, 236: 257. 1902. TYPE: Brazil. Bahia: without locality, without date (stam. fl), *Sellow 653* (lectotype, here designated, K; isolectotype, fragment at F). Figure 8.

Conomorpha macrophylla Martius, Herb. Fl. Bras. 260. 1837. TYPE: Colombia. Commisaría de Vaupés: Dtto. Japurensis, Serra do Araracoara, (pist. fl, fr), *Martius s.n.* (lectotype, here designated, M; isolectotypes, M—4 sheets).

Conomorpha utiarityi Hoehne, Relat. Commiss. Linhas Telegr. Estratég. Matto Grosso Amazonas, Ann. 5, Bot. 6: 64. 1915. TYPE: Brazil. Matto Grosso [Rondônia]: Salto de Utiarity, Rio Papagio, June 1909 (stam. fl), *Hoehne 2111* (holotype, R).

Shrub or small tree to 7 m tall; branchlets angular, 5–8 mm diam., the bark longitudinally ridged, creamish white, conspicuously lenticellate, densely lepidote. Leaves elliptic or obovate, coriaceous, 8–23 cm long, 4–12 cm wide, apex abruptly acuminate, the acumen to 1 cm, basally obtuse to acute, decurrent on the petiole, midrib depressed above, prominently raised below, nerves 24–40 pairs, inconspicuous or slightly raised above, more conspicuous below, upper surface scrobiculate, densely lepidote at first, glabrescent, the lower surface densely lepidote, the scales not overlapping, sparingly pellucid punctate, the margin revolute, epunctate; petioles marginate, 1.0–3.5 cm long, densely lepidote. *Staminate inflorescence:* a racemose panicle, with 1–6(–8) branches, branching from near the base, 2.5–8.0 cm long; peduncle, axis, and branches densely lepidote; peduncle 0.1–0.5 cm long; pedicels 0.5–1.0 mm long; floral bracts ovate, triangular, or ovate-triangular, 0.6–1.0 mm long, 0.4–0.6 mm wide, apex acute, densely lepidote adaxially, the margin entire. Flowers 4(–5)-merous, white; calyx cupuliform, carnose, 0.7–1.1 mm long, the tube 0.2–0.4 mm long, the lobes triangular, deltate, or deltate-ovate, 0.5–0.8 mm long, 0.5–0.9 mm wide, the apex rounded or attenuate to a rounded tip, sparingly pellucid or brown punctate, sparingly lepidote medially, the margin entire, often densely lepidote; corolla cam-

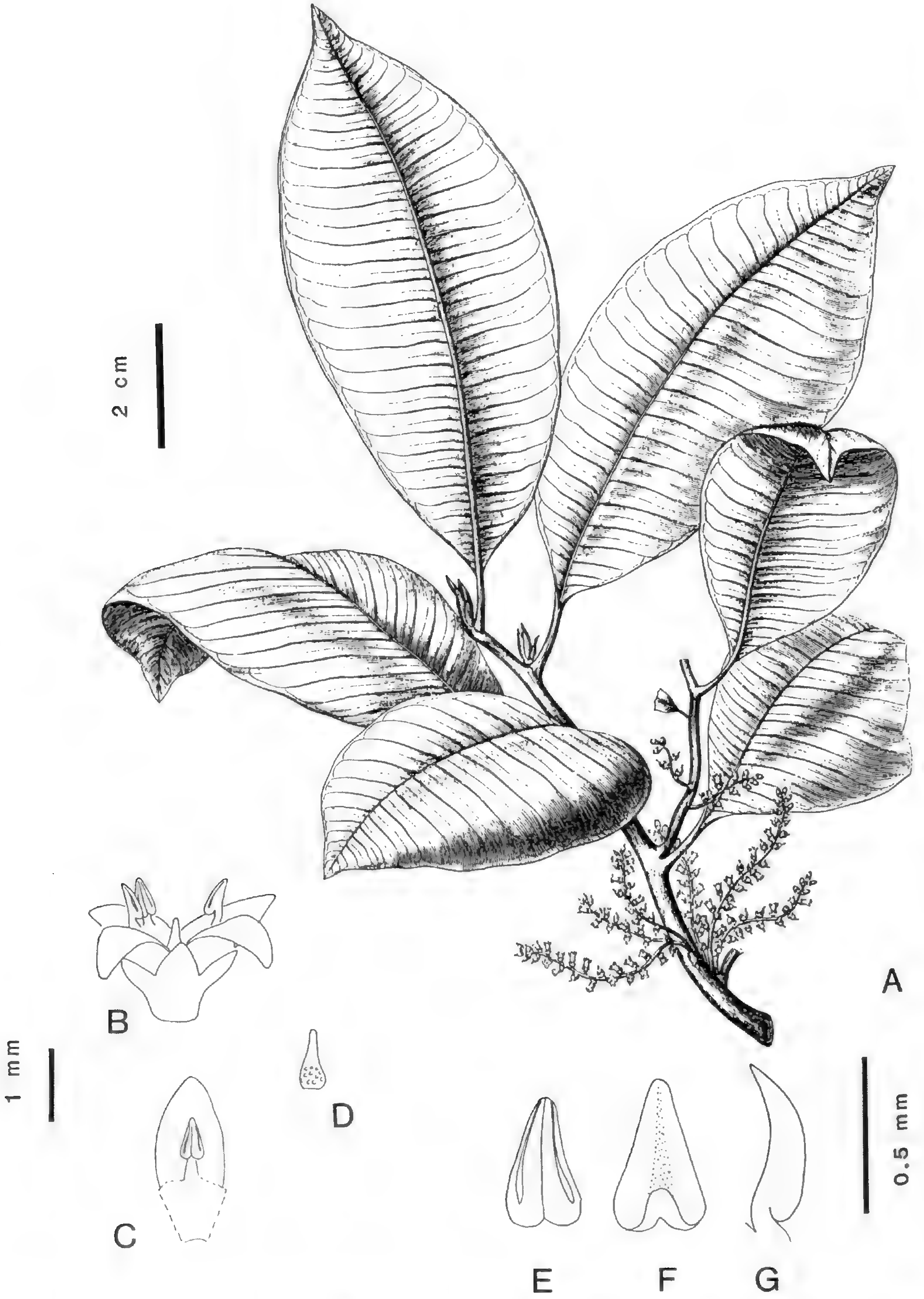


FIGURE 8. *Cybianthus amplus* (Mez) Agostini.—A. Habit.—B. Staminate flower.—C. Staminate corolla lobe, ventral view. D. Pistillode.—E. Anther, ventral view.—F. Anther, dorsal view, showing darkened connective.—G. Anther, lateral view. (A, modified from Miquel, 1856, fig. 47; B–G, from *Maguire & Wurdack 34861.*)

panulate, carnose, 2.3–2.7 mm long, the tube 0.8–1.1 mm long, the lobes elliptic to ovate, 1.5–2.0 mm long, 0.8–1.2 mm wide, apex rounded, flat, sparsely lepidote without, glandular-granulose within and without submarginally, inconspicuously pellucid or brown punctate along the margins, the margin entire, glandular-granulose; stamens 1.7–2.2 mm long, adnate 0.8–1.3 mm to the corolla, the tube inconspicuous, hyaline, 0.8–1.3 mm, elobate, the apically free filaments 0.1–0.3 mm long, flat, the anthers triangular to ovate-triangular, dorsifixed less than ¼ from base, 0.5–0.8 mm long, 0.3–0.4 mm wide, dorsally recurved, apex acute, base cordate, the connective inconspicuously brown punctate; pistillode elongate, subconic, 1.0–1.4 mm long, hollow, translucent glandular-lepidote basally. *Pistillate inflorescence:* a racemose panicle, with 1–5 branches, branching from near the base, 2.5–8.0 cm long; peduncle, axis, and branches densely lepidote; peduncle 0.1–0.5 cm long; pedicels 0.5–1.0 mm long; floral bracts ovate, triangular, or ovate-triangular, 0.6–1.0 mm long, 0.4–0.6 mm wide, apex acute, densely lepidote adaxially, the margin entire. Flowers 4(–5)-merous, white; calyx cupuliform, carnose, 0.7–1.1 mm long, the tube 0.2–0.4 mm long, the lobes triangular, deltate, or deltate-ovate, 0.5–0.8 mm long, 0.5–0.9 mm wide, the apex rounded or attenuate to a rounded tip, sparingly pellucid or brown punctate, sparingly lepidote medially, the margin entire, often densely lepidote; corolla campanulate, 2.3–2.7 mm long, the tube 0.8–1.1 mm long, the lobes elliptic to ovate, 1.5–2.0 mm long, 0.8–1.2 mm wide, apex rounded, flat, sparsely lepidote without, glandular-granulose within, and without in the marginal zone, inconspicuously pellucid or brown punctate along the margins, the margin entire, glandular-granulose; staminodes 1.7–2.2 mm long, adnate 0.8–1.3 mm to the corolla, the tube inconspicuous, hyaline, 0.8–1.3 mm, elobate, the apically free filaments 0.1–0.3 mm long, flat, the anthers triangular to ovate-triangular, dorsifixed less than ¼ from base, 0.5–0.8 mm long, 0.3–0.4 mm wide, dorsally recurved, apex acute, base cordate, the connective inconspicuously brown punctate; pistil obnapiform, 1.3–2.0 mm long, the ovary 0.7–1.2 mm long, 0.7–1.1 mm diam., glandular-lepidote, the style thick, 0.5–0.7 mm long, the stigma capitate, elobate, the placenta cotyliform, bearing 3 ovules, the ovules imbedded except at the apices. Fruit globose, 5–11 mm long, 6–12 mm diam., endocarp smooth or rugose, aril scanty, adnate to seed, embryo curved, 4 mm long.

Distribution. Colombia, Venezuela, Brazil, and Peru, at elevations below 1,100 m.

Ecology. *Cybianthus amplus* occurs in lowland, mostly seasonally inundated forests (várzea and igapó). It is a gap and forest margin species, and as such, thrives in areas of moderate disturbance.

Representative specimens examined. COLOMBIA. VAUPES: Cerro del Varador, Raudal Alto (Mariapire), right margin, 250 m, 3 Feb. 1953 (pist. fl), *Fernández 2056* (COL); Río Apaporis, Raudal de Jirijirimo, below mouth of Kanararí, 250 m, 25–26 Nov. 1951 (stam. fl), *García-Barriga 13715* (COL, US), 100 m, 15 Mar. 1952 (stam. fl), *Schultes & Cabrera 15928* (COL, GH, US); near mouth of Río Piraparana, Río Apaporis, 20 June 1952 (fr), *Schultes & Cabrera 16794* (COL, ECON, MO, US); along tributary of Río Macu Parana, 1–8 June 1970 (ster.), *Silverwood-Cope 3* (AMES). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: 0.5–3 km N of San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 120 m, 19 Nov. 1977 (stam. fl), *Liesner 3692* (MO, NY, VEN), 5 May 1979 (fr), *Liesner 7220*, (stam. fl bud), *7221* (MO, NY, VEN), 16 May 1979 (stam. fl), *Liesner 7468* (MO, VEN), 115 m, 17 Sep. 1975 (stam. fl), *Berry 1373* (MO, VEN); 15 km SW of Sta. Bárbara del Río Orinoco, 120 m, 26 June 1979 (stam. fl), *Huber 3861* (US, VEN); Río Cunucunuma, Caño Culebra, 1,000–1,100 m, 18 Nov. 1950 (pist. fl, fr), *Maguire et al. 29508* (NY, VEN); Cerro Duida, SE slopes along Caño Negro, 350–1,095 m, 25–26 Aug. 1944 (stam. fl), *Steyermark 57984* (F, NY, VEN); Sabana Grande, between Esmeralda and Cerro Duida, 175 m, 24 Mar. 1953 (stam. fl), *Maguire & Wurdack 34861* (COL, F, K, NY, S, U, US, VEN); Capibuara, alto Casiquiare, 120 m, 27 May 1942 (fr), *Williams 15574* (A, F, G, RB, US, VEN); Cerro Curiche, Tama-tama, without date (stam. fl), *Maguire 43662* (NY, VEN); vic. of N Cerro Vinilla, 30 km SSW of Ocamo, jct. of Río Orinoco, (stam. fl), *Steyermark et al. 130400* (MO, VEN); middle part of Río Baría, 80 m, 29 June 1984 (pist. fl), *Davidse & Miller 26773* (MO,VEN); Cerro Neblina Camp IV, 15 km NNE of Pico Phelps, N branch of river canyon, 780 m, 15–18 Mar. 1984 (stam. fl), *Liesner 16637* (MO, VEN). BOLIVAR: mid-basin, Río Paragua, near Minas de Manaima, 300 m, 13 June 1987 (fr), *Stergios 10284* (MO, PORT, US, VEN); Sierra Ichún, Salto Ichún, 27 Dec. 1961 (stam. fl), *Steyermark 90249* (VEN). BRAZIL. AMAZONAS: Yútica, left bank of Rio Vaupés, 15 Nov. 1952 (fr), *Romero-Castañeda 3536* (COL, GH, INPA, MO, NY, US).

Cybianthus amplus is most closely related to *C. plowmanii*, an endemic species of Cerro de la Neblina, and *C. peruvianus*, a western Amazonian species, but differs by its flat, symmetric, pellucid or brown punctate corolla lobes, leaves with revolute margins, the terete, lenticellate branchlets, and the acute anthers dorsally recurved.

Cybianthus amplus is a forest margin species and the only member of the subgenus that tolerates disturbance. Individuals growing in shady areas have longer leaves and longer, more highly branched panicles. Individuals growing in more open areas have thicker, obovate leaves with more prominently revolute margins. This variation has resulted in taxonomic overdescription. The type of *Conomorpha macrophylla* Martius represents populations with long, elliptic leaves, and narrowly campanulate flowers. It is otherwise identical to the other populations. Likewise, the type of *Conomorpha utiarityi* Hoehne differs only by the widely elliptic leaves and petioles at the longer end of the continuum, and the slightly larger and more broadly campanulate flowers.

8. Cybianthus quelchii (N. E. Brown) Agostini, Bol. Soc. Venez. Ci. Nat. 22(132–133): 388. 1976. *Ardisia quelchii* N. E. Brown, Trans. Linn. Soc., Bot. 2, ser. 6: 46. 1901. *Weigeltia quelchii* (N. E. Brown) Mez, Pflanzenr. IV, 236: 288. 1902. TYPE: Venezuela [Guyana]. Summit of Mt. Roraima, 2,860 m, autumn 1808 (stam. fl), *McConnell & Quelch 665* (holotype, K). [Steyermark (1981) reported that McConnell and Quelch arrived at the summit of Roraima from the Venezuelan side.]

Conomorpha depressa Steyermark, Fieldiana, Bot. 28(3): 458. 1953. TYPE: Venezuela. Bolívar: Carrao-tepui, 2,470–2,500 m, 7 Dec. 1944 (fr), *Steyermark 60898* (holotype, F; isotype, NY).

Shrub or tree to 5 m tall; branchlets terete, subsucculent, 0.5–1.2 cm diam., the bark yellowish brown, without lenticels, densely and minutely ferrugineous stipitate-lepidote at first, early glabrescent, densely black punctate and punctate-lineate. Leaves elliptic, oblanceolate, obovate, orbicular to oblate, coriaceous, (3.5–)4.5–11.5(–13) cm long, (2.0–)3.0–4.0(–6.0) cm wide, apex rounded, obtuse, truncate or emarginate, base acute, acuminate, or somewhat cuneate, not decurrent on the petiole, nitid and densely black punctate above and below, the midrib planer above, prominently raised and black punctate-lineate below, nerves 16–26 pairs, not usually conspicuous above, conspicuous below, the margin flat, punctate-lineate; petioles flat above, rounded below, (0.3–)1.0–1.5(–2.0) cm long, densely lepidote at first, glabrescent. *Staminate inflorescence:* a tripinnate panicle, 2.7–10 cm long, the peduncle, rachis, and pedicels lepidote at first, glabrescent; peduncle 1.2–2.3 cm; secondary branchlet bracts ovate-spathulate, membranaceous, 2.3–2.5 mm long, 1.2–1.3 mm wide, apex obtuse, prominently black punctate, sparsely lepidote, the margin entire, flat, the petioles to 0.2 mm long; floral bracts ovate, 0.9–1.1 mm long, 0.3–0.5 mm wide, apex acute, densely lepidote, the margin erose, irregular, sometimes denticulate, glabrous; pedicels terete, 0.1–0.5 mm long. Flowers 4–5-merous, erect; calyx cotyliform, carnose, 1.1–1.4 mm long, the tube 0.3–0.5 mm long, the lobes suborbicular to oblate, 0.8–1.1 mm long, 0.9–1.3 mm wide, apex obtuse, hyaline, densely and prominently black punctate medially, essentially glabrous, but sometimes with a few lepidote scales, the margin erose, irregular, often denticulate, glabrous; corolla campanulate, chartaceous, 2.9–3.0 mm long, the tube 0.6–0.9 mm long, the lobes ovate, reflexed, 1.9–2.2 mm long, 1.0–1.2 mm wide, ovate, the apex obtuse, prominently cucullate, glabrous without, densely glandular-granulose above staminal tube and apically along margin within, prominently black punctate and rugose without, the margin regular, entire except crenulate apically, glabrous; stamens 2.4–2.8 mm long, the filaments basally swollen and connivent to form an inconspicuous tube 0.5–0.7 mm long, terete and adnate to the corolla lobe 0.6–0.8 mm above tube, then apically free for 0.6–0.8 mm, ventrally recurved, terete, epunctate, the anther oblong to ovate, dorsifixed less than ¼ from base, 0.8–1.2 mm long, 0.5–0.6 mm wide, dorsally recurved, apex apiculate, the apiculum erect, base subcordulate, the connective black punctate at apex at point of insertion; pistillode lageniform, 0.9–1.1 mm long, ca. 0.5 mm diam., densely black punctate, the style and stigma not differentiated. *Pistillate inflorescence:* a tripinnate panicle, (1.0–)1.5–2.7(–4.0) cm long, peduncle, rachis, and pedicels lepidote at first, glabrescent; peduncle 0.7–2.0 mm long; secondary branchlet bracts ovate-spathulate, membranaceous, 2.2–2.3 mm long, 1.0–1.3 mm wide, apex obtuse, prominently black punctate, sparsely lepidote, the margin entire, flat, the petioles to 0.2 mm long; floral bracts ovate, 1.0 mm long, 0.5 mm wide, apex acute, densely lepidote, the margin irregular, denticulate, glabrous; pedicels terete, 0.1–0.5 mm long. Flowers 4-merous, erect; calyx deeply cupuliform, carnose, 0.9–1.1 mm long, the tube 0.3–0.5 mm long, the lobes orbicular to oblate, 0.3–0.5 mm long, 0.4–0.7 mm wide, apex obtuse, hyaline, sparsely glandular-papillate and ferrugineous lepidote, densely and prominently black punctate medially, essentially glabrous, the margin irregular, denticulate, glabrous; corolla campanulate, carnose, translucent, 2.5–3.0 mm long, the tube 0.5–0.7 mm long, the lobes oblate to suborbicular, reflexed, 1.7–2.1 mm long, 1.9–2.3 mm wide, the apex rounded to emarginate, prominently cucullate, glabrous without, densely glandular-granulose with and apically along margin within, prominently black punctate and punctate-lineate, the margin entire, irregular, glabrous; stamens 2.1–2.3 mm long, the tube inconspicuous, 0.5–0.7 mm long, the apically free filaments 0.9–1.1 mm long, ventrally recurved, subterete, epunctate, the anther erect, ovate, 0.5–0.7 mm long, 0.5–0.8 mm wide, dorsifixed less than ¼ from base, apex apiculate, the apiculum erect, base deeply cordate, the connective black punctate at apex at point of insertion; pistil obnapiform, 2.0–2.3 mm long, 0.4–0.5 mm diam., densely translucent-lepidote, the style 0.4–0.5 mm long, the stigma capitate, not lobed, 0.2 mm long, the placenta cupuliform, with 3–4 exposed ovules.

Fruit globose, 0.7–0.8 mm long, 0.9–1.2(–2.0) cm diam., exocarp thick, purple-black, juicy, edible, black punctate. *Bisexual inflorescence:* as in pistillate, but stamens 2.3–2.5 mm long, the tube 0.3–0.5 mm long, the filaments adnate to the corolla lobe 0.5–0.6 mm above tube, then apically free for 1.1–1.3 mm, the anther as in staminate flowers, but 0.8–0.9 mm long; pistil ellipsoid, 2.0–2.3 mm long, 1.1–1.4 mm diam., the style almost obsolete, the stigma capitate, 0.3 mm long, the placenta deeply cupuliform, with 2–3 exposed ovules. Fruit depressed-globose, 0.4–0.5 mm long, 0.5–0.7 mm wide, densely and prominently black punctate, exocarp thin, black, with little juice.

Distribution. Endemic to the Guayana Shield, known from most portions thereof, except Tafelberg and Macarena. It occurs at elevations from 1,150 to 2,330 m.

Ecology. *Cybianthus quelchii* is a conspicuous tree in gallery forests and dense thickets surrounding bogs on the plateaus of tepuis. It is frequently associated with *Archytaea multiflora* (Theaceae) and is one of the taller trees of the shrub islands growing on water-saturated soils. It is not a component of the cloud/elfin forest formations occurring in less exposed areas, nor is it present in the scrub formations in savannas.

This species is sexually labile, but it appears that polygamous individuals are rare (*Tillett et al. 45689*). Flowering occurs throughout the year on new growth, and within a given population there are usually some individuals in flower. During an inventory on the summit of Serra Aracá I observed that there are more staminate than pistillate individuals per population. In gallery forests studied on Chimantá Massif and Serra Aracá, flowers of this species produced a notable musklike odor and small dipterans were seen visiting the flowers. In populations bordering bogs on the summit of Muri-tepui, no odor was detectable in the flowers.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Río Negro, Cerro de la Neblina, plateau, NW range, summit N of base camp along Río Mawarinuma, affluent of Río Baría, 1,880 m, 7–8 Feb. 1984 (bud), *Luteyn & Steyermark 9442* (MO, NY, TEX, VEN), (fr), *9482* (MO, NY, TEX, US, VEN), upper basin of Cañon Grande above Salto Grande, 13 Dec. 1957 (fr), *Maguire et al. 42366* (F, MO, NY, S, US, VEN), S rim of upper basin, (fr), *Maguire et al. 42373* (F, MO, NY, US, VEN), ridge at Brazil/Venezuela divide, 26 km ENE of Neblina Base Camp, 2,000 m, 15 Apr. 1984 (pist. fl), *Plowman & Thomas 13598* (F, MO, NY, US, VEN); Depto. Atures, Serranía Sipapo, summit, S section, 17 Feb. 1981 (stam. fl), *Steyermark et al. 124531* (MO, VEN). BOLIVAR: Roraima, without date (ster.), *Schomburgk s.n.* (K); Dtto. Piar, Aparman-tepui, E of Auyán-tepui, 2,150 m, 23 Mar. 1987 (fr), *Delascio 13032* (MO, VEN), westernmost of 4 tepuis in Aparaman range, 2,100 m, 27 Mar. 1987 (fr), *Holst 3699* (MO, US, VEN); Auyán-tepui, Jan. 1949 (stam. fl), *Cardona s.n.* (US, VEN), summit, NE section, N of Camarata, 1,950 m, 28 Feb. 1978 (stam. fl), *Steyermark 116183* (F, MO, NY, US, VEN); Macizo del Chimantá, summit, Acopán-tepui, 2,200 m, Oct. 1947 (fr), *Cardona 2266* (US, VEN), SSE sector, SE plateau, headwaters of Río Arauai, 14–16 Feb. 1984 (stam. fl), *Luteyn et al. 9482* (AAU, MO, MYF, NY, S, US, VEN), NE plateau, headwaters of Río Yunek, 1,950 m, 8–11 Feb. 1985 (pist. fl), *Pipoly et al. 7163* (MO, MYF, NY, PH, TEX, US, VEN), SE sector, central–SE section of Churí-tepui, 10–12 Feb. 1984 (bud), *Huber & Colella 8964* (MYF, NY, VEN), 4 Feb. 1955 (stam. fl), *Steyermark & Wurdack 402* (F, MO, NY, U, US, VEN), central section, Chimantá-tepui, Upper Falls, Río Tirica, 2,150 m, 17 Feb. 1955 (bisex. fl, fr), *Steyermark & Wurdack 920* (F, MO, NY, US, VEN), central–S section, large valley between NE border of Torono-tepui and central section, Chimantá-tepui, 2,100 m, 11–15 Feb. 1985 (stam. fl), *Pipoly et al. 7256* (MYF, NY, TEX, US, VEN), Torono-tepui, summit, between base and upper falls and drop to escarpment, 1,895–1,910 m, 23 Feb. 1955 (stam. fl), *Steyermark & Wurdack 1088* (F, MO, NY, US, VEN); summit, Cerro Guaiquinima NE section, near cliffs, headwaters of NE branch of Río Carapo, 1,490–1,500 m, 25 May 1974 (bud), *Steyermark et al. 117322* (F, MO, NY, US, VEN); Dtto. Heres, Cerro Marutaní, summit, along Río Carla, affluent of Río Paragua at headwaters, 1,200 m, 11–12, 14 Jan. 1981 (bud), *Steyermark et al. 123866, 123906* (MO, NY, US, VEN); near Venezuelan–Brazilian frontier, 1,420 m, 13 Jan. 1981 (bud), *Steyermark et al. 123993*, (fr), *124023* (MO, NY, US, VEN); Ptari-tepui, SW-facing shoulder, 2,000–2,200 m, 2 Nov. 1944 (fr), *Steyermark 59797* (F, NY, VEN), vic. "Miss Kathy Camp," mesa between Ptari- and Sororopán-tepuis, 1,615 m, 15–17 Nov. 1944 (fr), *Steyermark 60240* (F, NY, VEN); summit of Mt. Roraima, NW portion, NNW of summit camp, 2,620–2,740 m, 27 Sep. 1944 (stam. fl), *Steyermark 58842* (F, NY, VEN); Tormeru, NW of Parupa, 1,200 m, 14 Dec. 1984 (fr), *Kral 72045* (MO, NY, US, VDB). GUYANA. Upper Mazaruni River Basin, Mt. Ayanganna, shoulder E flank above Thompson Camp, 1,418–1,525 m, 10 Aug. 1960 (polygamous), *Tillett et al. 45609* (F, FDG, MO, NY, S, US); Haieka savanna, E side of Haieka River, 4 km E of Chinoweing village, 740 m, 21 Aug. 1960 (stam. fl), *Tillett et al. 45219* (F, FDG, MO, NY, US, VEN). BRAZIL. AMAZONAS: plateau of Serra Aracá, S side of N mountain, 1,150–1,250 m, 11 Feb. 1984 (stam. fl), *Pipoly et al. 6695* (INPA, MG, MO, NY, PH, TEX, US, VEN), 14 Feb. 1984 (stam. fl), *6700*, (ster.), *6701*, *6706* (CM—2 sheets, INPA, MG, MO, NY, PH, TEX, US, VEN), plateau, N massif, 1,400 m, 20 Feb. 1984 (pist. fl), *Prance, Pipoly, et al. 29194* (INPA, MG, MO, NY, US). TERRITORIO DO RORAIMA: Serra do Sol (Uei-tepui), 2,333 m, 28 Dec. 1954 (pist. fl), *Maguire 40396* (F, MO, NY, S, US, VEN); Serra dos Surucucus, upper slopes of Serra Parima, S of Auaris, 1,400–1,520 m, 10 Feb. 1969 (pist. fl), *Prance et al. 9820* (F, INPA, K, MG, NY, S, U, US).

Cybianthus quelchii was placed in subgenus *Weigeltia* by Agostini (1971, 1980), but its campanulate corolla, with anthers distally recurved, indicate it shares common ancestry with the *Microconomorpha–Stapfia–Laxiflorus–Conomorpha* clade illustrated by Pipoly (1987). These synapomorphies, combined with its ferrugineous lepidote scales on the branchlets and leaves, indicate that it is a member of subgenus *Conomorpha*. Despite the fact that the scales of the branchlets are often early caducous, they are the same type of scale found in the other members of the subgenus, not like the furfuraceous scales encountered in subgenus *Weigeltia*. Also, the anthers are dorsifixed less than ¼ from the base, rather than versatile, as are all the members of subgenus *Weigeltia*.

This species is extremely variable throughout its range and often forms stands at the edge of bogs, or in gallery forests along watercourses on summits. Individuals occurring at the edges of bogs often have smaller leaves and larger inflorescences, while those of the gallery forests have correspondingly larger leaves and more compact inflorescences. The bark is extremely corky, and the wood is strong and flexible. The fruit is juicy, with a slightly tart, cherrylike flavor at maturity.

The type of *Conomorpha depressa* Steyermark represents populations in the eastern section of the state of Bolívar, which are notable only for their larger-than-average fruits. However, individuals from Cerro de la Neblina (*Luteyn & Steyermark 9442*) have the largest fruits known thus far, reaching 2 cm diam. It is not known whether the individuals from which fruits were collected on Neblina are pistillate or bisexual.

9. **Cybianthus punctatus** (Mez) Agostini, Acta Biol. Venez. 10: 155. 1980. *Conomorpha punctata* Mez, in Engler, Pflanzenr. IV. 236: 260. 1902. TYPE: Venezuela [Guyana]. Bolívar: Roraima, 1842–1843 (stam. fl), *Schomburgk 554* (lectotype, here designated, G; isolectotypes, BM, F, K, P, W). Figure 9.

Conomorpha sessilis A. C. Smith, Bull. Torrey Bot. Club 67: 294. 1940. TYPE: Venezuela. Bolívar: Roraima, vic. Arabupu, Arabupu River, Dec. 1938 (stam. fl), *Pinkus 55* (holotype, NY; isotypes, F, GH, S, US).

Shrub or small tree to 3 m tall; branchlets terete, 2.0–2.5 mm diam., densely lepidote. Leaves elliptic, narrowly elliptic, or elliptic-obovate, membranaceous to chartaceous, 7.5–10(–15) cm long, 2.5–4.5 cm wide, apex acuminate, the acumen 0.5–1.0 cm long, base acute, decurrent, midrib depressed above, prominently raised below, nerves 12–18 pairs, slightly raised above and below, upper surface whitish, sparsely and eglandular scrobiculate and densely lepidote when young, glabrescent, sparsely lepidote below, the margin revolute; petioles canaliculate, prominently winged, 1.0–2.2 cm long, densely lepidote. *Staminate inflorescence:* a somewhat pyramidal panicle with 3–7 lateral branches, 3.5–5.5 cm long, 2.5–3.5 cm broad, the peduncle, axis, branches, and pedicels densely lepidote; peduncle 0.3–1.5 cm long; pedicels terete, 1.0–1.5 mm long; floral bracts triangular to ovate-triangular, 0.5–0.7 mm long, 0.3–0.4 mm wide, apex acute, densely lepidote abaxially, the margin entire. Flowers (4–)5(–6)-merous; calyx cotyliform, carnose, 0.9–1.0 mm long, the tube 0.2–0.3 mm long, the lobes triangular, 0.7–0.9 mm long, 0.5–0.6 mm wide, apex attenuate to a rounded tip, brown punctate near the margin, the margin lepidote, entire; corolla campanulate, carnose, 2.0–2.5 mm long, the tube 0.7–0.9 mm long, the lobes ovate or broadly ovate, 1.3–1.6 mm long, 0.9–1.1 mm wide, reflexed, apically rounded or attenuate to a rounded tip, sparsely glandular-granulose without, densely glandular-granulose apically within, conspicuously brown punctate toward the margin, brown punctate-lineate medially, the margin entire, glabrous; stamens 1.7–2.0 mm long, adnate ca. 0.8 mm to the corolla tube, the staminal tube conspicuous, chartaceous, 0.8–1.0 mm long, elobate, the apically free filaments flat, 0.1–0.2 mm long, the anthers ovate-triangular, erect, 0.9–1.0 mm long, dorsifixed ca. ¼ from base, apex apiculate, the apiculum erect, cordate basally, the connective prominently brown punctate; pistillode lageniform, 1.2–1.5 mm long, ca. 0.4 mm diam., hollow, translucent glandular-lepidote basally. *Pistillate inflorescence:* a bipinnate or poorly formed panicle with 3–5 lateral branches, 2.0–4.5 cm long, 1.5–2.5 cm broad, the peduncle, axis, branches, and pedicels densely lepidote, the scales superposed; peduncle 0.6–0.8 cm long; pedicels terete, 2.7–3.8 mm long; floral bracts triangular to ovate-triangular, 0.5–0.7 mm long, 0.3–0.4 mm wide, apex acute, densely lepidote abaxially, the margin entire. Flowers 5-merous; calyx cotyliform, carnose, 0.9–1.0 mm long, the tube 0.2–0.3 mm long, the lobes deltate, 0.7–0.9 mm long, 0.7–0.9 mm wide, apex attenuate to a round tip, brown punctate near the margin, the margin lepidote, entire; corolla not seen. Fruit globose, 0.3–0.4 mm long and in diam. when dried, the exocarp verrucose.

Distribution. Endemic to the northeastern section of Pantepuí (sensu Mayr & Phelps, 1967) in the Auyán-tepui-Chimantá Complex of the Guyana Pakaraima–Venezuelan Gran Sabana Sub-

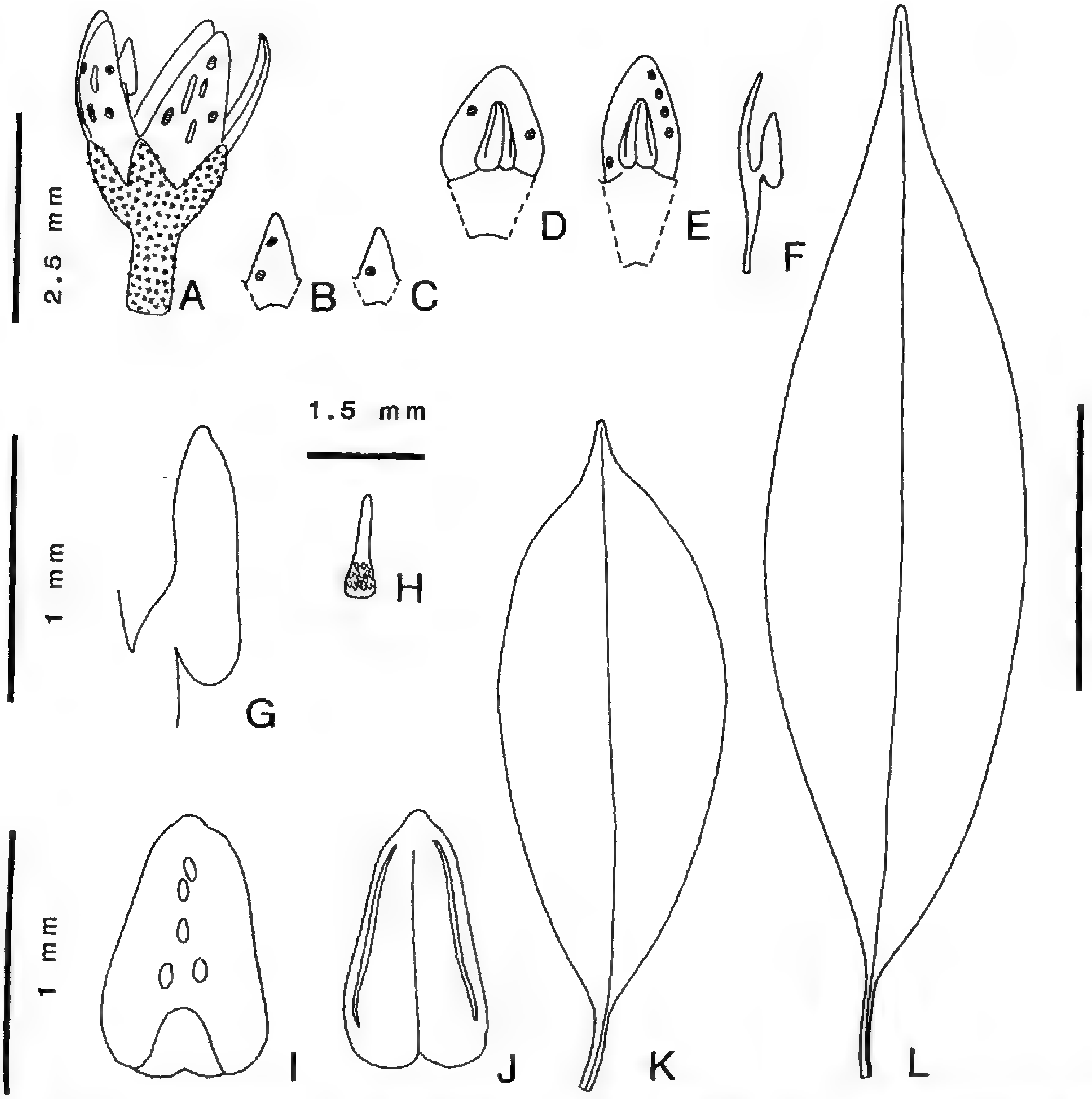


FIGURE 9. *Cybianthus punctatus* (Mez) Agostini.—A. Staminate flower.—B, C. Staminate calyx lobes, ventral view.—D, E. Staminate corolla lobes, ventral view.—F. Staminate corolla lobe, lateral view.—G. Anther, lateral view, showing erect habit.—H. Pistillode.—I. Anther, dorsal view, showing punctate connective.—J. Anther, ventral view.—K, L. Leaves. (A–K, from *Pinkus 55*; L, from *Forest Dept. Brit. Guiana WB331-5757*.)

province of Maguire (1979), at 1,000–1,400 m elevation.

Ecology. *Cybianthus punctatus* is an infrequently encountered element of cloud forests on talus slopes. Very little is known of its life history.

Specimens examined. VENEZUELA. BOLIVAR: Dtto. Piar, descent from Salto Hacha, upper basin of Río Purpur, along trail to Urimán, 850–1,100 m, (fr), *Davidse & Huber 22955* (MO, VEN); Gran Sabana, tributary of Río Kukenán, S of Mt. Roraima, 1,005–1,065 m, 2 Oct. 1944 (stam. fl), *Steyermark 59122* (F, NY, VEN); Kavanayén, forests of Oparuma, 1,400 m, 28 May 1946 (stam. fl), *Lasser 1836* (K, US, VEN); Arabapu, Mt. Roraima, 1,400 m, 13 Dec. 1938 (stam. fl), *Forest Dept. Brit. Guiana P49-282* (BRG, K); Ayavoparú, 10 km SW of Wadacapiapué, 1,100 m, without date, *Hernández 358* (NY, VEN). GUYANA. Wabuwak Kanuku Mts., Dec. 1948 (stam. fl), *Forest Dept. Brit. Guiana WB331-5757* (NY).

Within Guayana, *C. punctatus* may be most easily confused with *C. cardonae*, but is easily distinguished by its leaves 7.5–10(–15) cm long, (2.5–)3.5–4.5 cm wide, with acuminate apices, petioles canaliculate and winged, pedicels erect, and corolla carnose with reflexed lobes.

In sterile condition, *C. punctatus* may be confused with the sympatric *C. roraimae* and *C. lepidotus*. From *C. roraimae*, *C. punctatus* may be recognized by its branchlets 2.0–2.5 mm diameter, membranaceous to chartaceous leaves with upper surfaces shallowly eglandular scrobiculate, the nerves 12–18 pairs, and the petioles winged, 1.0–2.2 cm long. From *C. lepidotus*, *C. punctatus* is more difficult to separate, but may still be recognized by its leaves membranaceous to chartaceous, with nerves 12–18 pairs, and acute leaf bases, which are decurrent on the petiole. It appears that the two species are separated ecologically, *C. punctatus* being a talus forest species, while *C. lepidotus* occurs in protected cloud/elfin forest areas on the edges of the taller tepui summits.

10. Cybianthus cardonae Agostini, Bol. Soc. Venez. Ci. Nat. 22: 386. 1976. TYPE: Venezuela. Bolívar: Alto Paragua, Cerro Tabarerupá, 500 m, 1 July 1944 (stam. fl), *Cardona 1081* (holotype, VEN; isotypes, F, NY, US).

Shrub or tree to 8 m tall; branchlets subangular, 2–4 mm diam., densely lepidote, at times glabrescent. Leaves widely elliptic to elliptic, subcoriaceous to coriaceous, 10–18 cm long, 5–7 cm wide, apex acute or short-acuminate, base acute, decurrent on the petiole, midrib depressed above, prominently raised below, nerves 30–50 pairs, conspicuous above and below, densely glandular-scrobiculate above, densely ferrugineous lepidote below, the margin entire, epunctate, subrevolute; petioles marginate distally, squarrose proximally, 1.5–2.0(–3.0) cm long, densely lepidote. *Staminate inflorescence:* a lax pyramidal to subpyramidal panicle, erect, 8–15 cm long, about as long as the leaves, the peduncle 1–2 cm long, sparsely lepidote, the branches 5–6, racemose, 20–55-flowered, 2.5–10 cm long; floral bracts chartaceous, narrowly ovate, apex acute, 0.6–1.0 mm long, 0.1–0.2 mm wide, densely lepidote adaxially, the margin entire, glabrous; pedicels terete, thin, 1–3 mm long, apically recurved in anthesis and fruit, densely lepidote. Flowers 4-merous, whitish yellow; calyx cupuliform, chartaceous, 1.1–1.4 mm long, the tube 0.2–0.4 mm long, the lobes erect, deltate to ovate-deltate, symmetric, 0.7–0.9 mm long and wide, apex acutely rounded, with 2–6 conspicuous orange punctations, with few lepidote scales, the margin entire, irregular, lepidote; corolla campanulate, membranaceous, 2.5–3.1 mm long, the tube 0.8–1.0 mm long, the lobes ovate to ovate-elliptic, united ca. ⅓ length, 1.8–2.2 mm long, 0.9–1.4 mm wide, somewhat reflexed in anthesis, apex obtuse to rounded, symmetric, sparsely lepidote without, glandular-granulose apically within, glabrous without, inconspicuously pellucid punctate; stamens 2.1–2.2 mm long, the tube 0.9–1.0 mm long, inconspicuous, hyaline, elobate, the apically free filaments 0.2–0.5 mm long, terete, glabrous, the anthers lanceolate, dorsifixed ca. ¼ length, dorsally curved, 0.9–1.0 mm long, 0.2–0.3 mm wide, apex acute, base cordate, the connectives prominently brown punctate dorsally; pistillode conic, 1.5–1.7 mm long, 0.5–0.6 mm diam., the ovary lepidote, hollow, the style glabrous, the stigma punctiform when developed. *Pistillate inflorescence:* a subpyramidal panicle, erect, (6–)8–10 cm long, as long as or subequal to leaf length, the peduncle 1–2 cm long, sparsely lepidote, the branches 5–6, racemose, 12–15-flowered, 2.5–4 cm long; floral bracts chartaceous, narrowly ovate, apex acute, 0.6–1.0 mm long, 0.1–0.2 mm wide, densely lepidote adaxially, the margin entire, glabrous; pedicels terete, thin, 1–3 mm long, apically recurved in anthesis and fruit, densely lepidote. Flowers 4-merous; calyx cupuliform, chartaceous, 1.1–1.4 mm long, the tube 0.2–0.4 mm long, the lobes erect, deltate to ovate-deltate, symmetric, 0.7–0.9 mm long and wide, apex acutely rounded, with 2–6 conspicuous orange punctations, with few lepidote scales, the margin entire, irregular, lepidote; corolla unknown. Fruit depressed-globose, 4–6 mm long, 5–7 mm diam. when dried, smooth.

Distribution. Endemic to the Guayana Shield, in the Neblina, Duida, and Jaua complexes (Maguire, 1979). It is notable that it has thus far not been collected in the Sipapo-Yutajé Complex, which lies north of the Río Ventuari drainage. The absence of *Cybianthus cardonae* from Guaiquinima, along with data from other Myrsinaceae and Clusiaceae, support the notion that the affinities of Guaiquinima's flora lie with the Guyana Pakaraima-Venezuelan Gran Sabana Subprovince, rather than with the Caroní-Río Negro Subprovince, as postulated by Maguire (1979). The occurrence of this taxon on Serra Aracá, Amazonas, Brazil, once again reinforces the notion that Aracá's flora is intimately related to that of the Neblina and Duida complexes. It occurs in the region at 80–1,800 m altitude.

Ecology. *Cybianthus cardonae* is a conspicuous element of the cloud/elfin forest of the summit edge, near a large waterfall on the southern side of the northern mountain of Serra Aracá. These small patches of cloud and elfin forest located on plateau edges are floristically as well as physiognomically distinct from the more extended cloud forests below elfin forest formations on smaller, protruding plateaus scattered over the broad, principal plateaus of the tepuis. It appears that the pistillate flowers are ephemeral, as a number of fruiting specimens were seen and collected, while the pistillate corolla remains unknown. In the rest of its range, *C. cardonae* is infrequently encountered in small, elfin cloud forests in protected areas at the edge of steep cliffs on tops of the tepuis.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Río Negro, Cerro de la Neblina, S face of Pico Phelps Massif, 1,550–1,650 m, 13 Apr. 1984 (stam. fl), *Gentry & Stein 46610* (MO, NY, VEN).

Camp IV, 15 km NNE of Pico Phelps, N branch of river canyon, 780 m, 15–18 Mar. 1984 (fr), *Liesner 16678* (MO, VEN); Cerro Aracamuni, summit, Proa Camp, 1,400 m, 26 Oct. 1987 (fr), *Liesner et al. 22486* (MO, VEN), 2 Nov. 1987 (fr), *22760* (MO, VEN); Depto. Atabapo, Cerro Duida, 1,000 m, Jan.–Feb. 1969 (stam. fl), *Fariñas et al. 371* (VEN), saddle between Cerros Duida and Marahuaca, near base of Duida, 100 m, 27 Oct. 1988 (fr), *Liesner 25496* (MO, US, VEN), 28 Oct. 1988 (fr), *Liesner 25533* (MO, US, VEN); Cerro Marahuaca, slopes, "sima," 1,200 m, 16 Oct. 1988 (fr), *Liesner 24964* (MO, VEN); Cerro Huachamacari, E slope, 600–700 m, 3 Nov. 1988 (fr), *Liesner 25772* (MO, US, VEN). BOLIVAR: Río Orinoco, 30 km below la Urbana, 80 m, 14 Mar. 1949 (stam. fl), *Maguire & Politi 29071* (NY, VEN); Meseta de Jaua, Cerro Jaua, summit, 1,750–1,800 m, 22 Feb. 1974 (stam. fl), *Steyermark et al. 109300* (US, VEN). BRAZIL. AMAZONAS: plateau of Serra Aracá, S side of N mountain, 1,150–1,250 m, 17 Feb. 1984 (stam. fl), *Pipoly et al. 6704* (INPA, MG, MO, NY, US, VEN), plateau of N massif, N summit, 1,600 m, 23 Feb. 1984 (stam. fl), *Prance, Pipoly, et al. 29429* (INPA, K, MG, MO, NY, US, VEN).

Cybianthus cardonae may be confused with *C. punctatus* but may be separated by its acute leaves, recurved pedicels, and the membranaceous corolla.

11. **Cybianthus lepidotus** (Gleason) Agostini, Bol. Soc. Venez. Ci. Nat. 22: 388. 1976. *Conomorpha lepidota* Gleason, Bull. Torrey Bot. Club 58: 446. 1931. TYPE: Venezuela. Territorio Federal Amazonas: summit of Mt. Duida, 1,500 m, Aug. 1928–Mar. 1929 (pist. fl), *Tate 741* (holotype, NY; isotype, US). Figure 10.

Conomorpha curvivenia Gleason, Bull. Torrey Bot. Club 58: 444. 1931. TYPE: Venezuela. Territorio Federal Amazonas: Mt. Duida, 1,260 m, Aug. 1928–Mar. 1929 (stam. fl), *Tate 927* (holotype, NY; isotype, US).

Conomorpha lepidota Gleason f. *acutata* Steyermark, Fieldiana, Bot. 28(3): 465. 1953. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Duida, 2 Dec. 1944 (fr), *Steyermark 58265* (holotype, F; isotype, NY).

Shrub or small tree to 6 m tall; branchlets terete, 2–2.5 mm diam., densely lepidote. Leaves elliptic to narrowly elliptic, chartaceous to coriaceous, (3.1–)5–15 cm long, 1.6–6 cm wide, apically acuminate, the acumen 0.3–2.0 cm long, basally acute to obtuse, midrib depressed above, prominently raised below, nerves 24–28, inconspicuous above and below, pustulate and densely lepidote above at first, glabrescent, densely lepidote below, the scales not overlapping, inconspicuously pellucid punctate, the margin entire, subrevolute to revolute; petioles thin, marginate, 1.0–2.5 cm long, densely lepidote. *Staminate inflorescence:* a spike, rarely two subsessile spikes, (2–)6–16 cm long, 8–15-flowered, peduncle, pedicels, and axis densely lepidote, the scales not overlapping; peduncle (0.2–)0.5–0.8 mm long; floral bracts ovate to widely ovate, chartaceous, 0.5–0.6 mm long, 0.3–0.4 mm wide, apex acute, densely lepidote adaxially, the margin entire, glabrous. Flowers (4–)5-merous; calyx cupuliform, carnose, 0.9–1.2 mm long, the tube 0.2–0.4 mm long, the lobes deltate to ovate-triangular, 0.6–0.8 mm long and wide, apex acute or acuminate, rarely obtuse, attenuate to a rounded tip, conspicuously brown punctate, the margin entire, lepidote; corolla cupuliform, carnose, 1.5–2.5 mm long, the tube 0.5–1.0 mm long, the lobes ovate to broadly ovate, 1.2–1.7 mm long, 0.7–0.9 mm wide, apex attenuate to a round, cucullate tip, at times with a few, scattered lepidote scales without, glabrous without, glandular-granulose within over the entire surface, punctations brown, submarginal, the margin entire, glabrous; stamens 1.5–1.6 mm long, adnate 0.5–1.0 mm to corolla tube, the staminal tube 0.3–0.4 mm long, carnose, bearing lobes alternating with the apically free filaments 0.1–0.2 mm long, the filaments flat, 0.3–0.4 mm long, erect, glabrous, the anthers dorsifixed less than ¼ from base, ovate-triangular, 0.6–0.7 mm long, 0.4–0.5 mm wide, apex attenuate to a rounded tip, basally cordate, slightly dorsally reflexed, the connective epunctate; pistillode lageniform, 1.1–1.2 mm long, hollow, costate basally, sparingly translucent lepidote, pellucid-punctate. *Pistillate inflorescence:* a spike, (2–)6–16 cm long, 6–10-flowered, peduncle, pedicels, and axis densely lepidote, the scales not overlapping; peduncle 0.6–0.8 mm long; floral bracts ovate to widely ovate, chartaceous, 0.5–0.6 mm long, 0.3–0.4 mm wide, apex acute, densely lepidote adaxially, the margin entire, glabrous. Flowers 5-merous; calyx cupuliform, carnose, 0.9–1.2 mm long, the tube 0.2–0.4 mm long, the lobes deltate to ovate-triangular, carnose, 0.6–0.8 mm long and wide, apex acute or acuminate, rarely obtuse, attenuate to rounded tip, conspicuously brown punctate, the margin entire, lepidote; corolla cupuliform, carnose, 1.5–2.5 mm long, the tube 0.5–1.0 mm long, the lobes ovate to broadly ovate, 1.2–1.7 mm long, 0.7–0.9 mm wide, apex attenuate to a round, cucullate tip, at times with a few, scattered lepidote scales without, glabrous without, glandular-granulose within over the entire surface, punctations brown, submarginal, the margin entire, glabrous; staminodes 1.2–1.3 mm long, adnate 0.5–1.0 mm to corolla tube, the staminal tube 0.5–0.6 mm long, carnose, bearing lobes alternating with the apically free filaments 0.1–0.2 mm long, the filaments flat, 0.3–0.4 mm long, erect, glabrous, the anthers dorsifixed less than ¼ from base,

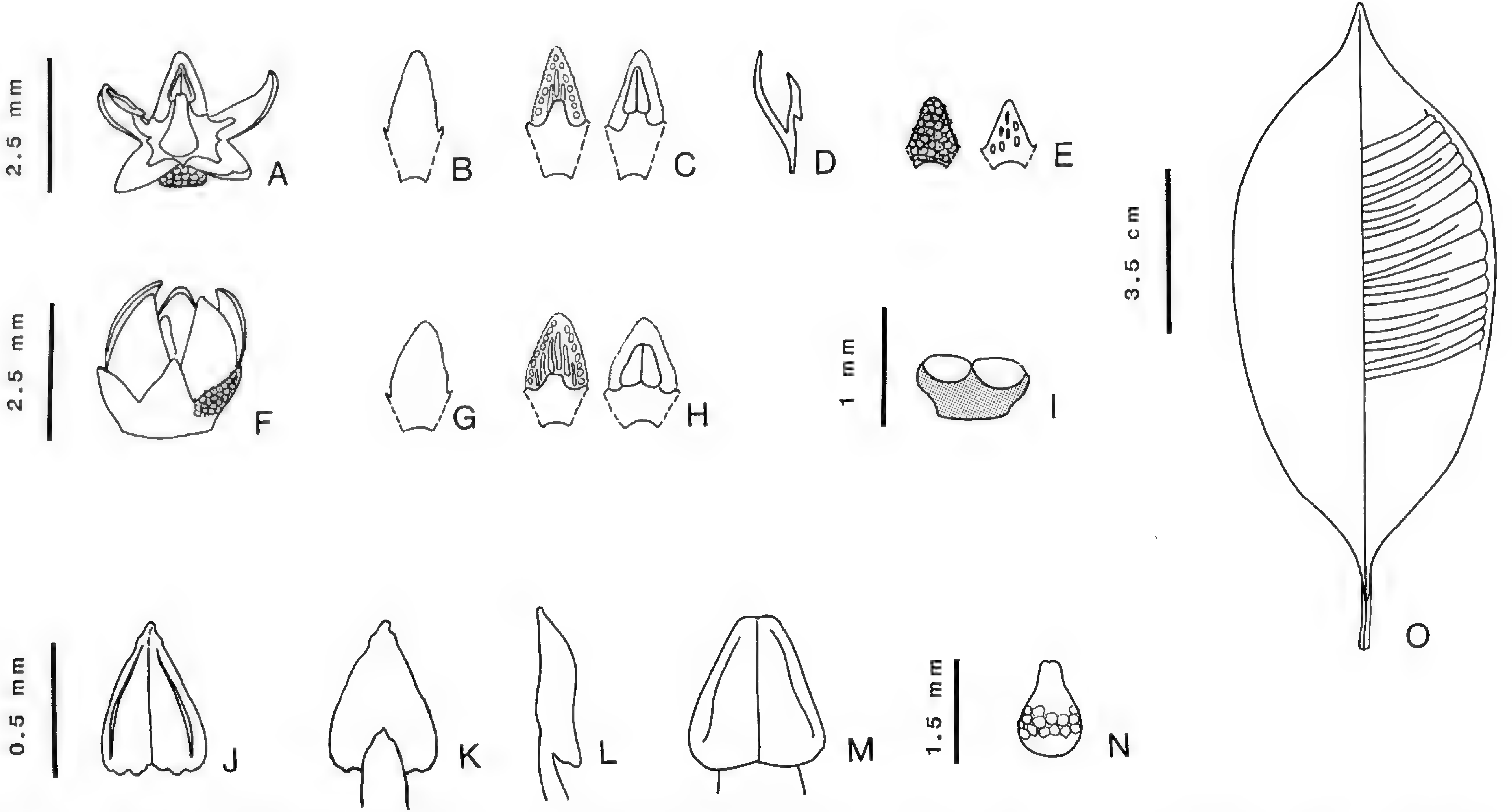


FIGURE 10. *Cybianthus lepidotus* (Gleason) Agostini.—A. Staminate flower, showing pistillode and conspicuous staminal tube.—B. Staminate corolla lobe, dorsal view.—C. Staminate corolla lobe, showing glandular granules, punctations, and anther habit.—D. Staminate corolla lobe, lateral view.—E. Staminate calyx lobe, dorsal and ventral views.—F. Pistillate flower.—G. Pistillate corolla lobe, dorsal view.—H. Pistillate corolla lobe, showing glandular granules, punctations, and anther habit.—I. Placenta, showing two naked ovules.—J. Anther, ventral view.—K. Anther, dorsal view.—L. Anther, lateral view.—M. Sterile anther, ventral view.—N. Pistil.—O. Leaf. (A–E, J–L, from *Steyermark 74900*; F–I, M, N, from holotype; O, from *Tate 927*.)

deltate, 0.7–0.8 mm long and wide, apex attenuate to a rounded tip, basally cordate, slightly dorsally reflexed, the connective epunctate; pistil pyriform, 1.4–1.5 mm long, the ovary 1–1.2 mm diam., the style not differentiated, the stigma punctiform, the placenta patelliform, bearing 2(–3) naked ovules. Fruit globose, purple at maturity, 0.5–1.0 cm long, 0.6–1.0 cm diam., the endocarp smooth, the embryo curved, 3.5–4.0 mm long.

Distribution. Guayana Highland of Venezuela and sandstone formations in Bolivia, 600–2,300 m in Venezuela, 850–950 m in Bolivia.

Ecology. *Cybianthus lepidotus* is restricted to large cloud forest formations in transition zones between sandstone and diabasic intrusions. It is often associated with species of *Erythroxylum,* which are also edaphic endemics. It is interesting to note that, in populations on Serra Aracá, I did not observe any flowering individuals less than 2 m in height. This is rather unusual in *Cybianthus,* where precocious flowering is frequent (Pipoly, 1981, 1983b, 1987). The cloud forest in which *C. lepidotus* was encountered was notably wetter and colder than the cloud/elfin forest in which *C. cardonae* had been found. The forest was located on a small plateau arising from the principal plateau of the mountain and was dominated by *Perissocarpa.* The soils were extremely wet, yet well-drained, humus with deep leaf litter.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atabapo, below Salto Los Monos on tributary of headwaters of Río Iguapo, 1,500–1,600 m, 11 Mar. 1985 (stam. fl), *Liesner 18537* (MO, NY, VEN); Cerro Huachamacari, E slope, 600–700 m, 3 Nov. 1988 (fr), *Liesner 25744* (MO, US, VEN), (stam. fl), *25745* (MO, US, VEN); Depto. Río Negro, Cerro de la Neblina, Camp VII, S slopes of Cañon Grande, 1,770–1,850 m, 30 Nov. 1984 (pist. fl, fr), *Croat 59505* (MO, NY, VEN), 7 Feb. 1985 (stam. fl), *Renner 2088* (US, VEN); Cerro Yaví, 2,200 m, 1 Mar. 1947 (stam. fl), *Phelps & Hitchcock 32* (NY, VEN), 1,800 m, (stam. fl), *Phelps & Hitchcock 174*; Cerro Parú, summit, 2,000 m, 4 Feb. 1951 (stam. fl), *Cowan & Wurdack 31221* (NY), (fr), *31342* (NY). BOLIVAR: Chimantá Massif, above middle falls of Río Tirica, 1,925 m, 5 Feb. 1955 (stam. fl), *Steyermark & Wurdack 501* (NY, VEN), Amurí-tepui (W sector of Acopán-tepui), 1,950 m, 2–5 Feb. 1983 (ster.), *Steyermark et al. 128734* (MO, NY, US, VEN), summit of Apacará-tepui, 2,125–2,300 m, 23 Mar. 1953 (stam. fl), *Steyermark 74900* (MO, NY, VEN), slope below summit, 2,000–2,150 m, 20 June 1953 (stam. fl), *Steyermark 75185* (MO, NY, VEN), wide valley in the SE sector of Apacará-tepui, 2,150 m, 6–9 Feb. 1985 (pist. fl), *Huber et al. 8882* (NY, US, VEN); Meseta de Jaua, Cerro Jaua, 1,922–2,100 m, 22 Mar. 1967 (pist. fl, fr), *Steyermark 98704* (VEN). BRAZIL. AMAZONAS: plateau of N massif of Serra Aracá, cloud forest of uppermost plateau, 1,600 m, 22 Feb. 1984 (stam. fl), *Prance, Pipoly, et al. 29239* (F, INPA, MG, MO, NY, US), 23 Feb. 1984 (stam. fl), *29247* (F, INPA, K, MG, MO, NY, US), S side of N plateau, 1,150–1,250 m, 14 Feb. 1984 (stam. fl), *Pipoly et al. 6703* (INPA, K, MG, MO, NY, RB, US, VEN). BOLIVIA. LA PAZ: Prov. Nor Yungas, valley of Río Coroico, Sacramento, 10 km NE of Chuspipata on Coroico Rd., 27 Jan. 1984 (ster.), *Gentry & Solomon 44668* (MO), 4 km NE (above) Inabuara, 13.5 km above San Pedro, 1,530–1,560 m, 22 Jan. 1984 (stam. fl), *Gentry & Solomon 44407* (MO); Prov. Larecaja, Maipiri, 6 Nov. 1926–28 Feb. 1927 (stam. fl), *Buchtien 1758* (HBG, NY, US), Copacabana, 10 km S of Maipiri, 850–950 m, 8 Oct.–15 Nov. 1939 (fr), *Krukoff 10987* (A, K, MICH, MO, NY, UC, US).

Cybianthus lepidotus, restricted to sizeable cloud forests in transition zones between sandstone and diabasic intrusions, is most easily recognized by its long, lax spikes. When sterile, it may be confused with *C. roraimae,* but may be easily distinguished by the branchlets 2–2.5 (not 3.5–4.5) mm in diameter. It may also be confused with *C. punctatus* and *C. cardonae.* For a discussion of the differences between these taxa in sterile condition, see *C. cardonae.*

The area of Bolivia in which this species has been collected is of biogeographic interest because it also supports several other Guayana Highland taxa in the Ericaceae and Clusiaceae. It is interesting that *Krukoff 10987* is identical, both qualitatively and quantitatively, to specimens of *C. lepidotus* from Cerro Duida.

12. Cybianthus sipapoensis Pipoly & Agostini, Ernstia 50: 36. 1988. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Sipapo, along middle of Caño Negro, 1,600 m, 6 Jan. 1949 (stam. fl), *Maguire & Politi 28181* (holotype, VEN; isotypes, F, LL, NY). Figure 11.

Shrub to small tree; branchlets terete, 2.5–3 mm diam., densely ferrugineous lepidote; leaves chartaceous, narrowly obovate, 9–13 cm long, 3.5–4.5 cm wide, apically subacuminate to acuminate, basally acute, midrib depressed above, prominently raised below, nerves 30–40 pairs, reticulate, conspicuous above and below, pellucid-punctate, sparsely lepidote and smooth above, glabrescent, moderately lepidote below, the margin entire, subrevolute; petioles canaliculate, 1.3–1.6 cm long. *Staminate inflorescence:* a condensed spike, 0.8–1.0 cm long, 5–8-flowered; floral bracts ovate to ovate-triangular, ca. 1 mm long, 0.8–1.2 mm wide, apex acute, pellucid-punctate, moderately lepidote below, the margin irregular, entire, glabrous; pedicels absent, rarely to 0.3(–0.6) mm long, sparsely lepidote. Flowers 2.5–3.3 mm long; clayx deeply cupuliform, carnose, 1.4–1.6 mm long, the tube

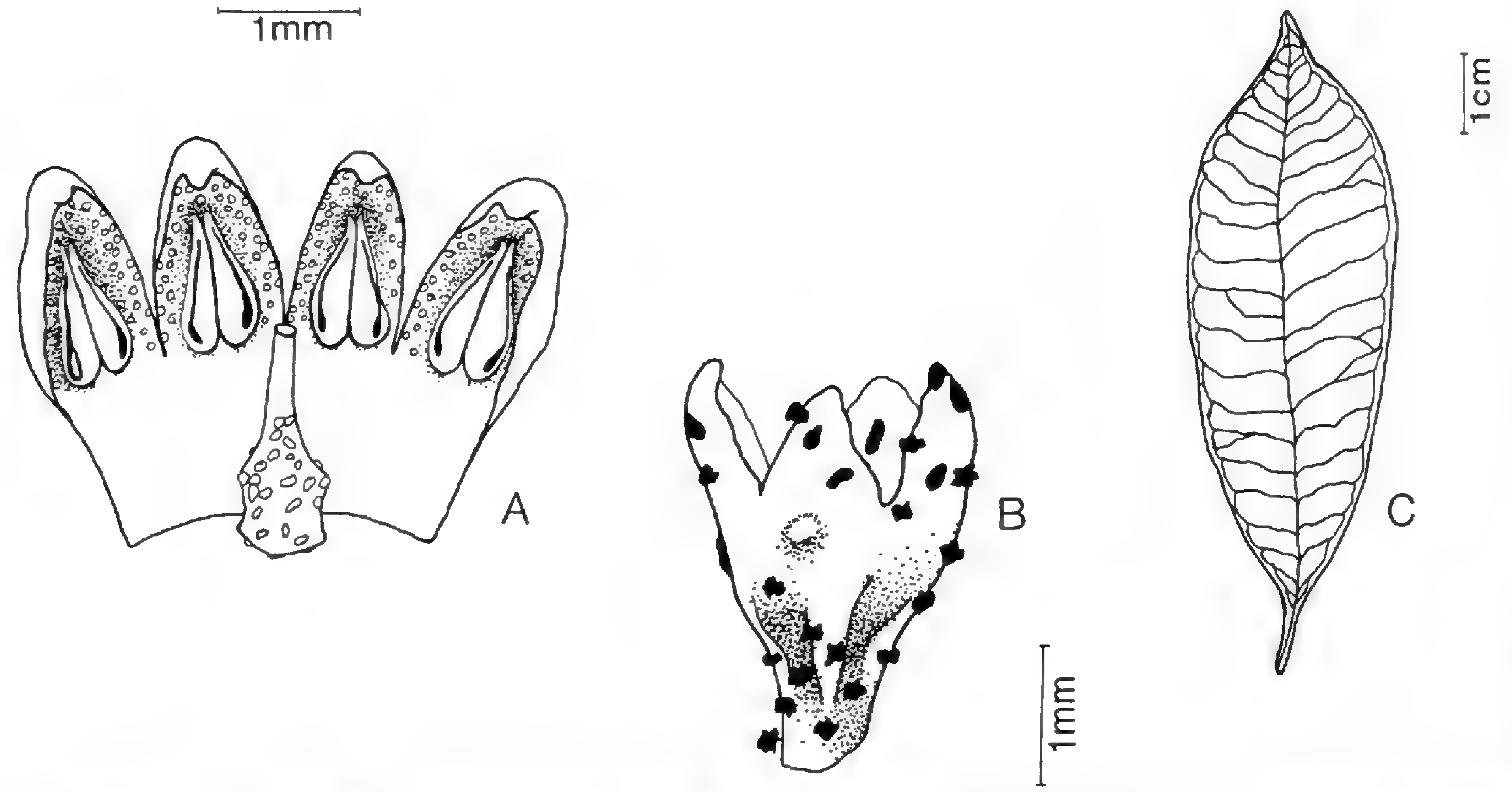


FIGURE 11. *Cybianthus sipapoensis* Pipoly & Agostini.—A. Opened staminate flower, showing cucullate corolla lobes, glandular granules, fused staminal tube, and pistillode.—B. Staminate calyx, showing lepidote scales.—C. Leaf, abaxial view. (From holotype.)

0.6–0.8 mm long, the lobes deltate or ovate-triangular, ca. 1.0 mm long, 0.8–1.2 mm long, apex acute, sparsely lepidote, conspicuously brown punctate, the margin irregular, entire; corolla cupuliform, carnose, 2.4–3.2 mm long, the tube 1.2–1.5 mm long, the lobes erect, ovate-triangular, 1.4–1.8 mm long, 0.9–1.1 mm wide, apex acute or subacute, cucullate, glabrous and sparsely lepidote without, densely glandular-granulose within and along the margin, pellucid-punctate; stamens 0.8–1.0 mm long, the tube 1.3–1.8 mm long, developmentally fused to the corolla, the anthers dorsally recurved, sessile, ovate-triangular, 0.8–1.1 mm long, 0.6–0.8 mm wide, apex long-attenuate, glabrous, prominently brown punctate dorsally; pistillode lageniform or obovoid, ca. 1.5 mm long, the ovary 0.8 mm long, 0.5 mm diam., translucent lepidote, the style ca. 0.8 mm long, prominently brown punctate. *Pistillate inflorescence:* unknown. Fruit unknown.

Distribution. Endemic to Cerro Sipapo (Paraque), 1,600 m. Known only from the type.

Ecology. Cybianthus sipapoensis is apparently restricted to cloud forests on steep slopes.

Cybianthus sipapoensis is easily recognized by the condensed spicate inflorescence and the apparently epipetalous sessile anthers. It may be confused with *C. spathulifolius*, but is easily separated by its leaves chartaceous (not coriaceous), with subrevolute (not flat) margins, and with petioles 1.3–1.6 (not 0.1–0.2) cm long, the petals erect (not tortuous), and the anthers sessile (not on filaments 0.3–0.4 mm long).

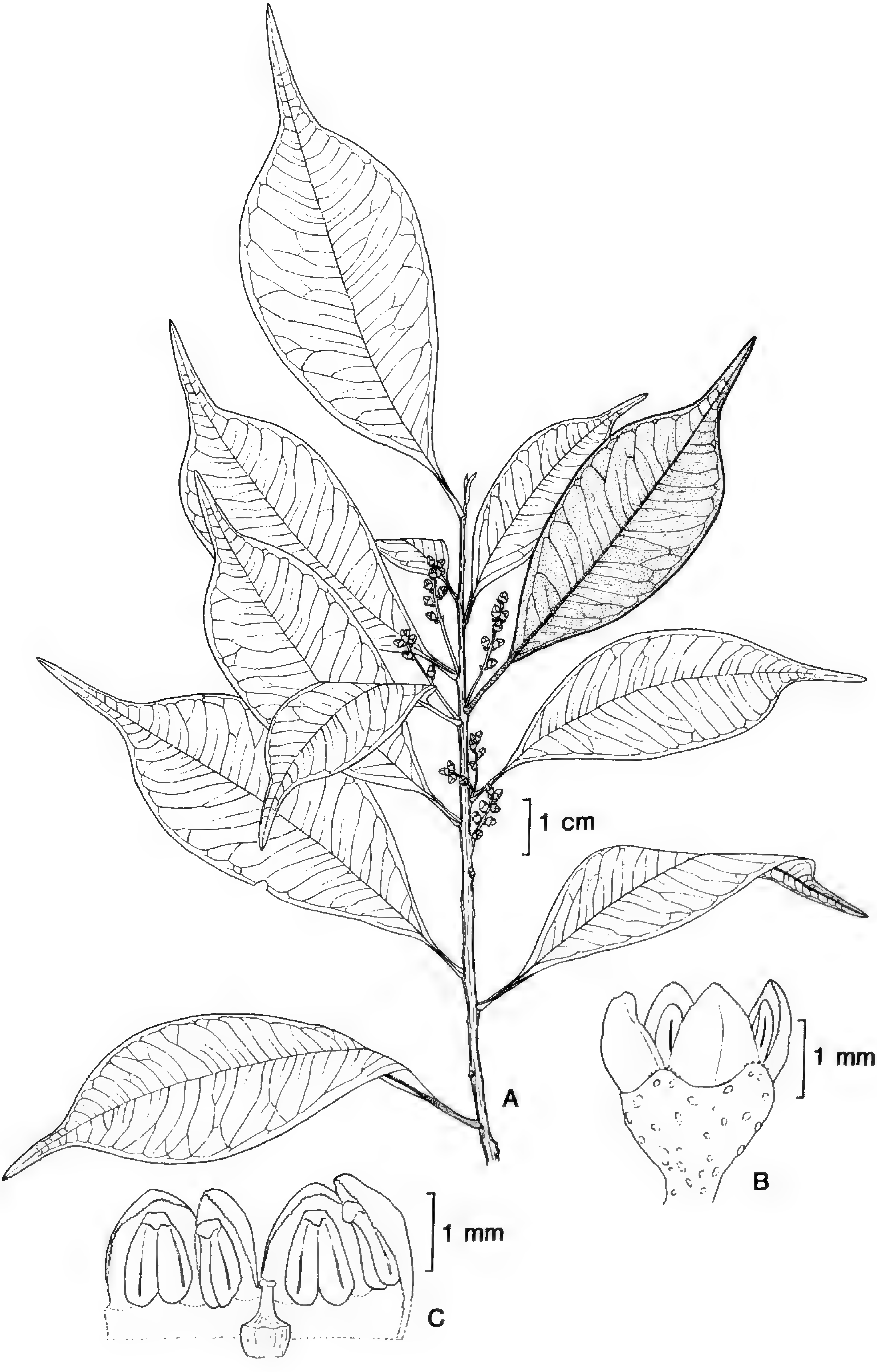
13. Cybianthus holstii Pipoly, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Ature, W side of valley of Río Coro-Coro, 8 km NNW of settlement of Yutajé, 500–1,000 m, 26 Feb. 1987 (pist. fl, fr), *Liesner & Holst 21418* (holotype, VEN; isotypes, MO, US). Figure 12.

Quoad inflorescentias spiciformes reductasque, calyces crateriformes, corollarum lobos abaxaliter carinatos erectos ad apicem cucullatosque pistillum apophysatum, *C. huberi* arcte affinis, sed illa ab hac laminis membranaceis (nec coriaceis) staminodii tubos inconspicuos (nec conspicuos) lobulis filamentis alterans destitutis (nec praeditis) antheris glabris eglandulosisque (nec rufo-papilosis brunneo-glandulosisque) fructibusque 4.0–4.5 (nec 5.5–10) mm diametris statim distinguitur.

Shrub to 2 m tall; branchlets thin, fragile, 1.5–2 mm diam., terete, densely stipitate-lepidote. Leaves obovate, membranaceous, 6.0–9.5 cm long (1.5–)2.2–3.5 cm wide, abruptly caudate apically,

→

FIGURE 12. *Cybianthus holstii* Pipoly.—A. Habit.—B. Pistillate flower, showing crateriform calyx.—C. Opened pistillate flower, showing apophysate ovary and subsessile sterile anthers. (From holotype.)


1 cm
A
1 mm
B
1 mm
C

the acumen 1.6–4.0 cm long, obtuse to rounded basally, slightly decurrent on the petiole, midrib depressed above, prominently raised below, nerves very fine, conspicuous above and below, very minutely scrobiculate above, moderately lepidote below, the scales along the midrib and margin slightly overlapping, pellucid-punctate; petioles thin, canaliculate, 1.2–1.5 cm long, ridged abaxially, densely lepidote toward the base. *Staminate inflorescence:* not seen. *Pistillate inflorescence:* a spike, 0.5–1.5(–2) cm long, 5–8-flowered, densely lepidote; floral bracts deltate, ca. 0.9–1.1 mm long and wide, apex acute, densely lepidote abaxially, the margin irregular, entire, glabrous; pedicels absent or rarely to 0.1 mm long. Flowers 4(–5)-merous, sessile or subsessile; calyx crateriform, coriaceous, 1.7–2.1 mm long, the tube ca. 1.0 mm long, the lobes very widely triangular, erect, 0.7–1.1 mm long, 1.1–1.5 mm wide, the apex rounded, prominently black punctate without, lepidote near the margin, the margin entire, glabrous; corolla cupuliform, coriaceous, 2.5–2.8 mm long, the tube 0.5 mm long, the lobes oblong, erect, 2.0–2.3 mm long, 0.7–1.1 mm wide, apex rounded, cucullate, strongly carinate without, pellucid punctate apically and along margin without, glandular granulose only along margin within, the margin entire, glabrous; staminodes 2.0 mm long, the tube inconspicuous, membranaceous, elobate, 0.5 mm long, the apically free filaments ca. 1.0 mm long, adnate to the corolla lobes, the anthers appearing epipetalous, ovate, 0.8 mm long, 0.5 mm wide, recurved distally, apically apiculate, the apiculum recurved ventrally, the base deeply cordate; pistil sessile, apophysate, costate, 1.8–2.1 mm long, the ovary 1.4–1.6 mm long and in diam., glandular-lepidote, the style short, 0.2–0.3 mm long, the stigma capitate, 2-lobed, the placenta cubic, 2-ovulate, the ovules covered by flaps of tissue. Fruit globose, 4.0–4.5 mm diam. when dry.

Distribution. Endemic to the Guanay and Yutajé complex, in forests on talus slopes under 1,000 m elevation.

Ecology. *Cybianthus holstii* is infrequently encountered in the margins of cloud forests on talus slopes.

Paratypes. VENEZUELA. Depto. Atures, Río Coro-Coro, W of Serranía de Yutajé, 9 km N of settlement, 600 m, 26 Feb. 1987 (pist, fl, fr), *Holst & Liesner 3185* (MO, US, VEN), Caño Yutajé, right branch, Río Manapiare, 1,400 m, 9 Feb. 1987 (pist. fl), *Maguire 35097* (F, MO, NY, US, VEN).

Cybianthus holstii is most closely related to *C. huberi* but can be easily separated from it by the membranaceous (not coriaceous) leaves with caudate (not short-acuminate) apices, the inflorescence 5–8(not 1–2)-flowered, and the glabrous (not rufous papillate) anthers. This species is dedicated to Bruce Holst, specialist in Myrtaceae and keen student of the Guayana flora.

14. Cybianthus guyanensis (A. DC.) Miquel in Martius, Fl. Bras. 10: 298. 1856. Figures. 13, 14.

Shrub or small tree to 8 m tall; branchlets terete, 2–3 mm diam., densely lepidote. Leaves narrowly obovate, narrowly elliptic, or oblong, membranaceous to chartaceous, 8–20 cm long, 2.0–3.5(–6.0) mm wide, apex acuminate to abruptly acuminate, the acumen 0.5–2 cm long, base acute, decurrent on the petiole, the midrib depressed above, prominently raised below, nerves (15–)20–40 pairs, inconspicuous or slightly raised above and below, the upper surface smooth or slightly wrinkled when dried, densely lepidote at first, glabrescent, lower surface sparsely to densely lepidote, pellucid-punctate, the margin entire, flat; petioles canaliculate and slightly marginate distally, 0.5–1.9(–2.3) cm long, densely lepidote. *Staminate inflorescence:* a raceme, a subsessile pseudoverticel of 2–3 racemes, or a panicle 2–8 cm long; peduncle, branches, and axis densely lepidote; peduncle 0.1–0.5 cm long; floral bracts ovate or ovate-triangular, 0.6–1.2 mm long, 0.3–0.4 mm wide, apex acute, densely lepidote abaxially, the margin entire, glabrous; pedicels erect, cylindrical, (0.3–)0.5–1.0 mm long, moderately lepidote. Flowers 4–5-merous; calyx cotyliform or subcupuliform, chartaceous, 0.8–1.1 mm long, the tube 0.2–0.4 mm long, the lobes ovate-triangular, 0.6–0.8 mm long, 0.5–0.7 mm wide, apex attenuate to a round or acute tip, inconspicuously pellucid or brown punctate, or prominently brown or black punctate, the margin lepidote, entire, glabrous; corolla campanulate, membranaceous or chartaceous, 2.0–2.6 mm long, the tube 0.6–1.0 mm long, the lobes erect or reflexed-recurved, elliptic or ovate-triangular, 1.2–1.7 mm long, 0.6–1.0 mm wide, apex acute to attenuate or attenuate to a rounded tip, inconspicuously or conspicuously brown punctate, the punctations few, glabrous externally, glabrous or densely glandular-granulose internally, sparsely lepidote or glabrous externally, the margins glabrous or glandular-granulose; stamens 1.1–1.8 mm long, the staminal tube inconspicuous, hyaline, membranaceous, 0.6–1.1 mm long, elobate, the apically free filaments terete, recurved ventrally, 0.2–0.9 mm long, eglandular, glabrous, the an-

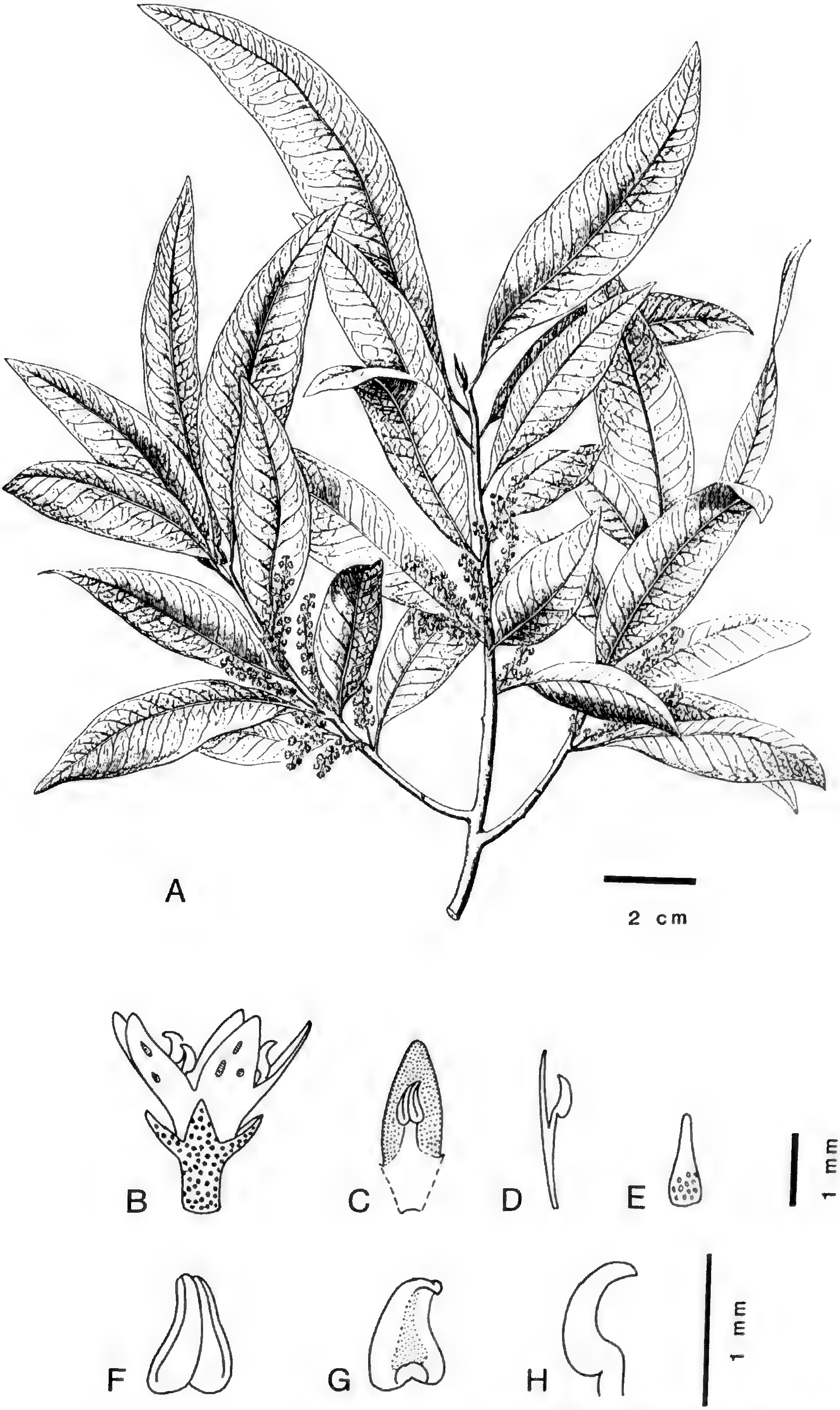


FIGURE 13. *Cybianthus guyanensis* (A. DC.) Miquel subsp. *guyanensis*.—A. Habit.—B. Staminate flower.—C. Staminate corolla lobe, showing elongate apically free filament and tortuous anther.—D. Staminate corolla lobe, lateral view.—E. Pistillode.—F. Anther, ventral view.—G. Anther, dorsal view, showing darkened connective.—H. Anther, lateral view. (A, modified from Miquel, 1856, fig. 49; B–H, from holotype.)

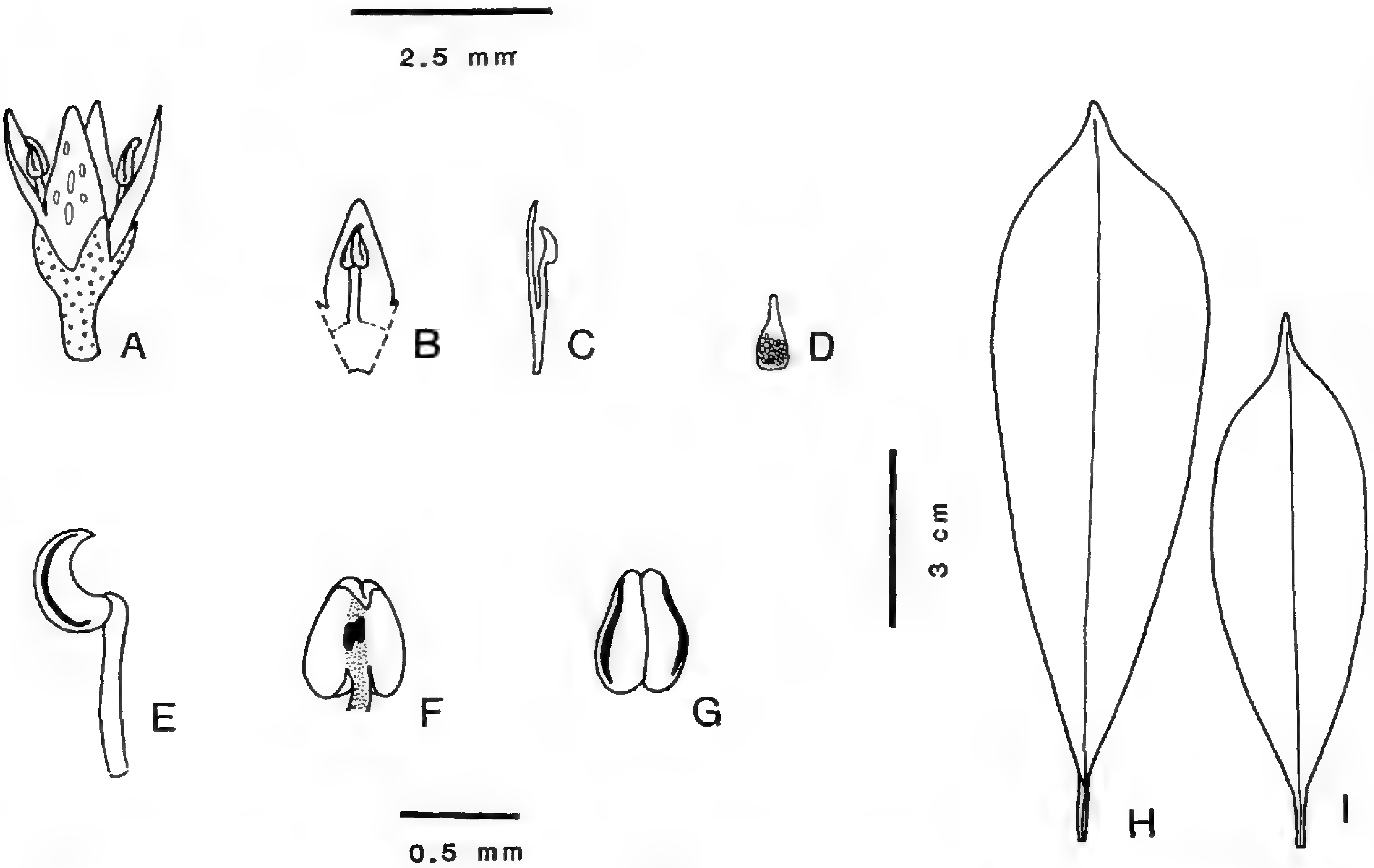


FIGURE 14. *Cybianthus guyanensis* (A. DC.) subsp. *multipunctatus* (A. DC.) Pipoly.—A. Staminate flower.—B. Staminate corolla lobe, ventral view, showing elongate apically free filament and tortuous anther.—C. Staminate corolla lobe, lateral view.—D. Pistillode.—E. Anther and filament, lateral view, showing wide dehiscence slit.—F. Anther, dorsal view, showing darkened and punctate connective.—G. Anther, ventral view.—H, I. Leaves. (A–G, from *Pinkus 252*; H, I, from *Sagot 1031*.)

thers dorsifixed just above the base, narrowly triangular, ovate, or ovate-triangular, dorsally recurved, 0.5–0.8 mm long, 0.3–0.4 mm wide, apiculate or attenuate to an acute tip at apex, the tip dorsally recurved, cordate basally, the connective inconspicuously brown punctate, or merely darkened; pistillode lageniform or conic, 0.9–1.4 mm long, basally translucent lepidote, the style not differentiated, the stigma not developed. *Pistillate inflorescence:* a raceme or panicle 2.5–8.0 cm long; peduncle, branches, and axis densely lepidote; peduncle 0.1–0.2 cm long; floral bracts ovate-triangular, 0.6–1.2 mm long, 0.3–0.4 mm wide, apex acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, (0.3–)0.5–1.0 mm long, moderately ferrugineous lepidote. Flowers 4–5-merous; calyx cotyliform or subcupuliform, chartaceous, 0.8–0.9 mm long, the tube 0.2–0.4 mm long, the lobes ovate-triangular, 0.6–0.8 mm long, 0.5–0.7 mm wide, apex attenuate to a rounded or acute tip, inconspicuously pellucid or brown punctate, or prominently brown or black punctate, the margin lepidote, entire, glabrous; corolla campanulate, membranaceous or chartaceous, 2.0–2.6 mm long, the tube 0.6–1.0 mm long, the lobes erect or reflexed-recurved, elliptic or ovate-triangular, 1.2–1.7 mm long, 0.6–1.0 mm wide, apex acute to attenuate or attenuate to a rounded tip, conspicuously brown punctate, the punctations few, glabrous externally, glabrous or densely glandular-granulose internally, sparsely lepidote or glabrous externally, the margins glabrous or glandular-granulose; staminodes 1.1–1.8 mm long, the staminodial tube inconspicuous, hyaline, membranaceous, 0.6–1.1 mm long, elobate, the filaments terete, recurved ventrally, 0.2–0.9 mm long, eglandular, glabrous, the anthers dorsifixed just above the base, tortuous, narrowly triangular, ovate, or ovate-triangular, dorsally recurved, 0.5–0.8 mm long, 0.3–0.4 mm wide, apiculate or attenuate to an acute tip at apex, the tip dorsally recurved, cordate basally, the connective inconspicuously brown punctate, or merely darkened; pistil pyriform, 1.4–1.6 mm long, the ovary 0.7–0.8 mm long, 1.0 mm diam., the style 0.7–0.8 mm long, or not well differentiated, the stigma capitate, 2-lobed, the placenta cotyliform, the ovules 2, naked. Fruit 0.5–0.6 cm long, 0.4–0.7 cm diam., exocarp thin to moderately thick, black, inconspicuously pellucid-punctate.

Distribution. *Cybianthus guyanensis* occurs from Venezuela (Amazonas and Bolívar) to Brazil (Amazonas and Pará), Guyana, Surinam, and French Guiana, from 80 to 1,000 m.

Ecology. *Cybianthus guyanensis* grows in lowland Amazonian igapó forests and montane forests. For more detailed discussion, see comments under each subspecies.

Preliminary phylogenetic analysis (Pipoly, unpublished) revealed that *C. guyanensis* is most closely related to *C. pseudoicacoreus* by the synapomorphic undulate anticlinal cell walls, subsessile inflorescence, pyriform pistil, and tortuous anthers of the staminodes. *Cybianthus pseudoicacoreus* may only be distinguished from *C. guyanensis* by its cupuliform, although deeply divided (not subcupuliform) calyx, the staminate corolla 2.8–3.2 (not 2–2.6) mm long, with the tube 1.2–1.8 (not 0.6–1.0) mm long. Further study may prove that *C. pseudoicacoreus* is best treated as another subspecies of *C. guyanensis*.

In his dissertation, Agostini (1971) recognized *C. guyanensis* as a distinct species and considered it most closely related to *C. peruvianus* and *C. amplus*. He separated it from those species by the combination of oblong-elliptic leaf blades, the short filaments, the corolla 2.3–2.6 mm long, with lobes internally glandular-granulose, the inconspicuous staminal tube, and the pedicels 0.5–1.0 mm long. The description provided here, based on many more collections, considerably alters the aforementioned quantitative characters. For a discussion of relationships among these species, see *C. plowmanii*.

In Guayana, *C. guyanensis* may be confused with *C. roraimae*, but is easily separated by the branchlets 2–3 (not 3.5–4.5) mm diam., leaves smooth (not pustulate) above with flat (not revolute) margins, the petioles (1.0–)1.5–1.9(–2.3) (not 2–3) cm long, pedicels 0.5–1.0 (not 2–3.5) mm long, corolla campanulate (not subrotate), the lobes erect to spreading (not perpendicular to the tube), the anthers distally recurved (not erect), and the sterile anthers apically tortuous (not erect).

As circumscribed here, *C. guyanensis* consists of two subspecies, *C. guyanensis* subsp. *guyanensis* and subspecies *multipunctatus*.

KEY TO GUAYANA SUBSPECIES OF
CYBIANTHUS GUYANENSIS

1a. Petioles (1.0–)1.5–1.9(–2.3) cm long; leaves symmetric, apical acumen 1–2 cm long; calyx subcupuliform, the lobes attenuate to an acute apex; corolla chartaceous, the tube 0.8–1.0 mm long, the lobes erect to spreading, 1.6–1.7 mm long, 0.9–1.0 mm wide, apically rounded, glandular-granulose within and along margins; stamens 1.5–1.8 mm long, the tube 0.9–1.1 mm long, the apically free filaments shorter than the anthers, 0.2–0.4 mm long, the anthers narrowly triangular to ovate-triangular, the apex apiculate, dehiscent by narrow, introrse slits; plants of igapó forests .... 14a. subsp. *guyanensis*

1b. Petioles 0.5–1.0 cm long; leaves slightly asymmetric, the acumen 0.5–1.0 cm long; calyx cotyliform, the lobes attenuate to a rounded apex; corolla membranaceous, the tube 0.6–0.7 mm long, the lobes distally reflexed-recurved, 1.2–1.6 mm long, 0.6–0.8 mm wide, apically acute, glabrous; stamens 1.1–1.4 mm long, the tube 0.6–0.8 mm long, the apically free filaments longer than the anthers, 0.6–0.9 mm long, the anthers ovate, the apex acute, dehiscent by wide, sublatrorse slits; plants of premontane forests on lateritic and sandstone substrates .... 14b. subsp. *multipunctatus*

14a. **Cybianthus guyanensis** (A. DC.) Miquel subsp. **guyanensis**. Figure 13.

Conomorpha guyanensis A. DC., Ann. Sci. Nat. 2 ser. 16: 92. 1841. *Peckia guyanensis* (A. DC.) O. Kuntze, Rev. Gen. 2: 402. 1891. *Conomorpha peruviana* var. *β guyanensis* (A. DC.) Mez in Engler, Pflanzenr. IV, 236: 262. 1902. TYPE: Venezuela. Bolívar [Guyana]: *sine loc.*, 1898 (stam. fl), *Schomburgk 975* (holotype, G-BOIS; isotypes, BM, F, G, GH, K, L. P, US, W).

Conomorpha heterantha Bentham ex Miquel in Martius, Fl. Bras. 10: 304. 1856. TYPE: Brazil. Prov. Rio Negro, Barra, Dec. 1850–Mar. 1851 (pist. fl), *Spruce 1041* (lectotype, here designated, M).

Shrub or small tree to 5 m tall. Leaves oblong to narrowly elliptic, symmetric, membranaceous to chartaceous, 9–20 cm long, 3–5.5 cm wide, apex acuminate, the acumen 1–2 cm long, nerves 20–40 pairs; petioles canaliculate and winged, (1.0–)1.5–1.9(–2.3) cm long, densely lepidote. *Staminate inflorescence:* a panicle 2–8 cm long; peduncle 0.2–0.5 cm long; floral bracts ovate, 0.7–0.8 mm long, 0.3–0.4 mm wide; pedicels 0.5–1.0 mm long. Flowers 4–5-merous; calyx subcupuliform, 0.8–1.2 mm long, the tube 0.3–0.4 mm long, the lobes subdeltate, 0.6–0.8 mm long, 0.5–0.6 mm wide, apex attenuate to an acute tip, inconspicuously pellucid or brown punctate, the margin lepidote, entire, glabrous; corolla chartaceous, 2.3–2.6 mm long, the tube 0.8–1.0 mm long, the lobes erect to spreading, elliptic, 1.6–1.7 mm long, 0.9–1.0 mm wide, apex attenuate to a rounded tip, inconspicuously brown punctate, glabrous externally, densely glandular-granulose internally, sparsely lepidote externally, the margins glandular-granulose; stamens 1.5–1.8 mm long, the staminal tube 0.9–1.1 mm long, the filaments shorter than the anthers, 0.2–0.4 mm long, the anthers narrowly triangular to ovate-triangular, 0.5–0.8 mm long, 0.3–0.4 mm wide, dehiscent by narrow introrse slits, apex apiculate, the tip dorsally recurved, cordate basally, the connective merely darkened; pistillode conic, 1.2–1.4 mm long. *Pistillate inflorescence:* a panicle 2.5–8.0 cm long; peduncle 0.2–0.5 cm long; floral bracts ovate, 0.7–0.8 mm long, 0.3–0.4 mm wide; pedicels 0.5–1.0 mm long. Flowers 4–5-merous; calyx subcupuliform, 0.8–1.1 mm long, the tube 0.3–0.4 mm long, the lobes subdeltate, 0.6–0.8 mm long, 0.5–0.6 mm wide, apex attenuate to an acute tip, inconspicuously pellucid or brown punctate, the margin lepidote, entire, glabrous; corolla campanulate, chartaceous, 2.3–2.6 mm long, the tube 0.8–1.0 mm long, the lobes erect or spreading, elliptic, 1.6–1.7 mm long, 0.9–1.0 mm wide, apex attenuate to a round tip, inconspicuously brown punctate, glabrous externally, densely glandular-granulose internally, sparsely lepidote externally, the margins glandular-granulose; staminodes 1.5–1.8 mm long, the staminodial tube 0.9–1.1 mm long, elobate, the filaments 0.2–0.4 mm long, narrowly triangular, or ovate-triangular, dorsally recurved, 0.5–0.8 mm long, 0.3–0.4 mm wide, apex apiculate, the tip dorsally recurved, cordate basally, the connective merely darkened; pistil pyriform, 1.4–1.6 mm long, the ovary 0.7–0.8 mm long, 1.0 mm diam., the style 0.7–0.8 mm long, the stigma capitate, 2-lobed, the placenta cotyliform, the ovules 2, naked. Fruit 0.5–0.6 cm long, 0.4–0.7 cm diam., exocarp thin to moderately thick, black, inconspicuously pellucid punctate.

Distribution. Venezuela and Brazil (Amazonas and Pará), at altitudes of 80 to 1,000 m. It is assumed that the type (*Schomburgk 975*) was collected in Venezuela rather than Guyana. Steyermark (1981) discussed the fact that the Schomburgk collections were probably Venezuelan.

Ecology. Subspecies *guyanensis* is restricted to inundated black water forests (igapó) in lowland Amazonia on white sands. It is apparently infrequent and is known from only 11 gatherings. Label data indicate that it grows on the banks of smaller streams and is shade tolerant.

Representative specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Río Negro, lower part of Río Baría, 80 m, 22–23 July 1984 (fr), *Davidse 27605* (MO, NY, VEN); Río Baría, near Río Marawinuma, 9 May 1984 (fr), *Thomas et al. 3450* (NY, US, VEN), (fr), *3412* (NY, US, VEN); upper Río Baría, 9 May 1984 (fr), *Gentry & Stein 47291* (MO, NY, US, VEN). BRAZIL. AMAZONAS: vic. Barra, Apr. 1851 (pist. fl, fr), *Spruce 1150* (F, K, LD), (stam. fl), *Spruce s.n.* (F, LD, M); 10 km upstream from jct. of Rios Cuieiras and Branquinho, 7 Apr. 1974 (stam. fl), *Campbell et al. P21936* (A, C, F, INPA, K, MICH, MO, NY, P, US).

Subspecies *guyanensis* may be distinguished from subspecies *multipunctatus* by the longer petioles (1.0–)1.5–2(–2.3) cm long, the corolla chartaceous (not membranaceous), with tube 0.8–1 (not 0.6–0.7) mm long, the lobes glandular-granulose within and along margins (not glabrous), 1.6–1.7 (not 1.2–1.6) mm long, 0.9–1.0 (not 0.6–0.8) mm wide, apically free filaments shorter than (not longer than) the anthers, and narrowly triangular (not ovate) anthers.

The type specimen of *Conomorpha heterantha* is pistillate, and therefore has shorter pedicels, stamens much shorter than the petals, and a broadly conic ovary. The feature that gave rise to the specific epithet, the heteromerous perianth, occurs frequently within the genus and is not constant among the specimens examined.

14b. Cybianthus guyanensis (A. DC.) Miquel in Martius subsp. **multipunctatus** (A. DC.) Pipoly, comb. et stat. nov. *Cybianthus multipunctatus* A. DC., Ann. Sci. Nat. 2 ser. 16: 94. 1841. *Conomorpha multipunctata* (A. DC.) Miquel, Stirp. Surinam. Select. 111. t. 34. 1850. TYPE: French Guiana. Cayenne, *Martin s.n.* (holotype, P not seen). Figure 14.

Shrub or small tree to 8 m tall; branchlets terete, 2–3 mm diam., densely lepidote. Leaves narrowly obovate to narrowly elliptic, asymmetric, chartaceous, or rarely membranaceous, 8–12(–15) cm long, 2.0–3.5(–6) cm wide, apex acuminate to abruptly acuminate, the acumen 0.5–1 cm long, nerves 15–30 pairs; petioles canaliculate, 0.5–1.0 cm long, densely lepidote. *Staminate inflorescence:* a raceme or rarely a subsessile pseudoverticel of 2–3 racemes, 2.5–5.0 cm long; peduncle 0.1–0.2 cm long; floral bracts ovate-triangular, 0.6–1.2 mm long, 0.3–0.4 mm wide, apex acute; pedicels (0.3–)0.5–1.0 mm long. Flowers 4-merous; calyx cotyliform, chartaceous, 0.9–1.0 mm long, the tube 0.2–0.3 mm long, the lobes ovate-triangular, 0.7–0.8 mm long, 0.5–0.7 mm wide, apex attenuate to a rounded tip, prominently brown or black punctate; corolla membranaceous, 2.0–2.5 mm long, the tube 0.6–0.7 mm long, the lobes reflexed-recurved, ovate-triangular, 1.2–1.6 mm long, 0.6–0.8 mm wide, apex acute to attenuate, dehiscent by wide, sublatrorse slits, conspicuously brown punctate, the punctations few, glabrous externally and internally; stamens 1.1–1.4 mm long, the staminal tube 0.6–0.8 mm long, the filaments 0.6–0.9 mm long, the anthers ovate, 0.5–0.7 mm long, 0.3–0.4 mm wide, attenuate to an acute tip at apex, the connective brown punctate, inconspicuous; pistillode lageniform, 0.9–1.0 mm long. *Pistillate inflorescence:* a raceme 2.5–5.0 cm long; peduncle 0.1–0.2 cm long; floral bracts ovate-triangular, 0.6–1.2 mm long, 0.3–0.4 mm wide; pedicels (0.3–)0.5–1.0 mm long. Flowers 4-merous; calyx cotyliform, 0.8–0.9 mm long, the tube 0.1–0.2 mm long, the lobes ovate-triangular, 0.6–0.7 mm long, 0.5–0.7 mm wide, apex attenuate to a rounded tip, prominently brown or black punctate; corolla membranaceous, 1.8–1.9 mm long, the tube 0.5–0.8 mm long, the lobes reflexed-recurved, ovate-triangular, 1.0–1.4 mm long, 0.6–0.8 mm wide, apex acute to attenuate, conspicuously brown punctate, the punctations few, glabrous externally and internally; staminodes 0.9–1.0 mm long, the staminal tube 0.2–0.3 mm long, the filaments 0.7–0.8 mm long, the anthers ovate, 0.4–0.5 mm long, 0.3–0.4 mm wide, attenuate to an acute tip at apex, pistil pyriform, 1.4–1.5 mm long, the ovary ca. 0.8 mm long, the style not well differentiated, the stigma capitate, 2-lobed, the placenta cotyliform, the ovules 2, naked. Fruit 0.5–0.6 cm long, 0.4–0.5 cm diam., the exocarp thick, black, inconspicuously pellucid-punctate.

Distribution. Venezuela (Bolívar), Guyana, Surinam and French Guiana, Brazil (Pará), 25–1,000 m elevation.

Ecology. Subspecies *multipunctatus* is found on lateritic and sandstone formations in the Guianas and eastern Venezuela. In Brazil, it has been collected on Serra do Cachimbo (*Prance et al. P24999*), a sandstone mountain that is known to contain a number of tepui elements, such as *Cybianthus spicatus* (HBK) Agostini, *C. fulvopulverulentus* subsp. *magnoliifolius* (Mez) Pipoly, *Clusia sessilis* Klotzch ex Engler, and *Clusia melchiori* Gleason.

Specimens examined. VENEZUELA. BOLIVAR: Morichal, 2 km E of Río Orinoco between Río Horeda and Cerro Gavilan (Cerro Carichana), 100 m, 17 Dec. 1955 (fr), *Wurdack & Monachino 39940* (F, MO, NY, US). GUYANA. UPPER DEMARARA: Mabura Hill, 100–200 m, 16 Sep. 1986 (ster.), *Pipoly & Boyan 8515* (BRG, FDG, NY, US); Moraballi Creek, Essequibo River, 30 Nov. 1938 (fr), *Davis 2764* (BM, FDG, K, NY, P, S, U), (stam. fl), *Forest Dept. Brit. Guiana D601-2764* (BM, FDG, K, NY, U); Eagle Mt., 500–700 m, 27 Jan. 1943 (pist. fl), *Forest Dept. Brit. Guiana F1158-3894* (FDG, K, NY); Kaieteur Plateau, 1 May 1944 (fr), *Maguire & Fanshawe 23122* (F, FDG, G, GH, IAN, NY, S, US, VEN), vic. Kaieteur Falls, and along W rim of Potaro Gorge, 450 m, 14 Feb. 1962 (pist. fl), *Cowan & Soderstrom 1860* (F, FDG, NY, US), forest along trail from airstrip to Kaieteur Falls, 450 m, 27 Feb. 1962 (pist. fl), *Cowan & Soderstrom 1988* (F, FDG, K, NY, US); 65 mi., Bartica–Potaro Rd., 28 Nov. 1947 (fr), *Forest Dept. Brit. Guiana F2790-5589* (FDG, K, NY, U), 10 mi., 14 Mar. 1948 (stam. fl), *Forest Dept. Brit. Guiana F2803-5602* (FDG, K, NY, RB, U, VEN); Upper Mazaruni River, 22 Sep. 1922 (fr), *De La Cruz 2045*, (fr), *2168* (CM, F, FDG, GH, MO, NY), Kamakusa, 15 Dec. 1922 (pist. fl), *Lang & Persaud 374* (BFG, F, FDG, K, NY), Coomaka, Nov. 1924 (fr), *Persaud 199* (F, FDG, K, NY), Makreba Falls, Kurupung River, 25 Feb. 1939 (stam. fl), *Pinkus 252* (BR, DUKE, G, GH, M, MO, RB, S, VEN), Mt. Ayanganna, 762 m, 3 Aug. 1960 (fr), *Tillett et al. 45017* (F, NY, P, S, U, VEN); Upper Rupununi River, near Dadanawa, without date (fr), *De La Cruz 1706* (CM, F, FDG, GH, MO, NY); without locality, *Appun 836* (K); without locality, Dec. 1890 (stam. fl), *Jenman 6220* (BRG, K). SURINAM. Hendriktop, 1,080 m, 14 Mar. 1922 (fr), *Boschwezen Surinam 5662* (BBS, U); ad fl. Carouany, Feb. 1844 (stam. fl), *Kappler 1729* (BM, P, S, U, W); in mountains called Nassau, 2 Mar. 1949 (stam. fl), *Lanjouw & Lindeman 2661* (BBS, NY, U), Nassaugbergette, line 13, 550 m, 5 Jan. 1955 (fr), *Lindeman & Cowan 7000* (BBS, U), along Marwoijne River, 400–550 m, 14 Mar. 1955 (fr), *Maguire et al. 40805* (BBS, NY, US, VEN). FRENCH GUIANA. Karouany, 1857 (stam. fl), *Sagot 1031* (BM, G, K, P, S, W); Montagne de Kaw, 275 m, 11 Dec. 1954 (fr), *Cowan 38722* (CAY, NY, U, US, VEN); Montagnes de la Trinité, sommet Nord, 350 m, 10 Jan. 1984 (stam. fl), *de Granville et al. 5813* (BR, CAY, G, MG, NY, U, US), Inselberg NW, 450 m, 17 Jan. 1984 (stam. fl), *de Granville et al. 5899* (CAY, NY, U), (stam. fl), *6087* (BR, CAY, G, NY, P, U); Montagnes Bellevue de l'Inini, 650 m, 15 Aug. 1985 (fr), *de Granville et al. 7511*, *7521* (B, BR, CAY, MG, MO, NY, P, U); Zone centrale, 600 m, 29 Aug. 1985 (fr), *de Granville et al. 7834* (B, BM, BR, CAY, F, G, GOET, INPA, MG, MO, NY, P, U); Saül, 220 m, 22 June 1988 (ster.), *Gentry et al. 63081* (CAY, MO, NY), La Fumée Mt., Antenne Est, 300 m, 18 May 1986 (fr), *Mori & Pennington 18050* (CAY, MO, NY). BRAZIL. PARA: Serra do Cachimbo, BR 163, Cuiabá–Santarém Hwy., km 823, 570 m, 7 Nov. 1977 (stam. fl), *Prance et al. 24999* (F, INPA, MG, NY, RB, US).

Subspecies *multipunctatus* may be distinguished from subspecies *guyanensis* by the filaments 0.7–0.8 (not 0.2–0.4) mm long, the corolla glabrous (not densely glandular-granulose within), and the petioles 0.5–1.0 (not 1.0–2.3) cm long. It is restricted to the Guianas, the easternmost portion of Guayana, and the Serra do Cachimbo.

15. Cybianthus roraimae (Steyermark) Agostini, Acta Biol. Venez. 10: 155. 1980. *Conomorpha roraimae* Steyermark, Fieldiana, Bot. 28(3): 468. 1953. TYPE: Venezuela. Bolívar: Mt. Roraima, ledge along SW-facing side, from bluffs to summit, 2,255–2,620 m, 27 Sep. 1944 (pist. fl), *Steyermark 58759* (holotype, F; isotype, NY). Figure 15.

Shrub or small tree to 5 m tall, the bark reddish brown; branchlets terete, 3.5–4(–4.5) mm diam.,

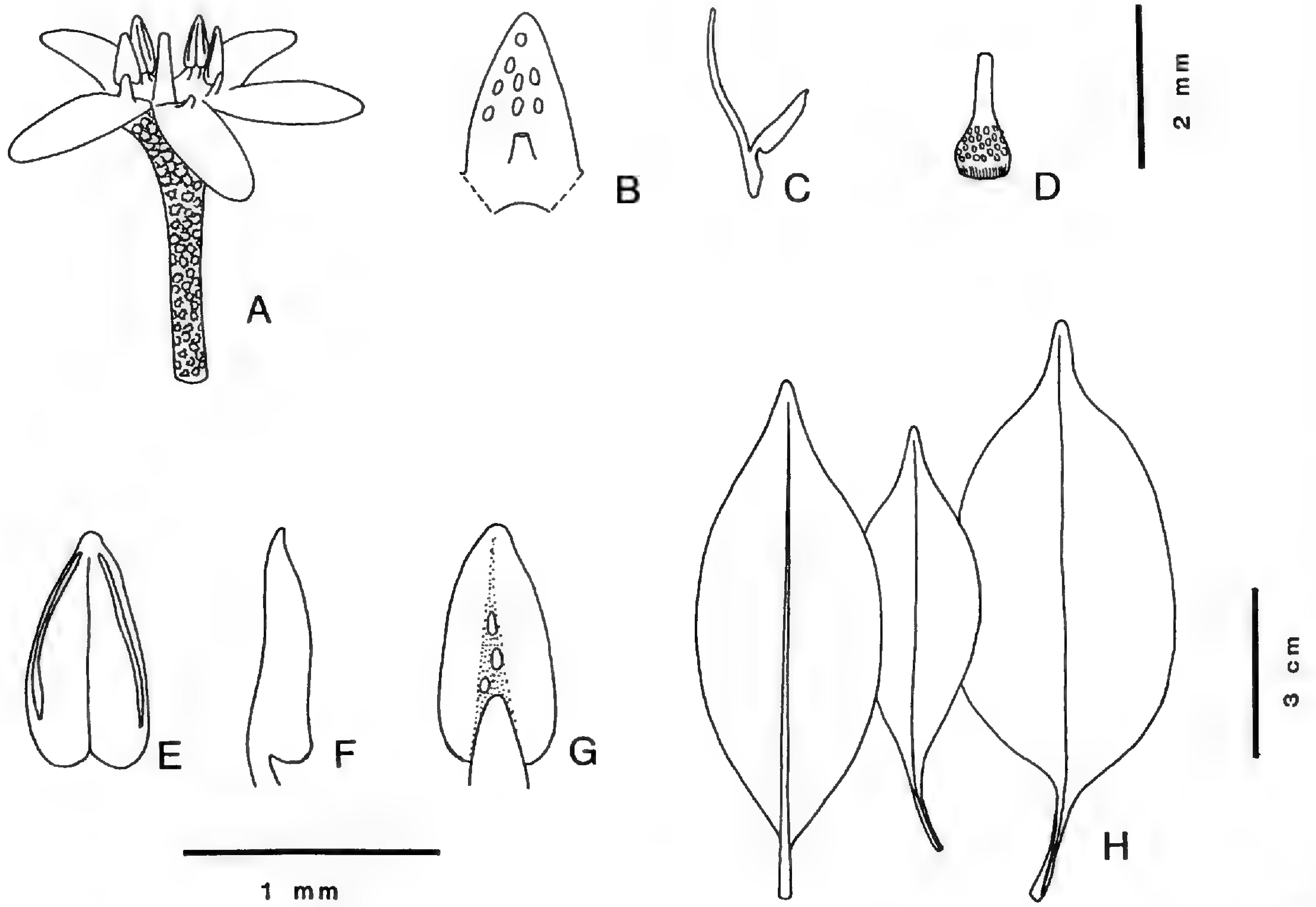


FIGURE 15. *Cybianthus roraimae* (Steyermark) Agostini.—A. Staminate flower.—B. Staminate corolla lobe, ventral view, showing pellucid punctations.—C. Staminate corolla lobe, lateral view showing anther habit.—D. Pistillode.—E. Anther, ventral view.—F. Anther, lateral view.—G. Anther, dorsal view showing darkened connective and pellucid punctations.—H. Leaves. (A–D, from *Maguire 33464*; E–G, from *Wurdack 34259*; H, left to right, from *Maguire 33464, Wurdack 34270,* and *Steyermark 58765.*)

densely lepidote. Leaves elliptic, coriaceous, 7–11 cm long, 2.5–4.5 cm wide, apex acuminate, the acumen 1.0–1.5 cm long, base rounded to obtuse, decurrent on the petiole, the midrib depressed above, prominently raised below, the nerves 26–30 pairs, conspicuous above and below, the upper surface pustulate, the lower surface densely lepidote, inconspicuously pellucid-punctate, the margin entire, epunctate, revolute; petioles marginate, 2–3 cm long, densely lepidote. *Staminate inflorescence:* a raceme, rarely a subsessile pseudoverticel of 2–3 racemes, 5–8 cm long; peduncle, axis, branches, and pedicels densely lepidote; peduncle 0.5–2.5 cm long; floral bracts ovate to broadly ovate, 0.5–1.0 mm long, 0.5–0.8 mm wide, apex acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, 2.0–3.5 mm long. Flowers nodding, (4–)5-merous, 2.1–2.4 mm long; calyx shallowly cotyliform, carnose, 0.7–0.9 mm long, the tube 0.3–0.4 mm long, the lobes deltate to subdeltate, 0.5–0.7 mm long, 0.5–0.8 mm wide, the apex rounded or attenuate to a rounded tip, epunctate or with a few, inconspicuous pellucid punctations, densely lepidote externally, the margin entire, lepidote; corolla rotate, membranaceous, 2.0–2.3 mm long, the tube 0.3–0.4 mm long, the lobes ovate, highly reflexed (perpendicular to the tube) in anthesis, apex attenuate to a rounded tip, glabrous without and within, the punctations pale brown or yellow, inconspicuous, the margin entire, glabrous; stamens 1.7–1.8 mm long, the staminal tube inconspicuous, hyaline, elobate, 0.4–0.6 mm long, the filaments flat, 0.3–0.4 mm long, epunctate, glabrous, the anthers dorsifixed near the base, ovate-triangular, 0.8–1.0 mm long, 0.4–0.6 mm wide, attenuate to an apiculate tip, the apiculum erect, slightly recurved dorsally, the connective dorsally brown or yellow punctate, the punctations not prominent; pistillode lageniform, 1.2–1.5 mm long, the base glandular lepidote with dark scales. *Pistillate inflorescence:* a raceme, rarely 2 racemes from a common peduncle, 5–8 cm long; peduncle, axis, branches, and pedicels densely lepidote; peduncle 0.5–2.5 cm long; floral bracts ovate to broadly ovate, 0.5–1.0 mm long, 0.5–0.8 mm wide, apex acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, erect, 2.0–3.5 mm long. Flowers (4–)5-merous, 2.1–2.4 mm long; calyx shallowly cotyliform, carnose, 1.0–1.1 mm long, the tube 0.2–0.3 mm long, the lobes very widely ovate, 0.8–0.9 mm long, 1.1–1.3 mm wide, the apex rounded or attenuate to a rounded tip, epunctate or with a few, inconspicuous pellucid punctations, densely lepidote externally, the margin entire, lepidote; corolla not seen. Fruit globose, wine-purple, 0.5–0.6 cm long, 0.4–0.5 cm diam. when dried.

Distribution. Endemic to the Auyán-tepui-Chimantá Complex (sensu Maguire, 1979), from 1,140 m to 2,600 m.

Ecology. *Cybianthus roraimae* occurs in cloud forests on talus slopes. Only a few of the fruiting collections also bear pistillate flowers, implying that the latter are ephemeral in this species, as they are in others of subgenus *Conomorpha* and throughout subgenus *Laxiflorus* (Pipoly, 1983a).

Specimens examined. VENEZUELA. BOLIVAR: Mt. Roraima, ledge along SW-facing side, 2,250–2,620 m, 27 Sep. 1944 (fr), *Steyermark 58765* (NY), 2,000 m, Dec. 1909 (fr), *Ule 8724* (L, K); Ilú-tepui, W-facing slopes, 2,100–2,400 m, 17 Mar. 1952 (fr), *Maguire 33464* (GH, NY, VEN), 21 Mar. 1952 (pist. fl, fr), *33504* (NY); NW slopes of Churi-tepui (Muru-tepui), 2,050 m, 29 Jan. 1953 (stam. fl), *Wurdack 34259* (K, NY, US, VEN), 30 Jan. 1953 (fr), *34270* (F, K, NY, US, VEN).

Cybianthus roraimae is unique within the genus in its purple flowers and rotate corollas. The densely lepidote pedicels and calyx lobes are reminiscent of *C. crotonoides*, which is easily separated by its overlapping (not merely adjacent) scales on the abaxial corolla surface and the longer calyx and corolla. In sterile condition, it may be confused with *C. cardonae*, *C. punctatus*, or *C. lepidotus*. Differences with those species are discussed under *C. cardonae*.

16. **Cybianthus breweri** Agostini, Bol. Soc. Venez. Ci. Nat. 22: 384. 1976. TYPE: Venezuela. Bolívar: Meseta de Jaua, Cerro Guanacoco, summit, 1,450 m, 3 Mar. 1974 (stam. fl), *Steyermark et al. 109754* (holotype, VEN).

Shrub or small tree to 3 m tall; branchlets terete, 3.5–5 mm diam., densely lepidote, glabrescent. Leaves obovate-spathulate to narrowly obovate-spathulate, coriaceous, 4–5 cm long, 1.5–2 cm wide, apically obtuse to rounded, at times abruptly short-acuminate, the acumen to 0.4 cm, base cuneate, pustulate above, sparsely lepidote below, midrib somewhat depressed above, prominently raised below, nerves inconspicuous above and below, inconspicuously pellucid punctate, the margin entire, epunctate, revolute; petioles canaliculate, 0.4–0.6 cm long, sparsely lepidote. *Staminate inflorescence:* a raceme 1–3 cm long, 8–16-flowered; peduncle 0.2–0.4 cm long; floral bracts deltate, carnose, 1.5 mm long and wide, apex acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, 2.0–3.0 mm long, erect. Flowers 4–5-merous; calyx cupuliform, carnose, 0.7–1.0 mm long, the tube 0.2–0.3 mm long, the lobes deltate to subdeltate, 0.5–0.7 mm long, 0.5–0.7 mm wide, apex acute, densely and prominently orange punctate, the margin entire, glabrous; corolla campanulate, ca. 2 mm long, the lobes sparsely lepidote without, densely glandular-granulose within; stamens ca. 1.5 mm long, the tube prominent, carnose, ca. 0.3 mm long, lobate, the lobes ca. 0.1 mm long, the anthers ovate-triangular, ca. 1.0–1.2 mm long, 0.5–0.6 mm wide, apex acute, base cordate, recurved distally, prominently punctate dorsally; pistillode conic, ca. 2.3 mm long, densely glandular-lepidote. *Pistillate inflorescence:* a raceme 1–3 cm long, 5–12-flowered; peduncle 0.2–0.4 cm long; floral bracts carnose, deltate, 1.5–1.6 mm long and wide, apex acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, 2.5–3.0 mm long, erect. Flowers 4–5-merous; calyx cupuliform, carnose, 0.7–1.0 mm long, the tube 0.2–0.3 mm long, the lobes deltate to subdeltate, 0.5–0.7 mm long, 0.5–0.7 mm wide, apex acute, densely and prominently orange punctate, the margin entire, glabrous; corolla not seen. Fruit depressed-globose, 0.7–0.8 cm diam., the exocarp thin, conspicuously pellucid–punctate.

Distribution. Endemic to the Meseta de Jaua, 1,400–2,100 m.

Ecology. *Cybianthus breweri* occurs in gallery forests and thickets at the margins of savannas.

Specimens examined. VENEZUELA. BOLIVAR: Meseta de Jaua, Cerro Jaua, summit, 1,922–2,100 m, 22–27 Mar. 1967 (fr), *Steyermark 97931* (VEN), 1,750–1,800 m, 22–28 Feb. 1974 (fr), *Steyermark et al. 109296, 109393, 109660* (VEN), 1,850–1,920 m, 4 Mar. 1974 (fr), *Steyermark et al. 109820* (VEN); Meseta de Jaua, Cerro Sarisariñama, 1,400 m, 16–18 Feb. 1974 (fr), *Steyermark et al. 109162* (VEN).

Cybianthus breweri may be distinguished by its coriaceous, obovate-spathulate leaves with inconspicuous secondary veins, and deltate calyx lobes with orange punctations.

17. **Cybianthus apiculatus** (Steyermark) Agostini, Acta Biol. Venez. 10: 168. 1980. *Conomorpha apiculata* Steyermark, Fieldiana, Bot.

28(3): 456. 1953. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Duida, SE-facing slopes along Caño Negro (tributary of Caño Iguapo), 305–1,095 m, 25–26 Aug. 1944 (fr), *Steyermark 57986* (holotype, F; isotypes, NY, VEN).

Shrub or small tree, to 3 m tall; branchlets thin, terete, 2–3 mm diam., densely lepidote at first, the scales not appressed, early glabrescent. Leaves membranaceous, translucent, elliptic to narrowly oblanceolate, asymmetric, (8–)10–17.5(–20) cm long, (2.0–)3–4(–5.9) cm wide, apically acuminate, the acumen (0.8–)1.5–1.9(–2.2) cm long, basally acuminate to acuminate-attenuate, decurrent on the petiole, nitid, smooth and glabrous above, pallid and densely orange lepidote below, the midrib depressed above, prominently raised below, lateral nerves 12–15, prominent above and below, the margin irregular, subrevolute at first, then flat at maturity, prominently punctate-lineate; petioles thin, marginate, and deeply canaliculate, (1–)1.3–1.7(–2.3) cm long. Prophylls 2, often persistent, chartaceous, elliptic, (1–)1.3–1.5(–2) cm long, 0.5–0.6 cm wide, apex acute, base acute, decurrent on the petiole; petiole thin, marginate, and deeply canaliculate, 0.2–0.4 cm long. *Staminate inflorescence:* a raceme, (0.6–)1.5–4.5(–6.2) cm long, lax, the rachis glandular-papillate and lepidote; floral bracts deltate, 0.8–1.1 mm long and wide, apex subulate, densely lepidote; pedicels terete, thin, 0.6–1.0 mm long, basally lepidote and glandular-papillate. Flowers 4–6-merous; calyx membranaceous, cotyliform, 1.3–1.5 mm long, unequally divided, translucent, the tube 0.3–0.4 mm long, the lobes hyaline, ovate to widely ovate, 0.9–1.2 mm long, 0.7–1.3 mm wide, apex acute, densely and prominently black punctate within and without, glabrous without, with a few glandular papillae at base within, lepidote scales absent, the margin erose, glandular-ciliate; corolla subrotate, chartaceous, translucent, 2.8–3.0 mm long, the tube 0.9–1.1 mm long, the lobes suborbicular to very broadly ovate, 1.8–2.2 mm long and wide, apex rounded, cucullate, glabrous without, densely glandular-granulose within except for a small (0.1 mm) marginal zone, densely and prominently black punctate and punctate-lineate, the margin entire, glabrous; stamens 2.6–3.0 mm long, the tube carnose, costate, 0.9–1.1 mm long, densely rufous glandular-granulose, without lobes, the apically free portion of the filaments terete, 0.6–1.2 mm long, ventrally recurved, the anthers ovate to widely ovate, 0.9–1.2 mm long, 0.6–0.8 mm wide, apex acute to rounded, the base cordulate, dorsally recurved, dorsifixed just above the base, slits very wide, glandular-papillate dorsally, the connective prominently black punctate; pistillode absent. *Pistillate inflorescence:* a simple raceme 2.0–4.5 cm long, erect; floral bracts linear-subulate, membranaceous, 0.6–0.8 mm long, 0.2–0.3 mm wide, apically attenuate, the margin entire, glabrous; pedicels terete, in fruit 1.2–2.3 mm long, incrassate. Flowers 4–5-merous; fruiting calyx subcotyliform, 1.1–1.3 mm long, the tube 0.2–0.3 mm long, the lobes deltate to subdeltate, 0.9–1.3 mm long, 0.9–1.2 mm wide, apex rounded, medially and dorsally thickened, the margin erose, glandular-ciliolate; corolla not seen; pistil pyriform, basally lepidote, persistent stigma capitate. Fruit ovoid, (0.5–)0.6–1.0 cm long, (0.3–)0.4–0.7 cm wide, the exocarp thin, rugulose, prominently black punctate.

Distribution. *Cybianthus apiculatus* is currently known only from the southernmost region of Territorio Federal Amazonas in Venezuela, including Cerros Neblina, Duida, and Marahuaca, and also from Mt. Ayanganna in Guyana.

Ecology. *Cybianthus apiculatus* occurs in mixed evergreen moist forest on talus slopes, where various species of *Dicymbe*, *Eperua*, and other legume species dominate. It specifically grows along the banks of black water streams in somewhat open, exposed areas, and has relatively few individuals per hectare, based on my observations in Guyana.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atabapo, slopes of Mt. Duida, 1,000 m, Aug. 1928–Apr. 1929 (fr), *Tate 901* (NY, US); Cerro Marahuaca, SE-facing slopes, headwaters of Río Iguapo, S section of SE range, 1,560 m, 13–14 Oct. 1983 (stam. fl), *Steyermark 129612* (MO, VEN), (stam. fl), *129683* (CAS, MO, NY, VEN), below Salto Los Monos, on tributary of headwaters of Río Iguapo, 1,500–1,600 m, 20 Oct. 1988 (stam. fl), *Liesner 25121* (MO, US, VEN); Sima Camp, S-central portion along branch of Caño Negro, 21–22 Feb. 1985 (stam. fl), *Steyermark & Holst 130492* (MO, NY, US, VEN), upper Río Yameduaka, 1,225 m, 17–18 Feb. 1985 (pist. fl), *Liesner 17606* (MO, US, VEN), (fr), *17819* (MO, US, VEN); Depto. Río Negro, Cerro de la Neblina, trail S from Camp V, 1,200–1,300 m, 12 Apr. 1984 (fr), *Gentry & Stein 46557* (MO, NY, VEN), Camp V, valley at N base of Pico Cardona, 1,250 m, 21–24 Mar. 1984 (stam. fl), *Liesner & Stannard 16896* (MO, NY, VEN), between Camps II and IV, 8 Nov. 1957 (fr), *Maguire et al. 42000* (F, NY—2 sheets, US, VEN), GUYANA. CUYUNI-MAZARUNI REGION VIII, MAZARUNI SUBREGION VIII-2: Ayanganna Plateau, 2 km W of base camp in Koatse River Valley, 3 Mar. 1987 (ster.), *Pipoly et al. 10940* (CAY, FDG, NY, US), (fr), *11000* (FDG, NY, US), Mt. Ayanganna, along base, NE side, 800–900 m, 1 Aug. 1960 (stam. fl), *Tillett et al. 44959* (F, FDG, NY, US, VEN).

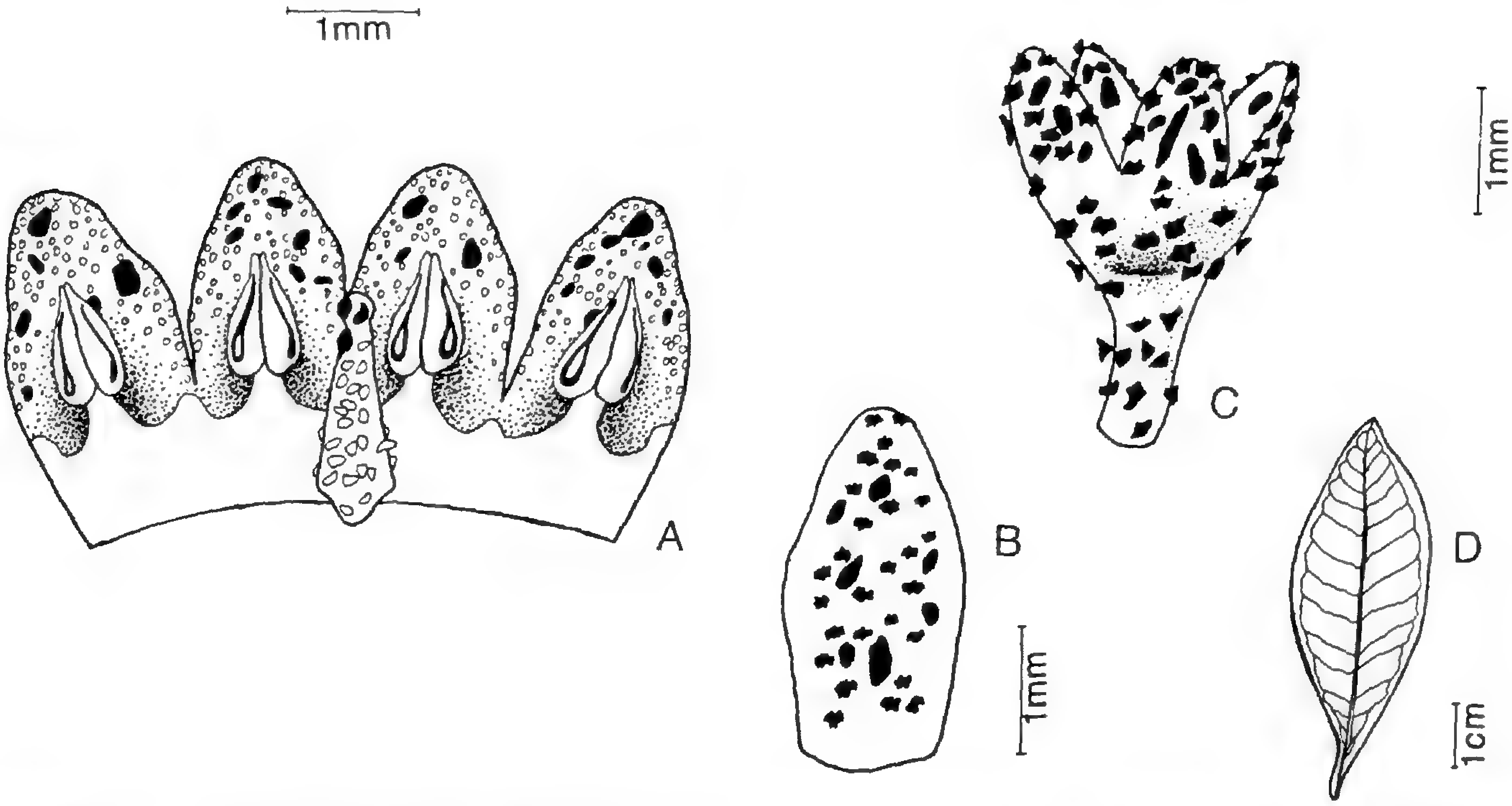


FIGURE 16. *Cybianthus agostinianus* Pipoly.—A. Opened staminate flower, showing prominent punctations, glandular granules, lobate staminal tube, and pistillode.—B. Staminate corolla lobe, dorsal view, showing lepidote scales and punctations.—C. Staminate calyx.—D. Leaf. (From holotype.)

Agostini (1980) placed *Cybianthus apiculatus* in subgenus *Cybianthus* on the basis of fruiting specimens available to him from Steyermark collections. In fruit, the simple raceme, with glandular-papillate rachis and subcotyliform calyx, indicated placement in that group. On the other hand, Agostini (1971) placed the Guyana populations (based on *Tillett et al. 4459*) in a new section, "Intermedius," on the basis of the lepidote branches and calyx with erose, glandular-ciliate margins.

Close examination revealed no qualitative differences between the Venezuelan and Guyanese collections. This species is here transferred to subgenus *Conomorpha* because the lepidote scales that define the subgenus are found on its branches. The anther morphology is entirely consistent with subgenus *Conomorpha* rather than *Cybianthus*, because the anthers are distally recurved (not erect), dorsifixed (not basifixed), and longitudinally (not poricidally) dehiscent. Because the erose and glandular-ciliate calyx lobe margin is a plesiomorphic character state (Pipoly, 1987), and the lepidote scales are homologous to those found in the rest of the subgenus, it is more parsimonious to hypothesize one reversal than to define a new infrageneric taxon on the basis of a homoplasy.

18. **Cybianthus agostinianus** Pipoly, Ernstia 50: 33. 1988. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Huachamacari, vic. summit camp, 1,800 m, 10 Dec. 1950 (fr), *Maguire et al. 30006* (holotype, VEN; isotypes, F, LL, NY, US). Figure 16.

Shrub or small tree to 4 m tall; branchlets, petioles, inflorescence rachis, and pedicels densely ferrugineous lepidote; branchlets terete, 3–4 mm diam. Leaves narrowly elliptic, elliptic, or rarely elliptic-obovate, chartaceous to coriaceous, 4.6–11.5 cm long, 2–3 cm wide, apically rounded to acute, basally acute, midrib depressed above, prominently raised below, nerves 15–40 pairs, somewhat conspicuous above and below, minutely pustulate above, sparsely to densely lepidote below, the margin flat, entire, epunctate, revolute; petioles canaliculate, 0.5–1.1 cm long, moderately lepidote. *Staminate inflorescence:* a simple, erect raceme, 1.5–3 cm long, 5–12-flowered; peduncle 0.2–0.5 mm long; floral bracts ovate or elongate-triangular, 0.7–1.1 mm long, 0.3–0.5 mm wide, apex acute, the margin entire, glabrous; pedicels terete, erect, 1.5–4.5 mm long. Flowers 4-merous; calyx cotyliform, chartaceous, 1.2–1.4 mm long, the tube 0.2–0.3 mm long, the lobes triangular or deltate, 1.0–1.1 mm long, 0.8–1.1 mm wide, apex acute, prominently black punctate, sparsely lepidote without, the margin irregularly dentate or undulate, glabrous; corolla campanulate, membranaceous, 2.6–2.8 mm long, the tube 0.6–0.7 mm long, the lobes elliptic, 1.9–2.0 mm long, 1.3–1.4 mm wide, erect, apex flat, rounded, prominently black punctate, sparsely lepidote without, sparsely glandular-granulose within, the margin flat, entire, hyaline, glandular-ciliate; staminal tube prominent, terete, chartaceous, 0.6–0.7 mm long, the lobes to 0.1 mm long, alternating with the apically free filaments; the apically free filaments ca. 0.4–0.5 mm long, prominently brown punctate, the anthers deltate, 0.8–0.9 mm long and wide, apex acute, dorsifixed ca. ⅓ from the base, distally recurved, prominently brown punctate dorsally; pistillode clavate, 1.4–1.6 mm long, 0.4 mm diam., prominently black punctate, densely translucent lepidote. *Pistillate inflorescence:* a simple, erect raceme, 1.5–3 cm long, 5–9-flowered; peduncle 0.2–0.5 mm long; floral bracts ovate or elongate-triangular, 0.9–1.3 mm long, 0.3–0.5 mm wide, apex acute, the margin entire, glabrous; pedicels terete, erect, 1.5–4.5 mm long. Flowers 4-merous; calyx cotyliform, chartaceous, 1.2–1.4 mm long, the tube 0.2–0.3 mm long, the lobes triangular or deltate, 0.9–1.2 mm long, 0.8–1.1 mm wide, apex acute, prominently black punctate, sparsely lepidote without, the margin irregularly dentate or undulate, glabrous; corolla not seen. Fruit subglobose, 3.0–3.5 mm diam., the exocarp moderately thick, inconspicuously pellucid punctate.

Distribution. Endemic to Cerros Duida and Huachamacari at 1,700–2,660 m.

Ecology. Cybianthus agostinianus grows in rocky, open areas where strong winds produce xeric effects. Label data imply that the species is locally common between rocks on the summits of Marahuaca and Huachamacari.

Specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atabapo, Cerro Huachamacari, elfin forest, vic. summit camp, 1,800 m, 10 Dec. 1950 (fr), *Maguire et al. 30102, 30103* (NY, VEN), summit, SW side of center, 2,660 m, 23 Oct. 1988 (stam. fl), *Liesner 25276* (MO, VEN), SE slopes, below Salto Los Monos on tributary of headwaters of Río Iguapo, 1,500–1,600 m, 20 Oct. 1988 (fr), *Liesner 25108* (MO, VEN), slopes, "sima area," 1,200 m, 16 Oct. 1988 (fr), *Liesner 24941* (MO, VEN); Cerro Duida, summit, 1,700–1,900 m, 1 Sep. 1944 (fr), *Steyermark 58153* (F, NY, US), (stam. fl), *Steyermark 59164* (F, NY, US), summit, slopes of Ridge 25, 26 Nov.–16 Dec. 1928 (fr) *Tate 435, 874* (NY).

Cybianthus agostinianus is unique within the subgenus for the prominently black punctate calyx and corolla. It is named in honor of the late Getulio Agostini, formerly of the Universidad Central de Venezuela, perceptive student of the genus, who suggested I take up a revision of the group.

19. Cybianthus spathulifolius Agostini ex Pipoly, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Cerro Sipapo, S and E rims, 2,000–2,200 m, 26–28 Jan. 1949 (stam. fl), *Maguire & Politi 28658* (holotype, VEN; isotypes, F, NY, S, US). Figure 17.

Ob inflorescentiam condensatamque tortuosam calycem profunde cupuliformem carnosumque, corollam carnosam et corollae lobos cucullatos atque manifeste punctatos ad *C. sipapoensem* valde affinis, sed ab ea foliis coriaceis (nec chartaceis) petiolis 0.1–0.2 (nec 1.3–1.6) cm longis secus marginem planis (nec revolutis), inflorescentia racemosa (nec spicata) pedicellis 1.0–1.5 (nec 0–0.6) mm longis, florum staminatorum calyce 1.1–1.2 (nec 1.4–1.6) mm longoque corolla 3.5–3.7 (nec 2.4–3.2) mm longa, denique corollae lobis tortuosis (nec rectis) statim recognoscitur.

Shrub or small tree; branchlets terete, 3–4 mm diam., densely lepidote. Leaves narrowly obovate-spathulate, coriaceous, 8–19 cm long, 3–7 mm wide, apex rounded to shortly acuminate, base truncate to subcuneate, decurrent on the petiole, the midrib depressed above, prominently raised below, nerves 30–60 pairs, conspicuous above and below, smooth and densely lepidote above at first, glabrescent, densely lepidote below, inconspicuously pellucid-punctate, the margin entire, epunctate, flat; petioles 0.1–0.2 cm long, densely lepidote. *Staminate inflorescence:* a tortuous axillary raceme, rarely several subsessile racemes from a common peduncle, 2–4 cm long, the peduncle, axis, and pedicels densely to sparingly lepidote; peduncle to 0.1 cm long; floral bracts depressed-ovate, carnose, 0.6–0.8 mm long, 0.7–1.0 mm wide, apex rounded to acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, 1.0–1.5 mm long, erect. Flowers 4(–5)-merous; 3.6–3.8 mm long; calyx deeply cupuliform, carnose, 1.1–1.2 mm long, the tube 0.3–0.4 mm long, the lobes deltate to subdeltate, 0.7–0.8 mm long, 0.7–0.8 mm wide, apex obtuse, rarely rounded, prominently orange punctate above, brown punctate below, the margin entire, at times lepidote; corolla tubiform, carnose, 3.5–3.7 mm long, yellowish brown; the tube 1.3–1.5 mm long, the lobes elliptic, erect, tortuous, 2.1–2.5 mm long, 1.1–1.4 mm wide, apex attenuate to a subacute to rounded tip, glabrous without, densely glandular-granulose within, prominently orange and brown punctate, the margin irregular, entire, densely glandular-granulose; stamens 3.8-3.9 mm long, the staminal tube inconspicuous, membranaceous, hyaline, 1.3–1.5 mm long, elobate, the filaments 0.1–0.3 mm long, adnate, 1.7–2.0 mm long, flat, glabrous, epunctate, the anthers narrowly triangular, 1.1–1.2 mm long, 0.3–0.4 mm wide, apex apiculate, the apiculum distally recurved, base cordate,

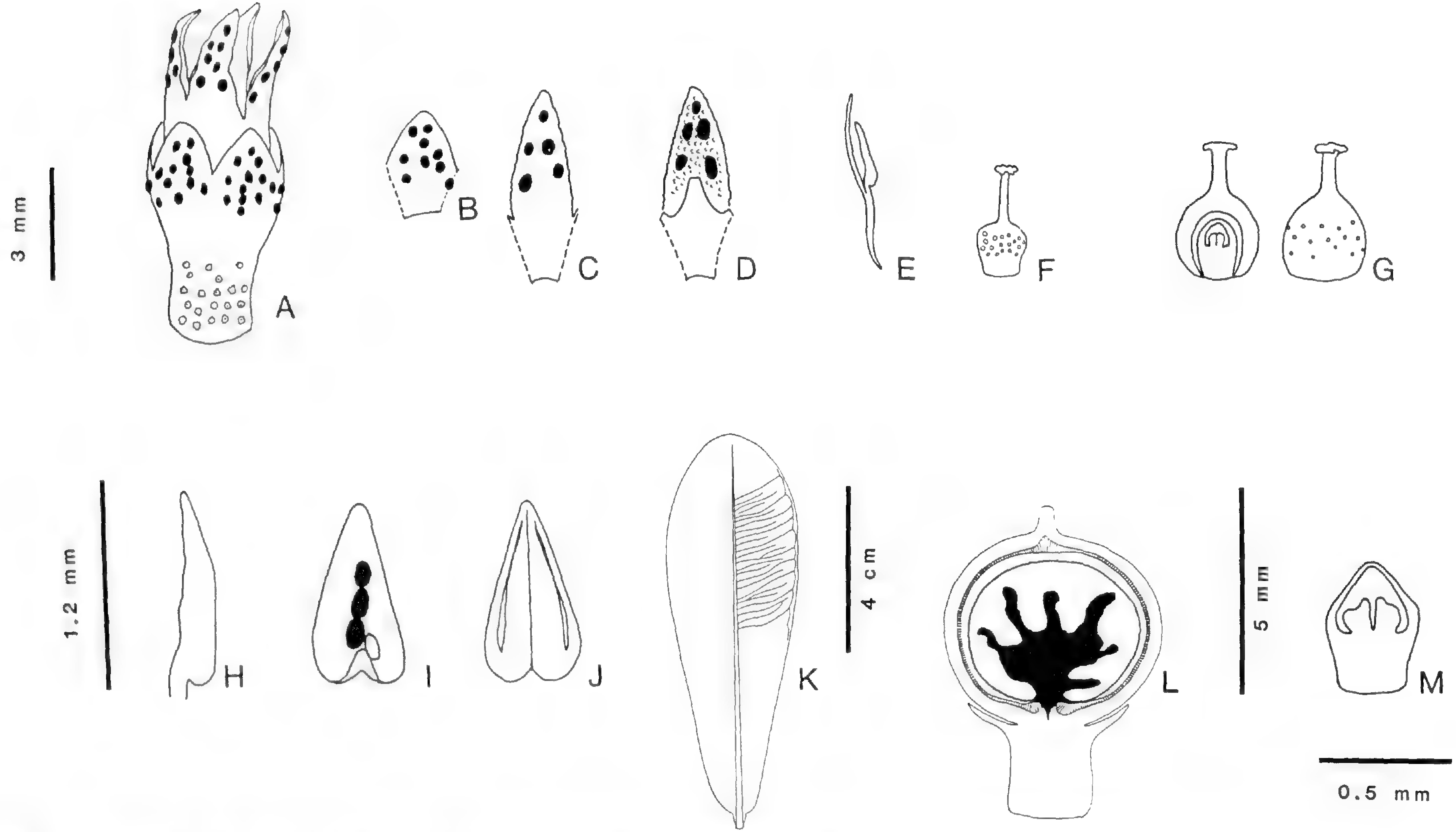


FIGURE 17. *Cybianthus spathulifolius* Agostini ex Pipoly.—A. Staminate flower.—B. Staminate calyx, ventral view, showing punctations.—C. Staminate corolla lobe, dorsal view.—D. Staminate corolla lobe, ventral view, showing punctations and glandular granules.—E. Staminate corolla lobe, lateral view.—F. Pistillode.—G. Pistil, in longisection and entire.—H. Anther, lateral view.—I. Anther, dorsal view, showing pellucid and black punctate connective.—J. Anther, ventral view.—K. Leaf.—L. Fruit longisection, showing lobed endosperm.—M. Placenta showing buried ovules. (A–E and H–K, from holotype; F, L, and M, from *Maguire & Politi 28461*.)

the connective prominently brown punctate dorsally; pistillode obnapiform, 1.4–1.5 mm long, the ovary 0.2–0.4 mm long, 0.3–0.5 mm wide, densely translucent lepidote, the style 1.0–1.2 mm long, prominently brown punctate, the style capitate, elobate. *Pistillate inflorescence:* a tortuous axillary raceme, rarely several subsessile racemes from a common peduncle, 1–3 cm long, the peduncle, axis, and pedicels densely to sparingly lepidote; peduncle to 0.1 cm long; floral bracts depressed-ovate, carnose, 0.6–0.8 mm long, 0.7–1.0 mm wide, apex rounded to acute, densely lepidote abaxially, the margin entire, glabrous; pedicels terete, 1.5–2.5 mm long, erect. Flowers 4(–5)-merous; 2.8–3.6 mm long; calyx deeply cupuliform, carnose, 1.5–1.6 mm long, the tube 0.6–0.8 mm long, the lobes ovate to elliptic, 0.8–1.0 mm long, 0.8–0.9 mm wide, apex obtuse, rarely rounded, prominently punctate, orange above, brown below, the margin entire, glabrous; corolla tubiform, carnose, 2.7–3.5 mm long, yellowish brown; the tube 0.9–1.0 mm long, the lobes elliptic, erect, tortuous, 1.7–2.0 mm long, 0.7–1.0 mm wide, apex attenuate to a rounded tip, glabrous without, densely glandular-granulose within, prominently orange and brown punctate, the margin irregular, entire, densely glandular-granulose; staminodes 0.9–1.0 mm long, the staminal tube inconspicuous, membranaceous, hyaline, 1.0–1.1 mm long, with lobes to less than 0.1 mm long alternating with the apically free filaments, the filaments 0.3–0.4 mm long, flat, glabrous, epunctate, the anthers ovate to ovate-triangular, 0.8–0.9 mm long, 0.3–0.4 mm wide, apex attenuate to a rounded tip, the tip dorsally recurved, base cordate, the connective prominently brown punctate dorsally; pistil obnapiform, 1.6–1.8 mm long, the ovary subglobose, 0.8–0.9 mm long, 0.8 mm diam., densely translucent lepidote, the style thin, 0.6–0.8 mm long, glabrous, prominently brown punctate, the stigma capitate, 2(–3)-lobed, the placenta cylindrical below, the apex obconic, the ovules 2–3, buried within. Fruit subglobose, 0.6–0.7 cm long, 0.7–0.8 cm diam., when dried.

Distribution. Endemic to Cerro Sipapo and the nearby Orinoco area, at 1,600–2,200 m.

Ecology. *Cybianthus spathulifolius* is a scrub forest species, occurring along cliffs.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro Sipapo, S Basin, 2,000–2,160 m, 26–28 Jan. 1949 (stam. fl), *Maguire & Politi 28668* (NY); Río Cuao, Río Orinoco, upper E Basin, 1,600–1,850 m, 20 Jan. 1949 (pist. fl, fr), *Maguire & Politi 28461* (NY).

Cybianthus spathulifolius appears to be closely related to the apparently sympatric *C. sipapoensis*, but may be easily distinguished by the coriaceous (not chartaceous) leaves with petioles 0.1–0.2 (not 1.3–1.6) cm long, and flat (not revolute) margins, the inflorescence racemose (not spicate), the pedicels 1.0–1.5 (not 0–0.6) mm long, the staminate calyx 1.1–1.2 (not 1.4–1.6) mm long, the staminate corolla 3.5–3.7 (not 2.4–3.2) mm long, and the lobes tortuous (not reflexed).

20. Cybianthus maguirei Agostini ex Pipoly, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Río Negro, Cerro de la Neblina, 6.5 km W of base camp, S extension of range, 0°47′N, 66°11′W, 1,600 m, 18 Apr. 1984 (pist. fl, fr), *Stein et al. 1616* (holotype, VEN; isotypes, F, K, MO, NY, US). Figure 18.

Ob inflorescentiam racemosam folia coriacea secus marginem revoluta et subter dense lepidota calycem cupuliformem tubum staminalem inconspicuum membranaceumque hyalinum corollae lobos secus marginem dense glandulari-granulosos, ad *C. crotonoideum* valde et arcte affinis, sed ab ea laminis desuper pustulatis (non scrobiculatis) atque subter squamis lepidotis adiacentis (nec marginibus ipsis superpositis) indutis, calycis lobis longioribus quam latioribus (nec latioribus quam longioribus), corolla staminata 2.7–3 (nec 2.5–2.7) mm longa, pedicello recto (non nutanti) necnon 0.4–0.6 (1–3) mm longo insidens, atque corolla pistillata 3.0–3.3 (nec 1.9–2.0) mm longa, pedicello recto (nec nutanti) necnon 0.6–1.0 (1–3) mm longo insidens, apicibus corollae staminatae pistillataeque lobis rectis (nec cucullatis) filamentis antheris brevioribus (nec longioribus) denique fructu verruculoso (nec laevi), 6–8 (nec 4.5–5) mm diametro praeclare distinguitur.

Shrub or small tree to 2 m tall; branchlets terete, 2–3 mm diam., densely appressed-lepidote, glabrescent. Leaves obovate or elliptic, coriaceous, 4–9.5 cm long, (2.3–)3–4 cm wide, apex short-acuminate, the acumen 0.4–0.6 cm long, attenuate to a rounded or subacute tip, base obtuse, short-decurrent on the petiole, midrib slightly depressed above, prominently raised below, nerves 24–30 pairs, densely pustulate and densely lepidote, then glabrescent above, moderately appressed-lepidote below, the scales adjacent but not overlapping, the punctations dark brown, inconspicuous, the margin entire, epunctate, revolute; petioles canaliculate, 1.0–1.2 cm long, thin, densely appressed-lepidote, the scales persistent. *Staminate inflorescence:* a straight raceme, rarely a cluster of 2–3 subsessile racemes 1.5–2.0 cm long; peduncle, axis, and pedicels densely lepidote; peduncle 0.2–0.3 mm long; floral bracts deltate or ovate, 0.5–1.0 mm long, 0.8–1.0 mm wide, apex acute, densely lep-

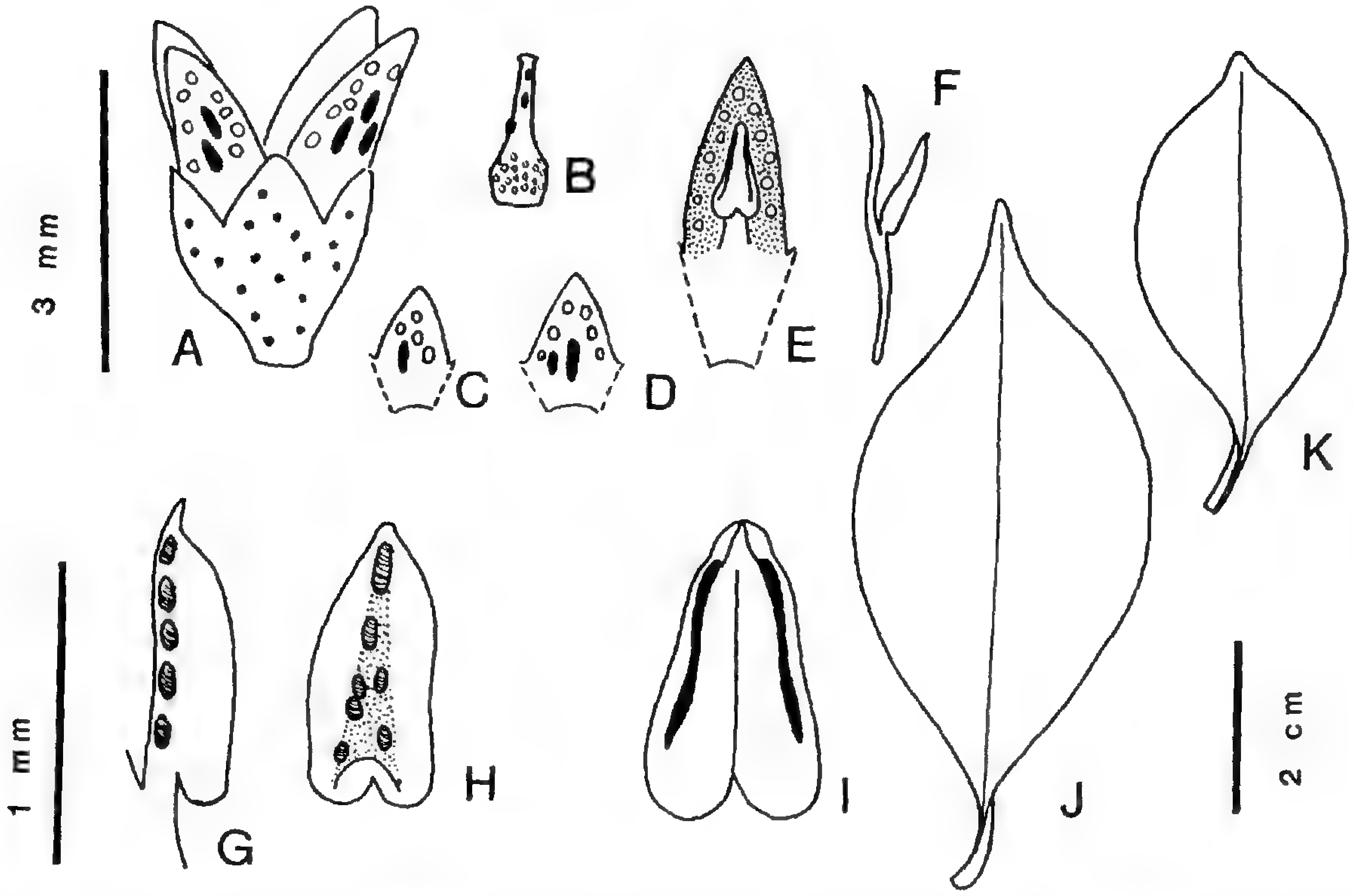


FIGURE 18. *Cybianthus maguirei* Agostini ex Pipoly.—A. Staminate flower, showing pellucid and black punctations.—B. Pistillode.—C, D. Staminate calyx lobes, ventral view.—E. Staminate corolla lobe, ventral view.—F. Staminate corolla lobe, lateral view.—G. Anther, lateral view, showing ventrally curved apiculum and erect habit.—H. Anther, dorsal view, showing darkened and punctate connective.—I. Anther, ventral view, showing apically confluent dehiscence slits.—J, K. Leaves. (A–I, from *Maguire 37042*; J, from *Maguire 37197*; K, from *Silva 60919*.)

idote abaxially, the margin entire, glabrous; pedicels terete, erect, 0.4–0.6 mm long. Flowers 4-merous, 2.8–3.1 mm long; calyx cupuliform, chartaceous, 1.0–1.5 mm long, the tube 0.4–0.5 mm long, the lobes ovate-triangular to deltate, 0.8–0.9 mm long, 0.4–0.7 mm wide, attenuate to an acute tip, prominently punctate and punctate-lineate, the distal punctations red, the proximal punctate-lineations black, the margin entire, densely lepidote; corolla campanulate, chartaceous, 2.7–3.0 mm long, the tube 0.9–1.2 mm long, the lobes erect, ovate, 1.6–1.9 mm long, 0.9–1.2 mm wide, flat, apex attenuate to acute tip, prominently punctate, the submarginal punctations red, the medial ones black, sparsely lepidote without except densely so along the margin, densely glandular-granulose within, densely glandular-granulose near margin without, the margin entire, densely glandular-granulose; stamens 2.1–2.4 mm long, the staminal tube inconspicuous, membranaceous, 0.9–1.2 mm long, hyaline, elobate, the apically free filaments flat, 0.1–0.3 mm long, sparsely brown punctate, the anthers ovate, 0.9–1.0 mm long, 0.4–0.5 mm wide, slightly recurved distally, apex apiculate, the apiculum somewhat recurved proximally, the base cordate, glabrous, the connective dark and prominently separating the thecae; pistillode obturbinate, 1.4–1.5 mm long, the ovary not well differentiated from the style, the base densely translucent glandular-lepidote. *Pistillate inflorescence:* a straight, simple, reduced raceme, 0.4–1.0 cm long; peduncle, rachis, and pedicels densely appressed-lepidote; peduncle 0.5–1.0 mm long; floral bracts triangular, 1.0–1.5 mm long, 0.3–0.5 mm wide, apex attenuate, densely lepidote, the margin entire, regular, glabrous; pedicels terete, 0.6–1.0 mm long; calyx cupuliform, 1.3–1.7 mm long, the tube 0.2–0.4 mm long, the lobes elliptic, 1.0–1.4 mm long, 0.3–0.6 mm wide, apex attenuate, medially thickened, plicate, prominently black punctate and punctate-lineate, moderately stipitate-lepidote except densely so along the margin, the margin entire, regular; corolla campanulate, chartaceous, 3.0–3.3 mm long, the tube 1.2 mm long, the lobes erect, oblong, 2.0–2.2 mm long, 0.7–1.4 mm wide, apex rounded to obtuse, sparsely lepidote medially without except densely so along the margin, glandular-granulose within and near margin without, prominently black punctate and punctate-lineate, the margin densely glandular-granulose; staminodes 2.3–2.6 mm long, the tube inconspicuous, hyaline, membranaceous, 1.0 mm long, the free apical portion of the filaments completely adnate to corolla lobes, 0.5–0.7 mm long, brown punctate, the anthers ovate, 0.9–1.1 mm long, 0.5–0.6 mm wide, apex acute, base deeply cordate, the connective prominently black punctate; pistil obnapiform, 2.1–2.3 mm long, the ovary 1.1–1.3 mm long, ca. 1.5 mm diam., densely translucent-lepidote, the style 0.9–1.1 mm long, the style capitate, 2-lobed, the placenta subglobose, with 4 naked ovules. Fruit depressed-globose, 4–5 mm long, 6–8 mm diam., verruculose, the exocarp thin, black punctate.

Distribution. Endemic to Cerro de la Neblina and adjacent mountains, at 1,300–2,000 m.

Ecology. *Cybianthus maguirei* grows among *Heliamphora* and Bromeliaceae patches on the summit of Cerro de la Neblina.

Paratypes. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Cerro de la Neblina, summit, 1,700–2,000 m, 4 Jan. 1954 (stam. fl), *Maguire et al. 37042* (NY, VEN), 10 Jan. 1954 (stam. fl), *37197* (NY). BRAZIL. AMAZONAS: Serra Pirapuçú, 1,300–1,700 m, 27 Jan. 1966 (stam. fl), *Silva & Brazào 60919* (INPA, NY, VEN).

Cybianthus maguirei is most closely related to *C. crotonoides*, a species endemic to the eastern state of Bolívar. *Cybianthus maguirei* is easily distinguished, however, by its leaves pustulate above, densely lepidote below, calyx lobes longer than broad, pedicels less than 1 mm long, flowers erect, longer corolla, apically free portion of the filaments shorter than the anthers, and finally, the larger fruit with verruculose exocarp.

It is a pleasure to dedicate this species to the late Bassett Maguire, former Curator Emeritus of the New York Botanical Garden, specialist in neotropical Clusiaceae and authority on Guayana floristics.

21. **Cybianthus crotonoides** (R. M. Schomb. ex Mez) Agostini, Acta Biol. Venez. 10: 153. 1980. *Conomorpha crotonoides* R. M. Schomb. ex Mez in Engler, Pflanzenr. IV, 236: 262. 1902. TYPE: Venezuela. Bolívar [Guyana]: Roraima, 1842–1843 (stam. fl), *Schomburgk 681* (*1027*) (lectotype, here designated, G-DEL; isolectotypes, K, P, W). [It should be noted that Steyermark (1981) determined that all of Richard Schomburgk's "Guyana-Roraima" collections were actually made within the borders of Venezuela.] Figure 19.

Shrub to 4 m tall; branchlets terete, thin, 2–3 mm diam., densely lepidote. Leaves elliptic to obovate-elliptic, coriaceous, 3.1–6 cm long, 1.0–2.5 cm wide, apically acute or short-acuminate, base acute, decurrent on the petiole, midrib slightly depressed above, prominently raised below, the nerves 22–26 pairs, inconspicuous above and below, the upper surface scrobiculate, densely lepidote at first, glabrescent, the lower surface densely lepidote, the margin entire, epunctate, revolute; petioles canaliculate, 0.9–1.3 cm long, densely lepidote. *Staminate inflorescence:* a simple raceme, 2.0–3.5 cm long, the axis and pedicels densely lepidote, the scales overlapping; peduncle 0.6–1.2 cm long; floral bracts linear-lanceolate, 0.3–0.6 mm long, 1.5–3.5 mm wide, apex acute, densely lepidote adaxially, the margin entire, glabrous; pedicels terete, nodding, 1–3 mm long. Flowers 4-merous, 2.6–2.9 mm long, cream-white; calyx cupuliform, carnose, 1.1–1.2 mm long, the tube 0.4–0.5 mm long, the lobes ovate or broadly ovate, 0.5–0.8 mm long, 0.7–1.0 mm wide, apically rounded, the punctations small, dark brown, conspicuous, the margin densely lepidote; corolla campanulate, carnose, 2.5–2.7 mm long, the tube 1.0–1.1 mm long, the lobes ovate to elliptic, 1.5–1.6 mm long, 1.1–1.2 mm wide, the apex attenuate to a rounded, cucullate tip, densely to sparingly lepidote medially without, glandular-granulose within, the margin irregular, finely crenulate, densely glandular-granulose; stamens 1.9–2.1 mm long, the staminal tube inconspicuous, hyaline, membranaceous, ca. 0.1 mm long, elobate, the apically free filaments 1.2–1.3 mm long, adnate to the corolla lobes, flat, epunctate, glabrous; the anthers ovate, 0.8–0.9 mm long, 0.6–0.7 mm wide, apex apiculate, the apiculum distally recurved, base cordate, the longitudinal slits thin, dorsifixed just above the base, the connective prominently brown punctate ventrally; pistillode pyriform, 1.3–1.4 mm long, the ovary ca. 0.3–0.4 mm long and in diam., densely translucent lepidote, the style ca. 0.9–1.0 mm long, prominently brown punctate, glabrous. *Pistillate inflorescence:* a simple raceme, 2.0–3.5 cm long, the axis and pedicels densely lepidote, the scales overlapping; peduncle 0.6–1.2 cm long; floral bracts ovate, 0.3–0.6 mm long, 1.3–2.7 mm wide, apex acute, densely lepidote adaxially, the margin entire, glabrous; pedicels terete, erect, 1–3 mm long. Flowers 4-merous, 2.0–2.1 mm long, cream-white; calyx cupuliform, carnose, 1.1–1.2 mm long, the tube 0.4–0.5 mm long, the lobes ovate-triangular, 0.5–0.8 mm long, 0.7–1.0 mm wide, apically rounded, inconspicuously pellucid-punctate, the margin densely lepidote; corolla campanulate, carnose, 1.9–2.0 mm long, the tube 1.0–1.1 mm long, the lobes ovate to elliptic, 0.7–0.8 mm long, 0.2–0.4 mm wide, the apex attenuate to a round, cucullate tip, densely to sparingly lepidote medially without, glandular-granulose within,

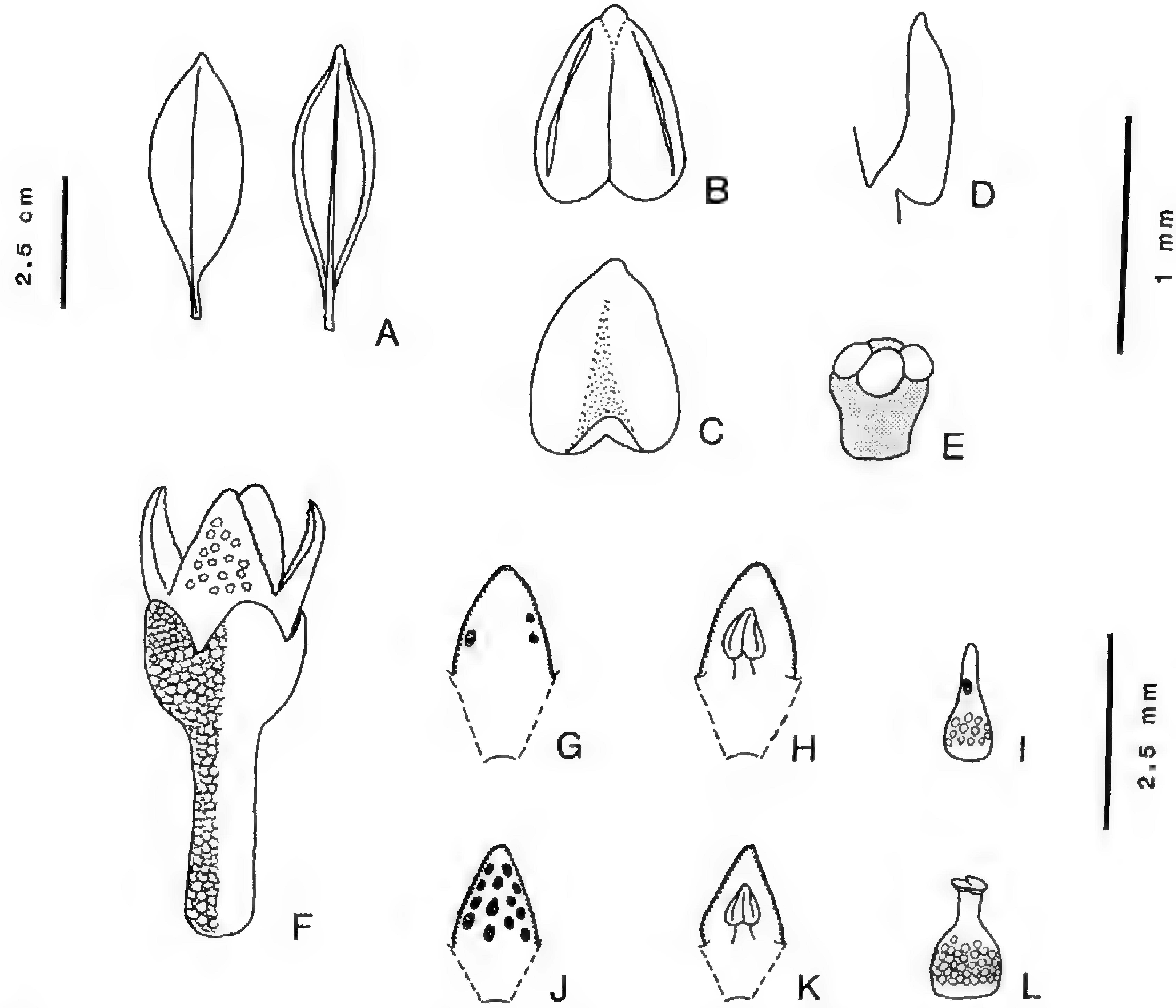


FIGURE 19. *Cybianthus crotonoides* (R. M. Schomb. ex Mez) Agostini.—A. Leaf, adaxial and abaxial views.—B. Anther, ventral view showing apiculum.—C. Anther, dorsal view showing darkened connective.—D. Anther, lateral view.—E. Placenta, showing naked ovules.—F. Staminate flower.—G. Staminate corolla lobe, dorsal view showing punctations.—H. Staminate corolla lobe.—I. Pistillode.—J. Pistillate corolla lobe, dorsal view showing punctations.—K. Pistillate corolla lobe, ventral view.—L. Pistil. (A–D and F–I, from *Cardona 2721*; E and J–L, from *Steyermark 59902.*)

the margin irregular, finely crenulate, densely glandular-granulose; staminodes 1.3–1.5 mm long, the staminodial tube inconspicuous, hyaline, membranaceous, ca. 0.1 mm long, elobate, the filaments 0.7–0.8 mm long, adnate to the corolla lobes, apically free for 0.1–0.2 mm, flat, epunctate, glabrous; the anthers ovate, 0.6–0.7 mm long, 0.5–0.6 mm wide, apex apiculate, the apiculum distally recurved, base cordate, dorsifixed just above the base, the longitudinal slits thin, the connective prominently brown punctate ventrally; pistil obnapiform, 1.6–1.8 mm long, the ovary 0.9–1.1 mm long and in diam., densely translucent glandular-punctate, the style short, 0.5–0.6 mm long, 4.5–5.0 mm diam., glabrous, epunctate, the stigma capitate and lobulate, the lobules ca. 2–3, the placenta subglobose, bearing 3–4 naked ovules. Fruit 3.5–4.5 mm long, 4.5–5.0 mm diam., purple-black at maturity, exocarp smooth.

Distribution. Endemic to Venezuela, state of Bolívar, 1,800–2,500 m.

Ecology. *Cybianthus crotonoides* grows in *Bonnetia roraimae* formations on the summits of various tepuis in the Auyán-tepui-Chimantá Floristic Complex (Maguire, 1979). It is notable that it occurs in the fissures of tall columns of rocks.

Specimens examined. VENEZUELA. BOLIVAR: Aparamán-tepui, 2,150 m, 22 Mar. 1987 (fr), *Holst 3487* (MO, US, VEN), (pist. fl, fr), *Holst 3497* (MO, US, VEN); Auyán-tepui, 2,100 m, Jan. 1949 (stam. fl), *Cardona 2721* (NY, VEN), 1,850 m, without date (stam. fl), *Pannier & Schwabe s.n.* (VEN), *Tate 1171* (NY, VEN), upper slopes of Auyán-tepui, 2,300 m, Apr. 1956 (stam. fl), *Vareschi & Foldats 4844* (VEN), summit of S portion, 2,050–2,300 m, 15 May 1964 (stam. fl), *Steyermark 93936* (F, NY, US, VEN); Camarcaibarai-tepui, summit, 2,400 m, 26 Mar. 1987 (pist. fl), *Holst 3624* (MO, US, VEN), SW-facing shoulder, 1,800–1,825 m, 22–24 May 1986 (stam. fl), *Steyermark et al. 132022* (MO, US, VEN); summit of Carrao-tepui, 2,470–2,500 m, 7 Dec. 1944 (pist. fl, fr), *Steyermark 60890* (F, NY, VEN); Murisipán-tepui, E of Auyán-tepui, 2,400–2,500 m, 25–26 Mar. 1987 (stam. fl), *Delascio 13063* (MO, VEN), second of 4 tepuis W to E in Apamarán range, 2,300 m, 26 Mar. 1987 (stam. fl), *Holst 3533* (MO, US, VEN); Ptari-tepui, along base of S-facing bluffs, 2,410 m, 6 Nov. 1944 (stam. fl), *Steyermark 59902* (F, NY, VEN); summit, Tereké-Yurén, W edge, 2,135 m, 26 May 1986 (pist. bud), *Liesner et al. 21118* (MO, US, VEN).

Cybianthus crotonoides is easily recognized by its coriaceous, revolute, acuminate leaves, that are so densely punctate below that the scales are superposed by their margins. It is most closely related to *C. maguirei* because of the subglobose placenta bearing naked ovules. However, *C. maguirei* is defined by its wide longitudinal dehiscence slits, which are apically confluent, and *C. crotonoides* is defined by its dense indument of lepidote scales, which overlap each other on the abaxial surface of the leaves, corolla, and calyx, on the pedicels, rachis, stem, and petioles, and by the nodding flowers, *Cybianthus crotonoides* shares several other characters with *C. maguirei* such as the inconspicuous, hyaline, membranaceous staminal and staminodial tube, the cupuliform calyx, and the corolla lobes densely glandular-granulose along the margin.

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3600(5); 3624(21); 3699(8). Huber, O. et al. 3861(7); 6990(4); 8882(11); 8964(8); 11005(2); 11590(5).

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Kappler, A. 1729(14b). Kral, R. 72045(8). Krukoff, B. A. 10987(11).

Lang, H. & C. Persaud 374(14b). Lanjouw, J. & J. Lindeman 2661(14b). Lasser, T. 1836(9). Liesner, R. et al. 3692(7); 7220(7); 7221(7); 7468(7); 16637(7); 16678(10); 16896(17); 17606(17); 18537(11); 21118(21); 21418(13); 22486(10); 22760(10); 24941(18); 24964(10); 25108(18); 25121(17); 25276(18); 25496(10); 25533(10); 25744(11); 25745(11); 25772(10). Lindeman, J. C. & R. Cowan 7000(14b). Luteyn, J. et al. 9442(8); 9482(8).

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Renner, S. 2088(11). Romero-C., R. 3536(7).

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Tate, G. 435(18); 741(11); 874(18); 901(17); 927(11); 1171(21). Thomas, W. & T. Plowman 3048(6); 3060(6); 3069(6); 3412(14a); 3450(14a). Tillett, S. et al. 44959(17); 45017(14b); 45056(1); 45219(8); 45609(8).

Ule, E. 8724(15).

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EVOLUTIONARY BIOLOGY OF *ACACIA CAVEN* (LEGUMINOSAE, MIMOSOIDEAE): INFRASPECIFIC VARIATION IN FRUIT AND SEED CHARACTERS[1]

James Aronson[2]

ABSTRACT

Six varieties are recognized in *Acacia caven* (Leguminosae, Mimosoideae; *Acacia* subg. *Acacia*, subsection *Polyseriae*), based on herbarium studies of vegetative characters, population-level studies of fruit and seed characters, and a map of the species' distribution and morphological variation patterns in southern South America. Two new varieties are described. Ecological and evolutionary aspects of carpological variations are discussed, and a framework is established for further studies in this and related species.

Within the huge pantropical genus *Acacia* Miller, subgenus *Acacia* sensu Vassal (= series *Gummiferae* Bentham, excluding *Faidherbia albida* (Del.) A. Chev.) appears to be a natural phyletic unit (Bentham, 1842; Pedley, 1986; Vassal, 1972). Its members occur primarily in the thornscrub and savannas of the Neotropics (ca. 50 species) and Africa (ca. 115 species) (Guinet & Vassal, 1978; Ross, 1979; Vassal, 1981; Rico Arce, 1984), but there are also 5–10 endemic species in western and northern Australia. The South American members of this subgenus (ca. 15 species) are among the least well known, despite the recent revision of the genus *Acacia* in Argentina by Cialdella (1984).

Although most abundant and variable in the warm temperate to subtropical biogeographical region known as the Chaco (Hueck & Seibert, 1972; Cabrera & Willink, 1973), one member of subgenus *Acacia, A. caven* (Molina) Molina, appears to have spread relatively recently into other biogeographical regions in northern Argentina, eastern Bolivia, western Paraguay, southern Brazil, Uruguay, and central Chile. This paper attempts to clarify infraspecific taxonomy of the species and set the stage for ecological, biogeographical, and other studies of *A. caven* and related species.

HISTORICAL SYSTEMATIC TREATMENT

Acacia caven was originally described (as *M. caven*) from central Chile by Molina (1782), who considered it very similar to *A. farnesiana* (L.) Willd., a species described over 29 years previously and widely cultivated in Italy and France during the eighteenth and nineteenth centuries. Unfortunately, leaflet size (and "a shorter pod") was the basis on which Bentham (1875: 502) separated the two taxa, thereby paving the way for subsequent authors, e.g., Kuntze (1898), Arechavaleta (1901), Hassler (1909), Spegazzini (1923), and Clos (1930), to lump the two together. By contrast, Hooker & Arnott (1830), Wight & Arnott (1834),

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Arata (1891), Burkart (1952, 1967, unpublished), Tortorelli (1956), Vassal (1972), Lombardo (1982), Cialdella (1984), Rodriguez et al. (1984), and Bernardi (1984) maintained separation of the two taxa on the basis of length to width ratio and anatomy of the pods, pericarp striations, length and pubescence of petioles, size of leaflets, and other morphological characters. Only Spegazzini (1923) and Cialdella (1984) treated *A. caven* in detail.

POSITION WITHIN SUBGENUS *ACACIA*

The small subsection *Polyseriae* (Vassal, 1972) is considered evolutionarily advanced compared to the far larger subsection *Uniseriae*, which contains all other members of the subgenus. *Acacia caven* and *A. farnesiana* are the only South American members of this subsection (*A. erioloba* E. Mey and *A. sphaerocephala* Cham. et Schldl. are the sole African and Mesoamerican representatives). Species of subsection *Polyseriae* have two, rarely three, rows of seeds per pod, as compared to only one row per pod in subsection *Uniseriae* (Vassal, 1972). This character led Wight & Arnott (1834) to propose the segregate genus *Vachellia*, a proposition accepted by Spegazzini (1923) but rejected by most subsequent workers. Many modern workers consider the subsection unnatural (D. Seigler & J. Ebinger, pers. comm.). Yet, it should be noted that indehiscent (or tardily dehiscent) pods are a diagnostic trait cited by Vassal (1972) for subsection *Polyseriae*, and that the group corresponds in part to the subseries *Summibracteatae* defined by Bentham (1875: 499) on the basis of floral as well as carpological characters.

INFRASPECIFIC TREATMENT

Cialdella (1984) recognized four varieties within *Acacia caven*. Three of these were characterized by pod size and shape (vars. *caven*, *microcarpa*, and *stenocarpa*) and corresponded to "forms" recognized by Spegazzini (1923) under *Vachellia farnesiana*. The fourth, *A. caven* variety *dehiscens* Burkart ex Cialdella, recognized the unusual populations with dehiscent pods in the hills between Córdoba and San Luis, Argentina. Three more of Spegazzini's (1923) "forms," characterized by short peduncles, small anthers, and large leaflets, respectively, were rejected by Burkart (unpublished) and Cialdella (1984). Furthermore, Burkart labeled several specimens var. *macrocarpa* or var. *sphaerocarpa*, but never prepared formal descriptions for them. Typical fruit types of the six putative varieties are shown in Figure 1.

HABITAT AND DISTRIBUTION

Acacia caven is one of the most widespread arboreal species of extra-tropical South America, occurring ca. 37°–18°S in six countries, where it is variously known as "espino," "espinillo," "aromita," and "churqui" (Fig. 2). It is a natural component of the deciduous thorn forest in all but the driest areas of the Chaco. This region covers more than 1,000,000 km^2 between 15° and 35°S in north-central Argentina, adjacent parts of Bolivia, a tiny portion of Mato Grosso, Brazil, and nearly half of Paraguay (Ragonese & Castiglioni, 1970; Cabrera & Willink, 1973; Ramella & Spichiger, 1989). Outside of the Chaco, it is considered invasive.

Like some other widespread acacias, e.g., *A. nilotica* (L.) Willd., *A. farnesiana*, *A. macracantha* Humbl. & Bonpl. ex Willd., and *A. karroo* Hayne, *A. caven* shows remarkable climatic tolerance and ecological adaptability, as well as a propensity to invade disturbed habitats. In central Chile, encroachment by *A. caven* affects over 2,000,000 ha, including natural ecosystems in the semiarid and subhumid portions of the mediterranean climate zone (Parsons, 1976; Fuentes et al., 1989; Ovalle et al., 1990). It occurs from sea level to nearly 3,200 m at its northern limits in central Bolivia. In Argentina and Chile it rarely occurs above 1,200 m, and in Bolivia it is sparse above 1,900 m. Freezing temperatures would appear to be a limiting factor. For unknown reasons, *A. caven* does not occur in close proximity to the sea. It occurs not only in diverse continental-climate areas but also in the mediterranean-climate region in Chile, both in seasonally inundated plains and on very dry slopes or inselbergs. Preferring open cow pastures or abandoned fields, it also enters clearings in various types of natural vegetation wherever livestock roam. Although usually seen as a much-coppiced shrub 1–3 m tall, *A. caven* can attain 8–10 m in height, with DBH of 80 cm, when left uncut in deep soils (Ovalle, 1986; pers. obs.).

REPRODUCTIVE BIOLOGY

Similar to several Australian and African acacias, *A. caven* possesses both hermaphroditic and masculine flowers, and thus should be considered an andromonoecious species (Spegazzini, 1923; Burkart, 1967; León et al., in prep.). These flowers occur in varying proportions, both within and among populations, possibly in response to changes in water availability (León et al., in prep.). *Acacia caven* seems to be largely allogamous, as more than 50 individuals tested have proven to be highly self-

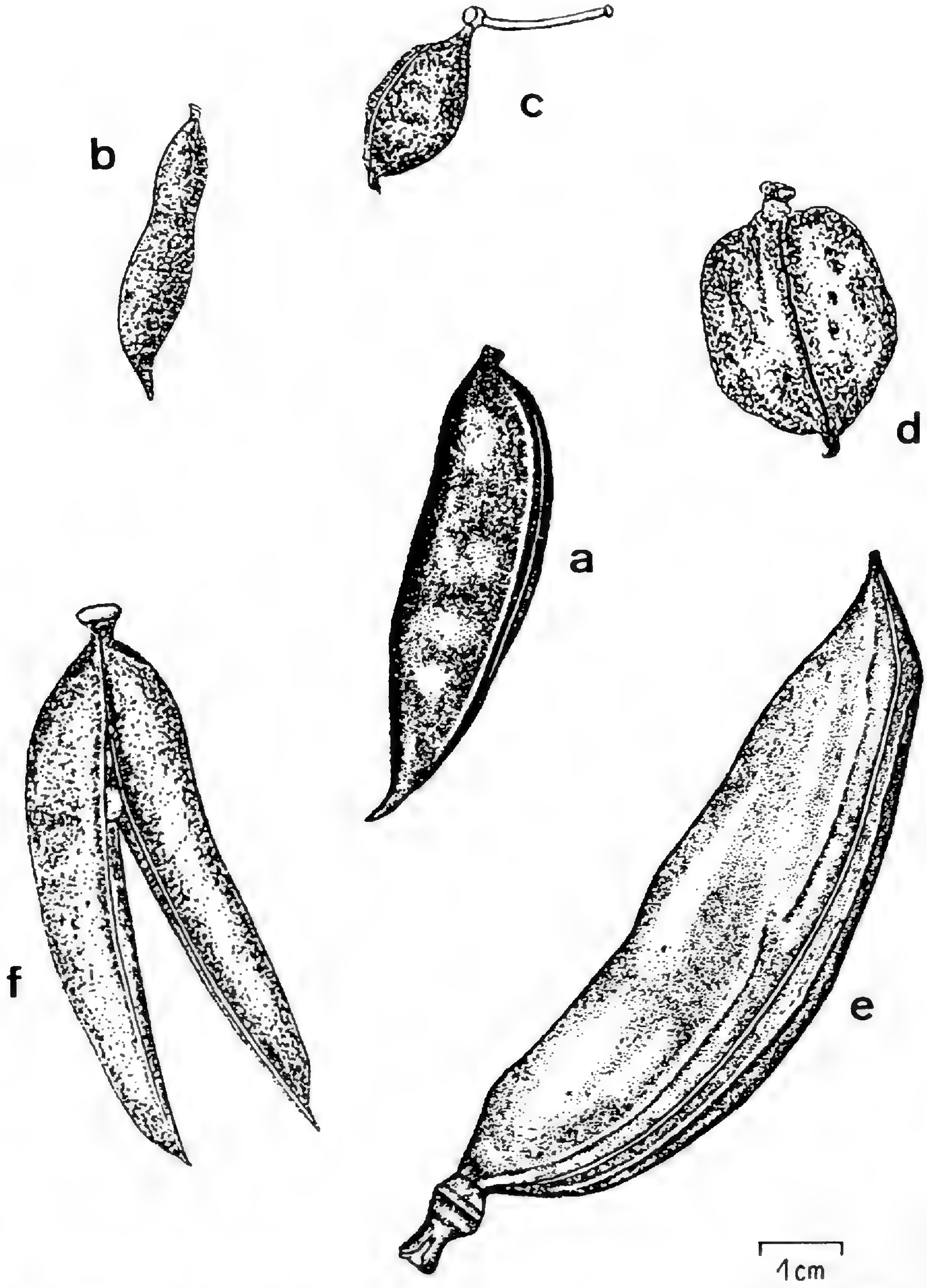

FIGURE 1. Typical fruits of the six varieties of *Acacia caven.*—a. Variety *caven Burkart 29343.*—b. Variety *stenocarpa Krapovickas 983.*—c. Variety *microcarpa Rojas 7697.*—d. Variety *sphaerocarpa Tressans & Radovancich 3539.*—e. Variety *macrocarpa Burkart 17577.*—f. Variety *dehiscens Burkart 15730.* All drawings life size.

incompatible, both in an Argentinian population near Córdoba (A. Anton, pers. comm.) and a Chilean population near Santiago (Peralta et al., in press). Pollination appears to be achieved—at least in central Chile—by small, crawling beetles, especially *Actylus trifaciatus* (Peralta et al., in press) rather than or in addition to, honey bees: the latter pollinator group is the most common for the genus (Arroyo, 1981).

SEED DISPERSAL

Most *Acacia caven* pods float in water, and some seeds are presumably dispersed in this fashion. For this reason, it has been suggested that its primary habitat within the Chaco was near seasonally active waterways, where it is often seen today (C. Saravia Toledo, pers. comm.). At the same time, most varieties of *A. caven* seem adapted for long-dis-

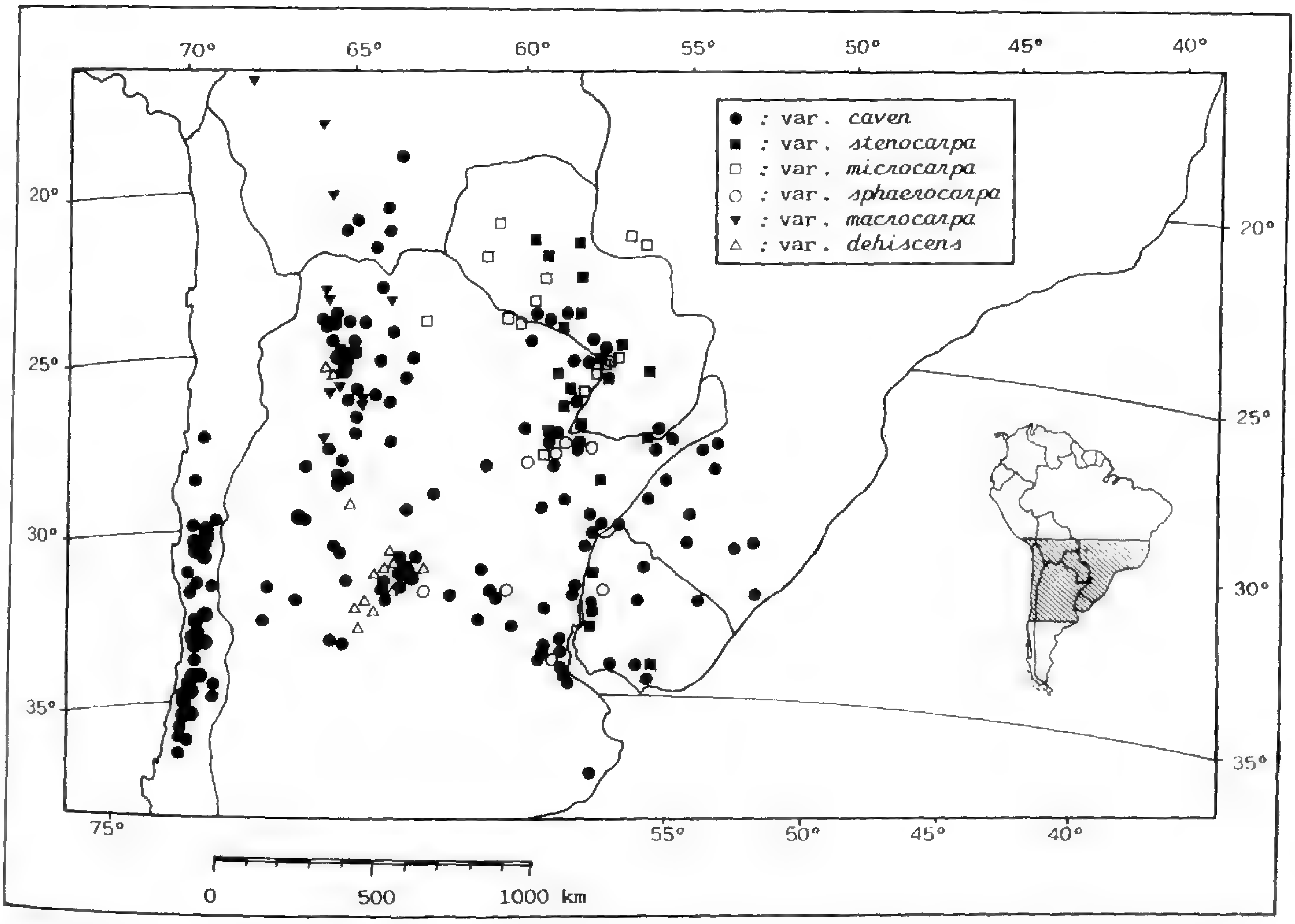

FIGURE 2. Continental distribution of *Acacia caven* in southern South America. Each point represents a single field collection.

tance dispersal by mega-vertebrates. In prehistoric times, there were numerous large animals such as camelids, stegomastodons, notoungulates, edentates, and giant sloths in the Chaco (Bucher, 1987). At present, domestic livestock are undoubtedly the most important agents of dispersal (Gutierrez & Armesto, 1981). Medium-sized birds such as "charata" (*Ortalis canicollis*), and "corzuela" (*Mazama americana, M. rufa*), as well as tapir (*Tapirus terrestris*), guanaco (*Lama guanicoe*), and sury (*Rhea americana*) are all probable dispersers of seed (C. Saravia Toledo, pers. comm.).

CYTOLOGY AND PALYNOLOGY

Chromosome numbers for *Acacia caven* have been recorded as $2n = 26$ (Castronovo, 1945) and $2n = 26, 52$ (Atchison, 1948). Similarly variable numbers occur in the closely related *A. farnesiana*, which is said to have $2n = 52, 104$ (Atchison, 1948). Pollen is shed in relatively large polyads consisting of ca. 32 grains (Caccavari, 1970; Heusser, 1971; Peralta et al., in press). Exceptions are *Rojas 7694* (SI) (var. *microcarpa*) with 16 grains and *Aronson 7977* (MO, SGO) (var. *macrocarpa*) with 48 grains (Guinet & Aronson, unpublished data).

MATERIALS AND METHODS

FRUITS AND SEEDS

Collections of seeds and pods were made at 49 sites covering the current range of distribution of *Acacia caven*. In addition, more than 750 herbarium fruit-bearing specimens of *A. caven* were compared for carpological and vegetative traits. Several fruit (pod) and seed characters appeared relatively constant within populations, and the three largest fruit samples from populations of each of the six putative varieties were selected for analysis. A total sample of 80 pods from each of five or more individuals was sufficient to represent each population, since the addition of further pods failed to alter the generalized variance (Tatsuoka, 1971; Farrell & Ashton, 1978). Only ripe pods free of bruchid damage were used. Voucher specimens for each population are deposited at herbaria in Chile (CONC, SGO), at Kew (K), and in Missouri (MO).

Length and width of 80 fully ripe pods per population were measured, and pod volume was

TABLE 1. Leaf and peduncle characters in six varieties of *Acacia caven*. Based on examination of fully developed leaves of 750 herbarium specimens.

Variety	Rachis length (cm)	Pairs of leaflets per pinna	Pubescence of rachis[1]	Peduncle length[2] (mm)	Position of nectary on rachis[3]
caven	5–7	4–6	±	5–15	A or absent
sphaerocarpa	3–4	8–14	±	5–15	A or absent
dehiscens	2–4	6–12	–	5–8	A
macrocarpa	3–4(–5)	6–10	–	3–5	A
microcarpa	3–7	4–6	±	10–15	A or B
stenocarpa	4–8	4–8	±	10–25	A or B

[1] – usually glabrous; ± variable.
[2] Not shown in Figure 1.
[3] A—at or near junction of first pair of pinnae; B—midway from A to base of rachis.

estimated as pod length × πr^2. Seeds were removed, counted, and weighed separately from pods. Average seed weight varied little within populations, as seen in a number of preliminary scale checks. To determine average seed weight for each population, all seeds from each sample were pooled, and three random subsamples of 100 seeds were weighed. The average weight of a single seed was calculated from the resulting mean values. Data were analyzed by Duncan's Multiple Range test and two-way ANOVA to evaluate the relative contribution of population and variety to overall variance.

RESULTS

Table 1 shows the comparison of selected morphological traits among the six putative varieties. Although some diagnostic differences occur, vegetative organs clearly do not display the most distinctive infraspecific variation. Table 2 shows intervarietal means of four pod and seed characters in 17 populations representing the six putative varieties. On the basis of pod volume and seed number per pod, three varietal groups can be distinguished: (i) *caven*, *sphaerocarpa*, and *dehiscens*, (ii) *macrocarpa*, and (iii) *microcarpa* and *stenocarpa*, which is further distinguished by narrow pod shape and small seed size.

Figure 2 shows collection localities for the six varieties. Partial geographic isolation occurs in some varieties, notably variety *dehiscens* in west-central Argentina, and variety *microcarpa* + variety *stenocarpa* in the Río Pilcomayo area of northeast Argentina and southern Paraguay. Geographic separation is correlated to ecological differentiation in most cases. Thus, variety *macrocarpa* is not only circumscribed geographically but also limited to sites above 2,000 m. Both variety *microcarpa* and variety *stenocarpa* are restricted to the portion of the Chaco that is periodically inundated for several months each year. Variety *dehiscens* is limited to the rather dry, isolated range of mid-altitudinal ranges stretching between San Luis and Córdoba, west-central Argentina; variety *sphaerocarpa* occurs only in high-rainfall areas of eastern Argentina and adjacent portions of Uruguay. Variety *caven* is the most widespread, demarking the outer periphery of the geographic range of the whole species, except in Bolivia and Paraguay.

A gap occurs in the distribution of *A. caven* in the middle of the Chaco, undoubtedly due to aridity. Moreover, the five varieties other than variety *caven* seem to spread out in an irregular pattern around this natural gap. This situation is remniscent of that found in *Acacia karroo* in southern Africa (Brain, 1989). In that species, three chemotypic races occur almost allopatrically around the treeless Drakensberg massif. The geographic distribution of these races appears correlated with changes in the quantity and distribution of precipitation. In 818 specimens of *A. caven*, polymorphism in a peroxidase banding pattern has been determined and a clear distinction was found between Chilean and non-Chilean populations (Brain & Aronson, in prep.). Further studies are needed in this area.

TAXONOMIC TREATMENT

Acacia caven (Molina) Molina, in Sag. Stor. Nat. Chili, 2nd ed., 163; 299, 1810.

Shrub or tree to 10 m high, but usually much smaller; single-stemmed or with 5–20 or more densely crowded basal stems, depending on history of cutting and burning; young branchlets mottled gray, sparingly puberulous, lenticels not prominent. Stipular spines 0.4–2.5 cm long, slender, not swollen at the base, white or gray, rarely brown, often mottled, borne in pairs at every node. Leaves bi-

TABLE 2. Means and ranges of four morphometric fruit and seed traits in six putative varieties of *Acacia caven*. For each variety, N = 240, from three populations. Means in a column followed by the same letter are not significantly different ($P = 0.05$).

	Fruits				Seeds	
Variety	Length (cm)	Width (cm)	Volume (cm^3)	Dry weight (g)[1]	Seeds per pod	Dry seed weight (g)
caven	5.1a	1.5a	9.0a	5.4a	21.3a	1.23a
Range	(4.6–8.4)	(1.4–2.3)	(7.0–14)	(3.7–9.7)	(9–39)	(1.2–1.3)
sphaerocarpa	4.0b	2.9ab	6.3b	3.5a	22.9a	1.15a
Range	(2.1–6.5)	(1.6–4.8)	(5.4–68)	(1.5–6.0)	(11–31)	(1.0–1.3)
dehiscens	5.5a	1.6a	11.9ab	6.3ab	18.4a	0.91b
Range	(3.3–7.5)	(0.9–2.2)	(7.1–18)	(5.2–8.3)	(4–28)	(0.90–0.93)
macrocarpa	8.4c	2.2b	31.9c	9.8b	30.2b	1.26a
Range	(6.2–11)	(1.8–2.5)	(26–38)	(8.4–12.7)	(16–41)	(1.25–1.27)
microcarpa	2.3d	1.2c	2.6d	0.9d	11.2c	0.47c
Range	(1.7–3.1)	(0.5–1.5)	(2.2–3.0)	(0.7–1.4)	(7–15)	(0.4–0.5)
stenocarpa	3.7a	0.8c	2.4d	1.4d	12.4c	0.51c
Range	(3.0–6.5)	(0.6–1.1)	(1.9–3.6)	(0.8–2.4)	(8–17)	(0.4–0.56)

[1] With seeds.

pinnate, deciduous; petiole 1–2 cm long, often with 1, rarely 2 or 0, conspicuous nectaries; primary rachis 2–5(–8) cm long, sparsely puberulous; pinna pairs typically 4–8(–14); rachillae 0.7–1.4 cm long; leaflets 4–10 pairs per pinna, invariably linear, 1.0 × 0.5 mm, glabrous; midrib and lateral nerves not readily distinct. Peduncles usually pubescent but sometimes glabrous, 3–15(–25) mm long, and relatively constant in length within populations. Flower head spherical or ellipsoid, 5–10 mm long; one or usually several per leaf axil, highly visible prior to the emergence of leaves. Flowers sessile, yellow, highly fragrant. Calyx 0.5–1.0 mm long, glabrous. Corolla 1–3 mm long, glabrous, approximately 30–55 flowers per head; stamens 44–58 per flower, with filaments free from the base and anthers eglandulate; pods brownish black or purplish brown, oblong-elongate or subglobose, straight or slightly falcate, frequently stipitate basally and/or acuminate, extremely variable in size, volume and weight; indehiscent, except in variety *dehiscens*; glabrous, usually not striate. Mesocarp ± spongy or quite sparse. Seeds olive brown, ± elliptic, 5–7 × 4–6 mm, areole 4–5 × 3–4 mm. Seeds 12–35 per pod in 2 (rarely 3) rows, or ± scattered in fully ripe pods.

KEY TO FRUITING SPECIMENS OF *ACACIA CAVEN*

1. Mature pod dehiscent .... var. *dehiscens*
1. Mature pod indehiscent 2
2(1). Pod subglobose, less than twice as broad as long, excluding beak and peduncle 3
2. Pod elongate-fusiform, more than twice as broad as long, excluding beak and peduncle 4
3(2). Pod usually 2.0–3.0 × 1.0–1.5 cm; mesocarp somewhat reddish, peduncle more than 15 mm long .... var. *microcarpa*
3. Pod 2.1–6.5 × 1.6–4.8 cm; mesocarp white, peduncle less than 15 mm long .... var. *sphaerocarpa*
4(2). Pod 3.0–4.0(–6.5) × 0.6–1.1 cm, narrowing at both ends, sometimes subtorulose, often light brown, occasionally reddish purple, peduncle usually more than 15 mm and rarely up to 30 mm .... var. *stenocarpa*
4. Pod 5–11 × 1.5–2.5 cm, elongate, acuminate, not torulose, peduncle less than 15 mm long 5
5(4). Pod dark brown, rarely black or slightly purple, 5–8 cm long, with one sutural ridge, this often indistinct; mesocarp evanescent .... var. *caven*
5. Pod usually reddish purple, usually more than 8 cm long, with three distinct sutural ridges, these often sharply distinct; mesocarp resinous .... var. *macrocarpa*

Acacia caven var. **caven**, *Mimosa caven* Molina, Sag. Stor. Nat. Chili 1st ed., 174. 1782. TYPE: not known. Neotype here designated: Rancagua, Chile, Oct. 1828, *Bertero s.n.* (SGO). Figure 1a.

Acacia adenopa Hook. & Arn., Bot. Miscell. 3: 206. 1833.

Acacia farnesiana (L.) Willd. var. *brachicarpa* O. Kuntze. Rev. Gen. Pl. 1:156. 1891. *Acacia farnesiana* (L.) Willd. var. *cavenia* (Hook & Arn.) O.Kuntze, Rev. Gen. Pl. 3:47. 1898. *Vachellia farnesiana* (L.) Wight & Arn. f. *cavenia* (Molina) Speg., Bol. Acad.

Nac. Cs. Córdoba 26(2): 298. 1923. *Acacia farnesiana* (L.) Willd. f. *cavenia* E. C. Clos, Bol. Min. Agric. Nac. 28(4): 455. 1930.

Shrub or tree to 10 m high, but usually much smaller; single-stemmed or with 5–20 or more densely crowded basal stems; young branchlets mottled gray, sparingly puberulous. Stipular spines 0.4–2.5 cm long, slender, white or gray, borne in pairs at every node. Leaves bipinnate, deciduous; peduncle 5–15 mm long, usually with one nectary at midpoint of petiole; primary rachis 5–7 cm long, sparsely puberulous; pinna pairs 4–6; rachillae 0.7–1.0 cm long; leaflets 4–6 pairs per pinna, linear, 1.0 × 0.5 mm, glabrous; midrib and lateral nerves not readily distinct. Peduncles usually pubescent, 3–15 mm long, and relatively constant in length within populations. Flower head spherical or ellipsoid, 0.5–1.0 cm long; one or usually several per leaf axil, highly visible prior to the emergence of leaves. Flowers sessile, yellow, highly fragrant. Calyx 0.5–1.0 mm long, glabrous. Corolla 1–3 mm long, glabrous, approximately 30–55 flowers per head; stamens 44–58 per flower; filaments free from the base; anthers eglandulate; pods brownish black or purplish brown, oblong-elongate or subglobose, straight or slightly falcate, frequently stipitate basally and/or acuminate ± 5–7 × 10–13 cm, 8–10 g; indehiscent, glabrous, usually not striate. Mesocarp ± spongy. Seeds olive brown, ± elliptic, 5–7 × 4–6 mm, areole 4–5 × 3–4 mm; 9–39 per pod in 2 rows in young pods but ± scattered in fully ripe pods.

Habit and distribution (Fig. 2). In disturbed sites in northern Argentina, southeastern Bolivia, and south-central Paraguay, occasionally an integrated element in xerophytic Chaco woodlands and along former river courses in adjacent areas. Also in the central valleys of Chile (36–27°S), parts of Uruguay, and southern Brazil. Especially frequent in much-burned, overgrazed cow pastures and in abandoned fields.

Representative specimens. ARGENTINA. CORDOBA: 32 km E of Córdoba, ca. 31°19′S, 64°57′W, 280 m, 11 Oct. 1988, *Aronson 7642* (CONC, K, MO). BOLIVIA. CHUQUISACA: 19 km S of Camargo, on road to Tarija, ca. 20°41′S, 65°15′W, 2,350 m, 26 Feb. 1989, *Aronson 7799* (CONC, MO); 53 km S of Palos Blancos, ca. 21°45′S, 63°38′W, 850 m, 28 Feb. 1989, *Aronson 7827* (MO). CHILE. 4 km E of Lo Ovalle, ca. 33°02′S, 71°22′W, 220 m, 18 Nov. 1988, *Aronson 7692* (K, MO); Cuesta de Chacabuco, 45 km N of Santiago, ca. 32°58′S, 70°42′W, 750 m, 23 Nov. 1988, *Aronson 7696* (K, MO). URUGUAY. 2 km E of Gauleguaychu, ca. 33°10′S, 58°22′W, 45 m, 23 Oct. 1988, *Aronson 7650* (CONC, MO, SGO).

Acacia caven var. **sphaerocarpa** Burkart ex Aronson, var. nov. TYPE. Argentina. Corrientes: ca. 27°27′S, 58°46′W, 60 m, "alrededores de la ciudad de Corrientes, antiguo camino a Matadero, 500 m de la ruta, 17 Feb. 1989, *S. G. Tressens & A. Radovancich 3539* (holotype, K; isotype, CTES). Figure 1d.

A varietatibus omnibus aliis var. *microcarpa* sola excepta legumine subgloboso differt, a var. *microcarpa* legumine maiore pedunculum crassum haud excedente differt.

Fruits are nearly spheroid when small (ca. 15 × 15 mm) or slightly ovoid when larger (ca. 25–30 × 20 mm), often with a sharp acuminate tip. Leaflets are numerous (8–14 pairs) and leaves are larger than in variety *caven*: 30–45 × 10–15 mm; stipular spines mostly less than 5 mm long.

Distribution (Fig. 2). In the more humid part of the Chaco and adjacent regions of Corrientes and Entre Ríos, Argentina, rarely in Santa Fe and Córdoba provinces, Argentina, and in western Paraguay and Uruguay. In damp fields where livestock roam.

Representative specimens. ARGENTINA. CORRIENTES: Empedrado, Estado La Yela, ca. 27°53′S, 58°49′W, 1954, *Pederson 3072* (K, LP); Arrocera Drews, 10 km NE of Colonia C. Pelligrini, Route 14, *Krapovickas et al. 29427* (CTES, SI). ENTRE RIOS: Depto. Islas del Ibicuy, 14.5 km N of the interprovince line with Buenos Aires, ca. 33°47′S, 58°20′W, 70 m, 22 Oct. 1988, *Aronson 7648* (MO). SANTA FE: Río Nah Tuli Piague, 9 Jan. 1937, *Ragonese 2444* (SI). URUGUAY. Laguna Guayaca, Apr. 1906, *Berro 4002* (MVFA).

In 1947, Burkart labeled one herbarium sheet (*Ragonese 2444*, SI) "forma sphaerocarpa n.f." but never described it formally. In all morphological traits except pod shape, this clearly shows affinity with variety *caven*. However, apart from carpological differences, limited geographical distribution (Fig. 2) and comparatively rapid growth rate under controlled environmental conditions (Aronson et al., 1991) support its recognition as a distinct variety. This variety seems to have unusually large leaves, regardless of water availability.

Acacia caven var. **dehiscens** Burkart ex Cialdella. Darwiniana 25: 76. 1984. TYPE: Argentina. Córdoba: Ascochinga, 22 Sep. 1936, *E. G. Nicora 962* (SI). Figure 1f.

Distribution. The mid-altitudinal hills of Córdoba and San Luis provinces, western Argentina. Very rare in the lower pre-Andean slopes of Catamarca and, according to Cialdella (1984), Salta. Tends to occur in heavily cut-over and frequently burned, heavily grazed, and otherwise disturbed sites in proximity to large, permanent human populations (Fig. 2).

Representative specimens. ARGENTINA. CATAMARCA: Las Peñas, *Brizuela 563* (LIL 206316). CORDOBA: Lago San Roque, Apr. 1945, *Hunziker 5984* (SI); Ascochinga, *Giardelli 405* (SI); 2 km E Villa de Totoral (jct. Rte. 9 and Rte. 17), ca. 31°15'S, 64°52'W, 500 m, 11 Oct. 1988, *Aronson 7644* (MO, SGO). SAN LUIS: Bajo Grande, Larca, *A. Maldonado 102* (SI); Larca, *Hunziker 2097* (SI); Embalse La Florida, 2 km E of Trapiche, ca. 33°06'S, 66°02'W, 930 m, 27 Mar. 1990, *Aronson 7907* (MERL, SGO).

Fruiting material is generally required to key out this variety. Variety *dehiscens* displays well-opened pods (see Fig. 1f) on the tree, especially at Embalse La Florida. Special caution is required with specimens from Lago San Roque, near Córdoba and from San Luis, since natural hybridization appears to occur between this variety and *A. atramentaria*. Moreover, pods on some herbarium sheets appear dehiscent due to crushing of specimens.

Acacia caven var. **macrocarpa** J. Aronson, var. nov. TYPE: Argentina. Salta: Chicoana, El Carril, 19 Oct. 1948, *Burkart 17577* (SI). Figure 1e.

A varietatibus aliis leguminibus multo maioribus pilis minutis glandulosis rubropurpureis omnimoobsitis et suturis prominentibus differt.

Mesocarp spongy and whitish.

Distribution. This variety has only been found at high altitudes (2,000–3,200 m) on the eastern flanks of the Andes, in Catamarca, Salta, Tucumán, and Jujuy provinces, northwestern Argentina and in Chuquisaca, Cochabamba, and La Paz departments of southern Bolivia. This variety is generally only found in dry streambeds and alluvial plains where groundwater is relatively near the surface (Fig. 2).

Representative specimens. ARGENTINA. CATAMARCA: Andalgalá, *Jorgensen 960* (MVM); Depto. Capital, "La Quebrada," *Krapovickas 1748* (SI). SALTA: between Guachipas y Alemania, ca. 25°38'S, 65°37'W, Jan. 1957, *Job 1511* (LP); Tolombón, 20 Oct. 1948, *Real 12084* (MERL); Quebrada de las Conchas, 14 Aug. 1936, *Cabrera 3758* (SI); Valle Santa María, Los Arcos, *Spegazzini 5983* (SI). JUJUY: Villa El Perchal, ca. 23°20'S, 65°30'W, 2,490 m, 7 Nov. 1988, *Aronson 7677* (MO, SGO). BOLIVIA. LA PAZ: Prov. Murillo, Mallasa, 16°32'S, 68°08'W, 3,200 m, 7 Aug. 1986, *Solomon 15483* (LBP, MBM). COCHABAMBA: Prov. Capinota, Santibañez to Capinota road, ca. 17°45'S, 66°17'W, 2,500 m, 1 Feb. 1985, *Pedrotti et al. 87* (LPB). CHUQUISACA: 27 km S of Las Careras, ca. 21°16'S, 65°17'W, 3,080 m, 26 Feb. 1989, *Aronson 7808* (K, MO).

Although Burkart had a drawing prepared for this variety in 1949 (Fig. 2e), he did not write a description. The three sutural ridges, the reddish purple pericarp, and the spongy, resinous mesocarp of the pod are unusual in *Acacia caven* and are reminiscent of some forms of *A. farnesiana*. Nevertheless, some Chilean, Bolivian, and one Uruguayan specimen of variety *caven* show morphologically intermediate pods that suggest possible gene flow with variety *macrocarpa*.

Acacia caven var. **microcarpa** (Speg.) Burkart ex Cialdella, Darwiniana 25(1–4): 77. 1984. TYPE: Argentina. Formosa. Depto. Patiño, Fortín Soledad, *A. Krapovickas 1283* (SI; isotype, LIL). Figure 1c.

Vachellia farnesiana (L.) Wight & Arn. f. *microcarpa* Speg., Bol. Acad. Nac. Ci. Córdoba 26: 301. 1923. fig. 20f, 3.

Compared to all other varieties except variety *stenocarpa*, the pod here is much smaller (2–3 × 1–2 cm) and the peduncle much longer (usually > 15 mm). The variety differs from variety *stenocarpa* by its much shorter, somewhat spherical or subglobose fruit, less than twice as long as broad. Mesocarp is white and evanescent.

Distribution. On heavy soils in the seasonally inundated portions of central Paraguay and northeastern Argentina (Formosa and Chaco provinces), in relative proximity to the Río Pilcomayo. Isolated specimens have also been collected in the small Brazilian portion of the Chaco. Found under relatively pristine as well as secondary, disturbed conditions in that region.

Representative specimens. ARGENTINA. CHACO: Pto. Barrangueras, 5 Dec., 1939, *Poiraberi 77* (LP, MVM). FORMOSA: R. Juarez, 10 Jan. 1957, *Burkart 201698* (SI); Río Pilcomayo, 12 Nov. 1986, *Vergara s.n.* (CTES). SALTA: between Colonia Castelli y Rivadavia, Mar. 1967, *Morello & Adamoli s.n.* (SI). BRAZIL. MATO GROSSO DO SUL: Mun. Porto Murtinho, estrada ao Fazenda Jererê, ca. 21°30'S, 57°44'W, 22 Dec. 1985, *Loureiro 161* (NY). MATO GROSSO: 20 km E of Pôrto Murtinho, 23 Oct. 1980, *Pires & Furtado 17287* (NY). PARAGUAY. PRESIDENTE HAYES: Palmas Chicas, near Puerto Mastinho, Dec. 1937, *Rojas 7694* (SI); Colonia, Menno, Misión Nueva, ca. 23°05'S, 59°40'W, *Arenas 200* (SI). BOQUERON: Mariscal Estigarribia, 23 Oct. 1980, *F. Casas & Molera 4431* (MO).

Acacia caven var. **stenocarpa** (Speg.) Burkart ex Cialdella, Darwiniana 25: 78, 1984. *Vachellia farnesiana* (L.) Wight & Arn. f. *stenocarpa* Speg., Bol. Acad. Nac. Ciencias Córdoba 262: 301. 1923. fig. 20. TYPE: Argentina, Misiones. Dept. Candelaria, Santa Ana, *Burkart 14734* (SI). Figure 1b.

Distribution. This variety is seen primarily in Formosa and Misiones provinces, Argentina and in adjacent Paraguay, especially within the area periodically flooded by the Río Pilcomayo. However, the few specimens from the Rió Uruguay collected before 1930 suggest that its former distribution, and possibly that of variety *microcarpa*, formerly included parts of Uruguay and possibly the Río Paraná region as well. Both of these areas are now transformed by agriculture and urban sprawl. There also exists one specimen from Tucumán, Argentina, nearly 800 km to the west of its current area of distribution.

Representative specimens. ARGENTINA. CHACO: Colonel Benitez, 7 July 1937, *Schinini 1987* (SI). CORRIENTES: 75 km N of Merced, Laguna Trinidad, Culantrillar, *Schinini et al. 11761* (MBM). FORMOSA: between Formosa and Mosou de Fierro, 7 Jan. 1945, *Ragonese & Cosso 2658* (SI); Clorinda, banks of the Río Pilcomayo, 14 Nov. 1944, *T. Rojas 12298* (LIL). ENTRE RIOS: 5 km S of Colón, ca. 32°20′S, 58°06′W, 20 m, *Aronson 7882* (CONC, K, MO). PARAGUAY. Trinidad, Bahia Caballero, Depto. Central, 11 Nov. 1950, *Sparre & Vervoorst 57* (K). PRESIDENTE HAYES: Mariscal Estigarribia, 11 Dec. 1987, *Schinini & Palacios 25934* (CORD, CTES, G); Presidente Hayes, 1 Dec. 1877, *Rojas 6979* (SI); Capitan López de Filippis, Oct. 1938, *Rojas 8419* (SI); Bajo Chaco, 30 km from Río Aguaray Guazu, 4 Jan. 1980, *P. Arenas 1571* (CTES). CAAGUAZU: *Hassler 9085* (LIL). URUGUAY. PAYSANDU: Santa Lucia, Bañado del Río Uruguay, ca. 34°28′S, 56°22′W, Nov. 1919, *J. Schroder 8865* (MVM).

This variety is distinguished by its short, narrow pod (> 10 mm) and long peduncle (≥ 15 mm). Fresh pods are usually light brown and often bear three strongly delineated suture ridges as in variety *macrocarpa* (and in much material of *A. farnesiana*). Leaves are big (80 × 50 mm), with pinnae up to 30 mm long. As in variety *stenocarpa*, trees tend to be weak and spindly compared to other varieties. Some introgression apparently takes place between variety *stenocarpa* and variety *microcarpa* (e.g., in *Sparre & Vervoorst 57*, K). Much more collection is needed in the Río Pilcomayo basin and in western Paraguay.

The few, rather old specimens of variety *stenocarpa* collected from Uruguay bear witness to the wider distribution of this variety in earlier times. They also raise the possibility that *A. caven* var. *stenocarpa* populations that existed in eastern Argentina and western Uruguay were eradicated, only to be replaced more recently by *A. caven* var. *caven*.

DISCUSSION

An infraspecific revision of a widespread and polymorphic *Acacia* based in large part on differences in shape and volume of pods and seed weight and number recalls the taxonomic revision of Brenan (1957) for *A. nilotica* (L.) Willd., the type species of *Acacia*. In *A. nilotica*, nine subspecies were delimited by Brenan, mainly on differences in the shape, size, and pubescence of the pods. Only fruiting specimens can be readily placed to subspecies, but geographic separation tends to confirm the validity of the infraspecific system proposed. Brenan's (1957) elaborate system for *A. nilotica* has been maintained by Ross (1979, 1981).

On a higher taxonomic level, Britton & Rose's (1928) subdivision of Bentham's (1875) series *Gummiferae* into 12 genera, partly on the basis of fruit characters, has been rejected by most subsequent workers. Moreover, for generic and tribal-level revisions throughout the Leguminosae, it has been argued that far too much emphasis in the past was placed on obvious fruit features, and that in the future these should be replaced, or at least supplemented, by consideration of flowers, inflorescences, seed, and seedlings in attempts to produce natural classification systems (Polhill et al., 1981: 25). However, at the specific and particularly the subspecific level in *Acacia caven*, fruit and seed parameters seem more conservative within populations than leaf pubescence, size of leaflets, capitulum diameter, and stipular spine length, all of which have been used to split up species complexes or to erect infraspecific categories within some widespread acacias and other Mimosoideae. For *A. caven*, and many related species, most pinnae, leaflet, and spinescent stipule parameters show such considerable infraspecific, and even within-population, variation that they gain taxonomic value only when substantiated by greenhouse or common-garden experiments, or when they are shown to be genetically fixed traits (cf. Aronson, 1992).

By contrast, the shape of mature legumes and the number and average weight of fully developed seeds per legume appear to be conservative within most populations of *A. caven*, though contrasted among varieties, and thus can play a role in systematic and other types of studies. Lewis & Elias (1981) consider that fruit characters provide excellent generic markers within the Mimoseae.

With regard to the evolutionary and ecological aspects of variation within *Acacia caven*, it seems that fruit and seed characters are subject to more intense selective pressure than other vegetative ones. At least four different types of seed dispersal strategies may have evolved in the varieties of *A. caven* described herein (Fig. 1). Variety *sphaerocarpa*, variety *microcarpa*, and variety *stenocarpa* may have undergone selection for seed dispersal by water in the regularly inundated regions they occupy. By contrast, high in the Andes, the unusually large pods of variety *macrocarpa* could have been selected for long distance dispersal by megavertebrates. Finally, variety *dehiscens* has possibly undergone selection for seed dispersal by rodents, ants, or avian granivores (Aronson, in prep.).

Studies on variation in polyad grain number among varieties of *Acacia caven*, e.g., those of Kenrick & Knox (1982) for *A. retinodes*, reveal a correlation between pollen grain number and maximum seed number per pod. Yet, there is no obvious correlation between seed number and average seed size in *A. caven*, such as predicted by Harper et al. (1970) and others. A related question is the possible correlation between ovule number in *Acacia caven* flowers and the number of seeds borne per pod (Lewis & Elias, 1981; Ph. Guinet, pers. comm.).

In Hispañola, Barneby & Zanoni (1989) used pod dehiscence as one of the diagnostic features for distinguishing *A. tortuosa* from *A. macracantha*. At a higher taxonomic level, the occasional occurrence of pod indehiscence is considered a diagnostic feature of subgenus *Acacia*, since nowhere in subgenus *Aculeiferum* or *Phyllodinae* can it be found (Elias, 1981). Within subgenus *Acacia*, as well as in various other legume taxa, it is observed that once pod indehiscence has arisen, it remains firmly fixed (B. Verdcourt, pers. comm.). The question arises whether *A. caven* variety *dehiscens* is the most primitive of the six varieties or a case of evolutionary "reversion." This latter hypothesis seems more likely in view of the fact that seed arrangement in variety *dehiscens* is polyseriate, just as in all the other varieties.

The significance of polyseriate seeds in a given pod should be noted in this context. In contrast to uniseriate seeded pods, pod length of *A. caven* (and of its close relative *A. farnesiana*) bears no correlation with seed number. Thus pod volume and dry weight are required, in addition to pod width and length, in order to adequately describe variation in reproductive output and therefore in evolutionarily significant phyletic groups. As Vassal (1972) put it: "The genus *Acacia* is endowed with great evolutionary dynamism; apparently it has not yet exhausted all its potentialities." Systematic treatments within the genus need to take this dynamism into account.

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DOCUMENTING SCIENTIFIC DATA: THE NEED FOR VOUCHER SPECIMENS

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Lucile M. McCook[3]

Like many botanists we have been following the developments in molecular systematics with interest and excitement. One aspect of most current work in nucleic acid sequencing and restriction enzyme analysis, C-value estimation, and natural products chemistry is, however, a growing source of concern. This is the question of voucher information for taxa studied.

A survey of papers on nucleic acid sequence data recently published has revealed a lack of consistency in the citation of voucher data (Cantino, 1992; Gianassi et al., 1992; Hufford, 1992; Olmstead et al., 1992; Downie & Palmer, 1992; Donoghue et al., 1992; Olmstead & Palmer, 1992). Some papers neither cite nor allude to any voucher data. Others refer to previous papers or individuals as documentation or sources of experimental material. Yet voucher data are not necessarily included in the referenced papers.

Vouchers are central to any serious questioning or reexamination of data and conclusions. An unexpected result may be due to convergence or to past misinterpretation of morphology and other characters, but it may also be caused by misidentification of the plant examined. The most prudent step to take before accepting an unexpected experimental result is to question the possibility of misidentification of experimental material or mislabeling in the laboratory. The next step is to duplicate the result. Because of the absence of voucher material, literally thousands of early chromosome counts, published over the past 50 years, have had to be discounted, and we suspect that fully half of the counts published before 1965 are based on plants the identity of which is questionable and cannot be verified.

Most systematists have had the experience of seeing species they know well misidentified in botanical garden collections. Not infrequently seeds raised from botanical garden sources are found to be species other than the one named on the package. Just as in commercial nurseries, botanical gardens receive seed and plants from commercial sources; few gardens have the personnel or the library and herbarium resources to verify the names of all the plants in their collection. Yet many molecular studies cite botanical garden accessions as if they were sources of accurate identifications. Some authors assume that any samples sent to them are adequately vouchered and documented. Our experience demands caution in this area. Misidentifications and mixing of labels occur with sufficient frequency that no systematist should be satisfied with procuring a sample from a botanical garden, or any other source, without being certain that a proper voucher exists that corresponds to the plant being sampled and that the plant is properly identified. Original locality data should also be established if possible.

Absence of a voucher makes it impossible to reassess identity. To avoid the potential for future problems we suggest that leading scientific journals insist on the citation of an existing herbarium voucher specimen and an indication of its location. Absence of a voucher for critical taxa should be explained so that readers are somehow assured of the identity of study materials. A statement that an author may be consulted personally for voucher data is not satisfactory. This rarely works. Are we simply going to have to discard dozens or possibly hundreds of sequences, obtained at huge cost in research dollars, because of inadequate voucher documentation? This seems likely.

We strongly urge that molecular systematists take the time and make the effort, sometimes not inconsiderable, to assure proper documentation of their experimental subjects. We also urge that journal editors insist on the inclusion of direct citation of voucher material in all papers presenting original data. As an example, the *Annals of the Missouri Botanical Garden* is instituting the following voucher policy. Papers presenting original data will not be accepted for consideration unless they include citation of voucher information. At the minimum this means citation of an extant herbarium specimen (minimally collector and number) and an

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ANN. MISSOURI BOT. GARD. 79: 969–970. 1992.

indication of the herbarium in which the voucher is located. Herbarium vouchers should clearly state by means of an annotation that the specimen represents a voucher for a particular study. Depending on the type of paper, reference to the original wild source may also be required, and is certainly appropriate for studies at infrafamilial level for widespread species. As always, authors are personally responsible for establishing the accuracy of their information.

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NOTICE

The Rupert Barneby Award

The New York Botanical Garden invites applications for the 1992 Rupert Barneby Award. The award of $500.00 is to assist researchers planning to come to The New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a letter describing the project for which the award is sought, and how the collections at NYBG will benefit their research. Travel to NYBG should be planned between Jan. 1, 1993 and Jan. 30, 1994. The letter should be addressed to Dr. Brian M. Boom, Vice President for Botanical Science, The New York Botanical Garden, Bronx, NY 10458, USA, and received no later than December 4, 1992. Announcement of the recipient will be made by December 20. Anyone interested in making a contribution to The Rupert Barneby Fund in Legume Systematics, which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Boom.

The recipient of the 1991 Rupert Barneby Award is Edith Gómez-Sosa, a legume taxonomist from the Instituto de Botánica Darwinion in Argentina. Professor Gómez-Sosa will use the award to further her studies of the genus *Astragalus* through the consultation of collections at The New York Botanical Garden during July and August of 1992. She will also have the opportunity to work together with Dr. Barneby during her stay in New York.

NOTICE

THE 1992 JESSE M. GREENMAN AWARD

The 1992 Jesse M. Greenman Award has been won by Sharon Elaine Bartholomew-Began for her publication "A morphogenetic re-evaluation of *Haplomitrium* Nees (Hepatophyta)," published as Volume 41 of Bryophytarum Bibliotheca. This study is based on a Ph.D. dissertation from Southern Illinois University at Carbondale, under the direction of Dr. Barbara Crandall-Stotler.

The Greenman Award, a certificate and a cash prize of $500, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Papers published during 1992 are now being accepted for the 25th annual award, which will be presented in the summer of 1993. Reprints of such papers should be sent to Dr. P. Mick Richardson, Greenman Award Committee, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. In order to be considered for the 1993 award, reprints must be received by 1 June 1993.

Volume 79, Number 3, pp. 447–736, of the ANNALS OF THE MISSOURI BOTANICAL GARDEN was published on July 17, 1992.

Instructions for Authors, *Annals of the Missouri Botanical Garden*

The *Annals* publishes original articles in systematic botany and related fields. Text may be in English or Spanish. When in Spanish, an English abstract in addition to a Spanish abstract is required. Papers whose purpose is the establishment of new nomenclatural entities in vascular plants and bryophytes are not accepted. Rather, they should be submitted to *Novon* for consideration. (*Novon* instructions are available from the editor.) Authors are urged to contact the editor prior to submitting manuscripts. Manuscripts sent already reviewed and revised are generally subject to the full normal review process initiated here. Manuscripts not properly prepared may be returned for revision prior to review.

Papers presenting original data must include the citation of a voucher(s). Herbarium vouchers should state the collector and number, the herbarium in which the voucher is located, and a clear annotation that the material represents the voucher for the study in question. Depending on the type of paper, reference to the original wild source may also be required. As always, authors are personally responsible for establishing the accuracy of their information.

Page costs are $80 per page, although charges may be reduced under certain circumstances. Corrections in proof will be billed nonnegotiably to the author at $3.00 per line.

Manuscripts (three copies) must be typed on one side of nonglossy 8½ × 11-inch paper. Draft-quality dot-matrix printouts are not acceptable. Leave at least one inch as margin all around, except on the first page. There three inches should be left blank at the top. **The text should be double-spaced or triple-spaced throughout,** including abstract, notes, legends, tables, specimen lists, Literature Cited, and footnotes. **Do not justify the right-hand margin, and do not break words there.** Italics, boldface, or other special typefaces should not be used—they will appear later as communicated to the printer by the editor. Words to be set in italics should be underlined. **Accents, umlauts, and other diacritical marks are the responsibility of the author.**

Manuscripts may be sent on MS-DOS 3½- or 5¼-inch diskettes, preferably as WordPerfect files, in addition to the printed documents. This is recommended, particularly for long articles, but not required.

Authors should include their full mailing address, telephone number, fax number, and electronic mail number in a letter sent with the submitted manuscript.

Footnotes should be typed double-spaced as paragraphs on the first page. The first footnote contains acknowledgments, including information on granting agencies and herbaria that loaned specimens. The second footnote is the author's address. Addresses for additional authors are each separate additional footnotes. No other footnotes are permitted, except footnotes in tables, and these are best avoided.

Long, complex tables are discouraged. Tables not neat and easily understood will be returned for improvement. Leave out vertical lines and avoid horizontal lines. Type table captions double-spaced as paragraphs at the tops of tables.

Periods are used after all abbreviations (which should be minimized) except metric measures, compass directions, and herbarium designations. States are not abbreviated, and cities are usually spelled out, although "St." is acceptable. **Abbreviate periodicals according to *B-P-H* (*Botanico-Periodicum-Huntianum*), authors according to *The Draft Index of Author Abbreviations Compiled at the Royal Botanic Gardens, Kew*, and books according to *Taxonomic Literature*, edition 2.** Note, however, that book abbreviations are to be capitalized, and that books listed in the Literature Cited section should have their titles spelled out when feasible. Note further that names of taxonomic authorities may be spelled out in major taxonomic citations such as the formal citation at the head of a taxonomic treatment. Except by prior arrangement with authors not having access to crucial references, the editor does not provide the service of looking up abbreviations.

The Literature Cited should include all references cited in the text. Periodicals should be listed as follows: author's last name, initial(s). Year. Full title of article. Journal abbreviated as in *B-P-H.* Volume: pages. Do not give parenthetical part numbers after volume numbers unless each part is paginated separately. For more than one author, follow this style: author's last name, initial(s), second author's initial(s) last name & third author's initial(s) last name. Citation of books should appear as follows: author's last name, initial(s). Year. Full Title (edited by Editor), 3rd ed., Vol. 2. Publisher, City of Publication. Citations of work "in prep." and similar references to inaccessible sources are strongly discouraged and should not be listed in the Literature Cited. Except by prior arrangement when necessary, the editor does not perform library research to fill in missing bibliographic information.

A brief Latin diagnosis for each new taxon is preferred to a complete Latin description.

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 Cordóba, *Bourgeau 1713* (holotype, K; isotypes, F, GH, P, US). Exclamation points are not used for specimens examined. Indicate unseen types as "not seen."

Do not cite nomina nuda, misapplied names, or superfluous names under synonymy; if relevant, include them in the discussion following the description.

If many specimens were examined, limit those cited in the text to one collection per geographical area. A full list of specimens may be placed at the end of the paper, following the Literature Cited. This list should be arranged alphabetically by collector, followed by collection number, followed by the number of the taxon in the text.

For those specimens cited in the text, follow this style: *Additional specimens examined* (or *Selected specimens examined* or *Paratypes*). MEXICO. Oaxaca: Sierra San Pedro Nolesco, Talea, 3 Feb. 1987 (fl), *Jergensen 865* (BM, G, K, US). Dates and reproductive status are optional.

Keys should be clear and consistent with descriptions.

Abbreviate herbaria according to *Index Herbariorum*, edition 8.

Send copies of illustrations; do not send originals until requested. Illustrations will be returned after publication. All illustrative materials should be mounted on stiff cardboard. The maximum size for printed illustrations is 5½ × 8¼ inches. Presize illustrations to fit either column width (2⅝ inches or ca. 68 mm) or full page width (5½ inches or ca. 140 mm). Figures are numbered in Arabic numerals in the order of their citation in the text. Parts of figures are labeled with capital letters. Photographs should be black-and-white prints. Transparencies and negatives are not accepted. Group figures into composite plates when possible, and abut edges of photographs. Do not use stripping between plate or figure segments. Make sure edges are squared.

Maps should include reference to latitude and longitude. Scale bars should appear on illustrations, on photographs, and on maps. Magnifications/reductions indicated in captions are unwelcome to the point of usually not being accepted. Scanning electron micrographs should be free of conspicuous charging. Axes on graphs should be labeled. No explanatory text is to appear in figures; rather, provide clear captions in sequential paragraphs apart from the other text, one paragraph for each group of figures, and following the style in current issues of the *Annals*.

For other aspects of style, consult a recent issue of the *Annals*; the latest edition of *The Chicago Manual of Style*; or write the editor. Communication with the editor at all points of the publication process is encouraged.

Manuscripts (**three copies**) and correspondence should be addressed to the Editor, *Annals of the Missouri Botanical Garden*, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.

ANNALS OF THE MISSOURI BOTANICAL GARDEN

VOLUME 79
1992

Colophon

This volume of the ANNALS of the Missouri Botanical Garden has been set in APS Bodoni. The text is set in 9 point type while the figure legends and literature cited sections are set in 8 point type.

The volume has been printed on 70# Vintage Gloss. This is an acid-free paper designed to have a shelf-life of over 100 years. Vintage Gloss is manufactured by the Potlatch Paper Company.

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The ANNALS is printed and distributed by Allen Press, Inc. of Lawrence, Kansas 66044, U.S.A.

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STATISTICAL SUMMARY OF SOME OF THE ACTIVITIES IN THE MISSOURI BOTANICAL GARDEN HERBARIUM, 1990–1991

	1990			1991		
	Vascular	Bryophyte	Total	Vascular	Bryophyte	Total
Acquisition of specimens						
Staff collections (includes bryophytes)	35,086		35,086	66,100		66,100
Purchase	1,350	0	1,350	586	0	586
Exchange	43,197	3,089	46,286	39,246	2,763	42,009
Gifts	11,040	1,081	12,121	12,309	875	13,184
Total acquisitions	90,673	4,170	94,843	118,241	3,638	121,879
Mountings						
Newly mounted	86,742	13,569	100,311	98,606	11,832	110,438
Mounted when received	1,843	0	1,843	455	0	455
Total specimens filed	88,585	13,569	102,154	99,061	11,832	110,893
Repairs						
Specimens repaired	15,852		15,852	14,641		14,641
Specimens stamped	8,054		8,054	6,033		6,033
Total repairs	23,906		23,906	20,674		20,674
Specimens sent						
On exchange	47,356	0	47,356	62,543	6,022	68,565
As gifts	14,765	1,020	15,785	28,536	425	28,961
Total	62,121	1,020	63,141	91,079	6,447	97,526
Loans sent						
Total transactions	596	29	625	672	25	697
Total specimens	24,828	1,339	26,167	36,859	1,346	38,205
To U.S. institutions						
Transactions	426	15	441	352	18	370
Specimens	17,554	288	17,842	22,018	1,124	23,142
To foreign institutions						
Transactions	170	14	184	320	7	327
Specimens	7,274	1,051	8,325	14,841	222	15,063
To student investigators						
Transactions	31	4	35	67	0	67
Specimens	3,818	861	4,679	8,897	0	8,897
To professional investigators						
Transactions	565	25	590	605	25	630
Specimens	21,010	478	25,306	27,962	1,346	29,308
Loans received						
Transactions	478	22	500	406	33	439
Specimens	32,414	1,490	33,904	23,422	2,699	33,904

	1990			1991		
	From U.S.	From abroad	Total	From U.S.	From abroad	Total
Visitors	458	124	582	477	133	610

On 31 December 1990 the total number of mounted, accessioned specimens in the herbarium was 3,805,381 (3,613,402 vascular plants and 191,979 bryophytes).

On 31 December 1991 the total number of mounted, accessioned specimens in the herbarium was 3,922,307 (3,718,496 vascular plants and 203,811 bryophytes).

Monographs in Systematic Botany from the Missouri Botanical Garden

Bibliografía Botánica Taxonómica de Chile.

Clodomiro Marticorena.

This comprehensive, up-to-date bibliography contains citations for over 6,100 references concerning the vascular plants of Chile. Each citation in the bibliography, which occupies about 450 of the book's 587 pages, is accessible through one or more of the subject indexes: taxonomic (by family and genus), geographical (by Chile's twelve political regions), and descriptors (including vernacular names, medicinal plants, cultivated plants, and others). The taxonomic index will be useful as a guide to the literature outside of Chile, since the bibliography contains citations for many generic and family revisions.

Monographs in Systematic Botany from the Missouri Botanical Garden, volume 41, 587 pages, hard bound, May 1992.

Index of Mosses 1963–1989.

Marshall R. Crosby, Robert E. Magill & Cheryl R. Bauer.

Index of Mosses is a guide to the names published for mosses, including all new taxa from the rank of genus and below. Entries include full references to places of publication, and, depending on the nature of the name, listings of basionyms, replaced names, and types. The Index for 1963–1989 lists about 8,500 names and contains appendixes giving full authors' names and fully spelled journal and book titles with references to their entries in TL-2 and B-P-H.

Monographs in Systematic Botany from the Missouri Botanical Garden, volume 42, 656 pages, hard bound, June 1992.

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